**Secondary production of macroinvertebrates as indicators of success in stream rehabilitation**

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**Abstract**

1. Hydromorphological rehabilitation is increasingly being used to reverse degradation of stream and river ecosystems. River rehabilitation projects have nevertheless been criticised for not meeting their goals or for not being monitored sufficiently well to assess whether their goals were met. There is therefore an urgent need to develop robust approaches to assessing treatment efficacy and to thus guide the increasing investment in rehabilitation.
2. A headwater tributary of the River Welland in Leicestershire, UK was rehabilitated in summer 2014. Rehabilitation included removal of weirs and the creation of a distinct and meandered low-flow channel with pool-riffle sequences.
3. Macroinvertebrates were collected in random sampling protocols stratified at in-stream biotope level. The rehabilitated reach was compared with a semi-natural upstream reach as a reference, and a similarly degraded reach as a control.
4. This study demonstrated that rehabilitation of the River Welland had clear beneficial effects on ecological processes. It demonstrated that active re-creation of lost biotope heterogeneity improved macroinvertebrate biodiversity and secondary production, which is the formation of heterotrophic biomass through time.
5. The rehabilitated reach yielded higher production estimates for Gastropoda, Bivalvia, Malacostraca, Odonata Arachnida and Ephemeroptera, Plecoptera & Trichoptera, and a lower estimate for Chironomidae relative to the control reach. The rehabilitated reach also had higher estimates of production for Shredder, Scraper, Filter-feeder and Predator feeding groups relative to the control reach. The rehabilitated reach clearly altered from being similar to the degraded reach before rehabilitation, to being more similar to the semi-natural reach afterwards. These outcomes demonstrate recovery of the reach’s entire macroinvertebrate community structure and function after rehabilitation.
6. The results provide a clear message to river rehabilitation practitioners: rehabilitation of the function of a physically degraded river ecosystem is possible if the rehabilitation is planned to actively restore the lost in-stream biotope diversity.

**Key Words**: biodiversity, hydromorphology, invertebrates, restoration, river, stream, sedimentation.

## Introduction

Natural streams are physically diverse because of the hydromorphological forces that structure them (Vannote *et al.*, 1980). Higher levels of physical heterogeneity in freshwater ecosystems are usually accompanied by more diverse biotic communities (Pilotto *et al.*, 2016). Physical habitat degradation is therefore regarded as a serious threat to biodiversity (Wilcove *et al.*, 1998); and aquatic ecosystems are generally more heavily affected than terrestrial ecosystems (Allan & Flecker, 1993; Sala *et al.*, 2000). Rehabilitation of lost hydromorphological features is commonly used in attempts to mitigate the ecological effects of river degradations (Ormerod, 2003; Pedersen *et al.*, 2006), which is an important component in achieving Good Ecological Status of the EU’s water framework directive (Friberg *et al.*, 2016). Hydromorphological rehabilitation in the absence of wider habitat enhancement to mitigate other abiotic stressors such as pollution may, however, have limited effectiveness in increasing invertebrate biodiversity in impacted streams and rivers (Palmer *et al.* 2010). Physical heterogeneity can be simply expressed as diversity of in-stream biotopes (Demars *et al.*, 2012). In-stream biotopes (e.g. ‘cobbles’, ‘leaf litter’ or ‘marginal plants’) are visually distinguishable, but typically small (50 cm2 – 5 m2 approximately), in-channel patches, made up of different mineral substrates, vegetation, or organic matter types, which form a dynamic mosaic structured by current speed and depth (Harper *et al.*, 1995; Kemp *et al.*, 1999). They conveniently sit between the forces which structure rivers and the biota (e.g. distinct macroinvertebrate assemblages) which inhabit them, as hydro-morpho-ecological units in river structure and function (Harper & Everard, 1998). In-stream biotopes can thus be used as a simple building-block approach to rehabilitation (Harper *et al.*, 1992; Kemp *et al.*, 1999; Buffagni *et al.*, 2000) because they are the interface between organisms and the physical processes of a stream and exist as distinct units, recognisable and classifiable on the basis of both their physical and biological attributes.

