Hydromorphological rehabilitation improves channel morphology, in-stream biotopes and macroinvertebrate communities, and thus enhances the conservation of an urban river

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Abstract

1. Many river rehabilitation projects have been criticised for failing to meet their goals or for being insufficiently monitored. There is, therefore, an urgent need to develop robust approaches to assessing treatment efficacy and to thus guide the increasing investment in rehabilitation.
2. In-stream biotopes (formerly called 'functional habitats' or 'mesohabitats' by different authors) and their macroinvertebrate assemblages were used to assess the effectiveness of entire-channel hydromorphological rehabilitation of a 1.8 km stretch of a lowland stream through the town of Market Harborough, Leicestershire, UK.
3. The project successfully enhanced the physical diversity, measured as the rehabilitated reach's coefficients of variability for channel water depth and width, wet surface area, number of in-stream biotopes and biotope diversity.
4. The project also enhanced the biodiversity conservation value, measured as macroinvertebrate total density, total biomass, richness, diversity, Ephemeroptera, Plecoptera & Trichoptera (EPT) richness, EPT diversity, EPT count%, and EPT biomass% - all of which significantly increased post-rehabilitation. Chironomidae count% and biomass% significantly decreased post-rehabilitation. Rehabilitation was also successful in significantly increasing macroinvertebrate shredder, scraper, and filter-feeder group density.
5. Changes in the rehabilitated reach's macroinvertebrate community metrics were significantly related to changes in the rehabilitated reach's percentages of cover of in-stream biotopes and increases in biotope diversity.
6. Macroinvertebrate structural and functional metrics can provide quantitative data for assessing reach-level rehabilitation outcomes, if samples are collected in a pre-defined sampling protocol stratified at the in-stream biotope level.
7. The practical implications of this work are that the design of rehabilitation projects, if based upon the re-creation of biotope heterogeneity, will succeed in improving biological value and restoring near-naturalness if a suitable upstream source of macroinvertebrate community for natural recolonisation is available. The study shows that the concept of biotopes has an important role to play in river conservation management.

Key Words: biodiversity, conservation, hydromorphology, invertebrates, channel reconfiguration, river rehabilitation.

1. Introduction

Riverine ecosystems have been altered by humans at different scales for millennia; with alterations ranging from catchment scale (e.g. through modifications of landscape and land use) to reach and in-stream scale (e.g. through channelisation and removal of large woody debris) (Allan, 2004; Vaughan *et al.*, 2009). Such hydromorphological degradations often create a “simplified, structurally-deficient, fragmented river system” (Ayres *et al.*, 2014) that negatively affects aquatic floral and faunal biodiversity (De Jalón *et al.*, 2013; Ayres *et al.*, 2014; Geist & Hawkins, 2016).

Rehabilitating major physical features by natural or artificial additions (such as stony riffles or flow deflectors) has been assumed to be the best way to minimise or reverse the ecological effects of stream and river morphological degradation (Mitsch & Jørgensen, 2003; Ormerod, 2003; Pedersen, Baattrup-Pedersen, & Madsen, 2006). Rehabilitation has been based on the belief that habitat heterogeneity promotes biodiversity (Palmer, Menninger, & Bernhardt, 2010) and enhances ecological functioning (Feld *et al.*, 2011). Its success, however, depends on whether population, community and ecological functions recover and attain the characteristics typical of non-degraded reference systems (Ormerod, 2003; Geist & Hawkins, 2016). Macroinvertebrates are at middle trophic levels within freshwater food webs and can thus offer valuable information about biological improvement. Increasing the area available for colonisation through rehabilitation affects macroinvertebrates more than fishes, as the former typically move less (Gore, Crawford, & Addison, 1998).

The European Water Framework Directive (WFD) implemented in 2000 (Council of the European Communities, 2000) specified that European Union (EU) countries should achieve ‘Good Ecological Status’ of their streams and rivers by 2015 (Muhar *et al.*, 2016). In practice, however, many EU countries failed to achieve these goals, so the deadlines were pushed back to 2021 or even 2027. All member states must now achieve Good Ecological Status by 2027 (European Commission, 2012). Although the UK left the EU at the end of 2020, it is claimed that this will not result in any deterioration of environmental standards. This seems unlikely, however, since the UK Environment Agency made 33% fewer inspections in 2019 than in 2014 because of financial constraints (Everett, 2020). Furthermore, success of rehabilitation for biodiversity conservation remains poorly quantified and limited (Al-Zankana, Matheson, & Harper, 2020). Only 10% of about 40,000 reported rehabilitation projects in the United States of America contained any post-rehabilitation monitoring (Palmer *et al.*, 2007) and only 30% of rehabilitation projects in Europe, including the UK, provided ecological monitoring information (Thompson, 2015). The apparently limited success of rehabilitation approaches is suggested to be due to: (a) failure of the rehabilitation to enhance hydromorphology (Tullos *et al.*, 2009; Selvakumar, O'Connor, & Struck, 2010; Violin *et al.*, 2011; Leal, 2012; Verdonschot *et al.*, 2015); (b) masking of small changes by confounding factors at the larger catchment scale, such as land use, erosion, high levels of heavy metals and nutrient pollution (Larson, Booth, & Morley, 2001; Harrison *et al.*, 2004; Roni *et al.*, 2006; Louhi *et al.*, 2011; Kail, Arle, & Jähnig, 2012; McManamay, Orth, & Dolloff, 2013) and constrained recolonisation; or (c) a combination of the two.

The conflicting results of post-rehabilitation monitoring studies, together with the relative infancy of stream rehabilitation science (Palmer, Hondula, & Koch, 2014) thus indicate the urgent need for better studies to address the links between hydromorphological rehabilitation and changes in stream biota in any river rehabilitation and conservation projects (Louhi *et al.*, 2011; Wolter *et al.*, 2013).

The planning and design of effective river rehabilitation projects requires critical assessment of the effectiveness of past use of relevant methods (Roni & Quimby, 2005). Clearly, such assessments must be based on data gathered through appropriate monitoring, measurement and reporting (Roni & Beechie, 2013). Unfortunately, most river rehabilitation schemes have failed to assess outcomes and effectiveness (Cowx *et al.*, 2013). In other cases, poor statistical designs or biological methods have undermined the monitoring (Friberg *et al.*, 2016). Increased social pressure to conserve and improve the environment has led to an increasing number of river rehabilitation projects (Everard, 2012; Smith, Clifford, & Mant, 2014; Reichert *et al.*, 2015; Geist & Hawkins, 2016), but there is only limited evidence that such hydromorphological rehabilitation has marked and long-term positive ecological effects – particularly on macroinvertebrates (Palmer, Menninger, & Bernhardt, 2010; Feld *et al.*, 2011; Friberg *et al.*, 2014; Al-Zankana, Matheson, & Harper, 2020), with only a few exceptions (Miller, Budy, & Schmidt, 2010; Kail *et al.*, 2015).

Rehabilitation projects – particularly in the UK – have generally focused on relatively large physical units: for example by installing large woody material to act as flow deflectors, by constructing riffle areas, or by widening reaches to reinstate multichannel planforms (e.g.

Biggs *et al.*, 1998; Harrison *et al.*, 2004; Pretty & Dobson, 2004; Smith & Chadwick, 2014; Thompson, 2015; White *et al.*, 2017; Al-Zankana, Matheson, & Harper, 2021).

An holistic approach to river rehabilitation, which rehabilitates the entire channel and addresses hydromorphological processes, is rare but has been attracting increasing attention (Ayres *et al.*, 2014). This approach creates improvements to the diversity of flow patterns through restructuring the channel morphology to a more natural form. It considers the whole physical and biological potential of the rehabilitated site, and the scale of implementation, to shape and sustain river habitats and biota. Thus, it enhances the recovery of both ecosystem structure and processes (Beechie *et al.*, 2010). Such holistic approaches (Friberg *et al.*, 2016) will help to avoid common pitfalls of engineered solutions, such as the creation of localised habitats that cannot be sustained by natural processes (Beechie *et al.*, 2010; Palmer, Hondula, & Koch, 2014). Rehabilitating free flow (channel longitudinal connectivity) will also restore natural erosion-sedimentation processes (Friberg *et al.*, 2016).

The present work reports on an entire-channel approach, using the concept of in-stream biotopes as the near-natural, predictable mosaic of a whole river channel, which underpinned our design for rehabilitation of an engineered channel 1.8 km long through a small town in England. The term "biotope" refers to the physical habitats of species (or trait) assemblages in physical and morphological units. This term was adopted by Demars *et al.* (2012) in preference to the earlier terms "functional habitats" of Harper *et al.* (1998) in the same study or "mesohabitats" of Armitage, Pardo, & Brown (1995). The original concept of 'functional habitats' had been proposed by Harper, Smith, & Barham (1992) as a simple visual tool for recognising distinct 'microhabitats' of 1-5 m^2 area in a mosaic along a river channel, which they showed through 'Twinspan' analysis to contain different assemblages of invertebrates. The method was developed in order to identify physically rich river channels in order to conserve them against engineering simplification in Eastern England. Later, the authors realised that such a method could also be used for rehabilitating over-simplified rivers (Harper *et al.*, 1998) in a 'building block' or 'jigsaw' fashion. Kemp, Harper, & Crosa (1999; 2000) then showed that these habitats could be predicted from hydrological first principles, and could therefore be used in designing rehabilitation of degraded rivers as well as conservation of rivers of higher ecological quality. Over the same time period, the concept of 'flow biotopes' had been introduced to indicate the physical diversity of a river system

(Newson & Newson, 2000) and clear relationships had been shown between surface flow diversity as 'flow biotopes' and channel biodiversity as 'functional habitats' (Newson *et al.*, 1998). Most of the functional habitats and flow biotopes were incorporated into the 'River Habitat Survey' of the UK National Rivers Authority (Harper & Everard, 1998). A subsequent re-analysis of the full set of original data, from 10 UK rivers used to identify functional habitats (Demars *et al.*, 2012), renamed, with ecological justification, these river micro-habitat units as 'biotopes'. They have recently been shown, on a smaller scale, to be an effective measure of restoration of Large Woody Material in a lowland stream (Al-Zankana, Matheson, & Harper, 2021).

To be effective, the present study required a near-natural undamaged river stretch and a degraded stretch which were similar to and could be compared against the stretch about to be rehabilitated. We used a near-natural upstream reach of the river as the reference (also as a potential source of aquatic biota for natural recolonisation) and a tributary, joining at the downstream end of the urban stretch, which was similarly degraded but also had a near-natural upstream section, as the control. The near-natural, reference reach was also used as our target state for macroinvertebrate community direction after rehabilitation (following Laasonen, Muotka, & Kivijärvi, 1998; Muotka *et al.*, 2002; Louhi *et al.*, 2011; Stranko, Hilderbrand, & Palmer, 2012; Winking, 2015; Lorenz, 2020). The entire project put back physical diversity into a degraded stretch of river (using our biotopes as measures of this) by creating meanders and their associated riffles, pool and runs, in a low-flow channel inside the straight, uniform, high-flow channel. We call this 'rehabilitation' or 'remediation' (Geist & Hawkins, 2016); we were not returning the channel to its former configuration. Particularly in urban settings, full restoration to some idealised (but generally unknown) 'pristine' state is impractical, but mitigation that reintroduces at least some ecosystem services and/or biodiversity can be considered to be a beneficial action. Geist & Hawkins (2016) argue, moreover, that in urban areas the outcomes of rehabilitation should be assessed not only on a biotic basis, but on value to the public. Pragmatic remediation is thus likely to address – and be a compromise between – the needs of both biota and the public.

Assessment of rehabilitation effectiveness was carried out at the three sites using a hierarchical method for quantitative measurement of biotopes, macroinvertebrate structure, and macroinvertebrate function. The specific hypotheses were that: (i) rehabilitation will enhance morphological complexity and physical heterogeneity; and (ii) macroinvertebrate community structure and functional metrics will improve significantly in the rehabilitated reach compared with before rehabilitation or the control reach and will come to resemble those of the reference reach.

