Effects of river restoration on ecosystem metabolism and trophic relationships

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Abbreviations

ANOVA	Analysis of Variance
ARIMA	Autoregressive Integrated Moving Average (ARIMA) model
CR	Carbon Range
DO	Dissolved Oxygen
ER	Ecosystem Respiration
FFG	Functional Feeding Group
$\mathbf{F_{med}^{200}}$	Fraction of median residence time due to transient storage, normalized for reach length
GPP	Gross Primary Production
$\mathbf{K_{oxy}^{20}}$	Normalized reaeration coefficient
NEP	Net Ecosystem Production
NR	Nitrogen Range
OTIS-P	One-Dimensional Transport with Inflow and Storage
POM	Particulate organic matter
REFORM	Restoring rivers for effective catchment management (EU project)
SEA	Standard Ellipse Area
$\mathbf{SEA_C}$	Standard Ellipse Area corrected for small sample sizes
$\mathbf{SEA_B}$	Bayesian Standard Ellipse Area
SIBER	Stable Isotope Bayesian Ellipses in R
SIAR	Stable Isotope Analysis in R
VPDB	Vienna Pee Dee Belemnite
WFD	Water Framework Directive

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1 Introduction

Following a long history of human pressures on riverine ecosystems, the European Water Framework Directive (WFD, Directive 2000/60/EC) came into force in 2000 and initiated a new period of river management in Europe. The directive aims at improving the ecological and chemical status of rivers in order to achieve the ‘good status’ of all surface waters until the year 2027. In Europe, degraded hydromorphology has been highlighted as a central impact to the ecological status of the rivers (EEA 2012). For instance, in countries such as Germany, the hydromorphology of almost all river sections is affected to an extent that they fail to meet the WFD goals (EEA, 2012). In response, river hydromorphology is nowadays being restored at an increasing rate.

The assessment of restoration success or failure 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). However, restoration of river hydromorphology has the potential to affect not only structural ecosystem features, including species composition and diversity, but also, and sometimes in a more pronounced way, functional aspects, such as key ecosystem processes and trophic transfers of energy and nutrients. Functional aspects can be influenced by restoration, while structural ecosystem features remain unaffected, and vice versa. Contrasting responses of functional aspects and community structural parameters have been reported in the context of impact assessments (e.g., Friberg et al. 2009, McKie & Malmqvist 2009, Niyogi et al. 2013). Thus, incorporating functional aspects into monitoring programs may enable a more holistic assessment of river health and a better mechanistic understanding of restoration effects. Although many studies have advocated that classical, community-based assessment needs to be complemented with functional approaches to evaluate river health (e.g., Young et al. 2008, 2009, Palmer & Febria 2012, Woodward et al. 2012), functional metrics are still rarely used in assessments of river restoration (Palmer et al. 2014). Consequently, the outcomes of river restoration for key ecosystem processes (e.g., river metabolism) and trophic relationships (e.g., trophic structure of benthic invertebrate communities and trophic connectivity between river and land) remain poorly understood.

Hydromorphological restoration has the potential to influence riverine food webs and associated transfers of energy and nutrients. A higher diversity of both feeding- and physical habitat-related niches can contribute to changes in food web structure, particularly if a higher variety of resources is available to increase the number of trophic pathways (Layman et al. 2007a, Woodward 2009). For instance, more complex river bed structures enhance the retention of allochthonous organic matter (Lepori et al. 2005b, 2006, Flores et al. 2011), which can further be increased by reconnecting rivers and floodplains and hence resource transfers from land to water. Autochthonous sources are also likely to increase, e.g. caused by enlarged shallow habitats providing more space for autotrophs (Lorenz et al. 2012, Friberg et al. 2016). Overall, improved river hydromorphology has the potential to increase the range of basal resources in riverine ecosystems with knock-on effects for consumers of higher trophic levels, including benthic invertebrates (Friberg et al. 2016).

River restoration may also promote the flux of aquatic biomass into terrestrial food webs. One particular food web linkage is the contribution of aquatic insects to the diet of predaceous riparian ground-beetles and spiders (Hering & Plachter 1997, Collier et al. 2002, Paetzold et al. 2005). Riparian arthropod predation on aquatic insects is concentrated along the shoreline where riparian arthropods aggregate, aquatic insects emerge, and surface drifting organisms accumulate (Paetzold et al. 2005). An improved shoreline structure (by creating a shallower river profile, removing bank fixations and providing habitats suited for riparian biota) enables riparian arthropods to stay close to the river channel and potentially makes aquatic prey more easily accessible to riparian predators. Consequently, river restoration is likely to increase the proportion of aquatic prey in the diet of riparian arthropods, promoting the trophic connectivity of river and land.

Food webs and trophic relationships of organisms are commonly analyzed by carbon and nitrogen stable isotopes (δ^{13}C and δ^{15}N). Stable isotope data provide information on the material assimilated by consumers (Abrantes et al. 2014). Because δ^{15}N is stepwise enriched with trophic transfers, i.e., consumers are enriched relative to their diet, it is generally used to characterize the relative trophic position of a consumer (Minagawa & Wada 1984, Post 2002, McCutchan et al. 2003). In contrast, δ^{13}C isotopic signatures change little with trophic transfers but vary among different producers, and thus can be used to identify the carbon sources of an organism (DeNiro & Epstein 1978, Vander Zanden & Rasmussen 1999, Post 2002). A common approach to study stable isotope data is to plot mean isotopic signatures of organisms in δ^{13}C -^{15}N -isotope bi-plots. The relative position of species or groups in this bi-plot space is used to investigate food web related aspects (Layman et al. 2007b). This approach may also be suitable to study effects of restoration on trophic relationships in order to obtain a more holistic characterization of restoration effects.

Ecosystem metabolism, i.e., the combination of gross primary production (GPP) and ecosystem respiration (ER), is a key ecosystem process in rivers. It is a measure of the production and use of organic matter within a river reach by the biota (Young et al. 2008, Tank et al. 2010). Hence, it provides information about a river's trophic and energetic base (relative contribution of autochthonous and allochthonous carbon sources to the food web) (Young et al. 2008, Tank et al. 2010, Beaulieu et al. 2013). Together with other characteristics of the river ecosystem, light availability, temperature, and organic matter supply are among the primary factors that control river ecosystem metabolism (Lamberti & Steinman 1997, Sinsabaugh 1997, Mulholland et al. 2001), and these factors are directly influenced by reach-scale characteristics (Bernot et al. 2010, Tank et al. 2010). Consequently, hydromorphological restoration can affect river ecosystem metabolism. For example, the widening of the river channel is a widely implemented restoration technique along mountainous rivers in central Europe. It increases light availability and water temperature, and hence primary productivity. Furthermore, river widening promotes macrophytes and other autotrophs through the creation of shallow, slow flowing areas and backwaters (Lorenz et al. 2012). These changes potentially lead to enhanced in-stream autotrophic processes. However, restoration can also promote heterotrophic metabolism in the river due to an increased input and retention of allochthonous organic matter (e.g., caused by an enhanced resource transfer from land to water and more complex river bed structures; compare previous paragraphs). There is only limited understanding of how restoration can influence ecosystem metabolism, especially for larger rivers (but see Colangelo 2007). Including ecosystem metabolism into river monitoring may enable a better mechanistic understanding of restoration effects.

1.1 Scope of the thesis

According to the previous chapter, hydromorphological restoration has the potential to influence functional aspects of riverine ecosystems, including river metabolism and trophic relationships. However, this has rarely been studied and the effects of river restoration on the trophic structure of benthic invertebrate communities, the trophic connectivity between river and land, and river ecosystem metabolism remain poorly understood. Against this background, the present thesis consists of three main chapters which are associated to the prior outlined topics. These chapters represent individual papers which have been partially submitted and published in peer-reviewed journals. They specifically address the following topics and associated objectives:

- *River restoration and the trophic structure of benthic invertebrate communities across 16 European restoration projects*
  In the second chapter, stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$) was applied to characterize changes in the trophic structure of benthic invertebrate communities between paired restored and unrestored river reaches. The study aimed to identify changes in the isotopic signatures of benthic invertebrate consumers indicative both of increased resource breadth (indicated by $\delta^{13}C$ range), and increases in trophic length (indicated by $\delta^{15}N$ range) following river restoration, which together favour larger isotopic niches of invertebrate assemblages. Moreover, it was investigated if restoration effects depend on the extent of restoration effort, and on the type of restoration measures applied.

- *River restoration enhances aquatic-terrestrial linkages: a stable isotope study of riparian arthropods in eleven restored floodplain sections*
  In the third chapter, the isotopic composition ($\delta^{13}C$, $\delta^{15}N$) of consumers in aquatic, riparian (within one meter distance to the river) and terrestrial (beyond the riparian zone) habitats was investigated. Stable isotope data were plotted in isotope space to examine the trophic organization across the aquatic-terrestrial interface. The study aimed to detect changes in the position of riparian arthropods in isotope space indicative both of a smaller share of terrestrial resources, and an increased use of aquatic prey following restoration. The isotopic distance of riparian consumers to benthic invertebrates and terrestrial arthropods was quantified as a measure of trophic linkage, and it was investigated how this varied with riparian habitat composition.

- *Hydromorphological restoration stimulates river ecosystem metabolism*
  In the fourth chapter, the effect of hydromorphological river restoration on ecosystem metabolism was investigated. The study was conducted in a 2.3 km long restored reach of a German mid-sized mountain river (Ruhr). The study aimed to assess reach-scale restoration effects on hydromorphology, habitat composition and hydrodynamics, and to determine the corresponding responses of river metabolism, i.e. whole-stream rates of GPP and ER, as well as the river's metabolic balance.

2 River restoration and the trophic structure of benthic invertebrate communities across 16 European restoration projects

2.1 Introduction

Restoration of river hydromorphology has the potential to affect not only structural ecosystem features, including species composition and diversity, but also ecosystem functioning (Palmer et al. 2014). Despite this, the most-widely used parameters for assessing the success or failure of restoration projects are almost exclusively based on changes in community composition of different biological groups. In the context of the EU Water Framework Directive the composition of organism groups like fish, phytoplankton and benthic fauna and flora are most commonly investigated, and the response of these assemblages to hydromorphological restoration has been relatively well characterized (Lepori et al. 2005a, Jähnig et al. 2010, Sundermann et al. 2011, Lorenz et al. 2012, Haase et al. 2013, Friberg et al. 2014, Schmutz et al. 2014, Stoll et al. 2014). Functional metrics, even though widely applied in basic studies of aquatic systems (e.g., Vander Zanden & Rasmussen 1999, Hieber & Gessner 2002, Fischer et al. 2005, Friberg et al. 2009, Gücker et al. 2009, McKie & Malmqvist 2009), are rarely in assessments of river restoration (but see Lepori et al. 2005b, 2006, Flores et al. 2011). Consequently, the outcomes of restoration for key ecosystem processes and trophic transfers of energy and nutrients remain poorly understood (Lepori et al. 2006).

Hydromorphological river restoration typically enhances not only habitat diversity in both the stream channel and riparian zone (Jähnig et al. 2010, Januschke et al. 2014), but also retention of organic matter (Lepori et al. 2005b, 2006, Flores et al. 2011), which together are expected to enhance aquatic-terrestrial linkages, and the availability of both autochthonous and allochthonous food sources. Therefore, significant alterations of food web structure and trophic relationships can be expected: A higher diversity of both feeding- and physical habitat-related niches can contribute to changes in food web structure, particularly if a higher variety of resources is available to increase the number of trophic pathways (Layman et al.

2007a, Woodward 2009). Apart from increases in retention of allochthonous matter (Lepori et al. 2005b, Flores et al. 2011), restoration also might increase the availability of autochthonous sources, e.g., caused by enlarged shallow habitats providing more space for autotrophs (Lorenz et al. 2012). Furthermore, stronger connections between river and floodplain, e.g., caused by a more shallow profile or the removal of hardened, channelized banks, has potential to increase inundation frequency and hence resource transfers from land to water. Furthermore, improving niche space for larger bodied predators through, e.g., the creation of pools or removal of dispersal obstacles are likely to increase food chain length (Woodward et al. 2005). These changes all have implications for complexity of the food web and the relative trophic position of different organisms within the web (Woodward & Hildrew 2002, Woodward 2009).

Stable isotope composition of carbon and nitrogen ($\delta^{13}C$, $\delta^{15}N$) are commonly used to study food web structure as they provide information on the material assimilated by organisms (Abrantes et al. 2014). $\delta^{15}N$ trophic fractionation changes about +3‰ between trophic levels (Minagawa & Wada 1984, McCutchan et al. 2003) and is generally used to calculate the trophic position of an organism (Post 2002). Because $\delta^{13}C$ trophic fractionation is less, changing only 0-1‰ from source to consumer (DeNiro & Epstein 1978, McCutchan et al. 2003) and can vary among different producers, it is often used to identify the resource base (Vander Zanden & Rasmussen 1999). A set of community-wide metrics has been introduced by Layman et al. (2007b) to gain more quantitative information from stable isotope data at the species or community level. These metrics have been used to investigate effects of ecosystem fragmentation on niche width (Layman et al. 2007a), to study effects of flooding on community structure (Calizza et al. 2012), to compare the trophic structure of communities within different lakes (Cooper & Wissel 2012), in invasion ecology (Jackson et al. 2012), and to identify patterns in food web structure related to different environmental conditions (Abrantes et al. 2014). Recently, these metrics have further been reformulated in a Bayesian framework by Jackson et al. (2011) which enables statistical comparison between sites without standardized sampling design or between different sampling periods (Jackson et al. 2012, Abrantes et al. 2014).

In this study, we applied stable isotope analysis of carbon and nitrogen to quantitatively characterize changes in trophic structure following both larger- and smaller scale river restoration projects. We sampled dominant benthic invertebrate taxa belonging to different functional feeding groups (FFG) on paired restored and degraded river sections in 16 catchments throughout Europe, allowing comparison of restored sections with degraded “control sites” located upstream (Hering et al. 2015). Two types of restoration projects were investigated; comprehensive flagship projects representing best-practice examples and typically involving extensively restored river sections at a larger scale, and smaller projects including single restoration measures only. We focus on benthic invertebrate communities, which are commonly applied indicators of ecosystem health, and which are trophically diverse, encompassing herbivorous, detritivorous, and predacious species. However, benthic invertebrates in streams also typically show a high degree of dietary flexibility, and thus have the potential to respond to new resources as they become available (Mihuc 1997, Layer et al 2013), leading to potentially rapid uptake into the food web (Göthe et al 2009). For example, species typically classified as detritivores are capable of incorporating algae into their diets when available (Friberg & Jacobsen 1994), and many species feed at different levels in the food web (both primary consumer and predator) at different points in their lifecycle (Wissinger et al 2004, Layer et al 2013). Furthermore, two of the largest feeding groups (collector-gatherers and filterers) feed on particulate organic matter, derived from both allochthonous and autochthonous sources, providing another pathway for novel sources of energy and nutrients to enter stream food webs following restoration (Webster and Meyer 1997).

We used a set of quantitative community metrics: $\delta^{13}C$ range (CR) and $\delta^{15}N$ range (NR) following Layman et al. (2007b), and standard ellipse area (SEA) according to Jackson et al. (2011) of the dominant feeding types of benthic invertebrate communities to quantify changes in trophic structure between restored and degraded sections. The restoration effect was quantified by comparing each restored river section to an upstream non-restored section. We expected that our isotopic metrics would show evidence for changes in trophic organization following river restoration, reflecting increases in habitat diversity, resource diversity, and aquatic-terrestrial linkages. Specifically, we hypothesized that (i) the CR metric would increase (i.e., an increase in $\delta^{13}C$ range), reflecting the availability of a more varied food source following restoration and that (ii) the NR metric would also increase (increasing $\delta^{15}N$ range), if changes in habitat diversity and increased availability of basal resources allow an increase on food chain length. Based on this, we further hypothesized that (iii) the SEA metric would increase, reflecting a larger isotopic niche of benthic invertebrate communities following restoration. We further expected these effects would (iv) increase with restoration extent, reflecting stronger changes in habitat complexity and aquatic-terrestrial connectivity, and that these effects are (v) related to the type of restoration measure employed, with projects which mainly aim at river widening (usually affecting both instream habitats and connectivity of water and land and thereby enhancing availability of autochthonous and allochthonous carbon resources) affecting food webs more strongly than projects which applied measures mainly affecting the river channel itself (e.g., instream measures or flow restoration).

2.2 Materials and Methods

2.2.1 Study sites

The study on benthic invertebrate communities and stable isotopes was undertaken in river sections in 16 catchments across Europe (Table 2.1, and compare Hering et al. 2015, Muhar et al. 2016), either medium-sized lowland rivers or medium-sized mountain rivers. In each of these catchments, a restored and a nearby non-restored river section were sampled. Two types of restoration projects were investigated: large restored river sections with an extensive restoration effort representing best-practice examples (R1) and smaller projects relying on mainly single, local restoration measures (R2). For each large and small project, a representative sampling reach was selected in the downstream part of the restored river section to account for effects of the restored river length. The restored sections were compared to non-restored, degraded "control sections" (D1/D2) located directly upstream of the corresponding restored sections. As the distance between restored and degraded reaches was small relative to overall stream size (mean distance: 3.0 km, n = 16), natural shifts in basal resources are not anticipated over this length of the streams, thus it is highly unlikely that anything other than the human impacts could cause shifts in isotopic signals.

Table 2.1: Overview of large-scale (R1) and small-scale (R2) restored sites (based on data presented in Muhar et al. 2016).

Site name	**FI_R1**	**SE_R1**	**DK_R1**	**PL_R1_1**	**DL_R1**	**DM_R1**	**CZ_R1**	**AT_R1**
Country	Finland	Sweden	Denmark	Poland	Germany	Germany	Czech Republic	Austria
River name	Vääräjoki	Emån	Skjern	Narew	Lippe	Ruhr	Becva	Drau
River type	Gravel-bed	Gravel-bed	Sand-bed	Sand-bed	Sand-bed	Gravel-bed	Gravel-bed	Gravel-bed
Latitude (N)	64.054433	57.149095	55.9380926	53.1500527	51.663675	51.44093	49.4968975	46.75454
Longitude (E)	24.2206639	16.441897	8.6279814	22.8716193	8.23248	7.96223	17.5211533	13.309393
Altitude (m a.s.l.)	60	10	10	139	72	153	232	570
Catchment geology	organic	siliceous	siliceous	organic	siliceous	siliceous	siliceous	siliceous
Catchment size (km^2)	835	4440	1553	3680	1896	1054	1532	2433
Mean discharge (m^3/s)	9.9	29.3	36.6	16.9	17.7	15.2	16.6	62.6
Stream order	4	6	5	2	3	3	7	7
Ecoregion	Fenno-scandian shield	Fenno-scandian shield	Central plains	Eastern plains	Central plains	Central Highlands	Hungarian lowlands	Alps
Restoration Length (km)	1.4	0.9	26	9	2	0.75	0.45	1.9
Restoration date	1997-2006	2006-2011	2003	1995-cont.	1997	2008	1997	2002-2003
Measure type	Other	Widening	Other	Other	Widening	Widening	Widening	Widening
Main restoration action	instream measures	Hydro RivCon (dam removal, naturalise flow regime, fishway construction, salmonid spawning gravel and boulder additions)	re-meandering and reconnection of wetlands	reconnection side channels (rise water level by thresholds)	re-meandering	riverbed widening	riverbed widening	riverbed widening; (partial removal of bank fixation; initiation of secondary channel; reconnection of one sidearm)
Time of sampling (together with degraded section)	August 2012	August 2013	August 2013	July 2012	August 2013	June 2013	September 2012	July 2013

Table 2.1: continued.