There have been many criticisms of river rehabilitation projects for not meeting their goals, or for not being monitored sufficiently well to determine whether their goals were met (Miller *et al.*, 2010; Barnes *et al.*, 2013; Al-Zankana *et al.*, 2020). Many hundreds of projects in the USA and EU, designed to rehabilitate natural flow and enhance habitat heterogeneity in streams and rivers, have been monitored to assess their effects on macroinvertebrate biodiversity, but their influence is still unclear (Miller *et al.*, 2010; Barnes *et al.*, 2013; Al-Zankana *et al.*, 2020). Indeed, biodiversity *per se* may not be a sufficiently nuanced criterion by which to gauge the ecological recovery or enhancement of rehabilitated streams (Dolph *et al.*, 2015). Macroinvertebrates as a group play an important role in stream ecosystems because they influence important stream processes such as nutrient cycling, primary production, decomposition and transformation of materials (Wallace & Webster, 1996). Rehabilitation of degraded streams may enhance ecosystem processes even in the absence of large increases in biodiversity, because different species can have similar functional roles (Palmer *et al.*, 1997; Hilderbrand *et al.*, 2005). For instance, recruitment of a few new taxa and/or increasing density and/or biomass of existing taxa could increase macroinvertebrate secondary production and thus enhance ecosystem processes to levels that approach those of undisturbed sites or the pre-degraded condition. Measures of ecosystem processes may thus provide a more comprehensive understanding of biotic condition than biodiversity alone (Bunn & Davies, 2000) and approaches that combine structure and function have been highly recommended as a means for assessing ecosystems (Naeem *et al.*, 2009).

A potentially valuable approach providing measures of both structure and function is thus through analysis of secondary production, which expresses the quality of the macroinvertebrate community ‘success’ over time, and it is directly related to ecosystem functioning (Dolbeth *et al.*, 2012). It integrates several measures of biological success beyond species richness, including changes in population density, biomass and growth rate over time (Benke & Huryn, 2006). Secondary production is the formation of heterotrophic biomass (Dry Mass, DM) through time (Benke, 1993). Many applications of secondary production studies in aquatic ecosystems have been published (see Dolbeth *et al.* (2012)), but little is known about how stream rehabilitation influences stream ecosystem function generally, and macroinvertebrate secondary production in particular. In-stream hydromorphological rehabilitation through installation of riffles or Large Woody Material (LWM) enhances channel stability, in-stream biotope availability, and hence food availability for macroinvertebrates (Smock *et al.*, 1989; Benke & Wallace, 2003). It can increase organic matter retention and consequently macroinvertebrate secondary production by increasing stability and quality of in-stream biotopes or resource availability (or both) for macroinvertebrates (Lemly & Hilderbrand, 2000; Johnson *et al.*, 2003; Lepori *et al.*, 2005; Dolph *et al.*, 2015).

Secondary productivity was used to gauge the recovery of stream ecosystem structure and function after reach-scale large woody material (LWM) installation (Wallace *et al.*, 1995; Entrekin *et al.*, 2009; Dolph *et al.*, 2015). To our knowledge however, the response of macroinvertebrate secondary production to reach-scale channel hydromorphological rehabilitation in urban areas has not yet been evaluated.

This study assesses changes in macroinvertebrate secondary production following the entire channel hydromorphological rehabilitation of an urbanised reach of the Upper Welland in Market Harborough, Leicestershire, UK (‘rehabilitated reach’ hereafter). The rehabilitated reach, a less-modified upstream reach (‘reference reach’ hereafter) and a degraded reach (‘control reach’ hereafter) were compared for two years following rehabilitation. The primary goal of rehabilitation was to increase the availability and heterogeneity of in-stream biotopes (both organic and inorganic) to resemble those of the upstream less-modified reference reach. The aim of the study was to determine whether rehabilitation would increase macroinvertebrate secondary production such that production of the rehabilitated reach would come to resemble that of the reference reach.

## Methods

### Study sites and rehabilitation activities

The River Welland rises in south west Leicestershire, UK, near Market Harborough. It flows for about 80 km through the gently rolling countryside of Northamptonshire, Leicestershire, and Rutland, and the flat countryside of Lincolnshire before it reaches the sea at the Wash. The main river and its tributaries together form more than 480 km of waterway. The average daily flow of the River Welland (at Ashley, approx. 10 km below Market Harborough) is 1.45 m3s-1 (<https://nrfa.ceh.ac.uk/data/station/meanflow/31021>), and in the reference reach the average river depth ranged between 0.08 m and 0.85 m, and average channel width ranged between 2.7 m and 4.1 m. The catchment area is approximately 1,554 km2. 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 1.8 km reach of the River Welland through Market Harborough, in Leicestershire, UK (Figure 1A, B), was restructured and rehabilitated by the Welland Rivers Trust and the University of Leicester as the ‘Welland for People and Wildlife’ project over two years starting Summer 2014 (Welland Rivers Trust, 2015). The rehabilitation process sought to re-create the in-stream biotopes as natural ‘jigsaw’ pieces that were formerly removed by degradation and which therefore needed to be returned in order to reintroduce channel complexity, biotope heterogeneity and biodiversity.