2. Methods

2.1. Study sites and rehabilitation process

The study was conducted in a Before-After-Control-Impact (BACI) design, which compared a 250 m section of the rehabilitated reach with an equivalently-sized near-natural upstream reach, and a similarly degraded tributary reach. The rehabilitated reach was within the 1.8 km long stretch of the Welland River flowing through Market Harborough (52.475427 N, -0.926341 W) (Figure 1). The near-natural reach of the Welland River was located upstream at Lubenham, 52.473637 N, -0.972636 W ('reference reach' hereafter), possessing a pool-riffle topography, a meandering platform and a wide range of organic and inorganic biotopes, including cobbles, gravel, sand, silt, marginal plants, macroalgae and submerged fine-leaved macrophytes. A straightened reach (250 m) of the Jordan River downstream of the rehabilitated reach at Market Harborough (52.476865 N, -0.909979 W) ('control reach' hereafter) was used as the control.

The Welland River rises in south west Leicestershire, UK, 10 km upstream of Market Harborough. It flows through the gently rolling countryside of Northamptonshire, Leicestershire and Rutland, with mixed agriculture on boulder clay. A dramatic change occurs when the river enters the flat, alluvial landscape of Lincolnshire (former swamp below sea level) for about 80 km before it reaches the sea at the Wash. The main river and its tributaries together form more than 480 km of waterway. Its full catchment area is 1,554 km^2 (Figure 1) and at Market Harborough its area is just 50 km^2. The landscape of the river valley is varied: changing from livestock-dominated hilly land of the upper Welland, with two market towns and several villages, into the largely arable fenlands of Lincolnshire below Stamford, and highly straightened channels that are tidal below Spalding, discharging to the Wash estuary. Natural meandering sections have been straightened and deepened, especially during the 1960s and 1970s, by engineering works to mitigate floods and improve land drainage. A near-natural reach of the Welland River at Lubenham is illustrated in Figure 4.1b of Al-Zankana (2018). The average daily flow of the Welland River at Ashley (approx. 10 km below Market Harborough, where the catchment area is about 5 times greater due to tributaries - at 250 km^2) is 1.45 m^3s^{-1} (https://nrfa.ceh.ac.uk/data/station/meanflow/31021); the average water depth at low-flow in the reference reach ranges between 0.08 m and 0.85 m and average active channel width ranges between 2.7 m and 4.1 m; in the control and rehabilitated reaches before rehabilitation the channel widths were 4-5 m and the depths rather uniform at around 0.03 m. The rehabilitated reach of the Welland River is illustrated prior to rehabilitation in Figure 4.1a of Al-Zankana (2018).

The Jordan River is about 6 km in length rising to the south of Braybrooke village in the county of Northamptonshire. It joins the Welland River within Market Harborough downstream of the rehabilitated reach (its ecological conditions were not affected by the rehabilitation activities). The control reach of the urban Jordan River had been modified similarly to the Welland River, its naturally meandering channel having been straightened and deepened (See Figure 4.1c of Al-Zankana (2018). Its channel is overly wide with steep banks, some of which are lined with concrete. The control reach thus had the same habitat conditions as the rehabilitation reach before the rehabilitation activities. Both the Jordan River and the Welland River rise in a similar landscape with only low-diffuse pollution of modern agriculture (Figure 1C). Both the Jordan River and the Welland River had similar upstream macroinvertebrate communities capable of supplying species for recolonisation (Welland Rivers Trust, Geoff Gilfillan, pers. comm.).

The 1.8 km reach of the Welland River through Market Harborough town was rehabilitated by the Welland Rivers Trust and the University of Leicester as the 'Welland for People and Wildlife' project over six months between autumn 2014 and spring 2015 (Welland Rivers Trust, 2015). Rehabilitation comprised the removal of six weirs and by-passing a further two by reconnecting a cut-off backwater channel. A new low-flow channel was created within the existing bank-full flood channel, known as a 'two-stage channel approach'. The new low-flow channel was meandered and narrowed, created by building berms constructed from the spoil derived from the digging of pools in meander bends. The coarser material was deposited between the bends, creating a series of pool-riffle sequences. These were expected to create variable width and depth, with wet area on berms for marginal plants to grow. These objectives were expected to create a gradual rather than the former sudden gradient (hence increasing current speed thus large particle biotopes with submerged fine-leaved macrophytes), create berms (hence emergent and marginal plant biotopes), pools (hence tree root and floating-leaved plant biotopes), to reduce the risk of erosion and provide safer access to the river for the community. Some native macrophytes were planted into coir mesh to initially stabilise the new berms, otherwise nothing was added.

The study measured physical and biological parameters before (spring 2014) and at quarterly intervals after rehabilitation (spring, summer, autumn 2015; spring, summer, autumn 2016), using the methods described below. This generated a very large quantity of data reported in Al-Zankana (2018), but for clarity this paper is restricted to a comparison of the pre-rehabilitation sampling (spring 2014, two sampling occasions, mid-March and mid-May) with the final post-rehabilitation sampling 18 months later in spring 2016 (two sampling occasions; mid-March and mid-May).

2.2. Channel morphology and in-stream biotope composition

In spring 2014 (the middle of March, April and again in May – three occasions), before the rehabilitation of the Welland River had begun, the wetted surface area (m^2), channel width (the wetted width) and depth (mid-river) were recorded every 5 m at all three sites. The channel depth was measured to the nearest centimetre at the centre of each 5 m cross section. The percentage of each in-stream biotope was estimated using lateral transects spaced every 5 m (perpendicular to the flow). The total number of biotopes and their coverage area for each 5 m transect were calculated following (Entrekin *et al.*, 2009). All transect measures were summed to give reach-level total wetted surface area, channel width, channel depth and biotope number and percentages for each study reach. Following rehabilitation, the same measurements were recorded quarterly in spring, summer and autumn, to record changes. In-stream biotopes were visually identified following Demars *et al.* (2012). The biotopes identified and sampled were: cobbles (CO), gravel (G) and sand (SA), silt (SI), tree-roots (TR), marginal plants (MP), leaf litter (LL), macroalgae (MA) and submerged fine-leaved macrophytes (MSF). Boulders (BL) and large woody debris (WD) were not sampled as there were not enough patches of them to collect three independent samples per visit. Metrics were calculated to describe the morphological condition of the study reaches, based on the data from the reach-level morphological survey and in-stream biotope mapping, as follows:

a) In-stream biotope diversity by the Shannon-Wiener diversity index (SWI) (Shannon & Weaver, 1949), following Kemp (1999) and Poppe *et al.* (2015), where 'species' were replaced by biotopes - named "SWI-biotope" hereafter. Number of in-stream biotopes was used rather than the number of species, and biotope proportions used instead of densities. The diversity index thus depends on both biotope richness and dominance. Greater values of SWI reflect both higher numbers of biotopes and greater equitability.

b) The coefficients of variation (CV) of channel water depth and of channel width (CV-depth, CV-width) were calculated from all the measurements made along the reach. Coefficient of Variation is defined as the ratio of the standard deviation to the mean.

2.3. Sampling and processing of macroinvertebrates

Pre-rehabilitation macroinvertebrate samples were collected in spring 2014 (two occasions, March and May). Post-rehabilitation samples were collected in spring 16 (two occasions, March and May). Samples were collected from all available biotopes (habitat patches) within the reaches and are referred to as biotope-specific samples. Three macroinvertebrate samples from separate patches of each existing biotope (those covering ≥1% area of the riverbed within a given reach) were collected on each sampling visit. Samples were collected using a Surber sampler (500 µm mesh size). The area (0.09 m^2) within the frame was disturbed for 30 s to dislodge all animals in the substrate; and the animals were subsequently swept by the water into the net for collection. In-stream macrophyte stems and leaves within the sampler frame were enclosed in the net and then cut off from the plant as close to the substratum as possible, and then sampled together with substrate. In-stream macroalgae were enclosed in the net and also sampled with the benthos. Flow was created manually in slow flowing biotopes (marginal plant and silt) to assist sample collection. Macrophyte or macroalgae surface areas were not added when expressing data from them as per m^2 of substratum.

In total, 228 macroinvertebrate samples were collected. In the control reach, in spring 2014, fifteen samples were collected on each occasion, from five biotopes (three samples per biotope) (G, SA, SI, MP and MSF). The same number of samples were collected in spring 2016.

In the reference reach, in spring 2014, twenty-one samples were collected on each occasion, from seven biotopes (CO, G, SA, SI, MP, MA and MSF). The same number of samples were collected in spring 2016.

In the rehabilitated reach, in spring 2014, eighteen samples were collected on each occasion, from six biotopes (CO, G, SA, SI, TR and LL). The same number of samples were collected after rehabilitation (spring 2016), together with three additional samples from each of MP and MSF, to give 24 samples on each occasion.

Macroinvertebrate samples were kept separate; specimens from each sampled biotope were identified and counted in the laboratory. Specimens were identified to the lowest practical taxonomic level (either species or genus) with the exception of Oligochaeta and

Coleoptera, which were identified to family; with Diptera also identified to family (except Chironomidae which were identified to sub-family). Macroinvertebrate biomass (mg Dry Mass (mgDM)) was estimated according to published size-specific mass regressions (Meyer, 1989; Wenzel, Meyer, & Schwoerbel, 1990; Burgherr & Meyer, 1997; Poepperl, 1998; González, Basaguren, & Pozo, 2002; Giustini *et al.*, 2008) except for Dry Mass of Oligochaeta and insect larvae, which were measured directly (following Rodriguez & Verdonschot, 2002; Benke & Huryn, 2006) as there were no appropriate length:mass regressions for them. Macroinvertebrate abundance data for each biotope were assigned to eight feeding strategies (hereafter called Functional Feeding Groups, FFG) according to Tachet *et al.* (2010).

Reach-level values of taxon count sample^{-1}, taxon biomass sample^{-1}, and FFG count sample^{-1} were calculated according to the relative coverage area of each sampled biotope in the given reach. The given reach-level variable lists were created by summing biotope-specific list values that were weighted by their availability percentage (following Huryn & Wallace, 1987; Lugthart & Wallace, 1992; Kedzierski & Smock, 2001; Pedersen *et al.*, 2007; Jähnig *et al.*, 2010).

Macroinvertebrate total density (individuals sample^{-1}), taxon richness, taxon diversity (Shannon-Wiener diversity), evenness, EPT richness, EPT diversity, EPT count%, and Chironomidae count% metrics were calculated (using a built-in option in PRIMER v.7 software (Clarke & Gorley, 2015)) from the reach-level taxon count sample^{-1} data lists. Total biomass (mgDM sample^{-1}), EPT biomass%, and Chironomidae biomass% were calculated from reach-level taxon biomass sample^{-1} data lists. The reach-level FFG count sample^{-1} data list was used to calculate the percentage of density contributed by each FFG (following Tullos *et al.*, 2009).

2.4. Data analysis

Wet surface area, CV-depth, CV-width, number of biotopes, SWI-biotope and in-stream biotope composition (predictor variables hereafter) were normalised (using a built-in option in PRIMER v.7 software (Clarke & Gorley, 2015)), Euclidean distance matrices were then calculated and used in a two-way permutational MANOVA (Anderson, Gorley, & Clarke, 2008). Principal Component Analysis (PCA) was conducted to visualise which predictor variables separated the study reaches. PCA results were ordinated by reaches; and variables contributing >0.5 Spearman's rank correlation (ρ) were included as vectors (following Clark, 2011). Two-way permutational MANOVA with *Period* (fixed factor, two levels: before, after) and *Reach type* (fixed factor, three levels: control, reference, rehabilitated), was used to run a BACI design test and all possible pair-wise tests. All tests used 9999 random permutations under a reduced model. When there were too few (< 100) possible permutations to obtain a reasonable test, a *P* value was calculated using 9999 Monte Carlo draws from the appropriate asymptotic permutation distribution (Anderson & Robinson, 2003).

Macroinvertebrate total density, total biomass and FFG densities were adjusted to show values per square metre before the data analysis. Macroinvertebrate total density, total biomass, taxon richness, taxon diversity, evenness, EPT richness, EPT diversity, EPT count%, EPT biomass%, Chironomidae count% and Chironomidae biomass% metrics (response variables hereafter) were log(*x*), Sqrt(*x*), or Asin(*x*) transformed prior to the analysis to improve the normality of the data distribution and satisfy the test requirements, where applicable. A Euclidean distance matrix was first used to calculate distances between samples for each metric separately and reaches were compared before-after rehabilitation period using the same permutational MANOVA design.