Site name	**FI_R2**	**SE_R2**	**DK_R2**	**PL_R2**	**DL_R2**	**DM_R2**	**CZ_R2**	**AT_R2**
Country	Finland	Sweden	Denmark	Poland	Germany	Germany	Czech Republic	Austria
River name	Kuivajoki	Mörrumsån	Stora	Warta	Spree	Lahn	Morava	Enns
River type	Gravel-bed	Gravel-bed	Sand-bed	Sand-bed	Sand-bed	Gravel-bed	Gravel-bed	Gravel-bed
Latitude (N)	65.6860429	56.336005	56.3614934	52.1930314	52.377747	50.86588	49.6570728	47.42112
Longitude (E)	25.6349874	14.700237	8.4982852	17.8974616	13.878897	8.79088	17.2179975	13.816094
Altitude (m a.s.l.)	74	87	10	75	35	191	218	692
Catchment geology	organic	siliceous	siliceous	calcareous	siliceous	siliceous	siliceous	calcareous/ siliceous
Catchment size (km^2)	976	3264	878	14519	6275	652	2305	809
Mean discharge (m^3/s)	12.8	12	16.1	45.3	14	12	17.7	21.5
Stream order	4	6	5	2	6	3	7	5
Ecoregion	Fenno-scandian shield	Fenno-scandian shield	Central plains	Central plains	Central plains	Central Highlands	Hungarian lowlands	Alps
Restoration Length (km)	0.4	3.3	0.3	3	0.95	0.24	0.22	0.6
Restoration date	2002-2006	2003-2012	2012	2008	2005	2000	1997	2003-2004
Measure type	Other	Other	Other	Widening	Other	Widening	Widening	Widening
Main restoration action	instream measures	Hydro RivCon (increased flow, fishway construction and salmonid spawning gravel additions)	instream measures (habitat restoration: salmonid spawning gravel)	reconnection floodplain	remeandering	riverbed widening	riverbed widening	riverbed widening (partial removal of bank fixation; initiation of one secondary channel)
Time of sampling (together with degraded section)	August 2012	August 2013	August 2013	July 2013	July 2013	July 2013	September 2012	July 2013

We therefore did not expect effects on isotopic signals due to the position of the sampling reaches in the river network. The degraded sections were selected to be similar to the restored reaches and to differ only in the absence of restoration activities (Hering et al. 2015). Therefore, comparing each restored river section with the nearby still degraded river section enabled quantifying the restoration effect. One flagship project (R1/D1) and one smaller project (R2/D2) were investigated in the following regions: Finland (FI), Sweden (SE), Denmark (DK), Poland (PL), Germany lowlands (DL) and mountains (DM), the Czech Republic (CZ), and Austria (AT). Further information about the general study design, restoration measures and environmental characteristics of the rivers is given in Muhar et al. (2016).

2.2.2 Sampling and laboratory analysis

Sampling was performed in summer 2012 or 2013, at the time of maximum biomass in each region (Table 2.1). We used a standardized sampling design across all 32 river sections, which allowed direct comparison of each restored river section with the nearby still degraded "control section": At each sample section, we collected dominant benthic invertebrate taxa representing different functional feeding groups (FFG) to obtain an overview of the isotopic signatures of consumers at different trophic levels. Restored and degraded sections were sampled in the same field campaign. The invertebrates were taken from different habitats in the section using a shovel sampler (mesh size 500 μm) and a hand net. We sampled late-instar larvae (and larger individuals in case of hololimnic species) representative taxa for the following functional feeding groups:

- Grazers (e.g., *Baetis* sp., *Rhithrogena* sp.)
- Shredders (e.g., *Gammarus* sp., *Asellus* sp., *Nemoura* sp.)
- Collector-gatherers (e.g., Oligochaeta)
- Collector-filterers (e.g., *Hydropsyche* sp., Simuliidae gen. sp.)
- Predators (e.g., *Rhyacophila* sp., *Sialis* sp.)

Each sample consisted of several individuals of the same taxon to obtain sufficient material for stable isotope analysis, and we aimed to collect at least one representative sample per FFG (see Appendix 1 for a list of taxa sampled at each section). In the field, individuals were presorted, counted and kept separated by functional feeding groups to avoid contact between predators and prey. The samples were placed in a cool box in the field and subsequently transported to the laboratory.

In the laboratory, the benthic invertebrates were kept individually in filtered stream water for 12 to 24 hours to allow for gut evacuation. Afterwards, the specimens were identified to the lowest level possible (most often genus). To prepare samples for stable isotope analysis, the animals were freeze-dried until all water was removed, and then ground with mortar and pestle. Four replicates of each taxon from each river section were loaded into tin capsules (~800 µg). Content of carbon and nitrogen and stable isotopes of carbon and nitrogen were analysed with an elemental analyser (CE Instruments EA 1110 CHNS, Carlo Erba, Milan, Italy) connected via a ConflowIV interface to a Thermo Finnigan MAT 253 isotope ratio mass spectrometer (both Thermo Fischer, Bremen, Germany) at University of Duisburg-Essen's Stable Isotope Facility (Instrumental Analytical Chemistry). Data from the stable isotope analysis are expressed as relative difference between ratios of samples and standards (VPDB for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$) as described by the equation:

$$\delta^{13}C, \delta^{15}N = [(R_{sample}/R_{standard}) - 1] \text{ x } 1000, \text{ where } R = {}^{13}C/{}^{12}C \text{ or } {}^{15}N/{}^{14}N.$$

The analytical precision over all measurements (standard deviation from 791 in-house standards) was 0.08‰ for $\delta^{13}C$ and 0.19‰ for $\delta^{15}N$.

2.2.3 Data analysis

We displayed the isotopic composition of benthic invertebrate assemblages in $\delta^{13}C$-$\delta^{15}N$-isotope space (see Appendix 2). Quantitative community metrics, as introduced by Layman et al. (2007b), were calculated independently for each section. These metrics describe the trophic structure of communities and their trophic diversity by the position of species or groups in the $\delta^{13}C$-$\delta^{15}N$-isotope space. Here, we particularly focused on two of these metrics: (i) $\delta^{15}N$ range (NR), calculated as maximum $\delta^{15}N$ minus minimum $\delta^{15}N$; and (ii) $\delta^{13}C$ range (CR), calculated as maximum $\delta^{13}C$ minus minimum $\delta^{13}C$. Both NR and CR describe the distance between the two species or groups with the most enriched and most depleted $\delta^{15}N$ or $\delta^{13}C$ values, respectively (Layman et al. 2007b). We used NR as an indicator for the trophic length of the communities and CR as an indicator of the range of assimilated carbon sources. We calculated two sets of metrics. The first were calculated across all invertebrate species sampled at each river section, and are subsequently referred to as total range values (NR_{total} and CR_{total}). The second were calculated by classifying the invertebrate species into five feeding groups (predators, shredders, grazers, collector-filterers, collector-gatherers), and then using the mean values of each feeding type to calculate ranges across the FFGs. They are hereafter referred to as mean FFG range ($NR_{meanFFG}$ and $CR_{meanFFG}$). Feeding types were assigned with data from www.freshwaterecology.info (Schmidt-Kloiber & Hering 2015).

Layman et al. (2007b) also calculated the area of a convex hull drawn around all species in $\delta^{13}C$-$\delta^{15}N$-isotope bi-plot to indicate the isotopic niche of the community. This approach was further extended by Jackson et al. (2011) by using standard ellipse area (SEA; expressed in ‰^{2}), which is to bivariate data as standard deviation is to univariate data (Batschelet 1981). The SEA contains c. 40% of the data and can therefore be used to measure the mean core community isotopic niche (Jackson et al. 2011). Here, the standard ellipse area corrected for small samples (SEA_C) was calculated as a measure of the isotopic niche, and was therefore used in the following analysis to quantify restoration effects. The small sample size correction leads to a slightly increased SEA_C in order to adjust bias towards underestimation (Jackson et al 2011). SEA_C was further applied to test for isotopic niche overlap between restored and corresponding degraded sections, which gives a measure of dietary similarity/dissimilarity (Jackson et al. 2012). We finally pairwise tested the probability if SEA of the degraded section is smaller than SEA of the restored section based on the Bayesian standard ellipse area (SEA_B). We refer to Jackson et al. (2011) for a comprehensive description of SEA, SEA_C and SEA_B.

To quantify restoration effects across all 16 catchments we first pairwise compared CR, NR and SEA_C between restored and corresponding degraded sections (R vs. D) and between large and small restored sections (R1 vs. D1 and R2 vs. D2). This allowed first investigation of patterns in trophic structure related to river restoration. We further used an effect size by calculating the response ratio according to Osenberg et al. (1997):

$$\Delta r = \ln\left(\frac{\bar{X}_R}{\bar{X}_D}\right)$$

with $\bar{X}_R$ and $\bar{X}_D$ being $\delta^{13}C$ range, $\delta^{15}N$ range or the standard ellipse area corrected for small samples of restored and degraded sections, respectively; values > 0 are denoting a positive effect (e.g. an increase in $\delta^{13}C$ range), and values < 0 are indicating a negative effect. One-sample t-test was used to assess if effect sizes differed significantly from 0. The effect sizes based on CR, NR and SEA_C were compared. Both, an overall comparison of effect sizes (R1 and R2 pooled) and a comparison between large and small restoration projects (R1 vs. R2) were carried out to test if there was an overall positive effect of restoration, and if the effect of restoration depends on the restoration effort. Although the restored sections were selected to differ only in terms of restoration intensity (R1 vs. R2), there were differences in restoration measures employed independently from restoration extent: some projects aimed at river widening, while others applied measures mainly affecting the river channel itself (e.g., instream measures or flow restoration) (Table 2.1). Therefore, we re-grouped the sections based on the restoration measure employed (widening vs. others) and tested if effect sizes differ between restoration projects which mainly aimed at river widening (usually affecting both instream habitats and connectivity of water and land and thereby enhancing availability of autochthonous and allochthonous carbon resources) and projects which established other, less extensive measures affecting the river channel itself (instream measures, flow restoration, remeandering, anastomosing). For selected restored and degraded sections, we worked out changes in trophic structure in more detail, based on niche overlaps and probabilities as inferred from SEA_C.

For the calculation of community-wide metrics (CR and NR), we used the package Stable Isotope Analysis (SIAR: Parnell et al. 2008, 2010) in R (R Development Core Team, 2007). The standard ellipse areas (SEA) were calculated using the SIBER package (Stable Isotope Bayesian Ellipses in R, Jackson et al. 2011) of SIAR (Parnell et al. 2008, 2010). Further statistical analyses, including Wilcoxon Matched Pair tests, t-tests (one-sample t-test against 0) and Mann Whitney U tests, were run in Statistica 12 (StatSoft).

2.3 Results

2.3.1 General patterns of river restoration on CR and NR metrics of benthic invertebrates

The pairwise comparison of benthic invertebrate communities between restored (R) and degraded (D) sections (large and small projects pooled) across all 16 catchments showed minor differences in both $\delta^{15}N$ range and $\delta^{13}C$ range. The difference between restored and degraded sections was not significant, neither for the total range, nor mean FFG range used for the calculation of NR and CR (Wilcoxon Matched Pair test, $p > 0.06$, $n = 16$, Table 2.2). The median NR_{total} was equivalent to the distance between two trophic levels (3.68 ‰ in restored sections and 3.12 ‰ in degraded sections, $n = 16$, Table 2.2). The $NR_{meanFFG}$ was smaller (restored sections: 2.21‰; degraded sections: 2.28‰).

For the general comparison of effect sizes according to Osenberg et al. (1997), values above zero indicate enhanced $\delta^{15}N$ range or $\delta^{13}C$ range in restored sections. Restoration had an overall positive effect on CR_{total} as the effect size ratio differed significantly from zero (t-test, $p < 0.05$, Figure 2.1), while $CR_{meanFFG}$ ratio was not significantly larger than zero (t-test, $p > 0.15$). Effect sizes for neither $NR_{meanFFG}$ nor for NR_{total} were different from zero (t-test, $p > 0.6$).

Table 2.2: Pairwise comparison of $\delta^{13}C$ and $\delta^{15}N$ ranges for R vs. D, R1 vs. D1 and R2 vs. D2 using Wilcoxon Matched Pair test. The analysis is based on total range values (i.e. all taxa are considered; not grouped into feeding types) and mean values (i.e. mean values of the feeding types were used). 25 and 75% percentiles are given in parentheses. Significant differences ($p < 0.05$) are indicated by bold median values.

	Total range values				**FFG mean range values**				
	$\delta^{15}N$ range (‰)		$\delta^{13}C$ range (‰)		$\delta^{15}N$ range (‰)		$\delta^{13}C$ range (‰)		
	Median	p	Median	p	Median	p	Median	p	n
R1 and R2 pooled									
R	3.68	0.80	6.29	0.06	2.21	0.96	4.70	0.18	16
	(2.24 - 4.8)		(5.42-8.89)		(1.62-3.02)		(3.89-5.93)		
D	3.12		5.64		2.28		3.80		16
	(2.45-4.27)		(4.12-8.33)		(1.53-3.12)		(3.22-5.08)		
Large projects									
R1	3.68	0.78	**7.46**	**0.01**	1.99	0.78	4.01	0.33	8
	(2.32-4.17)		(5.19-10.29)		(1.64-2.65)		(3.65-4.76)		
D1	2.94		**6.39**		1.80		3.43		8
	(2.4-4.01)		(4.12-8.33)		(1.52-2.51)		(3.22-4.43)		
Small projects									
R2	3.71	1.00	5.72	0.89	2.30	0.89	5.72	0.33	8
	(2.14-5.32)		(5.42-6.87)		(1.62-3.36)		(4.52-6.20)		
D2	3.14		5.20		2.89		4.35		8
	(2.54-4.49)		(4.17-7.98)		(1.83-3.66)		(2.81-6.00)		

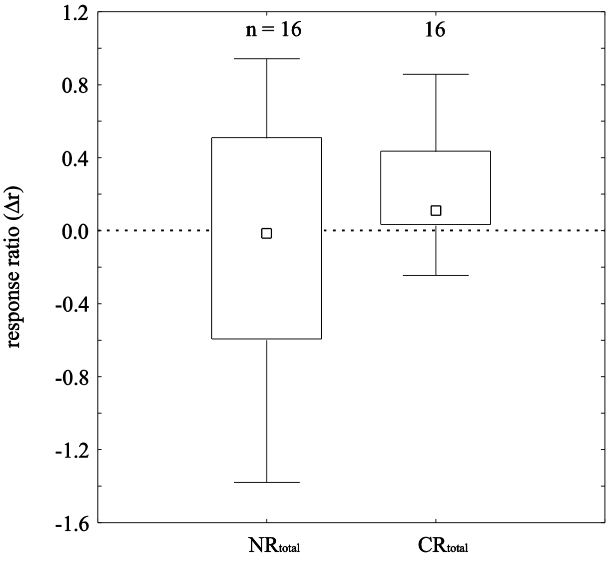

Figure 2.1: General restoration effect (R1 and R2 pooled) calculated as response ratio after Osenberg et al. (1997) for total range values of NR and CR (Median; Box: 25%–75%; Whisker: Min-Max). Effect sizes were pairwise calculated for each pair of restored and degraded sections.

2.3.2 Effects of large and small restored sections on CR and NR metrics of benthic invertebrates

The pairwise comparison between the four groups of sections (large restored sections: R1; corresponding degraded sections: D1; small restored sections: R2; corresponding degraded sections: D2) showed minor differences for $\delta^{15}N$ ranges and $CR_{meanFFG}$ (Table 2.2). In contrast, CR_{total} differed significantly between R1 and D1 (Wilcoxon Matched Pair test, $p < 0.05$, $n = 8$), but not between R2 and D2 (Wilcoxon Matched Pair test, $p > 0.89$, $n = 8$).

Similarly, the pairwise calculated effect sizes, expressed as response ratios following Osenberg et al. (1997), revealed a positive effect of restoration on CR_{total} on large restored river sections (R1) (t-test, $p < 0.05$, Figure 2.2) but not for the small restored sections (R2) (t-test, $p > 0.33$), suggesting that the range of assimilated sources is positively related to restoration extent. There were no significant effects of restoration on $CR_{meanFFG}$, NR_{total}, and $NR_{meanFFG,}$ neither for the large nor for the small restoration projects (t-tests, $p > 0.17$). Moreover, the comparison of the effect sizes between more- and less extensive restored sections (i.e., response ratios of R1 compared to the response ratios of corresponding R2 sections) did not reveal a significant difference for any of the metric values (Wilcoxon Matched Pair test, $p > 0.2$).

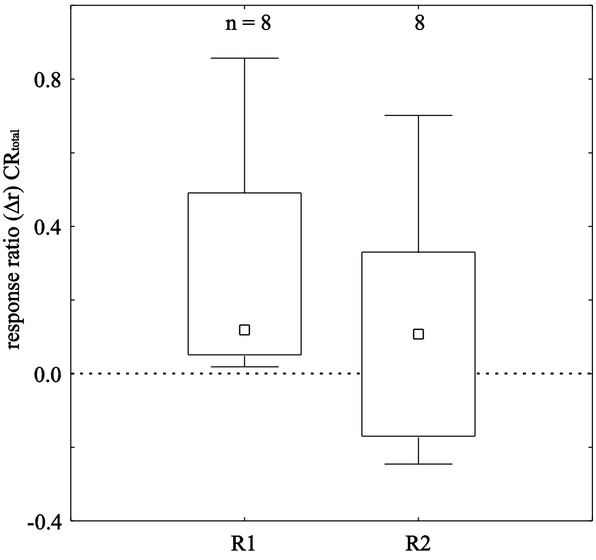

Figure 2.2: Comparison of response ratios after Osenberg et al. (1997) based on CR_{total} in large (R1) and small (R2) restoration projects; effect sizes were pairwise calculated (Median; Box: 25%–75%; Whisker: Min-Max).

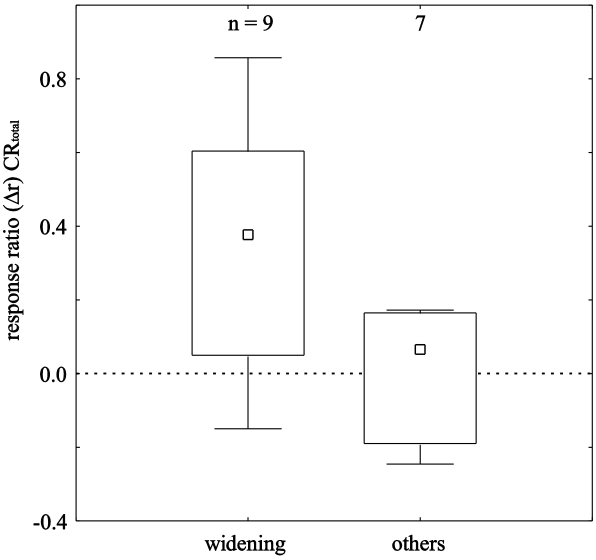

Figure 2.3: Comparison of response ratios after Osenberg et al. (1997) based on CR_{total} in restored sections with widening and restored sections with other measures (e.g., improvement of instream habitats); effect sizes were pairwise calculated (Median; Box: 25%–75%; Whisker: Min-Max).

2.3.3 Relationship of the metric values and the type of restoration measures

The alternative grouping of sections was based on the restoration measure employed (widening vs. others) and was therefore independent from restoration extent. The comparison of the effect sizes according to Osenberg *et al.* (1997) between restoration projects which mainly aimed at river widening (n=9) and projects which applied other less extensive measures mainly affecting the river channel itself (n=7) showed a positive effect for CR_{total} in sections where measures focused on river widening (Figure 2.3). Here, the effect size for $\delta^{13}C$ range was significantly larger than zero (t-test, $p < 0.05$). Effect sizes for $\delta^{15}N$ range were not significantly different from zero, neither using total range values nor mean values for the calculation of NR. The response ratios were not different between measures which aimed at river widening and other measures (Mann-Whitney U test, $p > 0.2$).