Rehabilitation included removal of six weirs, and by-passing of a further two weirs by reconnecting a cut-off backwater channel. The weirs had formerly trapped sediments (and hence decreased the proportion of coarse biotopes) and also acted as barriers to fish and eel movements. A natural meander running around a patch of woodland was re-opened where a flood channel had previously bypassed it. The channel was re-meandered and narrowed, with a distinct low-flow channel created by building berms constructed from the spoil derived from the digging of pools. Pools were dug in meander bends and the material excavated deposited between the bends, creating a series of pool-riffle sequences (see Figures 4.3 and 4.5 in Al-Zankana (2018) for illustrations). The overall objectives were to create a gradual rather than sudden gradient (hence increasing large particle biotopes), provide more marginal space for plants (hence increasing emergent and marginal plant biotopes), provide safer access to the river for the community and reduce the risk of erosion. Some native macrophytes were planted into coir mesh to initially stabilise the new berms.

This study was carried out on a 250 m section of the rehabilitated reach (within the 1.8 km long rehabilitation section) of the River Welland at Welland Park, Market Harborough (52.475427 N, -0.926341 W). A 250 m section of the reference reach of the Welland was located upstream at Lubenham, 52.473637 N, -0.972636 W). A 250 m section of control reach (a similarly physically degraded downstream reach of the River Jordan, was located downstream of the rehabilitated reach at Market Harborough (52.476865 N, -0.909979 W)) (Figure 1C).

The reference reach possessed 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 plants. The hydromorphology and macroinvertebrate community of the reference reach were used as targets for the success of the rehabilitated reach.

The River Jordan is a 6 km tributary of the Welland which it joins within Market Harborough downstream of the rehabilitated reach. Both the control reach of the River Jordan and the rehabilitated reach of the River Welland at the Welland Park had been modified (widened, deepened and straightened) during a previous flood alleviation project in the 1970s. The channels are overly wide with steep banks; some of which are lined with concrete. Both the Jordan and the Welland rise in a similar landscape with only the low diffuse pollution of modern agriculture. There were thus similar upstream invertebrate communities capable of supplying species for re-colonisation by drift in both rehabilitated and control sites. We identified no other abiotic stressors such as unresolved water quality or flow regimen issues that significantly affected or differed between the sites.

### Sampling and processing of macroinvertebrates

Macroinvertebrate samples were collected from the three reaches for two years post-rehabilitation 2015 and 2016; 8 intervals per year (Table S1). Water temperature was recorded for each study reach in parallel to the invertebrate sampling. In-stream biotopes were visually identified and named according to Demars *et al.* (2012). The biotopes identified and sampled were - cobbles (CO), gravel (G) and sand (SA) (mineral substrates); silt (SI) (soft substrate with organic matter), tree-roots (TR), marginal plants (MP), leaf-litter (LL), macroalgae (MA) and submerged fine-leaved plants (MSF) (vegetation types) (Table 1). Their coverage was estimated using lateral transects spaced every 5m following Entrekin *et al.* (2009). All transect measures were summed to give reach-level relative coverage area of each biotope for each study reach. In-stream biotope diversity was characterised by the Shannon-Wiener diversity index (SWI) (Shannon & Weaver, 1949), following Kemp (1999) and Poppe *et al.* (2015), where ‘species’ were biotopes - named “SWI-biotope” hereafter. This diversity index depends on both ‘species’ richness and dominance. Greater values of SWI refer to higher numbers of species and greater equitability. Here, we used the number of in-stream biotopes (rather than the number of invertebrate species), and the biotope proportions (instead of species densities).