When a permutation MANOVA gave a significant (P<0.05) overall interaction (Reach × Period) in predictor variables or in any response variable, all pairwise comparisons were made to examine which elements contributed to the overall interaction (significant dissimilarities). If there was no overall effect but there were only Reach or Period effects, all the pairwise comparisons related to that Reach effect or Period effect were examined, because the aim of the study was to capture all changes (all significant dissimilarities).

The relationships between response variables and predictor variables of the rehabilitated reach were analysed using distance-based linear modelling (DISTLM) (following Eddy & Roman, 2016; Heerhartz *et al.*, 2016). Euclidean distance matrices of all response variables used for the previously described permutational MANOVA analyses were used separately. Sequential tests were used to determine which predictor variable or combinations of which predictor variables best explained variability in each response variable. Each sequential test was performed with a step-wise selection procedure using Akaike's information criterion (AIC_c). The relationship between response variables and predictor variables was determined using Spearman's rank correlation (ρ>0.5).

3. Results

3.1. Channel morphological variables and in-stream biotope composition

The creation of a low-flow channel clearly provided more area for marginal macrophytes to grow and increased the number of organic and mineral biotopes, so that the rehabilitated reach had more in-stream biotopes and higher biotope diversity (SWI-biotope) than either the control reach or the reference reach (Table 1). PCA of the predictor variables (wet surface area, CV-depth, CV-width, number of biotopes, SWI-biotope and in-stream biotope composition) showed that, before rehabilitation, both control and rehabilitated reaches were separated from the reference reach along the first axis (PC1 in Figure 2, Table S1). PC1 described 60.9% of the differences between the control and rehabilitated reaches (which lay towards the left of PC1) and the reference reach (towards the right; Figure 2). This separation was driven by higher silty biotope percentages in the control and rehabilitated reaches (ρ = 0.54), than the reference reach (Table 1). The reference reach also had a higher proportion of gravel (ρ = 0.54) than the other two reaches (Table 1). PC2 captured 26% of the differences between the rehabilitated reach (towards the top of PC2) and the reference reach (towards the bottom; Figure 2). Leaf litter (ρ = 0.58), marginal plants (ρ = 0.54), SWI-biotope (ρ = 0.55), and number of biotopes (ρ = 0.57) were the most important contributors to PC2 (Table S1). They all remained higher in the rehabilitated reach than the reference reach (Table 1).

There were statistically significant interactions between Period and Reach for the predictor variables (Permutation MANOVA, *Pseudo-F* = 125.2, *df* = 2, *P*=0.001) (Tables S2). Before rehabilitation, the measured predictor variables of the control and rehabilitated reaches were similar but differed significantly (post-hoc Student's *t* test, *t* = 77.62, *df* = 4, *P*=0.001 and *t* = 71.49, *df* = 4, *P*=0.001) from that of the reference reach (Table S3).

Rehabilitation significantly increased the rehabilitated reach's variability in the measured predictor variables (*t* = 9.23, *df* = 4, *P*=0.002) (Table S4). Less of the surface area of stones & gravel was covered by silt compared to that in the pre-rehabilitation condition or in the control reach. The rehabilitated reach remained significantly different from the reference reach (*t* = 37.88, *df* = 4, *P*=0.001) (Table S3), despite the significant improvement in its channel morphology and biotope composition.

3.2. Macroinvertebrate community metrics

Forty macroinvertebrate taxa were recorded in both the control reach and the rehabilitated reach prior to rehabilitation; 71 in the reference reach (Table S5). Two years after rehabilitation, the number of taxa in the rehabilitated reach had increased to 55 but was unchanged in the other two reaches. All newly recorded species in the rehabilitated reach were also recorded in the reference reach. The rehabilitated reach's macroinvertebrate total density, total biomass, taxon richness, taxon diversity, evenness, EPT richness, EPT diversity, EPT count%, and EPT biomass% all increased significantly ($P<0.005$) by Spring 2016 compared with before rehabilitation (Figure 3, Table 2).

There were statistically significant interactions between Period and Reach for each of: macroinvertebrate total density (Permutation ANOVA, *Pseudo-F* = 23.92*, df* = 2, P=0.0001), total biomass (*Pseudo-F* = 31.43*, df* = 2, P=0.0001), taxon richness (*Pseudo-F* = 7.65*, df* = 2, P=0.002), taxon diversity (*Pseudo-F* = 56.19*, df* = 2, P=0.0001), evenness (*Pseudo-F* = 31.87*, df* = 2, P=0.0001), EPT diversity (*Pseudo-F* = 10.73*, df* = 2, P=0.0003), EPT count% (*Pseudo-F* = 13.49*, df* = 2, P=0.0001), Chironomidae count% (*Pseudo-F* = 38.63*, df* = 2, P=0.0001), Chironomidae biomass% (*Pseudo-F* = 18.20*, df* = 2, P=0.0001) (extra information is provided in Table S6). There was statistically significant Period effect for EPT richness (*Pseudo-F* = 5.95*, df* = 1, P=0.016) and statistically significant Reach effects for each of EPT richness (*Pseudo-F* = 39.62*, df* = 1, P=0.0001) and EPT biomass% (*Pseudo-F* = 11.94*, df* = 1, P=0.0003).

The control and rehabilitated reaches were statistically similar to each other ($P>0.05$) before the rehabilitation process (Spring 2014), shown by pairwise tests between reaches (extra information is provided in Table S7) according to their measured macroinvertebrate community metrics (Figure 3,Figure 4). The reference reach had significantly higher values ($P<0.005$) for total density, total biomass, taxon richness, taxon diversity, evenness, EPT richness, EPT diversity, EPT count%, and EPT biomass% compared to the control and rehabilitated reaches (Figure 3,Figure 4, Table 2). The control and rehabilitated reaches had significantly higher ($P<0.005$) Chironomidae count% and Chironomidae biomass% as compared to comparable values for the reference reach (Figure 4, Table 2).

Rehabilitation significantly ($P<0.005$) affected all measured macroinvertebrate community metrics of the rehabilitated reach (extra information is provided in Table S8) after just two years. Chironomidae count% and Chironomidae biomass% decreased significantly ($P<0.005$)

(Figure 4, Table 2). The rehabilitated reach differed significantly (*P*<0.005) by Spring 2016 from the control reach in terms of all measured metrics and moved toward the reference reach in terms of taxon richness, taxon diversity, EPT richness, EPT biomass%, Chironomidae count% and Chironomidae biomass% (Table S7). Evenness and EPT diversity metrics were improved beyond those of the reference reach (Table 2).

3.3. Functional Feeding Groups

There were statistically significant interactions between Period and Reach for each of shredder (permutation ANOVA, *Pseudo-F* = 45.41*, df = 2, P*=0.0001), scraper (*Pseudo-F* = 30.13*, df = 2, P*=0.001) and filter-feeder (*Pseudo-F* = 6.82*, df = 2, P*=0.003) (Table S9).

The control and rehabilitated reaches initially were statistically similar to each other (*P*>0.05) in terms of their shredder, scraper and filter-feeder densities, shown by pairwise tests between reaches (Table S10). The reference reach had higher values (*P*<0.005) for shredder, scraper and filter-feeder density than either other reach (Figure 5, Table 3).

Shredder density in the rehabilitated reach after rehabilitation increased significantly (*t* = 15.68, *df* = 10, *P*=0.0025) (Table S11) to 392 individuals m^{-2} from 61 individuals m^{-2} before. Scraper density also increased significantly (*t* = 13.08, *df* = 10, *P*=0.0026) to 249 individuals m^{-2} from 139 individuals m^{-2}. Filter-feeder density increased significantly (*t* = 6.20, *df* = 10, *P*=0.0026) to 141 individuals m^{-2} from 48 individuals m^{-2} (Figure 5, Table 3). Despite these significant increases, the rehabilitated reach remained significantly different from the reference reach (Table S10).

3.4. Relationships between response variables and predictor variables of the rehabilitated reach

DISTLM show that, post-rehabilitation increases of macroinvertebrate evenness were positively related to increases in in-stream biotope diversity (SWI-biotope). Increases in Gravel%, Marginal plant%, and leaf litter% were related positively to significant increases in most of the measured macroinvertebrate community metrics - total density, total biomass, taxon richness, taxon diversity, EPT richness, EPT diversity, and EPT biomass% . However, Gravel% was related negatively to variations in Chironomidae count% and Chironomidae biomass%. Silt% was related negatively to total biomass and EPT count%.

Before-after variations in macroinvertebrate FFG densities were explained mainly by post-rehabilitation changes in in-stream biotope percentages rather than by other channel morphological metrics. Significant increases in shredder macroinvertebrate density was related positively to post-rehabilitation increases in Gravel%, Marginal plant%, and leaf litter%. Scraper density increased significantly in a positive relationship to post-rehabilitation increase in Gravel%. Filter-feeder density increased significantly in a positive relationship to post-rehabilitation increase in SWI-biotope. The significant proportion of the variations (before-after changes) in each response variable explained by the given predictor variables are available in Table 4.

4. Discussion

Significant enhancements in the rehabilitated reach's macroinvertebrate community structure and function in this study were correlated with clear increases in in-stream biotope diversity and changes in biotope percentages. The significant relationship between increases in macroinvertebrate structural and functional metrics and changes in biotope percentages – rather than changes in measured channel morphology metrics – indicates the importance of in-stream biotopes as structural and functional units in stream ecology, and as indicators for monitoring the outcomes of stream rehabilitation projects. The significant post-rehabilitation increases in macroinvertebrate taxon richness, taxon diversity, total density and total biomass recorded in the rehabilitated reach indicate that rehabilitation increased the stability of coarse mineral biotopes and resource availability of organic biotopes for macroinvertebrates. Reduced embeddedness of coarse biotopes improved the suitability of these substrates for many taxa because of increased substrate stability, reduced deposition of fine sediments, and increases in the availability of food in epilithic biofilms (Wood & Armitage, 1997). It is known that organic biotopes support higher taxon richness and diversity (Friberg *et al.*, 1994; Friberg *et al.*, 1998; Harrison *et al.*, 2004; Friberg *et al.*, 2014; Verdonschot *et al.*, 2015).

Higher measurements of EPT richness, EPT diversity, EPT count%, and EPT biomass also indicate that environmental conditions, particularly water velocity, substrate availability and oxygen concentrations, were improved by rehabilitation – EPT is considered a good metric when physico-chemical measures are not taken – because the three taxa are sensitive to environmental stressors (Downes *et al.*, 1998). Only a few other river rehabilitation studies have shown clear improvement in macroinvertebrate communities (Friberg *et al.*, 1994; Biggs *et al.*, 1998; Laasonen, Muotka, & Kivijärvi, 1998; Pedersen *et al.*, 2007; Rios-Touma *et al.*, 2015; Lorenz, 2020). The primary source of new species here was expected to be downstream drift from an upstream reference reach, as aerial recolonisation by insects might be expected to take longer than two years (Matthaei, Werthmüller, & Frutiger, 1997; Lorenz, 2020).

The significant increase in abundance of shredder macroinvertebrates indicates greater in-stream complexity, as these taxa are dependent on the availability of coarse particulate organic matter being deposited in pool areas (Smock, Metzler, & Gladden, 1989; Fenoglio *et* *al.*, 2005). Conversely, the increase in areas of higher water velocities and larger, more stable substratum particles of riffles and boulders offer more profitable foraging areas for scrapers (algal grazers), and more suitable attachment sites for filter-feeders (Williams & Moore, 1986; Allan, 1995). We did not sample boulders (emergent or submerged boulders) in this study because there were not enough patches of them to collect three independent samples per visit, but their presence (as oviposition substrates) in the rehabilitated reach could have accelerated the recovery process and recolonisation of many taxa. Larger interstitial pores could also increase retention of particulate organic food and act as refugia from diverse flow conditions (Gee, 1982; Culp, Walde, & Davies, 1983). Absence of a resource (biotope) can result in unsuccessful or limited success of rehabilitation projects as macroinvertebrate species often have specific biotope requirements at different stages of their life, requiring that all these biotopes must be present and of sufficient quality to guarantee recolonisation and development of sustainable populations (Demars *et al.*, 2012; Verdonschot *et al.*, 2015).