2.3.4 Effects of river restoration on isotopic niche metric of benthic invertebrate communities

The entire statistical comparisons described above were simultaneously run based on standard ellipse area corrected for small samples (SEA_C). There was no support for a general restoration effect on SEA_C across all 16 catchments, i.e., neither pairwise comparison nor the effect sizes calculated according to Osenberg et al. (1997) revealed a significant difference; including the general comparison between R vs. D, the test if restoration extent has an effect (R1 vs. D1 and R2 vs. D2), and the re-grouping considering the type of restoration measure applied (widening vs. others). However, changes in SEA_C were apparent between some specific restored and degraded sections (Figure 2.4, Table 2.3).

In five of our eight study regions, SEA_C was bigger in R1 sections compared to the corresponding D1 sections, suggesting a larger isotopic niche following restoration. These sections are located in Finland, Sweden, Poland, Germany (mountains), and Austria (Figure 2.4, Table 2.3). Similarly, the probabilities that D1 had smaller SEA_B than the corresponding R1 were 72% in Finland, 92% in Sweden, 95% in Poland, 86% in Germany (mountains), and 81% in Austria, respectively. The comparison between small restored sections with the degraded "control-sites" only showed bigger SEA_C in the R2 sections in Finland, Sweden, Germany (lowlands), and Austria. The associated probabilities that D2 had smaller SEA_B than the corresponding R2 sections were 71% in Finland, 72% in Sweden, 93% in Germany (lowlands), and 67% in Austria. In contrast, there were no larger SEA_C in R1 nor R2 sections compared to the corresponding D1/D2 in Denmark and in the Czech Republic. There were no distinct patterns in dietary similarity/dissimilarity by comparing the overlap between R2/D2 sections with those of the corresponding R1/D1 sections. In some cases, the overlap between R2/D2 was bigger compared to the corresponding R1/D1 sections (e.g., Czech Republic), suggesting that the diets of invertebrate communities were more similar in the less intensively restored sections (Figure 2.4, Table 2.3). However, this effect did not appear across all sections (e.g., in Denmark), and more often the difference between isotopic niches of restored and corresponding degraded section seemed to be independent from restoration extent (Figure 2.4).

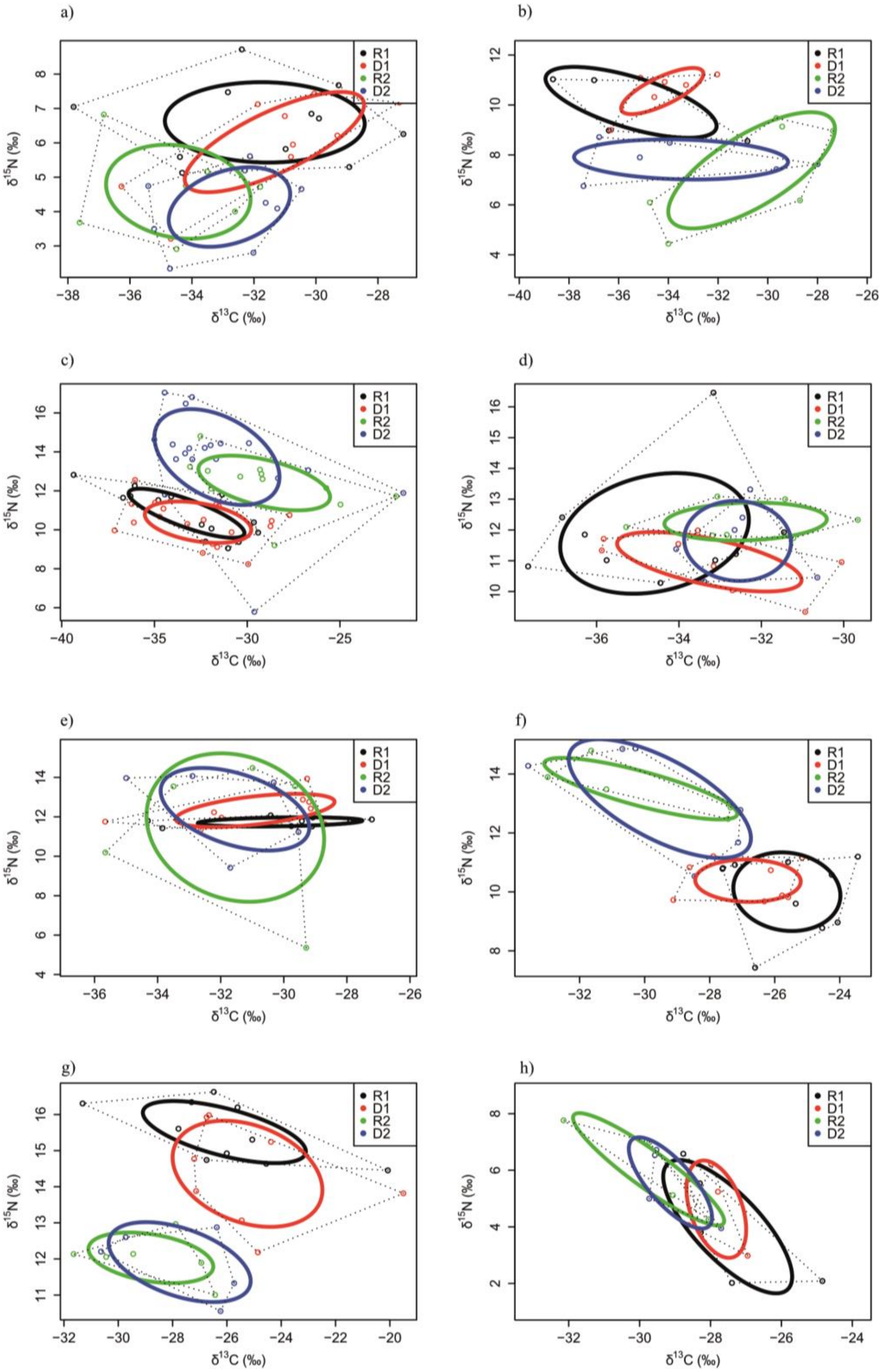

Figure 2.4: Mean stable isotope composition of the different benthic invertebrates from the eight study regions: a) Finland, b) Sweden, c) Denmark, d) Poland, e) Germany lowland, f) Germany mountain, g) Czech Republic, and h) Austria. *Solid lines* enclose the standard ellipses area (SEA$_C$), containing *c*. 40% of the data, showing the isotopic niche of representative benthic invertebrate communities at each site. *Dotted lines* are the convex hull areas of benthic invertebrate communities for each site, corresponding to the area encompassing all invertebrates in the δ^{13}C-δ^{15}N plot. R1 = large restoration, R2 = small restoration, and D1/D2 = corresponding degraded control-sites. Axes are idealized for each region.

Table 2.3: Standard ellipse area corrected for small samples (SEA_C), probability that the SEA in the degraded section is smaller than the SEA in the restored section, overlap in SEA_C between pairs of sites (restored and degraded), and overlap in % of respective area.

	SEAc (‰²)	**Probability that SEA_B D < SEA_B R**	**Overlap in SEA_C between R and D(‰²)**	**Overlap in % of respective SEA**
Large restored (R1)				
FI_R1	11.8	0.723	6.1	51.76
SE_R1	11.5	0.916	1.8	16.03
DK_R1	7.4	0.320	5.5	74.34
PL_R1	13.7	0.953	3.1	22.51
DL_R1	1.8	0.185	0.8	44.75
DM_R1	6.9	0.860	2.3	33.47
CZ_R1	6.3	0.173	3.6	56.12
AT_R1	8.9	0.810	3.9	43.44
Degraded (D1)				
FI_D1	8.8			69.22
SE_D1	3.2			57.55
DK_D1	8.9			61.47
PL_D1	5.4			57.59
DL_D1	5.7			14.39
DM_D1	3.7			62.66
CZ_D1	12.1			29.31
AT_D1	4.1			93.56
Small restored (R2)				
FI_R2	9.9	0.705	3.8	38.87
SE_R2	17.3	0.715	3.9	22.41
DK_R2	13.5	0.055	8.0	59.36
PL_R2	3.8	0.416	2.4	64.32
DL_R2	32.9	0.926	13.9	42.24
DM_R2	5.7	0.170	5.1	90.81
CZ_R2	4.7	0.309	4.0	84.36
AT_R2	5.3	0.666	3.1	57.45
Degraded (D2)				
FI_D2	6.7			57.05
SE_D2	10.8			35.93
DK_D2	23.7			33.80
PL_D2	5.3			46.01
DL_D2	13.9			99.99
DM_D2	13.2			38.78
CZ_D2	8.0			50.01
AT_D2	3.9			78.22

2.4 Discussion

Restoration of rivers is expected to increase the diversity of both habitat- and resource-based niches, which together have potential to affect the trophic structure of invertebrate communities. In line with this, we expected changes in the isotopic signatures of benthic invertebrate consumers indicative both of increased resource breadth (indicated by $\delta^{13}C$ range), and increases in trophic length (indicated by $\delta^{15}N$ range) following river restoration, which together favour larger isotopic niches of invertebrate assemblages (indicated by SEA_C). We further expected that the larger the restoration the bigger the impact. We found some support for an increase in resource breadth associated with restoration across all 16 restored sections, with these effects stronger for larger-scale restoration projects, and especially projects which aimed at river widening. In contrast, there was no support for a general increase in trophic length across all 16 catchments, though increases in NR ratios were apparent between some specific degraded and restored sections, suggesting such effects depend on local assemblage composition and/or environmental conditions. In line with this, changes in isotopic niche width of invertebrate assemblages were obvious between some specific restored and degraded sections. These findings suggest that river restoration results in modest changes in trophic structure. However, this is largely dependent on positive effects on the variety of resources assimilated by consumers (confirming hypothesis 1), rather than trophic length (rejecting hypothesis 2), with both effects further depending on restoration extent, the type of restoration measures employed and local environmental and community characteristics.

2.4.1 Restoration effects on trophic structure of benthic invertebrate communities

When using total community range values (CR_{total}), shifts in the $\delta^{13}C$ isotopic signatures of benthic consumers indicate an overall increase in the variety of resources assimilated following restoration (widening of CR). We further found that the increase in CR_{total} was significantly greater in more extensively restored sections (i.e., comparing R1 and D1), relative to the less extensive restorations (between R2 and D2). Similar results are apparent when comparing pairwise calculated effect sizes, expressed as response ratio after Osenberg et al. (1997), confirming the importance of restoration effort in dictating potential changes in the resource base and consumer responses. The increased CR_{total} ratio might reflect an increased availability of habitats suitable for autochthonous productivity, and/or a higher availability of allochthonous carbon resources either due to an intensified aquatic-terrestrial interaction or to the higher retentivity of restored sections. These possibilities are supported by results presented in Poppe et al. (2016) who showed that measures were significantly impacting the hydromorphology of our sections, and by Göthe et al. (2016) who found positive effects of restoration on riparian vegetation adjacent to our reaches. Effects on hydromorphology in particular were greater in the more extensively restored sections (Poppe et al. 2016). We sampled representatives of the same functional groups from all reaches, hence the change in the CR_{total} of invertebrates can partly be attributed to the dietary flexibility of many species, including those representing more specialized functional groups, allowing the food web as a whole to respond to the availability of novel resources (Mihuc 1997, Göthe et al. 2009, Layer et al. 2013). Increases in the variety of available resources may also help support the more flexible taxa among the invertebrates, at times or year or during particular disturbances when their preferred resource may be scarce. Overall, a greater range of basal resources allows for heterogeneous energy flow pathways, which is an important factor for stabilizing food webs (Rooney et al. 2006, Layman et al. 2007b). We found that river widening is a particularly effective restoration measure for increasing the breadth of resources available to consumers. Whereas CR_{total} increased markedly following river widening, projects which applied other less extensive measures mainly affecting the river channel itself (instream measures, flow restoration, remeandering, anastomosing) had no similar effects. River widening increases the surface area of instream habitats, and increases lateral connectivity between the river and its floodplain and can thereby enhance the availability of autochthonous and allochthonous carbon resources. Lepori et al. (2006) found no effect of increased detritus retentivity following restoration on the $\delta^{13}C$ signature of consumers, suggesting either that detritus was not limiting for consumers, or that the increase in retentivity was insufficient to alter carbon flows in the food web. The type of restoration studied by Lepori et al (2006) aimed primarily at restoring instream habitats, and thus may be comparable to the predominantly “instream” measures assessed in our study. Overall, our results provide strong evidence that the magnitude of food web changes following restoration can indeed depend strongly not only on the scale, but also type of restoration.

In contrast with the relatively consistent changes in the range of resource assimilation following restoration at the European scale, there were no overall effects on trophic length. Thus, regardless of whether we compared NR_{total} directly between reaches, or analysed response ratios, we could not detect any shifts in the range of $\delta^{15}N$ signatures. Effects on NR also did not differ between restoration measures. Furthermore, when considered in light of trophic fractionation, we also have no evidence for the clear addition of trophic levels following restoration. The value of trophic fractionation within food webs is often given with *c.* 3 ‰ (e.g., 3.4 ‰ in Minagawa & Wada 1984, Post 2002). We therefore assumed the $\delta^{15}N$ value of a consumer to be enriched by this value over that of its diet (Vander Zanden &

Rasmussen 2001). We observed the median $\delta^{15}N$ range of our invertebrate communities (NR_{total}) to span the space between two trophic levels (median restored sections: 3.68 ‰, median degraded sections: 3.12 ‰, n = 16). The results are in line with our expectations, as we sampled primary and secondary invertebrate consumers (e.g., grazers and predators) that should be separated by approximately one trophic level. Thus, based on the organisms we sampled, it appears that effects of the restoration on both the hydromorphology of the restored sections (increased habitat diversity and habitat size, e.g. depth, compare Poppe et al. 2016) and the variety of basal resources (indicated by CR) assimilated by consumers have not altered the trophic length of food chains. One possible reason for this is that, in choosing the most abundant invertebrate predators at each site, we were not sampling high enough in the food chain to detect real changes in food chain length, associated with large predators such as fish that might enter the food web due to increased habitat size and diversity (Woodward & Hildrew, 2002, Woodward et al. 2005, 2010). Other factors which might have obscured a change in food chain length include the possibilities that isotopic signatures of primary consumers might already be higher enriched (e.g., by scavenging on dead animal material), and reducing the relative difference between primary consumer and predator (i.e., minimum $\delta^{15}N$ and maximum $\delta^{15}N$) may not show the absolute higher position of predators in restored sections. Nevertheless, we did see increases in NR in some instances, suggesting that given the right community configurations and/or local environmental conditions, increases in trophic position lower in the food chain are possible following restoration.

We expected SEA to be larger in the restored sections compared to the degraded "control sections" following Layman et al. (2007a), who showed that the trophic niche width of the top predator *Lutjanus griseus* collapsed due to ecosystem fragmentation. He explains this effect with the reduction in diversity of prey taxa, which in turn is related to uniform energy flow pathways throughout the food web. Therefore, we assumed the isotopic niche of benthic invertebrate assemblages to increase with restoration, due to the higher diversity of both habitat- and resource-based niches (Poppe et al. 2016). We found no support for a general increase of isotopic niche width following restoration across our 16 catchments, though increases in SEA_C ratios were apparent between some specific degraded and restored sections. For those sections, the increases in SEA_C were further supported by the probabilities that degraded sections had smaller SEA_B than the corresponding restored sections (calculated based on Bayesian statistics). It is well known that the isotopic niche of a community largely depends on CR and NR as it is based on the distribution of the mean core community in isotope space (Jackson et al. 2011) and thereby combines nitrogen and carbon ranges. This explains why an overall positive effect following restoration is absent: The missing general restoration effect on trophic length (indicated by NR) also negatively affects a potential increase in SEA_C. For example, SEA_C in R1 of the Czech Republic was smaller compared to the degraded “control section”, although the corresponding CR was bigger. Thus, it appears that the smaller SEA_C results from a corresponding smaller NR. Overall, our results indicate that the primary effect of restoration on food web structure lower down in the benthic food web is an increase in the variety of resources assimilated, rather than an extension of food chain length.

2.4.2 Type of data used

The results of our analysis were partly determined by the type of data used: Significant differences in $\delta^{13}C$ range, e.g., between long restored sections compared to the corresponding degraded sections (R1 and D1), were only obtained with values for the total range of community signatures. Mean values of the organisms representing individual feeding types possibly reduced the corresponding $\delta^{15}N$ and $\delta^{13}C$ range, minimizing the influence of species occurring at either end of the isotopic gradients. This indicates that the increased variety of resources assimilated was primarily driven by a few taxa extending their range of resource intake. In fact, the outliers might reflect a higher diversity of the resource base, as stated in our first hypothesis. Consequently, outliers might be a result of restoration as the corresponding invertebrates assimilated sources that were only present at the restored sections.

2.4.3 Recommendations for river management

In this comparative analysis across multiple, heterogeneous restoration projects, we used a representative set of samples to test for restoration effects on trophic structure of benthic invertebrates communities, using a selected set of isotope-based community-wide metrics. To cover a large number of restored sites, we aimed to be pragmatic, straightforward, cost- and time-effective, i.e., we used a representative set of samples, considered time in the lab, and applicability of metrics. This approach could easily be adapted for more expanded sampling, particularly in more regional assessments focused more strongly on particular restoration projects. For instance, future sampling for stable isotope analysis could be coupled to the multihabitat sampling design (Haase et al. 2004). In this case, data about abundance of different taxa would be considered in later assessment of restoration effects to account for the relevance of different basal resources. If a standardized sampling design cannot be implemented or data from different sampling campaigns should be compared, we recommend the Bayesian approach to these metrics introduced by Jackson et al. (2011), and see McCarthy (2007) for an introduction to Bayesian statistics. Overall, this study demonstrates that these isotope-based metrics are useful to identify patterns in trophic structure related to river restoration and that the integration of functional metrics in river management practice can be useful to determine the outcomes of restoration for key ecosystem processes such as trophic transfers of energy and nutrients.

3 River restoration enhances aquatic-terrestrial linkages: a stable isotope study of riparian arthropods in eleven restored floodplain sections

3.1 Introduction

Rivers are an important source of energy and nutrients for riparian biota, particularly in the form of the dispersing adult stages of aquatic insects. The flux of biomass between the river and its riparian zone is determined by habitat structure and assemblage composition in riverine landscapes (e.g., Baxter et al. 2005, Paetzold et al. 2005, Burdon & Harding 2008, Carlson et al. 2016). For instance, emerging aquatic insects and stranded organisms substantially contribute to the diet of predaceous arthropods - such as ground beetles and spiders - inhabiting river shores (Hering & Plachter 1997, Collier et al. 2002, Paetzold et al. 2005). Consequently, riparian arthropods are a central component of floodplain biota, as they contribute to the linking of aquatic and terrestrial food webs (Baxter et al. 2005, Paetzold et al. 2005). Riparian arthropods subsequently serve as prey for other species, such as birds and bats, providing energy for higher trophic levels of terrestrial food webs (Jackson & Fisher 1986, Hammond 1998).

However, the flux of aquatic biomass into terrestrial food webs can be strongly altered by human activities (Carlson et al. 2016). One particularly pervasive impact in Europe is the modification of river channel hydromorphology (EEA 2012), which typically involves the degradation and loss of riparian habitats (Godreau et al. 1999, Tockner & Stanford 2002, Tockner et al. 2008). Negative effects of hydromorphological degradation on the quality of riparian habitats and diversity and composition of biota are well documented (e.g., Paetzold et al. 2008, Lambeets et al. 2009, Januschke et al. 2011). It can be assumed that also the fluxes of aquatic biomass to the terrestrial zone are affected as the river channel is disconnected from its riparian zone by many measures of hydraulic engineering.