Deposit-feeders continually dominated in the control reach, indicating that sedimentation - as the dominant physical process - was detrimental to a diverse macroinvertebrate community. Similarly, degraded reaches are characterised by homogeneous habitat conditions (because of reduced flow diversity) and limited biotope availability (e.g. surface coverage of biotopes by siltation). Siltation can shift the macroinvertebrate composition towards taxa with low dissolved oxygen requirements (Angradi, 1999; Zweig & Rabeni, 2001) and decrease those vulnerable to fine sediments (due to damage of filter-feeding apparatus or delicate gills) (Wood & Armitage, 1997; Larsen, Vaughan, & Ormerod, 2009). The low abundance of scrapers and filter-feeders in the control reach provided more evidence of the negative effects of silt on macroinvertebrate functional composition. Deposition of fine sediment is associated with reduced food quality or impaired access to food resources for scraper and filter-feeder invertebrates (Kreutzweiser, Capell, & Good, 2005; Rabení, Doisy, & Zweig, 2005).

The rehabilitated reach attained conditions similar to those of the reference reach two years after rehabilitation. Few other rehabilitation studies have evidenced such clear, combined structural and functional recovery of macroinvertebrate populations and communities in such a short time. Some of these others have indicated that hydromorphological rehabilitation did not generally promote macroinvertebrate biodiversity, even if habitat changes were considerable (Lepori *et al.*, 2005; Jähnig *et al.*, 2010; Northington *et al.*, 2011; Ernst, Warren, & Baldigo, 2012; Stranko, Hilderbrand, & Palmer, 2012; Haase *et al.*, 2013; Friberg *et al.*, 2014; Pedersen, Kristensen, & Friberg, 2014), whilst others reported only moderate levels of improvement (Purcell, Friedrich, & Resh, 2002; Harrison *et al.*, 2004; Roni *et al.*, 2006; Schiff, Benoit, & Macbroom, 2011; Testa, Shields, & Cooper, 2011; Smith *et al.*, 2019). These earlier studies may have failed to fully capture positive effects of rehabilitation on macroinvertebrate biodiversity because of the methods used to sample macroinvertebrates. Most of the above evaluations sampled only riffle or riffle-pool habitats, and thus did not cover all available in-stream biotopes. These are the least likely to change as a result of habitat enhancement (Brooks *et al.*, 2002; Palmer, Menninger, & Bernhardt, 2010). One resolution to the problem of adequate sampling comes from the multi-habitat sampling protocol set out in the EU WFD. This reflects the proportions of microhabitat types (equivalent to in-stream biotopes) that are present with ≥5% cover (Jähnig *et al.*, 2010; Haase *et al.*, 2013; Verdonschot *et al.*, 2015; Funnell, 2019; Lorenz, 2020).

The failure of some of many earlier rehabilitation projects to increase biotope composition and diversity may also explain a consequent lack of positive response by macroinvertebrates (e.g. Jähnig & Lorenz, 2008; Verdonschot *et al.*, 2015). Macroinvertebrate species often have specific biotope requirements at different stages of their life, requiring that all these biotopes must be present and of sufficient quality to guarantee recolonisation and development of sustainable populations (Demars *et al.*, 2012; Verdonschot *et al.*, 2015). Limitation of the availability of key organic biotopes in rehabilitated rivers can hinder colonisation by additional species (Lorenz, Jahnig, & Hering, 2009).

The present study highlights the importance of rehabilitating in-stream biotopes in river channel conservation improvements, because they are ecologically relevant for the biodiversity of macroinvertebrates. It also highlights the importance of them as a monitoring design that can measure both structural and functional outcomes. In-stream biotopes were first shown to be the building blocks of river conservation and should become the prime focus of river managers (Harper, Smith, & Barham, 1992; Harper & Everard, 1998; Newson *et al.*, 1998; Harvey, Clifford, & Gurnell, 2008). We show here that they still have a place within the new priorities of river conservation (Boon, 2012). For example, understanding biotopes goes some way towards addressing the lack of basic research addressing the relationships between physical habitat and biological communities as highlighted by Vaughan *et al.* (2009) and Boon (2012). If we understand biotopes, we may be in a better position to not only rehabilitate waterways, but to identify and conserve those with high conservation value. Pre-defined sampling of the macroinvertebrate community - stratified at in-stream biotope level - is better than random sampling of the entire reach to capture hydromorphological rehabilitation outcomes. Both structural and functional aspects of ecological integrity in macroinvertebrate communities need to be assessed, because maintaining functional redundancy through taxonomic biodiversity is the main rehabilitation target (Palmer, Ambrose, & Poff, 1997).

Conclusion

This study spanned only 18 months, but it nevertheless demonstrated that biodiversity improvements can begin within such a short period. Although it may have failed to detect changes in some taxa, or longer-term changes, it demonstrates the importance of post-rehabilitation monitoring which, as recently reported, is infrequently implemented (Al-Zankana, Matheson, & Harper, 2020).

Rehabilitation schemes need clearly defined target states, and judging success against reference or control sites (Geist & Hawkins, 2016). The lack of any differences in the control or reference reaches' macroinvertebrate structural (Table S8) and functional (Table S11) metrics (before *vs* after) strongly suggested that the positive changes in the rehabilitated reach's metrics were induced by the morphological effects of the rehabilitation applied to that reach only and not by any climatic or other environmental changes between years.

Rehabilitation projects should be evidence based and well monitored so that lessons can be learnt from successes and failures to inform best practice (Geist & Hawkins, 2016). The UK River Habitat Survey (Environment Agency, 2003) and IUCN's river restoration strategy (Addy *et al.*, 2016) provide landscape-scale monitoring methods, but these methods rely on the smaller underlying units of assessment being accurate, robust and replicable. In riverine environments, biotopes represent the smallest hydromorphological scale at which macroinvertebrate community structure or function can be meaningfully quantified (Harvey, Clifford, & Gurnell, 2008), so assessment at this level is crucial for the success of large-scale methods. We show by biotope analysis the rehabilitation of whole-channel hydromorphological heterogeneity, enhancing biotope biodiversity and thus macroinvertebrate community matrices. Our work demonstrates the utility of in-stream biotope analysis in the assessment of river rehabilitation outcomes.

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Declaration of interests

The authors have no conflict of interest to declare.

References

Addy, S., Cooksley, S., Dodd, N., Waylen, K., Stockan, J., Byg, A., *et al.* (2016). *River restoration and biodiversity: Nature-based solutions for restoring rivers in the UK and Republic of Ireland*. Retrieved from www.crew.ac.uk/publications

Al-Zankana, A., Matheson, T. & Harper, D. (2021). Adding large woody material into a headwater stream has immediate benefits for macroinvertebrate community structure and function. *Aquatic Conservation: Marine and Freshwater Ecosystems, 31*(4), 930-947. doi:https://doi.org/10.1002/aqc.3529

Al-Zankana, A. F. A. (2018). *Using in-stream biotopes to assess the effectiveness of stream rehabilitation projects.* (PhD Thesis). University of Leicester, UK, Retrieved from http://hdl.handle.net/2381/43147

Al-Zankana, A. F. A., Matheson, T. & Harper, D. M. (2020). How strong is the evidence – based on macroinvertebrate community responses – that river restoration works? *Ecohydrology & Hydrobiology, 20*(2), 196-214. doi:https://doi.org/10.1016/j.ecohyd.2019.11.001

Allan, J. D. (1995). *Stream ecology: Structure and function of running waters*. London, UK: Chapman and Hall.

Allan, J. D. (2004). Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution, and Systematics, 35*, 257-284.

Anderson, M., Gorley, R. N. & Clarke, R. K. (2008). *Permanova+ for Primer: Guide to software and statisticl methods*: PRIMER-E, Plymouth, UK.

Anderson, M. J. & Robinson, J. (2003). Generalized discriminant analysis based on distances. *Australian & New Zealand Journal of Statistics, 45*(3), 301-318.

Angradi, T. R. (1999). Fine sediment and macroinvertebrate assemblages in Appalachian streams: a field experiment with biomonitoring applications. *Journal of the North American Benthological Society, 18*(1), 49-66.

Armitage, P., Pardo, I. & Brown, A. (1995). Temporal constancy of faunal assemblages in'mesohabitats'—application to management? *Archiv für Hydrobiologie, 133*(3), 367-387.

Ayres, A., Gerdes, H., Goeller, B., Lago, M., Catalinas, M., García Cantón, Á., *et al.* (2014). *REFORM D1.4 Inventory of river restoration measures: effects, costs and benefits*. Retrieved from http://www.reformrivers.eu/deliverables/d1-4

Beechie, T. J., Sear, D. A., Olden, J. D., Pess, G. R., Buffington, J. M., Moir, H., *et al.* (2010). Process-based principles for restoring river ecosystems. *BioScience, 60*(3), 209-222.

Benke, A. C. & Huryn, A. D. (2006). Secondary production of macroinvertebrates. In *Methods in Stream Ecology* (2nd ed., Vol. 2, pp. 691-710). San Diego, California: Elsevier Academic Press.

Biggs, J., Corfield, A., Grøn, P., Hansen, H. O., Walker, D., Whitfield, M., *et al.* (1998). Restoration of the rivers Brede, Cole and Skerne: a joint Danish and British EU-LIFE demonstration project, V—short-term impacts on the conservation value of aquatic macroinvertebrate and macrophyte assemblages. *Aquatic Conservation: Marine and Freshwater Ecosystems, 8*(1), 241-255. doi:10.1002/(SICI)1099-0755(199801/02)8:1<241::AID-AQC269>3.0.CO;2-9

Boon, P. J. (2012). Revisiting the case for river conservation. In P. J. Boon & P. J. Raven (Eds.), *River Conservation and Management* (pp. 3-14). Chichester: John Wiley.

Brooks, S. S., Palmer, M. A., Cardinale, B. J., Swan, C. M. & Ribblett, S. (2002). Assessing stream ecosystem rehabilitation: Limitations of community structure data. *Restoration Ecology, 10*(1), 156-168. doi:10.1046/j.1526-100X.2002.10117.x

Burgherr, P. & Meyer, E. I. (1997). Regression analysis of linear body dimensions vs. dry mass in stream macroinvertebrates. *Archiv für Hydrobiologie, 139*(1), 101-112.

Clark, B. (2011). *Does habitat restoration increase macroinvertebrate diversity of urban streams in Perth, Western Australia?* (PhD Thesis). The University of Western Australia,

Clarke, K. R. & Gorley, R. N. (2015). *PRIMER v7: User Manual/Tutorial* (1st ed.): PRIMER-E: Plymouth.

Council of the European Communities. (2000). Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. *Official Journal of the European Communities, L327*, 1-73.

Cowx, I., Angelopoulos, N., Noble, R., Slawson, D., Buijse, T. & Wolter, C. (2013). *Measuring success of river restoration actions using end-points and benchmarking*. Retrieved from https://reformrivers.eu/system/files/5.1%20Measuring%20river%20restoration%20success.pdf

Culp, J. M., Walde, S. J. & Davies, R. W. (1983). Relative importance of substrate particle size and detritus to stream benthic macroinvertebrate microdistribution. *Canadian Journal of Fisheries and Aquatic Sciences, 40*(10), 1568-1574.

De Jalón, D. G., Alonso, C., González del Tango, M., Martinez, V., Gurnell, A., Lorenz, S., *et al.* (2013). *REFORM D1.2 Review on pressure effects on hydromorphological variables and ecologically relevant processes*. Retrieved from http://www.reformrivers.eu/deliverables/d1-2

Demars, B. O. L., Kemp, J. L., Friberg, N., Usseglio-Polatera, P. & Harper, D. M. (2012). Linking biotopes to invertebrates in rivers: Biological traits, taxonomic composition and diversity. *Ecological Indicators, 23*(0), 301-311. doi:10.1016/j.ecolind.2012.04.011

Downes, B. J., Lake, P. S., Schreiber, E. S. G. & Glaister, A. (1998). Habitat structure and regulation of local species diversity in a stony, upland stream. *Ecological Monographs, 68*(2), 237-257.