In Europe, the hydromorphology of a large number of river sections is nowadays being restored, which typically enhances habitat diversity not only in the river channel, but also in the riparian zone (e.g., Jähnig et al. 2010, Januschke et al. 2014, Poppe et al. 2016). Riparian biota are positively affected by restoration, e.g. through increasing species richness and abundance of riparian carabid beetles (Jähnig et al. 2009, Januschke et al. 2014, Januschke & Verdonschot 2016). A major driver of change is the provision of habitats suited for riparian biota, e.g. open sand and gravel bars. In addition, hydromorphological restoration may impact the riparian food web. A stronger connection of river and floodplain, e.g. caused by a more shallow profile or the removal of bank fixations, potentially makes aquatic prey more easily accessible to riparian predators as the shoreline is more open for cross habitat movements of organisms including emerging aquatic insects that crawl on the shore (Paetzold et al. 2005). Consequently, restoration not only provides habitats for riparian arthropods, but is also likely to increase the proportion of aquatic prey in the diet of riparian predators resulting in an improved trophic linkage between river and land.

However, the effect of restoration on energy and nutrient transfer between river channel and its adjacent riparian zone has not yet been sufficiently characterized. More generally, restoration effects have rarely been viewed from a functional point of view (but see Lepori et al. 2005b, 2006, Flores et al. 2011, Kupilas et al. 2016). Studying the effect of restoration on the linkage between these ecosystems is crucial to understand if restoration reestablishes this particular food web linkage and how the provision of riparian habitats promotes trophic reconnection. This is of interest for wider ecosystem management, as rivers most often represent habitats of high productivity that can fuel less productive systems (e.g. riparian and terrestrial) and thereby support other species of conservation interest (Jackson & Fisher 1986, Hammond 1998, Paetzold et al. 2005).

Stable isotope composition of carbon and nitrogen ($\delta^{15}N$, $\delta^{13}C$) is commonly used to study food webs. Trophic fractionation, i.e. the enrichment or depletion in $\delta^{15}N$ and $\delta^{13}C$ between diet and consumer, is important to evaluate food web relationships. According to Post (2002), the trophic fractionation of $\delta^{15}N$ is 3.4 ± 1‰ and of $\delta^{13}C$ is 0.4 ± 1.3‰. Based on this isotopic shift between prey and predator, $\delta^{15}N$ is generally used to characterize the trophic position of a consumer and $\delta^{13}C$ can be used to identify the ultimate carbon sources for an organism (Post 2002). Consequently, stable isotopes of carbon and nitrogen can be used to study food web organization and to trace affiliation of species or groups to each other in isotope space.

To assess effects of hydromorphological restoration on trophic patterns across the aquatic-terrestrial interface, we conducted a large scale comparative study targeting eleven river restoration projects in central and northern Europe. We analyzed stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) for a representative set of consumers sampled in the river and its floodplain indicating their aquatic, riparian (within one meter distance from the river) or terrestrial (beyond the riparian zone) origin due to their position in isotope space. We hypothesized that (i) isotopic signatures (δ^{13}C and δ^{15}N) of benthic invertebrates and terrestrial arthropods show a clear separation, and that isotopic signatures of riparian arthropods show evidence for an intermediate position in isotope space, reflecting the use of both in-stream and terrestrial resources. Rather than an exhaustive quantification of different potential basal resources in the aquatic and terrestrial habitats, our analyses focused on detecting shifts in the position of the organisms themselves in isotope space. In particular, we sought to detect changes in the position of riparian arthropods in isotope space following restoration. We calculated the isotopic distance of riparian arthropods to benthic invertebrates and terrestrial arthropods as a measure of trophic linkage, and hypothesized that (ii) isotopic signatures of riparian arthropods in restored reaches show evidence for an increased trophic linkage of river and land: increased distance to terrestrial arthropods reflecting a smaller share of terrestrial prey, and higher similarity to benthic invertebrates reflecting an increased use of aquatic resources. Finally, we assumed that (iii) riparian habitat diversity and the provision of unvegetated side bars are positively related to the strength of aquatic-terrestrial linkages as reflected by our measures of trophic linkage.

3.2 Materials and Methods

3.2.1 Study sites

We investigated the isotopic composition of consumers in aquatic, riparian and terrestrial habitats associated with eleven restoration projects conducted across central and northern Europe (Table 3.1, Muhar et al. 2016), encompassing both medium-sized lowland rivers and medium-sized mountain rivers. On each river, we selected a representative sampling reach at the downstream end of a restored river section (R) and compared it to a non-restored, hydromorphological degraded "control section"(D) located upstream of the restored section. As the distance between restored and degraded river sections was small relative to overall river size (2.8 km, n = 11), background shifts in isotopic composition (e.g. arising from geological or vegetation change) unrelated to the restoration are not anticipated between the sections. The degraded river sections were similar to the restored sections and differed only in the absence of restoration activities (Hering et al. 2015). The rivers are located in the following regions: Finland (FI), Sweden (SE), Germany lowlands (DL) and mountains (DM), the Czech Republic (CZ) and Austria (AT). Detailed information about the restoration measures and environmental characteristics of the rivers is given by Muhar et al. (2016).

Table 3.1: Overview of restored study reaches (compare Muhar et al. 2016).

Site name	**FI_R1**	**SE_R1**	**DM_R1**	**CZ_R1**	**AT_R1**	**FI_R2**	**SE_R2**	**DL_R2**	**DM_R2**	**CZ_R2**	**AT_R2**
Country	Finland	Sweden	Germany	Czech Republic	Austria	Finland	Sweden	Germany	Germany	Czech Republic	Austria
River name	Vääräjoki	Emån	Ruhr	Becva	Drau	Kuivajoki	Mörrumsån	Spree	Lahn	Morava	Enns
River type	Gravel-bed	Gravel-bed	Gravel-bed	Gravel-bed	Gravel-bed	Gravel-bed	Gravel-bed	Sand-bed	Gravel-bed	Gravel-bed	Gravel-bed
Latitude (N)	64.054433	57.149095	51.44093	49.4968975	46.75454	65.6860429	56.336005	52.377747	50.86588	49.6570728	47.42112
Longitude (E)	24.2206639	16.441897	7.96223	17.5211533	13.309393	25.6349874	14.700237	13.878897	8.79088	17.2179975	13.816094
Altitude (m a.s.l.)	60	10	153	232	570	74	87	35	191	218	692
Catchment geology	organic	siliceous	siliceous	siliceous	siliceous	organic	siliceous	siliceous	siliceous	siliceous	calcareous/ siliceous
Mean discharge (m^3/s)	9.9	29.3	15.2	16.6	62.6	12.8	12	14	12	17.7	21.5
Stream order	4	6	3	7	7	4	6	6	3	7	5
Ecoregion	Fenno-scandian shield	Fenno-scandian shield	Central Highlands	Hungarian lowlands	Alps	Fenno-scandian shield	Fenno-scandian shield	Central plains	Central Highlands	Hungarian lowlands	Alps
Restoration Length (km)	1.4	0.9	0.75	0.45	1.9	0.4	3.3	0.95	0.24	0.22	0.6
Restoration date	1997-2006	2006-2011	2008	1997	2002-2003	2002-2006	2003-2012	2005	2000	1997	2003-2004
Main restoration action	instream measures	Hydro RivCon (dam removal, naturalise flow regime, fishway construction, salmonid spawning gravel and boulder additions)	riverbed widening	riverbed widening	riverbed widening; (partial removal of bank fixation; initiation of secondary channel; reconnection of one sidearm)	instream measures	Hydro RivCon (increased flow, fishway construction and salmonid spawning gravel additions)	remeandering	riverbed widening	riverbed widening	riverbed widening (partial removal of bank fixation; initiation of one secondary channel)
Time of sampling	August 2012	August 2013	June 2013	September 2012	July 2013	August 2012	August 2013	July 2013	July 2013	September 2012	July 2013

3.2.2 Sample collection, preparation and laboratory analysis

Study reaches were sampled in summer 2012 and 2013, at the time of maximum biomass (Table 3.1). Field personnel were trained on a standard agreed field protocol during a workshop in spring 2012 (Hering et al. 2015), to ensure uniformity in the sampling methods employed. At each study reach, representative samples of aquatic, riparian and terrestrial consumers were collected to obtain an overview of the isotopic signatures across the aquatic-terrestrial interface. We collected riparian and terrestrial arthropods (predaceous ground-dwelling beetles and spiders) and dominant benthic invertebrate taxa representing different functional feeding groups. Basal resources (fine and coarse particulate organic matter in the river and most abundant terrestrial plant material) were taken for background information on isotopic signatures. Restored and degraded sections were sampled in the same field campaign.

Predaceous riparian ground beetles or spiders (formerly referred to as riparian arthropods; compare Appendix 3) were sampled within one meter distance to the river edge at randomly chosen locations of the study reach using exhausters and forceps (Figure 3.1). Potential terrestrial food sources of riparian arthropods were indirectly inferred from predaceous ground-dwelling beetles or spiders sampled adjacent to the riparian zone (referred to as terrestrial arthropods). Each sample of riparian and terrestrial arthropods consisted of several individuals.

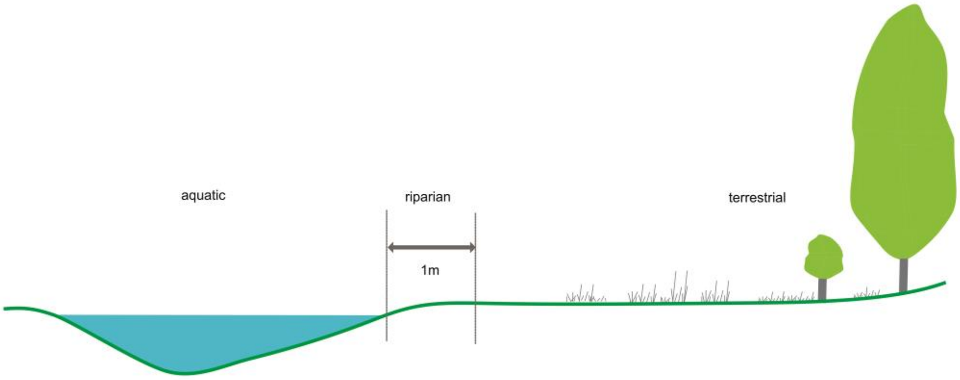

Figure 3.1: Schematic overview of aquatic, riparian, and terrestrial habitats sampled at each study reach.

We collected late-instar larvae (and larger individuals in case of hololimnic species) of the dominant benthic invertebrate taxa representing different functional feeding groups (FFG) to obtain an overview of the isotopic signatures of aquatic consumers at different trophic levels and to infer isotopic signals of potential aquatic food sources of riparian arthropods. The late-instar larvae reflect the isotopic composition of an aquatic insect at the time close to emergence, and thus most closely represent the composition of the adult stage most prone to predation by riparian arthropods (Paetzold et al. 2005). The sampling of benthic invertebrates is described in more detail by Kupilas et al. (2016). Briefly, invertebrates were collected from different habitats along the study reach using a shovel sampler (mesh size 500 µm) and a hand net. Each sample consisted of several individuals of the same taxon.

Riparian arthropods, terrestrial arthropods and benthic invertebrates were presorted, counted and kept separated. The samples were placed in a cool box in the field and subsequently transported cool to the laboratory. In the laboratory, specimens were kept individually for 12 to 24 hours to allow for gut evacuation (benthic invertebrates were hold in filtered stream water). Afterwards, the specimens were identified to the lowest level possible (most often species or genus; compare Appendix 3). To prepare samples for stable isotope analysis, we freeze-dried the samples to remove water, and then ground them with mortar and pestle to obtain a homogenized composite sample. Depending on the amount of sample material, up to four replicates of each sample from each river section were loaded into tin capsules (~800 µg).

At each study reach, we collected terrestrial basal resources from randomly selected locations along the shoreline for background information on isotopic composition of the resources. Fine and coarse particulate organic matter (POM), e.g. decaying leaves from riparian trees and herbaceous riparian vegetation, was collected from deposition zones in the river reach. In the laboratory, samples were rinsed and examined visually to remove all inorganic matter, benthic invertebrates or fragments of fresh plants. Samples of the most abundant terrestrial plants were collected from randomly selected locations along the shoreline of the study reach, e.g. herbaceous riparian vegetation from shallow banks. Plant samples were taken without roots. In the laboratory, samples were rinsed and examined visually to remove all material and specimens were identified to the lowest level possible (species or genus). The resource samples were freeze-dried in case of POM and dried at 60°C in case of plants until all water was removed. Afterwards, the samples were ground with mortar and pestle to obtain a homogenized composite sample. Several replicates of each sample were loaded into tin capsules.

Content of carbon and nitrogen and stable isotopes of carbon and nitrogen were analysed with an elemental analyser (CE Instruments EA 1110 CHNS, Carlo Erba, Milan, Italy) connected via a ConflowIV interface to a Thermo Finnigan MAT 253 isotope ratio mass spectrometer (both Thermo Fischer, Bremen, Germany) at University of Duisburg-Essen's Stable Isotope Facility (Instrumental Analytical Chemistry). Data from the stable isotope analysis are expressed as relative difference between ratios of samples and standards (VPDB for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$) as described by the equation:

$$\delta^{13}C, \delta^{15}N = [(R_{sample}/R_{standard}) - 1] \text{ x } 1000, \text{ where } R = {}^{13}C/{}^{12}C \text{ or } {}^{15}N/{}^{14}N.$$

The analytical precision over all measurements (standard deviation from 791 in-house standards) was 0.08‰ for $\delta^{13}C$ and 0.19‰ for $\delta^{15}N$.

3.2.3 Data analysis

We displayed the isotopic composition of each study reach in $\delta^{13}C$-$\delta^{15}N$-isotope space (Appendix 4). For benthic invertebrate communities we computed the area of a convex hull drawn around all species in isotope space to indicate the isotopic niche of the community. For further analyses, we calculated mean isotopic values of each community (separately for $\delta^{13}C$ and $\delta^{15}N$), reflecting the average isotopic signature of the particular aquatic system; the arithmetic mean of a community is similar to its centroid in isotope space. We used multiple Wilcoxon Matched pair tests between organism groups (aquatic, riparian, terrestrial) to explore the general trophic organization across the aquatic-terrestrial interface for the total population of restored and degraded sections (n=22). We inferred the trophic relationship of riparian arthropods to either the aquatic or the terrestrial system based on their position in isotope space considering trophic fractionation.

We calculated two metrics based on the relative position of groups to each other in the $\delta^{13}C$-$\delta^{15}N$-isotope space independently for each reach: the distance of riparian arthropods to terrestrial arthropods, calculated as riparian arthropods minus terrestrial arthropods; and the distance of riparian arthropods to benthic invertebrates, calculated as riparian arthropods minus benthic invertebrates separately for $\delta^{13}C$ and $\delta^{15}N$. Both metrics indicate trophic linkage of riparian arthropods to the terrestrial and aquatic system considering trophic fractionation. To quantify the restoration effect, we then pairwise compared isotopic distances of riparian arthropods to terrestrial arthropods and benthic invertebrates between restored and corresponding degraded reaches using Wilcoxon Matched pair tests.

To explore the relationship between riparian habitat composition and the strength of trophic linkages, we used data on riparian habitats recorded by Poppe et al. (2016). Briefly, for each study reach riparian habitats were recorded along ten equidistant transects vertical to flow directions containing the entire flood-prone area. The length of each riparian habitat feature was measured and proportions were computed. We calculated riparian habitat diversity (Shannon-Wiener Index) based on the habitat composition at each study reach and correlated the resulting habitat diversity to the trophic linkage metrics (i.e. isotopic distances). In addition, the proportion of open side bars as key habitats for ground-dwelling riparian arthropods was correlated to the trophic linkage metrics. All statistical analyses were performed in R (Version 3.2.2, http://www.r-project.org/).

3.3 Results

3.3.1 Isotopic signatures across the aquatic-terrestrial interface

Benthic invertebrates were significantly different in their isotopic signatures ($\delta^{13}C$, $\delta^{15}N$) from terrestrial arthropods collected beyond the riparian zone, indicating a clear differentiation between aquatic and terrestrial food webs (Wilcoxon Matched pair test, $\delta^{15}N$: $p < 0.001$, $\delta^{13}C$: $p < 0.001$, n=22, Figure 3.2, Appendix 4). The $\delta^{15}N$ isotopic signatures indicated that the aquatic system (benthic invertebrates) was significantly more enriched than the terrestrial system (terrestrial arthropods). Both systems were separated by approximately one trophic level considering trophic fractionation of $\delta^{15}N$: the median of pairwise calculated distances between benthic invertebrates and terrestrial arthropods in isotope space was +3.7‰ (n = 22). Furthermore, benthic invertebrates were significantly more depleted in $\delta^{13}C$ than terrestrial arthropods (median: -1.8‰, n = 22). Therefore, isotopic signatures suggest that predaceous arthropods collected beyond the riparian zone relied more on a terrestrial diet. However, $\delta^{13}C$ isotopic signatures of benthic invertebrates showed a large range, reflecting an overlap in $\delta^{13}C$ across the aquatic-terrestrial interface for the majority of study reaches (Figure 3.2c, Appendix 4).

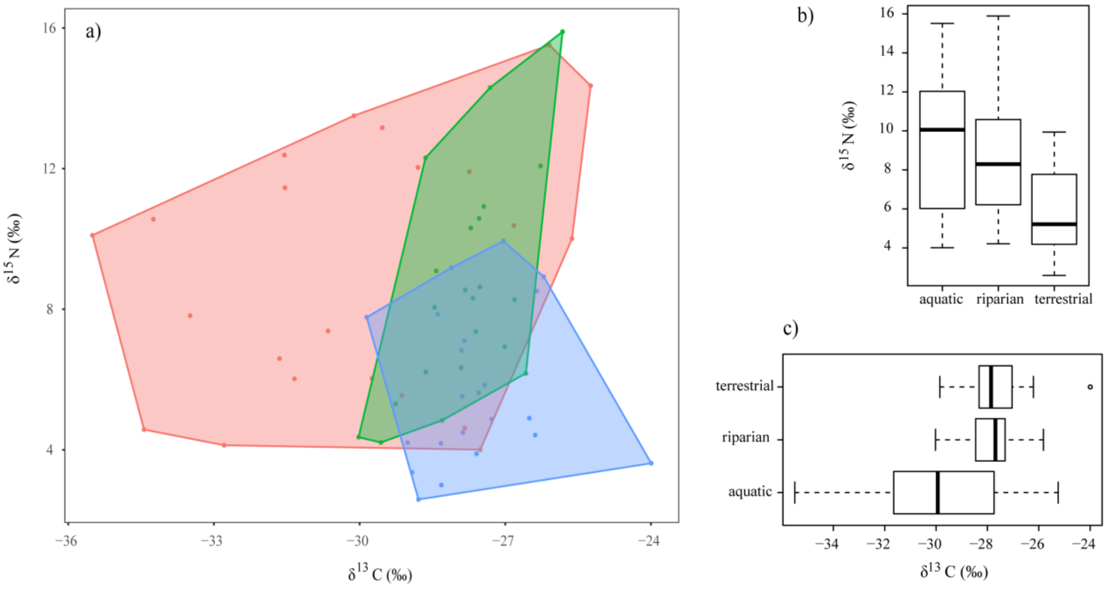

Figure 3.2: Trophic organization across the aquatic-terrestrial interface as indicated by mean stable isotope composition (δ^{15}N, δ^{13}C) of benthic invertebrate communities, riparian arthropods and terrestrial arthropods across all study reaches (n=22): a) general distribution of benthic invertebrates (red), riparian arthropods (green) and terrestrial arthropods (blue) in isotope space, and pairwise comparison of b) δ^{15}N and c) δ^{13}C isotopic signatures between benthic invertebrates (aquatic), riparian and terrestrial arthropods (Median; Box: 25–75%; Whisker: Min–Max excluding outliers, ○ = Outliers).

Riparian arthropods were similar in their δ^{15}N isotopic signatures to benthic invertebrates and significantly different from terrestrial arthropods (Wilcoxon Matched pair test, δ^{15}N: $p < 0.001$, n=22, Figure 3.2b), indicating a large proportion of higher δ^{15}N enriched aquatic prey in the diet of riparian arthropods. Therefore, riparian arthropods were also higher δ^{15}N enriched than their terrestrial counterparts (median of pairwise calculated distances between riparian and terrestrial arthropods: +2.1‰, n = 22). Considering trophic fractionation, however, δ^{15}N isotopic signatures of riparian arthropods reflected a mixed diet with significant proportion of aquatic insects and hence, an intermediate position in isotope space.

In terms of δ^{13}C isotopic signals we observed the opposite pattern, with isotopic signatures of riparian arthropods being more similar to terrestrial arthropods and significantly different from benthic invertebrates (Wilcoxon Matched pair test, δ^{13}C: $p < 0.001$, n=22, Figure 3.2c). Considering trophic fractionation of δ^{13}C (0.4 ± 1.3‰, Post 2002), however, the median of pairwise calculated distances between riparian arthropods and benthic invertebrates across all study reaches was still within the range of one trophic level (+1.5‰, n = 22). Overall, there were large differences between study reaches and riparian arthropods were more closely linked to the aquatic system in Austria, Germany (mountain) and partly in the Czech Republic and Finland. The majority of study reaches in Sweden, Finland and Germany (lowland) revealed more marked differences between riparian arthropods and benthic invertebrates, reflecting that their diet predominantly relied on terrestrial carbon resources (Appendix 4). Accordingly, $\delta^{15}N$ patterns were more consistent for describing trophic linkages of riparian arthropods.

3.3.2 Restoration effect

We compared the isotopic distances of riparian arthropods to terrestrial arthropods and benthic invertebrates between restored and corresponding degraded reaches (separately for $\delta^{15}N$ and $\delta^{13}C$). The $\delta^{15}N$-distance of riparian arthropods to terrestrial arthropods revealed differences between the two groups of sites (Wilcoxon Matched pair test, $p < 0.05$, $n = 11$, Figure 3.3a): The $\delta^{15}N$ isotopic signatures of riparian arthropods were more differentiated from terrestrial arthropods in restored reaches than in degraded reaches, suggesting a significant decrease in the use of terrestrial resources following restoration. Accordingly, riparian arthropods in restored reaches also took a relative higher trophic position than in degraded reaches (as reflected by higher $\delta^{15}N$, Table 3.2), suggesting an increased proportion of higher $\delta^{15}N$ enriched aquatic prey in the diet of riparian consumers following restoration and enhanced trophic linkage. This pattern is further supported by the pairwise comparison between restored and degraded reaches using the $\delta^{15}N$-distance of riparian arthropods to benthic invertebrates: although the comparison showed a minor effect (Wilcoxon Matched pair test, $p = 0.08$, $n = 11$), the findings suggest a closer relation between aquatic and riparian biota in restored reaches (Figure 3.3b).

The pairwise comparison between restored and corresponding degraded reaches using $\delta^{13}C$-distances of riparian arthropods to terrestrial arthropods and benthic invertebrates did not reveal significant patterns. Consequently, the restoration effect was mostly a result of increased distance between riparian and terrestrial arthropods based on $\delta^{15}N$ signatures and hence higher trophic enrichment of riparian predators following restoration.

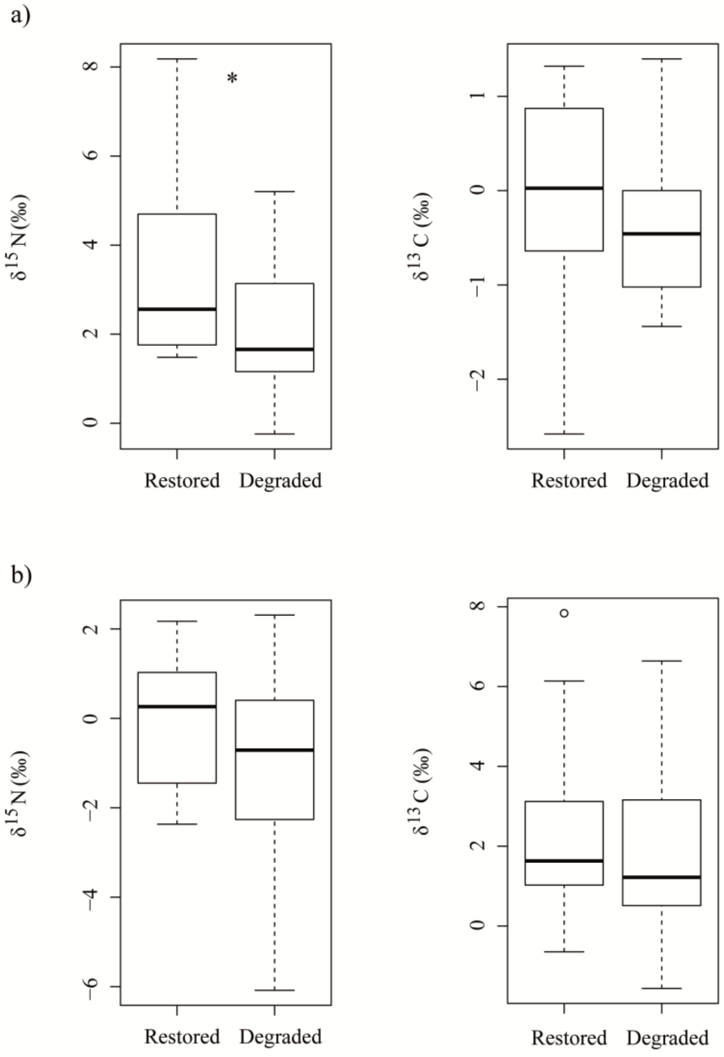

Figure 3.3: Pairwise comparison of the isotopic distances of riparian arthropods to a) terrestrial arthropods and b) benthic invertebrates between restored and corresponding degraded study reaches (Median; Box: 25–75%; Whisker: Min–Max excluding outliers, ○ = Outliers): Significant differences ($p < 0.05$) between pairs are indicated with *.

Table 3.2: Median $\delta^{13}C$ and $\delta^{15}N$ values of consumers in aquatic, riparian and terrestrial habitats separately for restored (R) and degraded (D) study reaches.

	aquatic		**riparian**		**terrestrial**		
	$\delta^{13}C$	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**	**n**
R	-30.12	10.01	-27.52	8.64	-27.87	4.88	11
D	-29.53	10.38	-27.82	8.05	-27.84	5.53	11

3.3.3 Relationship between riparian habitat composition and trophic linkage

We tested if habitat composition was positively related to trophic linkage metrics. Given the above presented results, we limited our analysis to $\delta^{15}N$-distance of riparian arthropods to terrestrial arthropods that displayed the most pronounced differences between restored and degraded sites. We tested the relationship between the metric values and the diversity of riparian habitats (Shannon-Wiener Index) and between the metric values and the proportion of unvegetated side bars. There was a positive relationship between riparian habitat diversity and our trophic linkage metrics as well as between the proportion of open side bars and trophic linkage metrics (Figure 3.4).

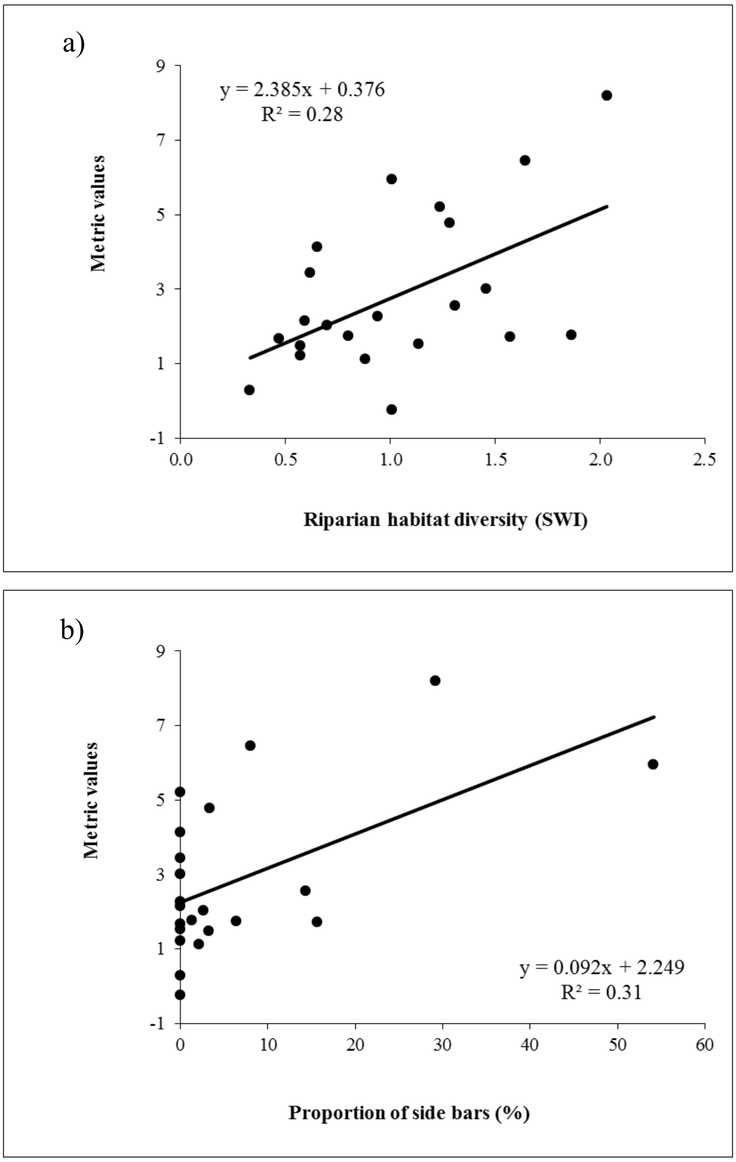

Figure 3.4: Relationship between metric values ($\delta^{15}N$-distance of riparian arthropods to terrestrial arthropods in isotope space) and a) diversity of riparian habitats (Shannon-Wiener Index) and b) proportion of unvegetated side bars.

3.4 Discussion

Stable isotopes indicate trophic positions and ultimate carbon resources of consumers in food webs (Post 2002). We therefore expected that isotopic signatures of consumers sampled in rivers and their floodplains reflect their aquatic, riparian or terrestrial origin (hypothesis i). Hydromorphological restoration of rivers is expected to increase habitat diversity of the riparian zone, favouring the occurrence of riparian arthropods such as ground beetles and spiders. Moreover, restoration can increase cross-habitat movements of consumers between the river and its riparian zone by creating a shallower river profile or the removal of bank fixations, making aquatic prey more easily accessible to riparian predators. Following restoration, we thus expected changes in isotopic signatures of riparian arthropods, due to a smaller share of terrestrial prey in their diet (indicated by increased distance to terrestrial arthropods in isotope space), and increased use of aquatic resources (higher similarity to benthic invertebrates in isotope space) (hypothesis ii). We further expected that riparian habitat diversity and the provision of unvegetated side bars are positively related to the strength of aquatic-terrestrial linkages (hypothesis iii).

Our study revealed a general differentiation between benthic invertebrates and terrestrial arthropods in isotope space, with riparian arthropods taking an intermediate position, reflecting the use of both in-stream and terrestrial resources (confirming hypothesis i). However, $\delta^{15}N$ patterns were more consistently useful for describing trophic linkages of riparian arthropods than $\delta^{13}C$. We found some support for an enhanced aquatic-terrestrial linkage associated with restoration across all eleven projects (confirming hypothesis ii). However, this was largely dependent on $\delta^{15}N$ isotopic signatures of riparian arthropods, rather than on $\delta^{13}C$ signatures, as $\delta^{15}N$ signatures revealed a higher relative trophic position of riparian biota following restoration reflecting decreased use of terrestrial and increased use of aquatic prey (i.e. preservation of the aquatic signature). We further observed that riparian habitat diversity is positively related to the strength of aquatic-terrestrial linkages, pointing to the importance of habitat diversification in the riparian zone in promoting trophic linkages between river and floodplain (confirming hypothesis iii). In general, these findings suggest that restoration results in enhanced trophic linkages between river and riparian zone, which is not only controlled by the provision of open sand and gravel bars but by the general diversification of riparian habitats.

3.4.1 Isotopic signatures across the aquatic-terrestrial interface

We found a clear separation between benthic invertebrates and predaceous terrestrial arthropods using stable isotopes ($\delta^{13}C$, $\delta^{15}N$). The higher trophic position of benthic invertebrates over terrestrial arthropods has to be emphasized: $\delta^{15}N$ signatures revealed that benthic invertebrate communities were approximately one trophic level higher than terrestrial arthropods across all 22 study reaches. Riparian arthropods also took a higher trophic position than predaceous terrestrial arthropods, indicating a significant proportion of higher $\delta^{15}N$ enriched emerging aquatic insects and stranded organism in their diet. Riparian arthropods subsequently can make aquatic biomass further available for the terrestrial food web as they represent important prey for terrestrial consumers of higher trophic levels (Jackson & Fisher 1986). Our large scale comparison therefore supports previous findings that characterized riparian arthropods as a central component of floodplain biota, as they contribute to the linking of aquatic and terrestrial food webs (Baxter et al. 2005, Paetzold et al. 2005).

3.4.2 Restoration effect and influence of riparian habitat composition on trophic linkage

In accordance with our hypothesis, restoration not only promotes riparian habitat diversification (e.g., Jähnig et al. 2010, Januschke et al. 2011, Poppe et al. 2016) and riparian arthropod assemblages (e.g., Jähnig et al. 2009, Januschke et al. 2014) but also promotes trophic connectivity between river and floodplain. Our findings indicated a significantly smaller share of terrestrial prey in the diet of riparian arthropods following restoration and suggested a modest increase of aquatic prey. This effect is largely inferred from the $\delta^{15}N$ isotopic signatures of riparian arthropods, rather than changes in $\delta^{13}C$ signatures, as $\delta^{15}N$ signatures revealed a higher relative trophic position of riparian biota following restoration. In terms of $\delta^{13}C$ isotopic signals we observed almost no changes, though $\delta^{13}C$ was originally expected to be a better indicator of changes in resource use (Post 2002). For instance, Collier et al. (2002) showed that the ultimate carbon resources of riparian predators can shift between streams (indicated by $\delta^{13}C$) while the trophic position of riparian predators remained the same ($\delta^{15}N$). However, Collier et al. (2002) compared two streams differing in a range of environmental characteristics (e.g., catchment conditions) while we studied paired reaches, which were located close to each other and differed only in habitat changes induced by restoration measures. Our findings therefore suggest that there was no considerable shift in the use of ultimate carbon resources following restoration and that $\delta^{15}N$ patterns were more consistent for describing trophic linkages of riparian arthropods.

Overall, patterns of $\delta^{13}C$ across the aquatic-terrestrial interface were inconsistent between all 22 river reaches and were independent of their restored or degraded state: in some regions the sections showed large differences between terrestrial and aquatic $\delta^{13}C$, while others reflected an overlap in $\delta^{13}C$ signatures (Appendix 4). These findings suggest that differences in $\delta^{13}C$ isotopic signatures between water and land were dictated by regional environmental characteristics rather than restoration measures. One possible reason for a $\delta^{13}C$-overlap across the aquatic-terrestrial interface is the utilization of terrestrial carbon (leaves, wood) by benthic invertebrates. Even aquatic biofilms are often "contaminated" with terrestrial carbon (trapped particles, bacteria growing in the biofilm, uptake of DOC of terrestrial origin). Hence, grazing or shredding benthic invertebrates reflect isotopic signatures initially derived from terrestrial carbon instead of aquatic carbon.

Riparian arthropod predation is concentrated along the shoreline and habitat structure of the riparian zone determines not only composition of riparian arthropod assemblages but also aquatic insect emergence and the accumulation of surface drifting organisms (Paetzold et al. 2005). Open sand and gravel bars are major drivers of aquatic-terrestrial transfers as the boundary between river and shore is open for cross-habitat movements (Paetzold et al. 2005). Furthermore, aquatic insects leaving the water for emergence are particularly vulnerable to predation on open bars providing a minimum of shelter (Hering & Plachter 1997). In line with this, we found a positive relationship between the provision of such habitats and the strength of aquatic-terrestrial linkages. However, we further highlighted that overall riparian habitat diversity is important in dictating strength of trophic linkages between river and floodplain. One possible reason is that different habitats (such as vegetated banks together with open bars) promote riparian taxa with different hunting strategies: web-building spiders benefit from vegetated shorelines, complementing ground-dwelling predation, thus utilizing a larger proportion of the available prey.

Our findings provide evidence for an enhanced qualitative linkage following restoration. However, hydromorphological restoration typically enhances riparian arthropod abundances and species richness in the riparian zone (Günther & Assmann 2005, Lambeets et al. 2008, Jähnig et al. 2009, Januschke & Verdonschot 2016), which has potential to increase quantitative energy flow into the terrestrial food web as more riparian predators are consuming more aquatic prey. This is in line with numbers of arthropods caught in our paired restored and degraded reaches: the three reaches with highest trophic linkage metrics ($\delta^{15}N$-distance of riparian arthropods to terrestrial arthropods indicating a smaller share of terrestrial prey in the diet of riparian consumers) revealed the twelve-, six- and four-fold numbers of riparian arthropods in restored compared to degraded reaches. This also applies for the expected increase in aquatic insect biomass as a result of restoration, which can serve as potential prey for riparian predators. Hering & Plachter (1997) and Burdon & Harding (2008) showed positive associations between aquatic insect biomass and riparian predator densities.

3.4.3 Recommendations for future research

Stable isotopes ($\delta^{15}N$, $\delta^{13}C$) can be particularly useful to investigate the trophic organization across the aquatic-terrestrial interface as they reflect integrated feeding patterns that incorporate spatiotemporal scales (Paetzold et al. 2005, Abrantes et al. 2014). Stable isotopes have been successfully used to estimate feeding linkages between river channels and their adjacent areas based on riparian arthropods (e.g., Collier et al. 2002, Sanzone et al. 2003, Paetzold et al. 2005) and have been further applied to test for land use effects on aquatic prey subsidies to riparian spiders (Krell et al. 2015) and for inundation pressures on prey selection of riparian beetles (O'Callaghan et al. 2013). In this study, we quantified the isotopic distance of riparian arthropods to terrestrial arthropods and benthic invertebrates as a measure of trophic linkage (considering trophic fractionation). Our metrics follow the objectives of Layman et al. (2007b) who introduced a set of metrics to gain more information from stable isotope data at the community level. Such metrics have a fundamental advantage, as they allow the organisms to "speak" for themselves. For future applications, we suggest to classify different floodplain-inhabiting organism groups by species or genus or by body size. We further propose to calculate standard ellipses to identify isotopic niches of the different organism groups according to Jackson et al. (2011). Standard ellipses can be applied to analyse isotopic niche overlaps as a measure of dietary similarities among groups (Jackson et al. 2012), and can therefore be used to identify the position of riparian consumers between aquatic and terrestrial food webs as well as changes following restoration. Recently, increasing attention has been given to the response of floodplain-inhabiting organism groups to restoration (e.g., Hering et al. 2015, Göthe et al. 2016, Januschke & Verdonschot 2016). Moreover, the recovery of ecological functioning has been emphasized in river restoration research (Palmer et al. 2014). The above suggested approach combines the response of floodplain organisms to restoration with a functional metric to characterize the trophic organization across the aquatic-terrestrial interface. Consequently, it enables a more holistic characterization of river restoration effects and should therefore be of key interest to restoration research.