Eddy, E. N. & Roman, C. T. (2016). Relationship between epibenthic invertebrate species assemblages and environmental variables in Boston Harbor's intertidal habitat. *Northeastern Naturalist, 23*(1), 45-66. doi:10.1656/045.023.0104

Entrekin, S. A., Tank, J. L., Rosi-Marshall, E. J., Hoellein, T. J. & Lamberti, G. A. (2009). Response of secondary production by macroinvertebrates to large wood addition in three Michigan streams. *Freshwater Biology, 54*(8), 1741-1758.

Environment Agency. (2003). *River habitat survey in Britain and Ireland field survey guidance manual: version 2003*.

Ernst, A. G., Warren, D. R. & Baldigo, B. P. (2012). Natural-Channel-Design restorations that changed geomorphology have little effect on macroinvertebrate communities in headwater streams. *Restoration Ecology, 20*(4), 532-540. doi:10.1111/j.1526-100X.2011.00790.x

European Commission. (2012). Commission staff working document, European overview (1/2) accompanying the document: “Report from the commission to the European Parliament and the Council on the Implementation of the Water Framework Directive (2000/60/EC) River Basin Management Plans”. COM (2012) 670 Final.

Everard, M. (2012). Why does ‘good ecological status’ matter? *Water and Environment Journal, 26*(2), 165-174.

Everett, S. (2020). Conservaton News; By the Water. *British Wildlife, 31*(6), 459-461.

Feld, C. K., Birk, S., Bradley, D. C., Hering, D., Kail, J., Marzin, A., *et al.* (2011). From natural to degraded rivers and back again: a test of restoration ecology theory and practice. *Advances in Ecological Research, 44*, 119-209. doi:http://dx.doi.org/10.1016/B978-0-12-374794-5.00003-1

Fenoglio, S., Bo, T., Agosta, P. & Malacarne, G. (2005). Temporal and spatial patterns of coarse particulate organic matter and macroinvertebrate distribution in a low-order Apennine stream. *Journal of Freshwater Ecology, 20*(3), 539-547.

Friberg, N., Angelopoulos, N. V., Buijse, A. D., Cowx, I. G., Kail, J., Moe, T. F., *et al.* (2016). Chapter Eleven: Effective river restoration in the 21st century: From trial and error to novel evidence-based approaches. *Advances in Ecological Research, 55*, 535-611. doi:10.1016/bs.aecr.2016.08.010

Friberg, N., Baattrup-Pedersen, A., Kristensen, E. A., Kronvang, B., S.E. Larsen, Pedersen, M. L., *et al.* (2014). The River Gelså restoration revisited: Habitat specific assemblages and persistence of the macroinvertebrate community over an 11-year period. *Ecological Engineering, 66*, 150-157. Retrieved from https://doi.org/10.1016/j.ecoleng.2013.09.069

Friberg, N., Kronvang, B., Hansen, H. O. & Svenden, L. M. (1998). Long-term, habitat-specific response of a macroinvertebrate community to river restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems, 8*, 87-99.

Friberg, N., Kronvang, B., Svendsen, L. M., Hansen, H. O. & Nielsen, M. B. (1994). Restoration of a channelized reach of the River Gelså, Denmark: Effects on the macroinvertebrate community. *Aquatic Conservation: Marine and Freshwater Ecosystems, 4*(4), 289-296. doi:10.1002/aqc.3270040402

Funnell, L. J. (2019). *Short term impacts of physical instream restoration works on the invertebrate community in Waituna Creek, measured by Surber and kick-net sampling methods.* (Master Thesis). University of Otago, New Zealand,

Gee, J. H. R. (1982). Resource utilization by Gammarus pulex (Amphipoda) in a Cotswold stream: a microdistribution study. *Journal of Animal Ecology, 51*(3), 817-831.

Geist, J. & Hawkins, S. J. (2016). Habitat recovery and restoration in aquatic ecosystems: current progress and future challenges. *Aquatic Conservation: Marine and Freshwater Ecosystems, 26*(5), 942-962. doi:https://doi.org/10.1002/aqc.2702

Giustini, M., Miccoli, F., De Luca, G. & Cicolani, B. (2008). Length–weight relationships for some plecoptera and ephemeroptera from a carbonate stream in central Apennine (Italy). *Hydrobiologia, 605*(1), 183-191. doi:10.1007/s10750-008-9353-9

González, J. M., Basaguren, A. & Pozo, J. (2002). Size-mass relationships of stream invertebrates in a northern Spain stream. *Hydrobiologia, 489*(1-3), 131-137.

Gore, J. A., Crawford, D. J. & Addison, D. S. (1998). An analysis of artificial riffles and enhancement of benthic community diversity by physical habitat simulation (PHABSIM) and direct observation. *Regulated Rivers: Research & Management, 14*(1), 69-77. Retrieved from <Go to ISI>://WOS:000073949100006

Haase, P., Hering, D., Jähnig, S., Lorenz, A. & Sundermann, A. (2013). The impact of hydromorphological restoration on river ecological status: a comparison of fish, benthic invertebrates, and macrophytes. *Hydrobiologia, 704*(1), 475-488.

Harper, D. M. & Everard, M. (1998). Why should the habitat-level approach underpin holistic river survey and management? *Aquatic Conservation: Marine and Freshwater Ecosystems, 8*(4), 395-413.

Harper, D. M., Smith, C., Kemp, J. & Crosa, G. (1998). The use of 'functional habitats' in the conservation, management and rehabilitation of rivers. *Advances in River Bottom Ecology.*, 315-326.

Harper, D. M., Smith, C. D. & Barham, P. J. (1992). Habitats as the building blocks for river conservation assessment. In P. J. Boon, P. Calow, & G. E. Petts (Eds.), *River Conservation and Management* (pp. 311-319). Chichester, UK: John Wiley & Sons Ltd.

Harrison, S. S. C., Pretty, J. L., Shepherd, D., Hildrew, A. G., Smith, C. & Hey, R. D. (2004). The effect of instream rehabilitation structures on macroinvertebrates in lowland rivers. *Journal of Applied Ecology, 41*(6), 1140-1154. doi:10.2307/3505789

Harvey, G. L., Clifford, N. J. & Gurnell, A. M. (2008). Towards an ecologically meaningful classification of the flow biotope for river inventory, rehabilitation, design and appraisal purposes. *Journal of Environmental Management, 88*(4), 638-650. doi:https://doi.org/10.1016/j.jenvman.2007.03.039

Heerhartz, S. M., Toft, J. D., Cordell, J. R., Dethier, M. N. & Ogston, A. S. (2016). Shoreline armoring in an estuary constrains wrack-associated invertebrate communities. *Estuaries and Coasts, 39*(1), 171-188. doi:10.1007/s12237-015-9983-x

Huryn, A. D. & Wallace, J. B. (1987). Local geomorphology as a determinant of macrofaunal production in a mountain stream. *Ecology, 68*(6), 1932-1942.

Jähnig, S. C., Brabec, K., Buffagni, A., Erba, S., Lorenz, A. W., Ofenböck, T.*, et al.* (2010). A comparative analysis of restoration measures and their effects on hydromorphology and benthic invertebrates in 26 central and southern European rivers. *Journal of Applied Ecology, 47*(3), 671-680.

Jähnig, S. C. & Lorenz, A. W. (2008). Substrate-specific macroinvertebrate diversity patterns following stream restoration. *Aquatic Sciences, 70*(3), 292-303.

Kail, J., Arle, J. & Jähnig, S. C. (2012). Limiting factors and thresholds for macroinvertebrate assemblages in European rivers: empirical evidence from three datasets on water quality, catchment urbanization, and river restoration. *Ecological Indicators, 18*, 63-72. Retrieved from https://doi.org/10.1016/j.ecolind.2011.09.038

Kail, J., Brabec, K., Poppe, M. & Januschke, K. (2015). The effect of river restoration on fish, macroinvertebrates and aquatic macrophytes: A meta-analysis. *Ecological Indicators, 58*, 311-321. doi:http://dx.doi.org/10.1016/j.ecolind.2015.06.011

Kedzierski, W. M. & Smock, L. A. (2001). Effects of logging on macroinvertebrate production in a sand-bottomed, low-gradient stream. *Freshwater Biology, 46*(6), 821-833.

Kemp, J. L. (1999). *Physical controls on the diversity and distribution of river channel habitats.* (PhD Thesis). University of Leicester, UK, ProQuest Dissertations & Theses: UK & Ireland database.

Kemp, J. L., Harper, D. M. & Crosa, G. A. (1999). Use of ‘functional habitats’ to link ecology with morphology and hydrology in river rehabilitation. *Aquatic Conservation: Marine and Freshwater Ecosystems, 9*(1), 159-178. doi:10.1002/(SICI)1099-0755(199901/02)9:1<159::AID-AQC319>3.0.CO;2-M

Kemp, J. L., Harper, D. M. & Crosa, G. A. (2000). The habitat-scale ecohydraulics of rivers. *Ecological Engineering, 16*(1), 17–29. doi:10.1016/S0925-8574(00)00073-2

Kreutzweiser, D. P., Capell, S. S. & Good, K. P. (2005). Effects of fine sediment inputs from a logging road on stream insect communities: a large-scale experimental approach in a Canadian headwater stream. *Aquatic Ecology, 39*(1), 55-66.

Laasonen, P., Muotka, T. & Kivijärvi, I. (1998). Recovery of macroinvertebrate communities from stream habitat restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems, 8*(1), 101-113.

Larsen, S., Vaughan, I. P. & Ormerod, S. J. (2009). Scale-dependent effects of fine sediments on temperate headwater invertebrates. *Freshwater Biology, 54*(1), 203-219.

Larson, M. G., Booth, D. B. & Morley, S. A. (2001). Effectiveness of large woody debris in stream rehabilitation projects in urban basins. *Ecological Engineering, 18*(2), 211-226. doi:10.1016/s0925-8574(01)00079-9

Leal, C. C. (2012). *The effects of restored aquatic large woody debris structures on invertebrate populations in the Napa River.* (Master Thesis). San Jose State University, USA, Retrieved from http://scholarworks.sjsu.edu/etd_theses (4240)

Lepori, F., Palm, D., Brannas, E. & Malmqvist, B. (2005). Does restoration of structural heterogeneity in streams enhance fish and macroinvertebrate diversity? *Ecological Applications, 15*(6), 2060-2071. doi:10.1890/04-1372

Lorenz, A. W. (2020). Continuous riverine biodiversity changes in a 10-years-post-restoration-study—Impacts and pitfalls. *River Research and Applications*.

Lorenz, A. W., Jahnig, S. C. & Hering, D. (2009). Re-meandering German lowland streams: qualitative and quantitative effects of restoration measures on hydromorphology and macroinvertebrates. *Environmental Management, 44*(4), 745-754. doi:10.1007/s00267-009-9350-4

Louhi, P., Mykrä, H., Paavola, R., Huusko, A., Vehanen, T., Mäki-Petäys, A.*, et al.* (2011). Twenty years of stream restoration in Finland: little response by benthic macroinvertebrate communities. *Ecological Applications, 21*(6), 1950-1961.

Lugthart, G. J. & Wallace, J. B. (1992). Effects of disturbance on benthic functional structure and production in mountain streams. *Journal of the North American Benthological Society, 11*(2), 138-164. doi:10.2307/1467381

Matthaei, C. D., Werthmüller, D. & Frutiger, A. (1997). Invertebrate recovery from a bed-moving spate: the role of drift versus movements inside or over the substratum. *Archiv für Hydrobiologie, 140*(2), 221-235.

McManamay, R. A., Orth, D. J. & Dolloff, C. A. (2013). Macroinvertebrate community responses to gravel addition in a southeastern regulated river. *Southeastern Naturalist, 12*(3), 599-618.

Meyer, E. I. (1989). The relationship between body length parameters and dry mass in running water invertebrates. *Archiv für Hydrobiologie, 117*(2), 191-203.