4 Hydromorphological restoration stimulates river ecosystem metabolism

4.1 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 & 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 suitable 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 are implemented at the reach-scale, covering short river stretches typically of 1 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 & 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 & 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 interannual 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 have measured metabolism of larger streams and rivers (e.g., Uehlinger 2006, Dodds et al. 2013, Hall et al. 2015, 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. 2005b, 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 & 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.

4.2 Materials and Methods

4.2.1 Study site

This study was conducted in the upper river Ruhr (Federal State of North Rhine-Westphalia, Germany, Figure 4.1, Table 4.1) 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 km², 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, and industrial and residential areas in the floodplain. More recently, the hydromorphology of several river sections has been restored.

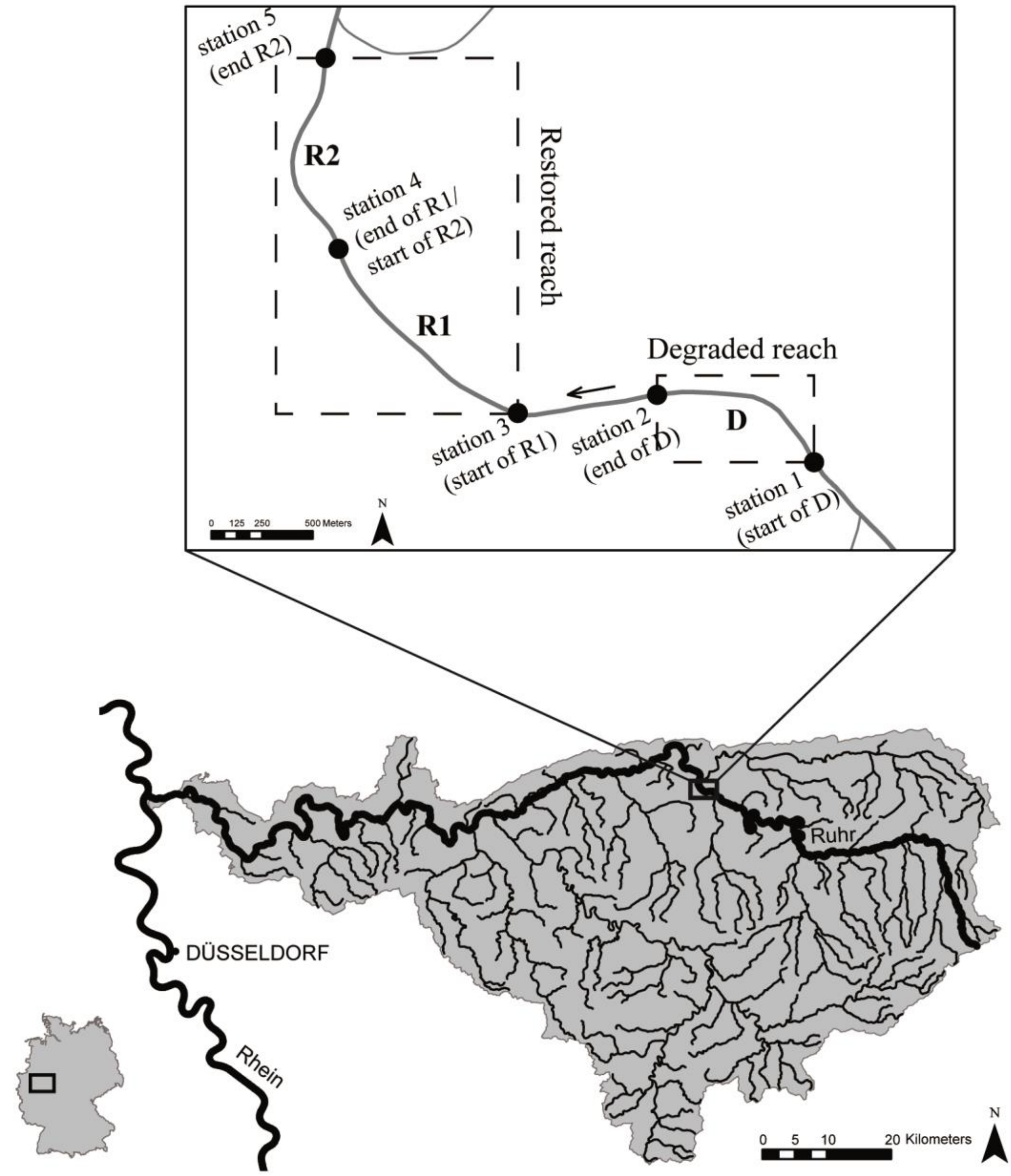

Figure 4.1: Location of the study site in the upper catchment of the river Ruhr in Germany. Stations represent start and end of the investigated river reaches (degraded, first restored and second restored reach).

Table 4.1: 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 ($m^3 s^{-1}$)	21.3
Catchment geology	siliceous
Restoration length (km)	2.3
Restoration date	2007-2009
Main restoration action	riverbed widening
pH **	8.3
Electric conductance ** ($\mu S\ cm^{-1}$)	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).

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 5).

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; 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 5). 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 5). 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.

4.2.2 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 (Figure 4.2). 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 five-point scale developed by Kohler (1978), ranging from 1 (“very rare”) to 5 (“abundant, predominant”). The empirical relationship between the values of the five-point Kohler scale (x) and the actual surface cover of macrophytes (y) is given by the function $y = x^3$ (Kohler & 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.

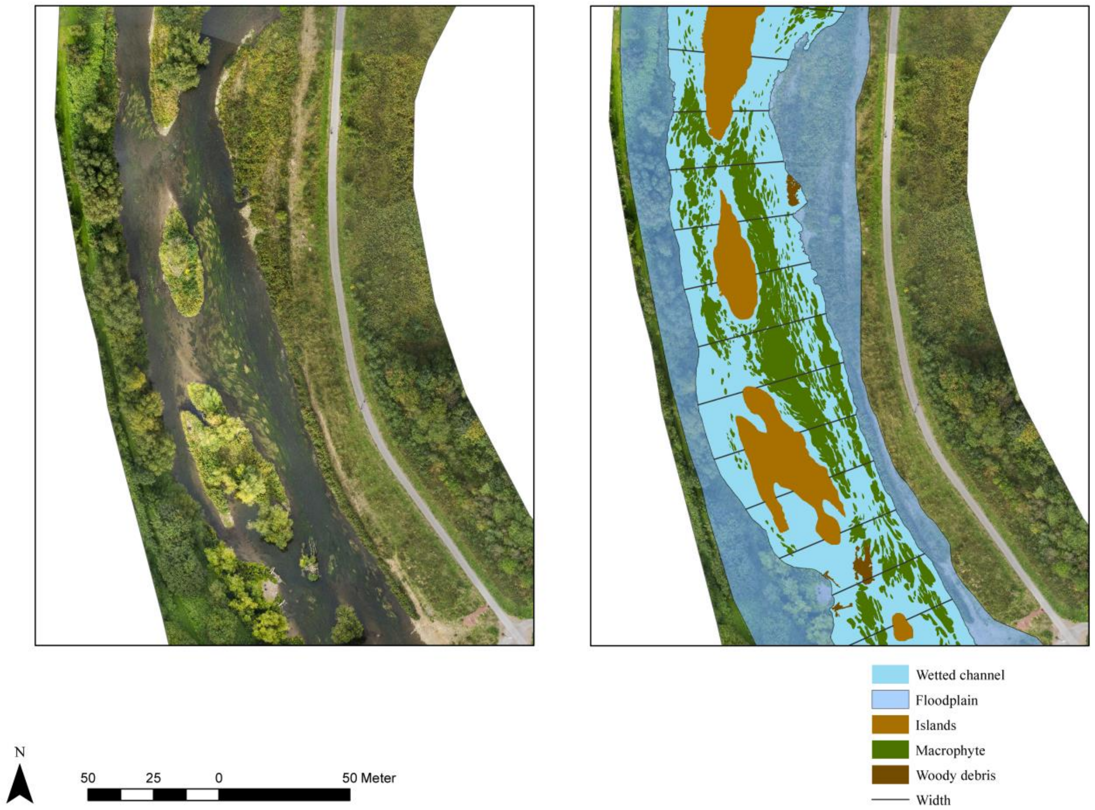

Figure 4.2: Analysis of aerial photos. A representative river section of the second restored reach is shown.

4.2.3 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 (Figure 4.1). 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 & Wagner 2000).

4.2.4 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.

4.2.5 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 & 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 & 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 1 h 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 & 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 6) 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 6). Subsequently, we calculated ER and GPP as described in detailed elsewhere (Marzolf et al. 1994, Young & 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 7). 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.

4.2.6 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).

4.3 Results

4.3.1 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 4.2). Furthermore, the restored reaches had larger wetted channel areas, floodplain areas, island areas, and patches of woody debris than the degraded river reach (Table 4.2). The intensively restored reach R2 showed the highest values for hydromorphological variables (Table 4.2). The share of macrophyte cover of total wetted area was also highest in R2.

Table 4.2: 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 ($m^2\ s^{-1}$) **	0.28	0.59	10.21
Channel cross-sectional area, A (m^2) **	12.11	14.96	27.05
Storage zone cross-sectional area, A_S (m^2) **	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.

4.3.2 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 4.2). 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 4.2). Damköhler numbers between 0.5 and 5.0 indicated reliable transient storage parameter estimates for the reaches (Harvey & Wagner, 2000, Table 4.2). Tracer breakthrough curves estimated by transport modeling closely corresponded to measured tracer concentrations (Figure 4.3).

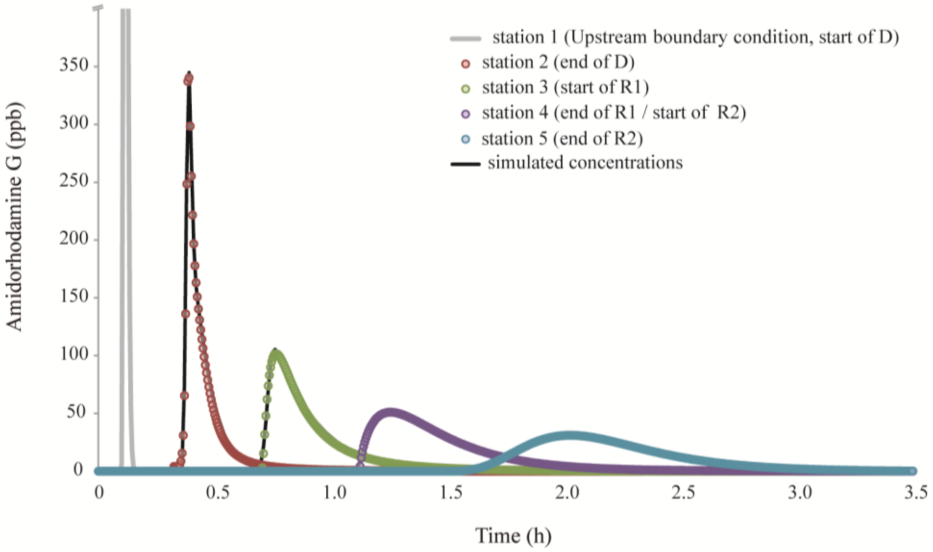

Figure 4.3: Tracer breakthrough curves for the conservative tracer addition experiment in the river Ruhr. Upstream boundary condition based on concentrations at sampling station 1 (start of degraded reach, D, grey solid line), observed concentrations at sampling stations 2 (end of degraded reach, empty circles), 3 (start of first restored reach, R1, empty squares), 4 (end of first restored reach, start of second restored reach, R2, empty triangles), 5 (end of second restored reach, crosses), and simulated concentrations based on final parameter estimates with OTIS-P (solid lines).

4.3.3 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 (Figure 4.4a). 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 (Figure 4.4 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, $p < 0.0001$; Tukey's HSD post hoc tests, $p < 0.0005$).

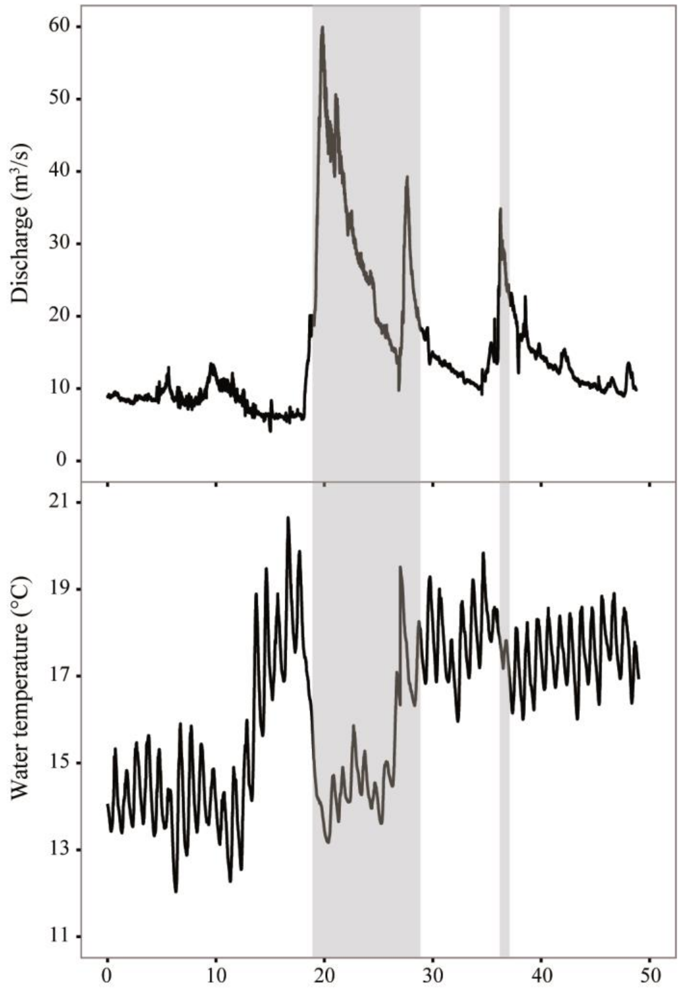

Figure 4.4: (a) discharge and (b) water temperature in the river Ruhr during the study period in summer 2014. Trend in water temperature during study period is exemplarily shown for the second restored reach (R2).

4.3.4 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, net ecosystem production (NEP), and GPP:ER at the restored river sections (R1 and R2 versus station D; estimated with the one-station method; Figure 4.5). Moreover, GPP, ER, NEP, and GPP:ER were also higher (Figure 4.5) 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.

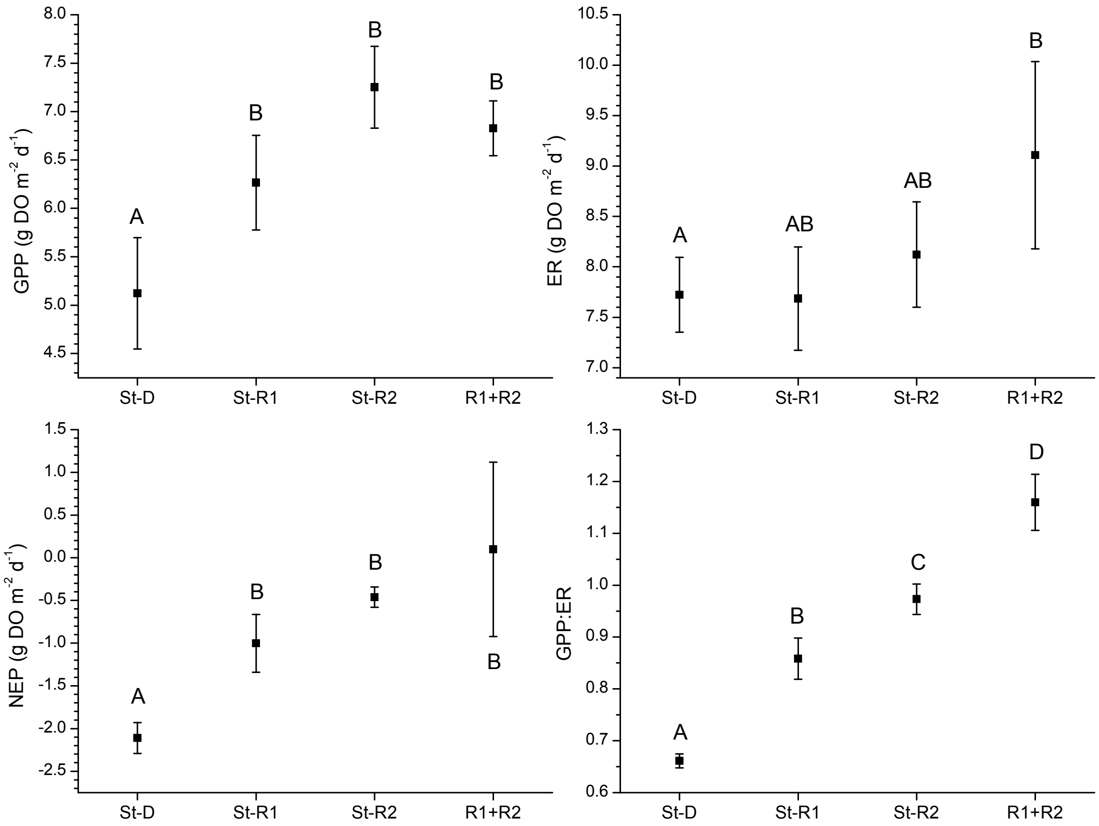

Figure 4.5: Average predicted metabolic parameters and 95% confidence intervals of time series estimated by the one-station open-channel method at river stations downstream of reaches D, R1, and R2, and by the two-station open-channel method for river reach R1+R2. F-tests for all variables were significant (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 ($p < 0.05$).

The three sampling stations at the downstream ends of the reaches generally exhibited similar metabolism patterns (Figure 4.6). 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 (Figure 4.6a). 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 (Figure 4.6b). 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 (Figure 4.6). However, NEP of the total restored river reach (R1+R2) was positive and the average GPP:ER ratio was higher than 1 during most of the sampling period, indicating a slight change in the river's metabolic balance following restoration.

4.4 Discussion

Restoration of river hydromorphology usually covers short river stretches of less than 1 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 & Pusch 2006).

4.4.1 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.