Miller, S. W., Budy, P. & Schmidt, J. C. (2010). Quantifying macroinvertebrate responses to in-stream habitat restoration: applications of meta-analysis to river restoration. *Restoration Ecology, 18*(1), 8-19.

Mitsch, W. J. & Jørgensen, S. E. (2003). Ecological engineering: A field whose time has come. *Ecological Engineering, 20*(5), 363-377. doi:10.1016/j.ecoleng.2003.05.001

Muhar, S., Januschke, K., Kail, J., Poppe, M., Schmutz, S., Hering, D.*, et al.* (2016). Evaluating good-practice cases for river restoration across Europe: context, methodological framework, selected results and recommendations. *Hydrobiologia, 769*(1), 3-19.

Muotka, T., Paavola, R., Haapala, A., Novikmec, M. & Laasonen, P. (2002). Long-term recovery of stream habitat structure and benthic invertebrate communities from in-stream restoration. *Biological Conservation, 105*(2), 243-253.

Newson, M. D., Harper, D. M., Padmore, C. L., Kemp, J. L. & Vogel, B. (1998). A cost-effective approach for linking habitats, flow types and species requirements. *Aquatic Conservation: Marine and Freshwater Ecosystems, 8*(4), 431-446. doi:10.1002/(sici)1099-0755(199807/08)8:4<431::aid-aqc302>3.3.co;2-n

Newson, M. D. & Newson, C. L. (2000). Geomorphology, ecology and river channel habitat: mesoscale approaches to basin-scale challenges. *Progress in Physical Geography, 24*(2), 195-217.

Northington, R. M., Benfield, E. F., Schoenholtz, S. H., Timpano, A. J., Webster, J. R. & Zipper, C. (2011). An assessment of structural attributes and ecosystem function in restored Virginia coalfield streams. *Hydrobiologia, 671*(1), 51-63.

Ormerod, S. J. (2003). Restoration in applied ecology: Editor's introduction. *Journal of Applied Ecology, 40*(1), 44-50. doi:10.1046/j.1365-2664.2003.00799.x

Palmer, M. A., Allan, J. D., Meyer, J. & Bernhardt, E. S. (2007). River restoration in the twenty-first century: data and experiential knowledge to inform future efforts. *Restoration Ecology, 15*(3), 472-481.

Palmer, M. A., Ambrose, R. F. & Poff, N. L. (1997). Ecological theory and community restoration ecology. *Restoration Ecology, 5*(4), 291-300.

Palmer, M. A., Hondula, K. L. & Koch, B. J. (2014). Ecological restoration of streams and rivers: Shifting strategies and shifting goals. *Annual Review of Ecology, Evolution, and Systematics, 45*, 247-269.

Palmer, M. A., Menninger, H. L. & Bernhardt, E. (2010). River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? *Freshwater Biology, 55*(s1), 205-222. doi:10.1111/j.1365-2427.2009.02372.x

Pedersen, M. L., Friberg, N., Skriver, J., Baattrup-Pedersen, A. & Larsen, S. E. (2007). Restoration of Skjern River and its valley - Short-term effects on river habitats, macrophytes and macroinvertebrates. *Ecological Engineering, 30*(2), 145-156. doi:10.1016/j.ecoleng.2006.08.009

Pedersen, M. L., Kristensen, K. K. & Friberg, N. (2014). Re-meandering of lowland streams: will disobeying the laws of geomorphology have ecological consequences? *PloS One, 9*(9). doi:10.1371/journal.pone.0108558

Pedersen, T. C. M., Baattrup-Pedersen, A. & Madsen, T. O. M. V. (2006). Effects of stream restoration and management on plant communities in lowland streams. *Freshwater Biology, 51*(1), 161-179. doi:10.1111/j.1365-2427.2005.01467.x

Poepperl, R. (1998). Biomass determination of aquatic invertebrates in the Northern German lowland using the relationship between body length and dry mass. *Faunistisch-Ökologische Mitteilungen, 7*, 379-386.

Poppe, M., Kail, J., Aroviita, J., Stelmaszczyk, M., Giełczewski, M. & Muhar, S. (2015). Assessing restoration effects on hydromorphology in European mid-sized rivers by key hydromorphological parameters. *Hydrobiologia, 769*(1), 21-40.

Pretty, J. L. & Dobson, M. (2004). The response of macroinvertebrates to artificially enhanced detritus levels in plantation streams. *Hydrology and Earth System Sciences Discussions, 8*(3), 550-559.

Purcell, A. H., Friedrich, C. & Resh, V. H. (2002). An assessment of a small urban stream restoration project in Northern California. *Restoration Ecology, 10*(4), 685-694. doi:10.1046/j.1526-100X.2002.01049.x

Rabení, C. F., Doisy, K. E. & Zweig, L. D. (2005). Stream invertebrate community functional responses to deposited sediment. *Aquatic Sciences-Research Across Boundaries, 67*(4), 395-402.

Reichert, P., Langhans, S. D., Lienert, J. & Schuwirth, N. (2015). The conceptual foundation of environmental decision support. *Journal of Environmental Management, 154*, 316-332.

Rios-Touma, B., Prescott, C., Axtell, S. & Kondolf, G. M. (2015). Habitat restoration in the context of watershed prioritization: the ecological performance of urban stream restoration projects in Portland, Oregon. *River Research and Applications, 31*(6), 755-766. doi:10.1002/rra.2769

Rodriguez, P. & Verdonschot, P. (2002). *Aquatic Oligochaete Biology VIII: Proceedings of the 8th International Symposium on Aquatic Oligochaeta, Held in Bilbao, Spain, 18-22 July 2000* (Vol. 158): Springer.

Roni, P. & Beechie, T. (2013). *Stream and watershed restoration: A guide to restoring riverine processes and habitats*. Chichester, West Sussex, UK: Wiley-Blackwell.

Roni, P., Bennett, T., Morley, S., Pess, G. R., Hanson, K., Van Slyke, D*., et al.* (2006). Rehabilitation of bedrock stream channels: The effects of boulder weir placement on aquatic habitat and biota. *River Research and Applications, 22*(9), 967-980. doi:10.1002/rra.954

Roni, P. & Quimby, E. (2005). *Monitoring stream and watershed restoration*. Maryland, USA: CABI.

Schiff, R., Benoit, G. & Macbroom, J. (2011). Evaluating stream restoration: a case study from two partially developed 4^{th} order Connecticut, USA streams and evaluation monitoring strategies. *River Research and Applications, 27*(4), 431-460. doi:10.1002/rra.1365

Selvakumar, A., O'Connor, T. P. & Struck, S. D. (2010). Role of stream restoration on improving benthic macroinvertebrates and in-stream water quality in an urban watershed: case study. *Journal of Environmental Engineering, 136*(1), 127-139.

Shannon, C. E. & Weaver, W. (1949). *The Mathematical Theory of Communication*. Urbana, USA: University of Illinois Press.

Smith, B. & Chadwick, M. A. (2014). Litter decomposition in highly urbanized rivers: influence of restoration on ecosystem function. *Fundamental and Applied Limnology, 185*(1), 7-18. doi:10.1127/fal/2014/0581

Smith, B., Clifford, N. J. & Mant, J. (2014). The changing nature of river restoration. *Wiley Interdisciplinary Reviews: Water, 1*(3), 249-261.

Smith, R. F., Neideigh, E. C., Rittle, A. M. & Wallace, J. R. (2019). Assessing macroinvertebrate community response to restoration of Big Spring Run: Expanded analysis of before-after-control-impact sampling designs. *River Research and Applications, n/a*(n/a). doi:10.1002/rra.3556

Smock, L. A., Metzler, G. M. & Gladden, J. E. (1989). Role of debris dams in the structure and functioning of low-gradient headwater streams. *Ecology, 70*(3), 764-775. doi:10.2307/1940226

Stranko, S. A., Hilderbrand, R. H. & Palmer, M. A. (2012). Comparing the fish and benthic macroinvertebrate diversity of restored urban streams to reference streams. *Restoration Ecology, 20*(6), 747-755.

Tachet, H., Richoux, P., Bournaud, M. & Usseglio-Polatera, P. (2010). *Invertébrés d'Eau Douce: Systématique, Biologie, Écologie*: CNRS éditions Paris.

Testa, S., Shields, F. D. & Cooper, C. M. (2011). Macroinvertebrate response to stream restoration by large wood addition. *Ecohydrology, 4*(5), 631-643.

Thompson, M. (2015). *The effect of large woody debris restoration on stream ecosystems.* (PhD Thesis). University College London, UK, Retrieved from http://discovery.ucl.ac.uk/id/eprint/1455018

Tullos, D. D., Penrose, D. L., Jennings, G. D. & Cope, W. G. (2009). Analysis of functional traits in reconfigured channels: implications for the bioassessment and disturbance of river restoration. *Journal of the North American Benthological Society, 28*(1), 80-92.

Vaughan, I., Diamond, M., Gurnell, A., Hall, K., Jenkins, A., Milner, N., *et al.* (2009). Integrating ecology with hydromorphology: a priority for river science and management. *Aquatic Conservation: Marine and Freshwater Ecosystems, 19*(1), 113-125.

Verdonschot, R. C. M., Kail, J., McKie, B. G. & Verdonschot, P. F. M. (2015). The role of benthic microhabitats in determining the effects of hydromorphological river restoration on macroinvertebrates. *Hydrobiologia, 769*(1), 55-66. doi:10.1007/s10750-015-2575-8

Violin, C. R., Cada, P., Sudduth, E. B., Hassett, B. A., Penrose, D. L. & Bernhardt, E. S. (2011). Effects of urbanization and urban stream restoration on the physical and biological structure of stream ecosystems. *Ecological Applications, 21*(6), 1932-1949. doi:10.1890/10-1551.1

Welland Rivers Trust. (2015). People and Wildlife Project. Retrieved from http://www.wellandriverstrust.org.uk/index.php/people-and-wildlife-project/

Wenzel, F., Meyer, E. & Schwoerbel, J. (1990). Morphometry and biomass determination of dominant mayfly larvae (Ephemeroptera) in running waters. *Archiv für Hydrobiologie, 118*(1), 31-46.

White, J. C., Hill, M. J., Bickerton, M. A. & Wood, P. J. (2017). Macroinvertebrate taxonomic and functional trait compositions within lotic habitats affected by river restoration practices. *Environmental Management, 60*(3), 513-525. doi:10.1007/s00267-017-0889-1

Williams, D. D. & Moore, K. A. (1986). Microhabitat selection by a stream-dwelling amphipod: a muitivariate analysis approach. *Freshwater Biology, 16*(1), 115-122.

Winking, C. (2015). *Ecological evaluation of restored former sewage channels in the urbanised Emscher catchment.* (PhD Thesis). Universität Duisburg-Essen, Germany,

Wolter, C., Lorenz, S., Scheunig, S., Lehmann, N., Schomaker, C., Nastase, A., *et al.* (2013). REFORM D 1.3 Review on ecological response to hydromorphological degradation and restoration. *Project Report REFORM D, 1*.

Wood, P. J. & Armitage, P. D. (1997). Biological effects of fine sediment in the lotic environment. *Environmental Management, 21*(2), 203-217.

Zweig, L. D. & Rabeni, C. F. (2001). Biomonitoring for deposited sediment using benthic invertebrates: a test on 4 Missouri streams. *Journal of the North American Benthological Society, 20*(4), 643-657.

Table 1. Mean and Standard Deviation (SD) of predictor variables (channel morphology metrics and biotope composition) of the three study reaches recorded before and after rehabilitation. Sample size of each mean=3. CV-depth; coefficients of variation of channel depth, CV-width; coefficients of variation of channel width, SWI-biotope; in-stream biotope diversity characterised by the Shannon-Wiener diversity index.