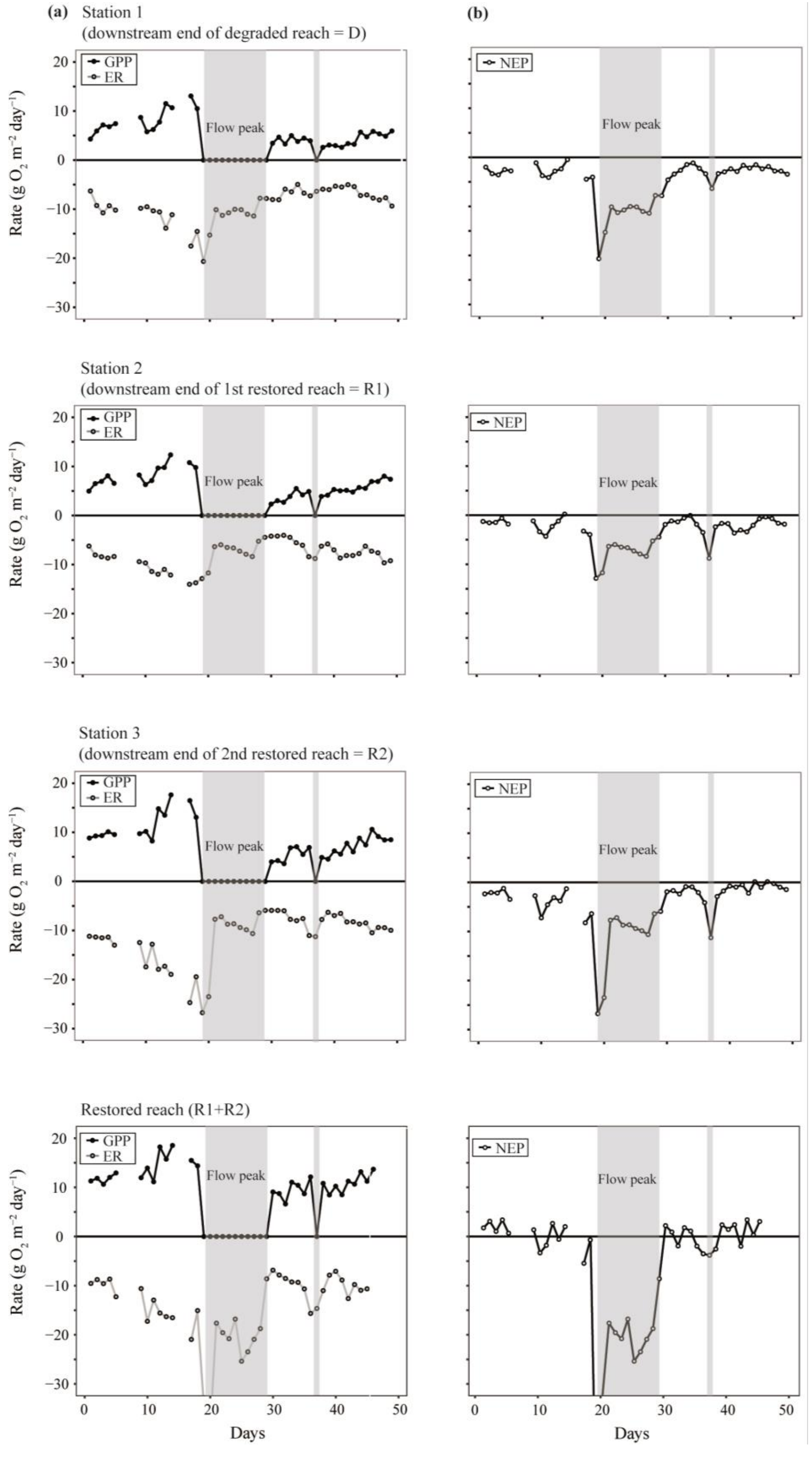

Figure 4.6: Daily rates of (a) gross primary production (GPP: positive values, black line) and ecosystem respiration (ER: negative values, grey lines) and (b) net ecosystem production (NEP) measured at the downstream ends of the investigated reaches (degraded = D; first restored = R1; second restored = R2) and for the combined reaches R1+R2 of the river Ruhr in summer 2014. Vertical grey bars indicate peak flow events.

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 4.1). 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.

4.4.2 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 (Figure 4.6). 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 and 50 $m^3 s^{-1}$; see Appendix 8, 9). 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 8, 9). Considering the limited knowledge about natural geographical gradients in river metabolism, it was not possible to assess whether 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 chapter 4.2.5). 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 what 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 situations, 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 & Gücker 2005), thereby positively affecting water quality.

4.4.3 Recommendations for restoration monitoring

For most regions and river types, data are 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.

5 Summary, conclusion and future prospects

5.1 Summary

Restoration of river hydromorphology has the potential to affect not only structural ecosystem features, including species composition and diversity, but also functional aspects, such as key ecosystem processes and trophic transfers of energy and nutrients. Despite this, the most-widely used parameters for assessing the success or failure of restoration projects are almost exclusively based on changes in community composition of different biological groups (e.g., fish, benthic invertebrates, and macrophytes). Functional metrics, even though increasingly recognized as a valuable addition to classical assessments, are rarely used to study restoration effects. Consequently, the outcomes of river restoration for key ecosystem processes (e.g., river metabolism) and trophic relationships (e.g., trophic structure of benthic invertebrate communities and trophic connectivity between river and land) remain poorly understood. Against this background, the present thesis focused on the following objectives:

- The application of stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$) together with quantitative community metrics to characterize changes in the trophic structure of benthic invertebrate communities following restoration.
- The characterization of the isotopic composition ($\delta^{13}C$, $\delta^{15}N$) of consumers in aquatic, riparian, and terrestrial habitats to assess restoration effects on the trophic connectivity between river and land.
- The assessment of reach-scale restoration effects on hydromorphology, habitat composition and hydrodynamics and the estimation of the corresponding responses of river ecosystem metabolism.

According to the previously outlined objectives, this thesis is divided into three main chapters. In the following paragraphs, background information and main results of the three chapters are summarized.

Chapter 2: River restoration and the trophic structure of benthic invertebrate communities across 16 European restoration projects

River restoration is expected to increase the diversity of both habitat- and resource-based niches, which together have potential to influence food web structure and trophic relationships. Stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$) was applied to characterize changes in the trophic structure of benthic invertebrate communities between paired restored and degraded river reaches across 16 European catchments. Dominant taxa of invertebrate assemblages belonging to different functional feeding groups were sampled. Quantitative community metrics were calculated independently for each reach: $\delta^{13}C$ range was calculated to estimate the range of basal resources assimilated, $\delta^{15}N$ range was estimated as an indicator of the trophic length and standard ellipse area corrected for small samples was used as a measure of isotopic niche width. It was analyzed if restoration influenced the trophic structure of invertebrates, if restoration effects depended on the extent of restoration effort, and on restoration measures applied.

The results indicated an increase in resource breadth associated with restoration across all 16 restored reaches. These effects were stronger for larger-scale restoration projects and especially for projects where river widening was conducted. In contrast, there was no support for a general increase in trophic length, though increases in trophic length ratios were apparent between some specific degraded and restored reaches, suggesting such effects depend on local assemblage composition and/or environmental conditions. In line with this, changes in isotopic niche width were obvious between some paired restored and degraded reaches. This European-scale comparison indicates that river habitat restoration results in modest changes in trophic structure, primarily by increasing the breadth of resources assimilated by consumers; this effect increases with restoration effort and it depends on restoration measure type.

Chapter 3: River restoration enhances aquatic-terrestrial linkages: a stable isotope study of riparian arthropods in eleven restored floodplain sections

Riparian arthropod predation on aquatic insects is concentrated along the river shoreline where riparian consumers aggregate, aquatic insects emerge, and surface drifting organisms accumulate. An improved shoreline structure (by creating a shallower river profile, removing bank fixations and providing habitats suited for riparian biota) enables riparian arthropods to stay close to the river channel and potentially makes aquatic prey more easily accessible to riparian predators. Consequently, river restoration is likely to increase the proportion of aquatic prey in the diet of riparian arthropods, promoting the trophic connectivity of river and land.

A large scale comparative study targeting eleven river restoration projects in central and northern Europe was conducted to assess effects of river restoration on trophic patterns across the aquatic-terrestrial interface. The isotopic composition ($\delta^{13}C$, $\delta^{15}N$) of consumers in rivers and their floodplains was investigated reflecting their aquatic, riparian (sampled within one meter distance to the river) or terrestrial (collected beyond the riparian zone) origin. The study aimed to detect changes in the position of riparian arthropods in isotope space indicative both of a smaller share of terrestrial prey, and an increased use of aquatic insects following restoration. The isotopic distance of riparian consumers to benthic invertebrates and terrestrial arthropods was quantified as a measure of trophic linkage, and it was investigated how this varied with riparian habitat composition.

The study revealed a general differentiation between benthic invertebrates and terrestrial arthropods in isotope space, with riparian arthropods taking an intermediate position, reflecting the use of both in-stream and terrestrial prey. Overall, patterns in $\delta^{15}N$ isotopic signatures of consumers were more consistently useful for describing the trophic linkages of riparian arthropods than $\delta^{13}C$: Benthic invertebrates were significantly more enriched in $\delta^{15}N$ than terrestrial arthropods (by approximately one trophic level) and riparian arthropods also took a higher trophic position than terrestrial consumers, indicating a significant proportion of higher $\delta^{15}N$ enriched aquatic prey in their diet. Following restoration, $\delta^{15}N$ isotopic signatures of riparian arthropods revealed a higher relative trophic position, lending support to the conjecture that restoration increased the proportion of aquatic prey and reduced the share of terrestrial prey in the diets of individuals. Riparian habitat diversity and the provision of open sand and gravel bars were positively related to the strength of aquatic-terrestrial linkages as reflected by measures of trophic linkage, pointing to the importance of habitat diversification in the riparian zone in promoting trophic linkages between river and floodplain.

Chapter 4: Hydromorphological restoration stimulates river ecosystem metabolism

Restoration of river hydromorphology is expected to increase the river's habitat and hydrodynamic heterogeneity. Together, these changes may stimulate ecosystem metabolism, i.e. whole-stream rates of gross primary production (GPP) and ecosystem respiration (ER), as well as affect the river's metabolic balance. Yet, little is known about the effects of hydromorphological restoration on ecosystem metabolism, especially for mid-sized and large rivers. Against this background, three reaches of the third-order, gravel-bed river Ruhr in

Germany were compared: two reaches restored with moderate (R1) and substantial effort (R2) and one upstream degraded reach (D). Hydromorphology, habitat composition, and hydrodynamics were assessed. GPP and ER were estimated using the one-station open-channel diel dissolved oxygen change method over a 50-day period at the end of each reach. Moreover, the metabolic rates of the combined restored reaches (R1+R2) were estimated 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 net ecosystem production 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.

5.2 Conclusion and future prospects

The present thesis contributes to a more holistic understanding of river restoration effects and can help to develop novel assessment approaches that consider functional aspects. In this paragraph, main conclusions are presented and suggestions for future research and application in river restoration practice are made.

The results obtained from the second chapter provide evidence that the magnitude of food web changes following restoration can depend not only on the scale, but also type of restoration measures applied. River widening was particularly effective for increasing the breadth of resources available to consumers. This should be of key interest for restoration practice as a greater range of basal resources allows for heterogeneous energy flow pathways up through the food web, which is important for stabilizing food webs. A web consisting of numerous energy flow pathways that originate from a diverse pool of resources is likely to be more resilient against disturbances than a food web relying on a single basal resource.

Consequently, river widening should be considered a key measure in future restoration practice in order to promote food web stability.

In contrast with the relatively consistent changes in trophic structure of benthic invertebrates communities following restoration (chapter 2), there was no positive effect on benthic invertebrate richness and diversity (Verdonschot et al. 2016). This is of particular interest as the study of Verdonschot et al. (2016) was conducted in the same project but with classical, community-based assessment approaches. The contrasting results of these studies stress the potential for classical assessments to miss important effects of river restoration. This highlights the need to evaluate restoration effects in a holistic way, incorporating novel approaches that consider functional aspects. The use of community-wide metrics based on stable isotopes appears to be particularly suitable to study changes in the trophic structure of communities following restoration. Future research should focus on a more expanded sampling of benthic invertebrates, particularly in more regional assessments of restoration projects. Moreover, other metrics introduced by Layman et al. (2007b) can be used to gain further information about restoration effects on the trophic diversity of communities. This approach combines traditional taxonomic research with patterns in trophic structure and has the potential to complement classical assessments in order to provide a better mechanistic understanding of restoration effects.

The third chapter stresses the need to address rivers and their adjacent riparian zones as a functional unit in restoration assessments since they are closely linked by the reciprocal flow and use of energy and nutrients. The results obtained from this thesis suggest that enhanced riparian habitat diversity and the provision of shallow bars along the shoreline can promote trophic connectivity of river and land mediated through riparian arthropods feeding on aquatic insects. Accordingly, river manager should increasingly aim at improving shoreline structures in the future. Shallow side bars (such as gravel and sand bars along the shoreline) appear to be key habitats for aquatic-terrestrial transfers as the shoreline is particularly open for cross habitat movements of consumers. More generally, increased habitat diversity in the riparian zone can promote riparian taxa with different hunting strategies. For instance, web-building spiders benefit from vegetated shorelines, complementing the ground-dwelling predation on side bars. The recovery of aquatic-terrestrial linkages should also be of interest for wider ecosystem management as riparian arthropods can subsequently serve as prey for other floodplain-inhabiting organisms, including species of conservation interest (e.g., birds and bats).

In order to develop a sound understanding of restoration effects on the trophic organization across the land- water interface, future research should also include other riparian and floodplain-inhabiting organism groups, especially in more regional assessments.

In this context, Layman-metrics (see chapter 2) can be used to study restoration effects on the trophic structure and diversity of these communities. Moreover, the degree of lateral trophic connectivity between river and land should be considered in future restoration research. This can be achieved by sampling terrestrial consumers in defined distances from the river edge in paired restored and degraded floodplain sections.

The results obtained from chapter 4 indicate an increase in river ecosystem metabolism as response to the restoration of a mid-sized mountain river in Germany. Hydromorphological restoration enhanced habitat availability and abundance of macrophytes, promoting river primary productivity and respiration. This may be of interest for restoration practice as the occurrence of dense macrophyte stands and thus high rates of metabolism in restored river reaches are likely to increase the assimilation of dissolved nutrients and the sedimentation of particulate nutrients, thereby positively affecting water quality. Accordingly, these changes in ecosystem functioning are closely related to valuable ecosystem services such as self-purification and the provision of clean water.

The fourth chapter also revealed that for most regions and river types, data on metabolic rates are missing that could be used to establish limits of good, moderate or poor river conditions. This stresses the need to combine measures of river metabolism with classical assessments in different regions and river types in order to provide reference conditions and to facilitate interpretation of restoration outcomes. However, based on data from mainly small streams, Young et al. (2008) already proposed a framework to assess functional stream health using GPP, ER, NEP and GPP:ER. This framework can be used to establish an assessment approach for smaller river types in Germany. The findings obtained from this thesis (chapter 4) will help to develop a similar approach for larger rivers. Chapter 4 also reflected a good agreement of results obtained with the one-station and the two-station method in restored reaches, i.e. that both clearly suggested metabolism increases due to restoration. This may be an important finding for agency efforts to monitor restoration outcomes, because the one-station method may be more practical for routine measurements (especially in mid-sized and large rivers), while the two-station technique is often considered a research method that is too complex for such purposes. However, metabolic rates measured with the one-station method should be considered as qualitative indicators of metabolism as it is most likely that lengths of river reaches evaluated with the one-station method and reaches exclusively affected by restoration will differ.

In general, modern river restoration should consider a wide range of environmental characteristics, including functional ones, such as ecosystem metabolism and trophic relationships. Incorporating functional metrics into monitoring programs enables a more holistic assessment of river health and a better understanding of restoration effects.

6 Zusammenfassung

6.1 Hintergrund

In Folge der intensiven Nutzung und den daraus resultierenden Belastungen von Fließgewässern durch den Menschen wurde die Wasserrahmenrichtlinie (WRRL, Richtlinie 2000/60 / EG) im Jahr 2000 verabschiedet. Sie bietet die Basis für ein naturverträgliches Gewässermanagement in Europa. Das Ziel der WRRL besteht in dem Erhalt bzw. der Erreichung des guten ökologischen und chemischen Zustands aller Wasserkörper. Ein Großteil der Fließgewässer in Europa entspricht diesen Zielvorgaben nicht, in erster Linie aufgrund hydromorphologischer Beeinträchtigungen (EEA 2012). Daher liegt der Fokus europaweit auf der Verbesserung der Gewässerstrukturen, so dass die Zahl hydromorphologischer Renaturierungen stetig steigt.

Der Erfolg von Renaturierungsmaßnahmen wird bisher meistens an der Etablierung naturnaher Lebensgemeinschaften im Gewässer gemessen. Häufig werden z.B. Fische (z.B. Roni et al. 2008, Haase et al. 2013, Schmutz et al. 2016), Makrozoobenthos (z.B. Jähnig et al. 2010, Friberg et al. 2014, Verdonschot et al. 2016) und aquatische Makrophyten (z.B. Lorenz et al. 2012, Ecke et al. 2016) untersucht. Allerdings können Gewässerrenaturierungen auch funktionale Eigenschaften, wie Ökosystemfunktionen oder Stoff- und Energieflüsse durch Nahrungsnetze, beeinflussen. Es ist auch möglich, dass Renaturierungen funktionale Eigenschaften beeinflussen während sich die Zusammensetzung der Lebensgemeinschaften nicht verändert (und umgekehrt). Diese gegensätzlichen Reaktionen wurden bereits in Studien festgestellt, in denen Auswirkungen verschiedener Belastungen bzw. Umweltvariablen auf Ökosystemfunktionen und die Zusammensetzung von Lebensgemeinschaften verglichen wurden (z.B. Friberg et al. 2009, McKie & Malmqvist 2009, Niyogi et al. 2013). Eine ganzheitliche Bewertung des Gewässerzustandes sollte daher auch funktionale Aspekte berücksichtigen. Obwohl dies in den letzten Jahren zunehmend hervorgehoben wurde (z.B. Young et al. 2008, 2009, Palmer & Febria 2012, Woodward et al. 2012), werden funktionale Aspekte im Zusammenhang mit Renaturierungen bislang häufig außer Acht gelassen (Palmer et al. 2014). Daher sind Renaturierungseffekte auf die trophische Struktur von

Lebensgemeinschaften, die trophische Vernetzung von Gewässer und Ufer und den Ökosystem-Metabolismus kaum verstanden. Eine umfassendere Untersuchung von Renaturierungen unter Einbeziehung funktionaler Aspekte kann zu einem besseren Verständnis von Renaturierungseffekten und damit auch zu einer effektiveren und erfolgreicheren Maßnahmenplanung beitragen. Die vorliegende Arbeit widmet sich daher der Analyse von Renaturierungseffekten im Hinblick auf:

- Die trophische Struktur von Makrozoobenthos-Gemeinschaften unter Verwendung stabiler Isotope ($\delta^{13}C$, $\delta^{15}N$) und daraus abgeleiteter Isotopenmetrics.
- Die trophische Vernetzung von Gewässer und Ufer unter Verwendung stabiler Isotope ($\delta^{13}C$, $\delta^{15}N$) mit dem Fokus auf Makrozoobenthos, Uferarthropoden und terrestrischen Arthropoden.
- Habitatveränderungen innerhalb des Gewässers und daraus resultierende Veränderungen im Ökosystem-Metabolismus.

Ziel dieser Arbeit ist es, durch die Untersuchung der o.g. Teilaspekte den bisherigen Wissensstand zu Renaturierungseffekten zu erweitern. Zudem werden Möglichkeiten aufgezeigt, wie funktionale Aspekte künftig im Rahmen eines Monitorings untersucht werden können.

6.2 Methoden und Ergebnisse

Die Arbeit gliedert sich entsprechend der oben genannten Teilaspekte in drei Hauptkapitel. Die jeweiligen Kapitel stellen individuelle Manuskripte dar und werden in der Folge kurz zusammengefasst:

Kapitel 2: Effekte von Fließgewässer-Renaturierungen auf die trophische Struktur von Makrozoobenthos-Gemeinschaften an 16 Europäischen Renaturierungsprojekten

Morphologische Renaturierungen erhöhen die Habitatvielfalt im Gewässer und fördern damit auch autotrophe Organismen. In Folge komplexerer Gewässerbettstrukturen verbessert sich zudem das Retentionsvermögen für partikuläres organisches Material. Gemeinsam kann dies das Angebot an allochthonen und autochthonen Ressourcen erhöhen. Dies kann Veränderungen in der Struktur von Nahrungsnetzen im Gewässer zur Folge haben. Auf Grundlage der stabilen Isotope ($\delta^{13}C$ und $\delta^{15}N$) von Makrozoobenthos-Gemeinschaften in 16 renaturierten und 16 oberhalb gelegenen, verbauten Fließgewässerabschnitten in Europa wurde untersucht, inwieweit Renaturierungen die trophische Struktur von Makrozoobenthos-

Gemeinschaften beeinflussen. Beprobt wurden die dominanten Taxa verschiedener Ernährungstypen des Makrozoobenthos. Für jede Probestelle wurden die drei folgenden Isotopenmetrics berechnet, die über die Verteilung der Daten im Isotopenraum die trophische Struktur und Diversität einer Gemeinschaft beschreiben: Der $\delta^{13}C$ range wurde als Maß für den Umfang an assimilierten Ressourcen genutzt und der $\delta^{15}N$ range als Indikator für die trophische Länge der Makrozoobenthos-Gemeinschaften. Die Standardellipse wurde als Maß für die Nischengröße der Gemeinschaften im Isotopenraum berechnet. Anhand eines Vergleichs der Metrics zwischen renaturierten und oberhalb gelegenen, verbauten Gewässerabschnitten wurde untersucht, ob morphologische Renaturierungen die trophische Struktur der Makrozoobenthos-Gemeinschaften beeinflussen und ob Renaturierungseffekte vom Umfang der Renaturierung sowie dem Maßnahmentyp abhängig sind.

Der Umfang an assimilierten Ressourcen war in renaturierten Abschnitten größer als in verbauten. Dieser Effekt war stärker in großräumig renaturierten Fließgewässerabschnitten und an Probestellen an denen der Maßnahmentyp „Aufweitung“ umgesetzt wurde. Im Gegensatz dazu zeigte sich keine generelle Zunahme der trophischen Länge. Zunahmen der trophischen Länge waren jedoch zwischen einigen gepaarten renaturierten und verbauten Abschnitten nachweisbar, was darauf hindeutet, dass diese Effekte von der lokalen Artenzusammensetzung und/oder von Umweltbedingungen abhängig sind. Infolgedessen zeigten sich Veränderungen in der Nischengröße ebenfalls nur an einigen gepaarten renaturierten und verbauten Abschnitten. Dieser großräumige Vergleich zeigt, dass Renaturierungen zu moderaten Veränderungen in der trophischen Struktur von Makrozoobenthos-Gemeinschaften führen, in erster Linie durch die Vergrößerung des assimilierten Nahrungsspektrums. Dieser Effekt nimmt mit dem Umfang einer Renaturierung zu und ist zudem vom Maßnahmentyp abhängig.

Kapitel 3: Fließgewässer-Renaturierungen erhöhen die aquatisch-terrestrische Interaktion: Untersuchung der stabilen Isotope von Uferarthropoden in elf renaturierten Gewässerabschnitten

Räuberische Uferarthropoden spielen eine wichtige Rolle bei der trophischen Verknüpfung von aquatischen und terrestrischen Nahrungsnetzen, da sie sich u.a. von aquatischen Insekten ernähren. Die Prädation durch räuberische Uferarthropoden (wie z.B. Laufkäfer und Spinnen) konzentriert sich in starkem Maße auf die Uferbereiche von Fließgewässern, an denen das Nahrungsangebot in Form von emergierenden und angespülten aquatischen Insekten hoch ist. Eine strukturelle Verbesserung von Uferbereichen im Zuge morphologischer Renaturierungen (z.B. durch die Abflachung der Ufer, der Entfernung von Ufersicherungen und der Schaffung von Habitaten) bietet den Prädatoren gute

Besiedlungsbedingungen und einen guten Zugang zu ihrer aquatischen Beute. Auf Grundlage der Untersuchung stabiler Isotope ($\delta^{13}C$, $\delta^{15}N$) von Makrozoobenthos, Uferarthropoden und terrestrischer Arthropoden in elf renaturierten und elf oberhalb gelegenen, verbauten Fließgewässerabschnitten in Europa wurde analysiert, inwieweit morphologische Renaturierungen die trophische Vernetzung von Gewässer und Ufer begünstigen. Die Isotopendaten der Organismen wurden für jeden Gewässerabschnitt im Isotopenraum aufgetragen. Es wurde untersucht, ob sich die Positionen der Uferarthropoden im Isotopenraum zwischen renaturierten und verbauten Abschnitten unterscheiden, und ob dies auf eine geringere Nutzung terrestrischer Ressourcen und auf einen größeren Anteil aquatischer Beute hinweist. Als Maß für die trophische Vernetzung wurden die Distanzen von Uferarthropoden zum Makrozoobenthos und zu terrestrischen Arthropoden im Isotopenraum berechnet. Zusätzlich wurde der Zusammenhang zwischen Habitatzusammensetzung im Uferbereich und trophischer Vernetzung getestet.

Es zeigte sich eine deutliche Auftrennung von Makrozoobenthos und terrestrischen Arthropoden im Isotopenraum. Die intermediäre Stellung der Uferarthropoden deutet auf die Nutzung sowohl aquatischer als auch terrestrischer Beute hin. Generell waren die Stickstoff-Isotope ($\delta^{15}N$) im Hinblick auf die Untersuchung der trophischen Vernetzung in dieser Studie besser geeignet als die Kohlenstoff-Isotope ($\delta^{13}C$): Das Makrozoobenthos nahm eine signifikant höhere trophische Position ($\delta^{15}N$) ein als die terrestrischen Arthropoden (um etwa eine trophische Stufe). Die Uferarthropoden wiesen im Vergleich zu den terrestrischen Arthropoden ebenfalls eine höhere trophische Position auf, was auf einen erheblichen Anteil an höher $\delta^{15}N$ angereicherter aquatischer Beute in ihrer Nahrung hindeutet. Dabei zeigten die Uferarthropoden in renaturierten Abschnitten eine höhere trophische Position als an den verbauten Vergleichsabschnitten (basierend auf ihren $\delta^{15}N$-Werten). Dies lässt auf eine Erhöhung des Anteils aquatischer Beute und eine Reduktion des Anteils terrestrischer Beute in Folge der Renaturierung schließen. Sowohl der Anteil flacher Kies- oder Sandbänke als auch die Diversität an Uferhabitaten zeigten eine positive Korrelation zur Stärke der trophischen Vernetzung. Dies weist darauf hin, dass die Habitatzusammensetzung im Uferbereich die trophische Vernetzung von Gewässer und Ufer maßgeblich begünstigt.

Kapitel 4: Hydromorphologische Renaturierung erhöht den Ökosystem-Metabolismus im Gewässer

Fließgewässer-Renaturierungen erhöhen die Habitatvielfalt und verändern die hydrodynamischen Eigenschaften von Gewässerabschnitten. Diese Veränderungen können den Ökosystem-Metabolismus, d.h. Bruttoprimärproduktion (BPP) und Respiration (R), eines Fließgewässers beeinflussen. Bislang sind die Effekte morphologischer

Renaturierungen auf den Ökosystem-Metabolismus kaum untersucht worden, insbesondere für größere Flüsse. Im Rahmen dieser Studie wurden drei Gewässerabschnitte der Ruhr bei Arnsberg (Deutschland) verglichen: zwei renaturierte Abschnitte und ein oberhalb gelegener, verbauter Abschnitt. Die beiden renaturierten Abschnitte R1 und R2 unterschieden sich im Hinblick auf die Intensität morphologischer Veränderungen. Gewässermorphologie, Habitatzusammensetzung und Hydrodynamik der einzelnen Abschnitte wurden untersucht. Für die Quantifizierung des Ökosystem-Metabolismus wurden die Bruttoprimärproduktion (BPP) und Respiration (R) mit Hilfe der Ein-Stationen O2-Tagesgangmethode über einen Zeitraum von 50 Tagen jeweils am unteren Ende der drei Abschnitte erfasst. Zusätzlich wurde der Ökosystem-Metabolismus für die gesamte renaturierte Fließstrecke (R1+R2) mit Hilfe der Zwei-Stationen O2-Tagesgangmethode zur Messung des ökosystemaren Metabolismus definierter Fließstrecken untersucht.

Die Gewässermorphologie, welche über verschiedene Strukturelemente charakterisiert wurde, verbesserte sich mit zunehmender Intensität der Renaturierungen (D < R1 < R2). Die hydrodynamischen Eigenschaften der renaturierten Abschnitte änderten sich. Sie wiesen eine geringere Fließgeschwindigkeit, höhere Längsdispersion und größere hydrodynamische Totzonen auf. Die Totzonenaktivität war am höchsten in R1 und am niedrigsten in R2, mit mittleren Werten in D. Die Makrophytendeckung war am höchsten in R2 und am niedrigsten in R1, mit mittleren Werten in D. Bruttoprimärproduktion (BPP) und Respiration (R) waren am höchsten am Ende von R2. Die gesamte renaturierte Fließstrecke (R1+R2) wies im Vergleich zum verbauten Abschnitt (D) ebenfalls höhere Werte für BPP und R auf. Die Renaturierung erhöhte die autotrophen Eigenschaften der untersuchten Abschnitte, was durch höhere BPP:R und eine größere Nettoproduktivität angezeigt wurde. Generell spiegelte die Respiration den Verlauf der Bruttoprimärproduktion, was auf die hohe Bedeutung der autochthonen Produktion im Gewässer hindeutet. In der vorliegenden Studie konnte somit gezeigt werden, dass Renaturierung einen erheblichen Einfluss auf die Hydrodynamik und den Ökosystem-Metabolismus der untersuchten Gewässerabschnitte hatte. Dies war maßgeblich auf die Zunahme an Makrophyten zurückzuführen. Der erhöhte Ökosystem-Metabolismus und das Vorkommen dichter Makrophytenbestände in renaturierten Gewässerabschnitten können die Assimilation gelöster Nährstoffe sowie die Sedimentation von partikulärem Material begünstigen und dadurch die Wasserqualität verbessern.

6.3 Schlussfolgerungen und Ausblick

Die im Rahmen dieser Arbeit erzielten Ergebnisse tragen zu einem umfassenderen Verständnis von Renaturierungseffekten bei und können bei der Entwicklung funktionaler Bewertungsansätze helfen. In den folgenden Absätzen werden die wichtigsten Schlussfolgerungen der Kapitel dieser Arbeit zusammengefasst und Vorschläge für künftige Forschungsvorhaben sowie für die Anwendung in der Praxis formuliert.

Die Ergebnisse des zweiten Kapitels zeigen, dass Renaturierungseffekte auf Nahrungsnetze sowohl vom Umfang einer Renaturierung als auch vom Maßnahmentyp abhängen können. Die Aufweitung des Gewässerbettes hat sich hinsichtlich der Vergrößerung des Nahrungsspektrums für benthische Primärkonsumenten als besonders effizient herausgestellt. Das sollte von Interesse für den Gewässerschutz sein, da eine breite Nahrungsbasis heterogene Stoffflüsse durch das Nahrungsnetz begünstigt und damit zur Stabilisierung von Nahrungsnetzen beiträgt. Dies macht es im Vergleich zu einem Nahrungsnetz, das auf einem begrenzten Nahrungspool beruht, robuster gegenüber Störungen. Daher sollte die Gewässeraufweitung zukünftig als Schlüsselmaßnahme angesehen werden, um die Stabilität eines Nahrungsnetzes zu begünstigen.

Im Gegensatz zu den sehr konsistenten Renaturierungseffekten auf die trophische Struktur der Makrozoobenthos-Gemeinschaften (Kapitel 2), konnten keine positiven Auswirkungen auf Diversität und Artenreichtum des Makrozoobenthos festgestellt werden (Verdonschot et al. 2016). Dies ist von besonderer Bedeutung, da die Studie von Verdonschot et al. (2016) in dem gleichen Projekt (d.h. in denselben Gewässerabschnitten) durchgeführt wurde, jedoch unter Verwendung klassischer Bewertungsverfahren. Das unterstreicht die Notwendigkeit, Renaturierungseffekte in Zukunft mit einem ganzheitlichen Ansatz zu untersuchen, bei dem auch funktionale Aspekte wie die trophische Struktur von Lebensgemeinschaften berücksichtigt werden. Die Anwendung der in Kapitel 2 eingeführten Isotopenmetrics scheint in dieser Hinsicht besonders geeignet. Sie verbinden klassische taxonomische Analysen mit Veränderungen in der trophischen Struktur von Lebensgemeinschaften. In zukünftigen Studien könnte eine umfangreichere Beprobung des Makrozoobenthos im Fokus stehen, insbesondere wenn es sich dabei stärker um regionale Bewertungen handelt. Zudem können zusätzlich zu den in dieser Arbeit verwendeten Isotopenmetrics weitere der von Layman et al. (2007b) eingeführten Metrics verwendet werden, z.B. um die trophische Diversität der Gemeinschaften noch besser zu beschreiben. Dazu gehören *„mean distance to centroid“*, *„mean nearest neighbor distance“* und *„standard deviation of nearest neighbor distance“*. Dieser Ansatz hat das Potenzial, die klassischen Bewertungsansätze zu ergänzen.

Das dritte Kapitel verdeutlicht die Notwendigkeit Gewässer und Ufer in künftigen Bewertungen stärker als funktionale Einheit zu betrachten, da sie u.a. durch Stoff- und

Energieflüsse eng miteinander verbunden sind. Die im Rahmen dieser Arbeit erzielten Ergebnisse zeigen, dass morphologische Renaturierungen, insbesondere durch die Schaffung von Habitatvielfalt im Uferbereich sowie speziell durch offene und flache Uferbänke, die trophische Vernetzung von Gewässer und Ufer begünstigen können. Dementsprechend sollte in der künftigen Planung von Renaturierungsmaßnahmen die strukturelle Verbesserung der Uferzone stärker mit berücksichtigt werden. Flache Sand- und Kiesbänke, auf denen räuberische Uferarthropoden (z.B. Laufkäfer) einen guten Zugang zu emergierenden oder an Land gespülten Insekten haben, stellen entscheidende Habitate für die trophische Vernetzung dar. Generell kann die Schaffung von Habitatvielfalt im Uferbereich das Vorkommen von Arten mit unterschiedlichen Jagdtechniken begünstigen. Beispielsweise können Spinnen ihre Netze in die Ufervegetation bauen, so emergierende Insekten fangen und folglich ebenfalls zur trophischen Vernetzung beitragen. Spinnen und Laufkäfer können in der Folge selbst als Beute für andere Auenorganismen dienen (z.B. Vögel oder Fledermäuse). Deshalb sollte die Vernetzung von Gewässer und Ufer nicht allein im Fokus des Gewässerschutzes stehen, sondern auch für den allgemeinen Umweltschutz von Interesse sein.

Der im Rahmen dieser Arbeit verwendete Ansatz ist ein erster Versuch, Renaturierungseffekte auf die trophische Organisation zwischen Gewässer und Ufer zu untersuchen. Ein Aspekt, der in zukünftigen Studien unbedingt Beachtung finden sollte, ist das Ausmaß der lateralen Vernetzung. Dies kann beispielsweise untersucht werden, indem an gepaarten renaturierten und verbauten Gewässerabschnitten in definierten Abständen vom Gewässer Organismen gesammelt werden. Diese Untersuchungen können Aufschluss darüber geben, welche Uferstrukturen eine möglichst weitreichende trophische Vernetzung begünstigen. Darüber hinaus sollten in zukünftigen Untersuchungen auch weitere Organismengruppen der Ufer und Auen mit einbezogen werden. So kann ein fundiertes Verständnis über Renaturierungseffekte auf die trophische Organisation an der Schnittstelle von Gewässer und Aue erlangt werden. Unter Verwendung der bereits zuvor genannten Isotopenmetrics (Kapitel 2) können so u.a. Auswirkungen auf die trophische Struktur und Diversität der verschiedenen Organismengruppen untersucht werden.

Die im Rahmen des vierten Kapitels erzielten Ergebnisse zeigen, dass Renaturierung den Ökosystem-Metabolismus von Fließgewässern beeinflussen kann. In Folge der morphologischen Renaturierung werden Habitate für Makrophyten geschaffen, die den Ökosystem-Metabolismus fördern. Das sollte für die Praxis von Bedeutung sein, da dichte Makrophytenfelder und höherer Ökosystem-Metabolismus in renaturierten Abschnitten die Assimilation gelöster Nährstoffe und die Sedimentation partikulärer Substanzen fördern und dadurch die Wasserqualität verbessern können. Dementsprechend steht der Ökosystem-Metabolismus eng in Verbindung mit Ökosystemdienstleistungen, wie der Selbstreinigung von Gewässern und der Bereitstellung von sauberem Wasser. Die Untersuchungen im Rahmen dieser Arbeit zeigten auch, dass für viele Gewässertypen bislang keine Daten zum Metabolismus vorhanden sind. Daher ist es nach derzeitigem Stand nicht möglich, Grenzwerte für einen guten, mäßigen oder schlechten Zustand zu bestimmen. In Zukunft sollte daher der Ökosystem-Metabolismus gemeinsam mit klassischen Untersuchungen zum Gewässerzustand in verschiedenen Regionen und für verschiedene Gewässertypen bestimmt werden. Für kleine Fließgewässer wurde basierend auf dem Ökosystem-Metabolismus bereits ein Ansatz zur Bewertung des funktionalen Gewässerzustandes entwickelt (Young et al. 2008). Dieser Ansatz kann als Grundlage für die Entwicklung eines Bewertungssystems für kleine Gewässertypen in Deutschland dienen. Eine Erweiterung dieses Ansatzes auf Grundlage der im Rahmen dieser Arbeit erzielten Ergebnisse kann dabei helfen, ein entsprechendes Bewertungssystem für größere Fließgewässer zu entwickeln.

Die beiden Methoden zur Messung des Ökosystem-Metabolismus (Ein-Stationen und Zwei- Stationen O2-Tagesgangmethode) zeigten eine gute Übereinstimmung, d.h. beide wiesen auf eine deutliche Zunahme des Ökosystem-Metabolismus in Folge der Renaturierung hin. Dies könnte entscheidende Informationen zur Wahl der Methode im Rahmen eines Monitorings liefern. Die Ein-Stationen O_2-Tagesgangmethode scheint im Hinblick auf das Monitoring praktikabler zu sein (besonders in größeren Flüssen). Die Zwei-Stationen O_2-Tagesgangmethode wird hingegen häufig als sehr wissenschaftlicher Ansatz erachtet der für das routinemäßige Monitoring zu komplex ist. Bei der Bewertung von Renaturierungseffekten mit der Ein-Stationen O_2-Tagesgangmethode sollten die Ergebnisse als qualitative Veränderungen des Metabolismus gesehen werden, da die damit gemessenen Fließstrecken häufig nicht mit den renaturierten Gewässerabschnitten übereinstimmen.

Die vorliegende Arbeit hat gezeigt, dass hydromorphologische Renaturierungen funktionale Aspekte - wie die trophische Struktur von Lebensgemeinschaften, die trophische Vernetzung von Gewässer und Ufer und den Ökosystem-Metabolismus - beeinflussen können. Klassische Bewertungsverfahren sollten daher in Zukunft durch funktionale Ansätze ergänzt werden, um so eine umfassendere Abschätzung des Gewässerzustands und ein besseres Verständnis von Renaturierungseffekten zu ermöglichen.

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8 Appendix

Appendices are available on the enclosed CD-ROM.

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Eidesstattliche Erklärungen

Erklärung:

Hiermit erkläre ich, gem. § 6 Abs. (2) f) der Promotionsordnung der Fakultäten für Biologie, Chemie und Mathematik zur Erlangung der Dr. rer. nat., dass ich das Arbeitsgebiet, dem das Thema " Effects of river restoration on ecosystem metabolism and trophic relationships" zuzuordnen ist, in Forschung und Lehre vertrete und den Antrag von Benjamin Kupilas befürworte.

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