Predictor variables	Period	Control		Reference		Rehabilitated	
		Mean	SD	Mean	SD	Mean	SD
CV-depth	Before	0.36	0.07	0.61	0.06	0.34	0.30
	After	0.36	0.06	0.62	0.08	0.45	0.07
CV-width	Before	0.13	0.04	0.33	0.01	0.14	0.02
	After	0.13	0.02	0.34	0.03	0.35	0.02
SWI-biotope	Before	0.67	0.05	0.82	0.04	0.76	0.03
	After	0.67	0.04	0.81	0.06	0.94	0.03
Wet surface area (m^2)	Before	815	4	968	6	887	4
	After	818	5	970	4	875	4
Number of biotopes	Before	5	0	7	0	6	0
	After	5	0	7	0	8	0
Cobbles%	Before	0.0	0.0	11.3	0.5	4.3	0.1
	After	0.0	0.0	11.2	0.5	7.4	0.3
Gravel%	Before	36.0	1.5	71.7	1.3	38.1	1.6
	After	35.0	1.8	73.0	1.9	58.7	1.2
Sand%	Before	5.0	0.5	4.4	1.0	13.5	1.1
	After	8.5	0.9	4.9	1.2	4.0	0.4
Silt%	Before	52.0	2.3	2.2	0.1	41.1	3.1
	After	51.0	1.2	1.8	0.2	3.4	0.2
Tree root%	Before	0.0	0.0	0.0	0.0	1.7	0.2
	After	0.0	0.0	0.0	0.0	3.0	0.3
Marginal plants%	Before	1.3	0.0	1.6	0.0	0.0	0.0
	After	1.0	0.0	2.2	0.01	9.0	0.5
Leaf litter%	Before	0.0	0.0	0.0	0.0	1.2	0.0
	After	0.0	0.0	0.0	0.0	10.0	1.3
Macroalgae%	Before	0.0	0.0	6.7	0.8	0.0	0.0
	After	0.0	0.0	5.0	0.3	5.0	0.6
Submerged Fine-leaved Macrophytes%	Before	5.8	0.8	2.0	0.0	0.0	0.0
	After	4.5	0.1	2.0	0.0	4.5	0.2

Table 2. Mean and Standard Deviation (SD) of response variables (macroinvertebrate metrics) in three study reaches. Sample size of each mean=6.

Response variables	Period	Control		Reference		Rehabilitated	
		Mean	SD	Mean	SD	Mean	SD
Total density (individuals.m^{-2})	Before	853.7	176.7	1816.9	119.6	775.1	91.0
	After	868.7	208.9	1894.9	170.8	1188.1	234.7
Total biomass (mgDM.m^{-2})	Before	253.8	67.8	2618.3	532.1	300.2	205.8
	After	207.3	81.0	3238.0	640.1	1858.4	397.0
Taxon richness	Before	3.2	0.5	7.1	0.4	3.8	0.3
	After	3.1	0.4	6.6	0.6	6.6	0.3
Taxon diversity	Before	7.0	1.9	20.9	1.5	7.0	0.9
	After	6.7	1.8	20.8	3.4	23.2	1.4
Evenness	Before	0.6	0.1	0.8	0.0	0.5	0.0
	After	0.6	0.1	0.8	0.0	0.9	0.0
EPT richness	Before	1.4	0.7	3.5	0.1	1.6	0.7
	After	1.1	0.7	3.2	0.5	3.0	0.1
EPT diversity	Before	2.5	0.5	8.5	1.3	3.6	1.6
	After	2.2	0.8	7.8	2.9	11.7	1.2
EPT count%	Before	1.8	1.5	39.8	7.0	2.5	1.6
	After	1.6	1.4	32.8	7.3	16.9	1.0
Chironomidae count%	Before	51.3	11.2	10.6	1.2	48.5	7.0
	After	56.9	9.2	11.0	2.6	12.7	2.0
EPT biomass%	Before	6.7	13.5	25.1	10.2	10.1	9.2
	After	8.2	17.0	22.5	2.3	20.8	5.4
Chironomidae biomass%	Before	18.2	11.5	3.2	0.1	11.4	6.9
	After	22.4	11.4	3.6	0.4	2.8	0.4

Table 3. Mean and standard deviation (SD) of FFG density (individuals.m^{-2}) for three study reaches. Sample size of each mean=6.

FFG	Period	Control		Rehabilitated		Reference	
		Mean	SD	Mean	SD	Mean	SD
Absorber	Before	26.9	24.1	32.8	8.2	28.4	9.0
	After	26.6	23.0	23.0	5.9	16.6	5.7
Deposit-feeder	Before	302.3	54.7	285.0	35.8	284.6	24.1
	After	305.3	67.6	193.9	64.0	247.4	18.1
Shredder	Before	97.0	41.6	61.0	14.3	544.7	54.1
	After	100.9	40.8	392.0	66.3	560.1	99.8
Scraper	Before	145.7	49.0	139.0	9.0	613.3	80.5
	After	146.0	49.3	249.0	31.0	655.5	55.4
Filter-feeder	Before	86.3	38.1	48.3	15.4	170.9	26.6
	After	95.6	39.3	141.0	36.4	251.1	29.6
Piercer	Before	1.3	0.6	5.3	3.4	4.6	4.8
	After	1.2	0.5	18.7	9.2	9.5	5.4
Predator	Before	147.8	30.0	136.0	12.7	154.7	45.8
	After	140.6	38.4	151.0	12.3	127.3	31.0
Parasite	Before	46.3	20.1	33.2	4.4	15.7	3.8
	After	52.5	20.2	18.7	3.6	27.3	14.7

Table 4. Summary of sequential tests, obtained from distance-based linear models (DISTLM), seeking relationships between variations in response variables (macroinvertebrate metrics) and predictor variables (channel morphological and biotope composition) of the rehabilitated reach. Values displayed are significant at $P<0.05$ and indicate both the proportion of variability explained by each predictor variable and the cumulative variability explained by the models. + indicate additions to the model. Correlations were obtained using Spearman's rank correlation ($\rho>0.5$), 'positive' and 'negative' indicate positive or negative correlations. SWI-biotope, in-stream biotope diversity.

Response variables	Predictor variables	Proportion	Cumulative	Relationship
Total density	Gravel%	0.87	0.87	positive
Total biomass	Marginal plant%	0.64	0.64	positive
	+Silt%	0.15	0.79	negative
Taxon richness	Gravel%	0.39	0.39	positive
	+Marginal plant%	0.25	0.64	positive
Taxon diversity	Gravel%	0.58	0.58	positive
	+Marginal plant%	0.18	0.76	positive
Evenness	SWI-biotope	0.98	0.98	positive
EPT richness	Gravels%	0.52	0.52	positive
EPT diversity	Gravels%	0.78	0.78	positive
EPT count%	Silt%	0.96	0.96	negative
Chironomidae count%	Gravel%	0.95	0.95	negative
EPT biomass%	Gravel%	0.38	0.38	positive
	+Leaf litter%	0.23	0.61	positive
Chironomidae biomass%	Gravel%	0.70	0.70	negative
Shredder	Gravel%	0.43	0.43	Positive
	+Marginal plant%	0.33	0.76	positive
	+Leaf litter%	0.20	0.96	positive
Scraper	Gravel%	0.95	0.95	positive
Filter-feeder	SWI-biotope	0.78	0.78	positive

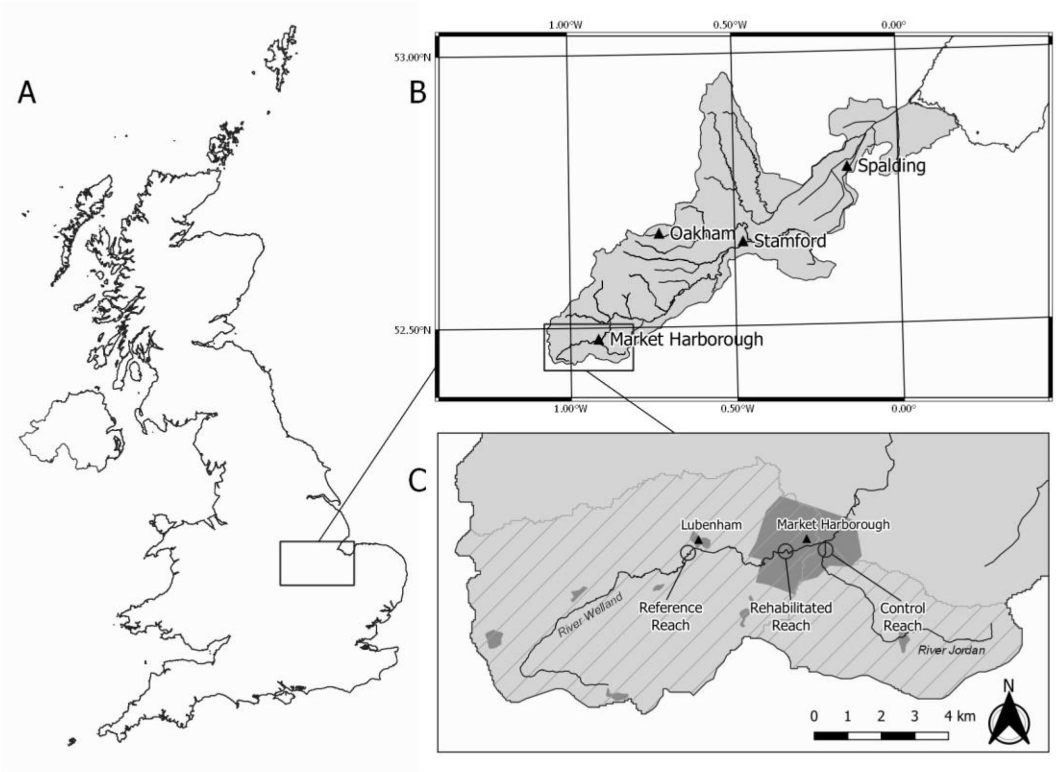

Figure 1. Map of the study area. A) Outline of the UK. B) Outline of the catchment of the River Welland and the location of Market Harborough. C) The location of the reference reach, the rehabilitated reach and the control reach. Drawn by Mr Chris French, Welland Rivers Trust.

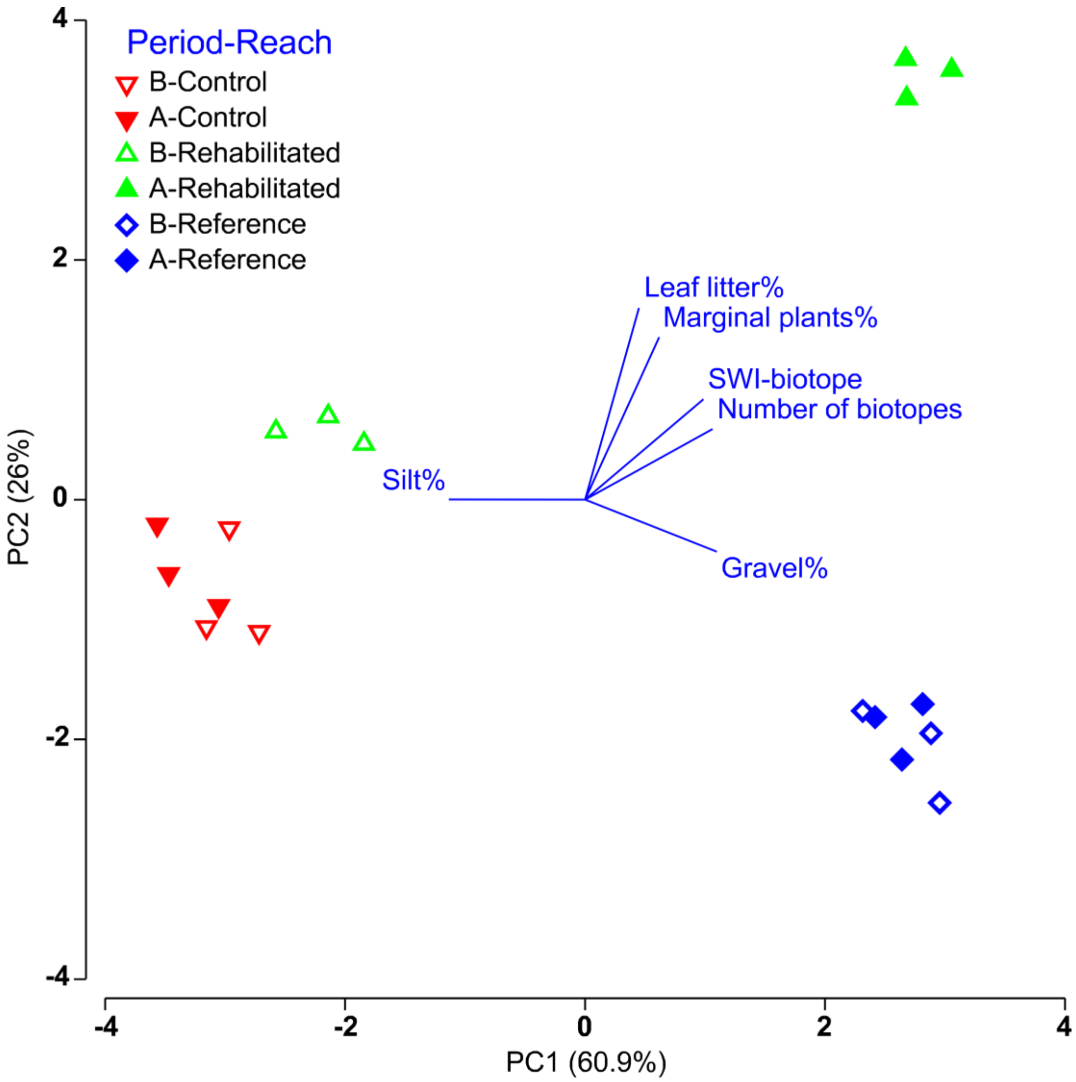

Figure 2. PCA ordination plots showing before-after trends of channel morphology metrics and in-stream biotope composition, based on reach-level data measured before and after rehabilitation. In the Period-Reach key, B refers to 'Before rehabilitation' and A to 'After rehabilitation'. Vectors indicate variables correlated at $\rho>0.5$. SWI-biotope, in-stream biotope diversity.

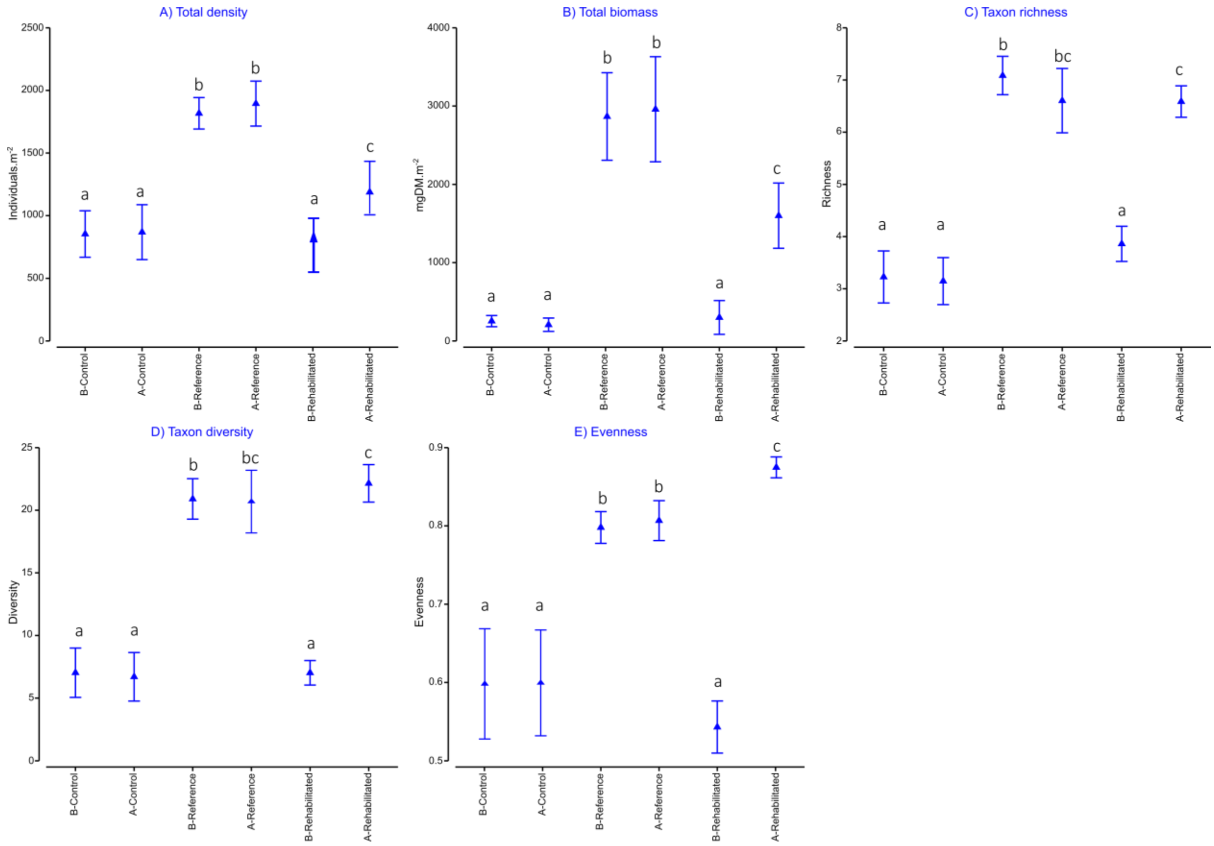

Figure 3. Before-after variations in: A) Total density. B) Total biomass. C) Taxon richness. D) Taxon diversity. E) Evenness. B, Before rehabilitation; A, After rehabilitation; DM, dry mass. Pairs of matching lowercase letters (a, b or c) indicate statistically indistinguishable data values.

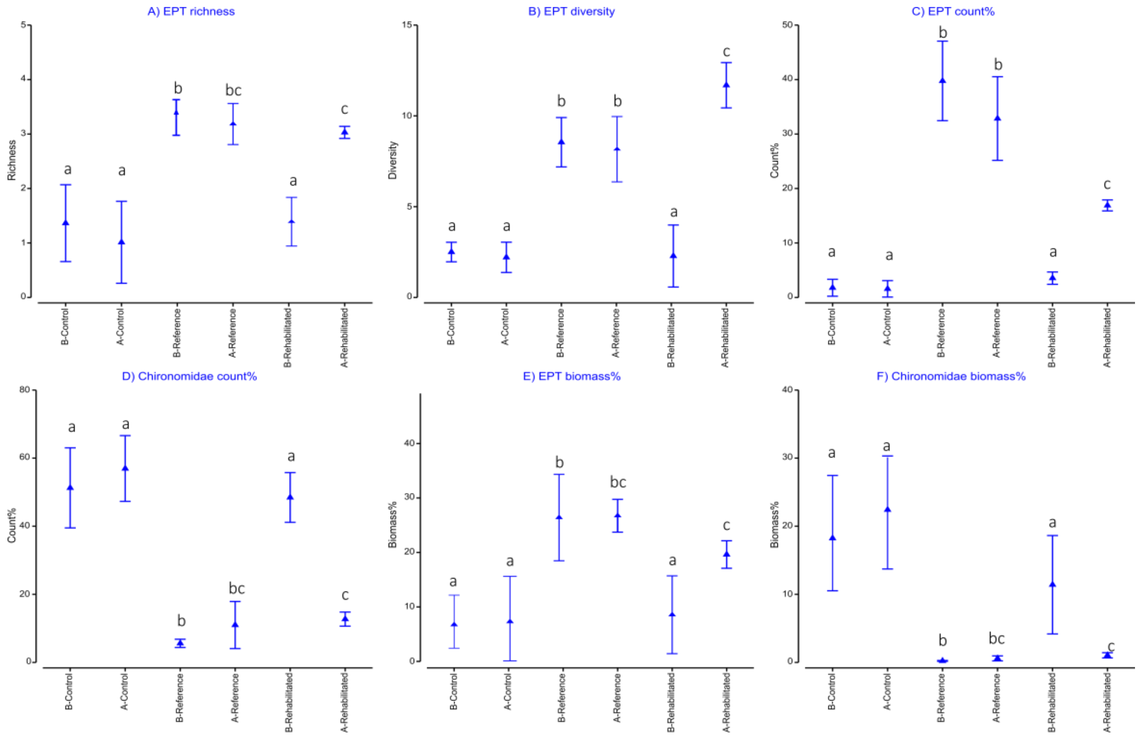

Figure 4. Before-after variations in: A) EPT richness. B) EPT diversity. C) EPT count%. D) Chironomidae count%. E) EPT biomass%. F) Chironomidae biomass%. B, Before rehabilitation; A, After rehabilitation; DM, dry mass; EPT, Ephemeroptera, Plecoptera & Trichoptera. Pairs of matching lowercase letters (a, b or c) indicate statistically indistinguishable data values.

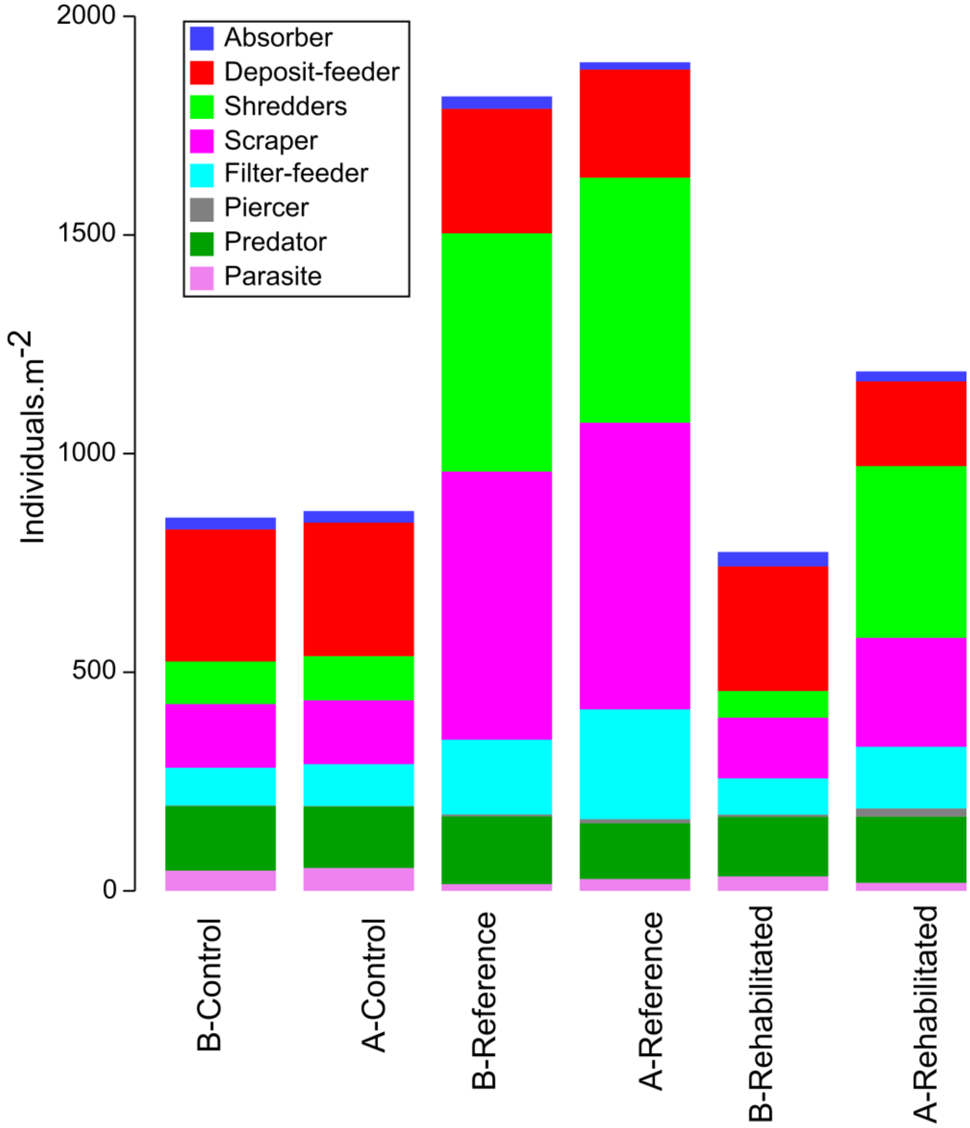

Figure 5. Before-after variations in macroinvertebrate functional feeding group average abundance (individuals m^{-2}). B, Before rehabilitation; A, After rehabilitation.