During the study, 960 macroinvertebrate samples were collected. In the control reach, 15 samples were collected per visit from 5 biotopes (3 samples per each biotope that covered ≥1% area of the riverbed). The biotopes were G, SA, SI, MP and MSF. In the reference reach, 21 samples in total were collected per visit from 7 biotopes (CO, G, SA, SI, MP, MA and MSF). In the rehabilitated reach, 24 samples in total were collected per visit from 8 biotopes (CO, G, SA, SI, TR, LL, MP and MSF). Samples were collected using a Surber sampler (500 µm mesh size and area of 0.09 m2). The area 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. More information is available in the Supplementary Information File; Section 1.

Specimens were identified to genus level (as the published size-specific mass regressions are at genus level) and counted (individual sample-1) using standard UK lotic invertebrate taxonomic keys and guidance books (Soar & Williamson, 1925; 1927; 1929; Mann & Watson, 1954; Hynes *et al.*, 1960; Brinkhurst, 1971; Gledhill *et al.*, 1976; Hynes, 1977; Macan & Cooper, 1977; Elliott & Mann, 1979; Cranston, 1982; Croft, 1986; Elliott *et al.*, 1988; Wallace *et al.*, 1990; Edington & Hildrew, 1995; Killeen *et al.*, 2004; Wallace, 2006; Greenhalgh & Ovenden, 2007; Elliott, 2009; Elliott & Humpesch, 2010; Dobson *et al.*, 2012; Waringer & Graf, 2013).

The population of each genus was divided into different size-classes based on either body length or head-capsule width. Body length was measured to the nearest 0.5 mm, and head capsule width to the nearest 0.1 mm, and size classes were defined by this measurement accuracy. Length was measured by using an ocular micrometer for small specimens, or a sheet of 1 mm graph paper placed directly on the dissecting-microscope’s stage for large specimens. Head capsule width (HW) was measured across the widest part of the head. Body length (BL) was measured as the distance between the anterior of the head to the posterior of the last abdominal segment (after Poepperl, 1998). In addition, for two species, other linear body dimensions were used: these were: for *Gammarus pulex*, the length of first thoracic segment (TL); and for *Asellus* spp. the length of the pleotelson (PL). Tricoptera larval head capsule width at eye level was measured to the nearest 0.2 mm (after Ross & Wallace, 1983).

Each genus’ dry-mass (mg Dry Mass, mgDM) was then estimated according to the following size-specific mass regression (following Meyer, 1989; Wenzel *et al.*, 1990; Burgherr & Meyer, 1997; Poepperl, 1998; González *et al.*, 2002; Giustini *et al.*, 2008) and summed to give the genus’ biomass per sample (mg DM sample-1).

log M = log a + b log L

where M is organism dry mass in mg (mgDM), L is any linear dimension (mm), and a and b are constants. A list of the constants used for each genus, and associated references are available in Table S2.

Population biomass of each genus (mgDM sample-1) was calculated using both population density (number of individuals sample-1), and dry mass (mg DM) of each individual organism within the population.

Reach-level values of density (individual sample-1) and biomass (mgDM sample-1) for each genus were compiled into a ‘genus list’ calculated according to the relative coverage area of each sampled in-stream biotope in each reach (Kedzierski & Smock, 2001; Pedersen *et al.*, 2007; Jähnig *et al.*, 2010), and then pooled to show values per square metre before estimating secondary production (Al-Zankana, 2018).

### Estimation of macroinvertebrates secondary production

During thefirst post-rehabilitation year (2015), reach-level secondary production (mgDM m-2 year-1) of each macroinvertebrate genus was estimated using the empirical model of Benke (1993).

log10*P* = -0.536 + 1.005 log10*B* - 0.035*T* – 0.245 log10 WMax

*P*, production (mgDM.m-2.year-1);

*B*, mean biomass (mgDM.m-2), (depending on 8 time-point samples in our study);

*T*, mean temperature (C);

WMax, maximum individual mass (mgDM.individual-1).

To assess secondary production of any macroinvertebrate genus in the control reach in 2015 for example, we depended on 8 sampling months (visits), and 3 replicates per visit. All genus-specific secondary production values in a reach were summed to obtain the total secondary production for that reach. The same steps were repeated for thesecond post-rehabilitation year. All genus-specific secondary production values in a reach were also assigned to one of eight functional feeding groups (FFG) according to Tachet *et al.* (2010). Each genus was coded using a “fuzzy coding” approach on the basis of the extent to which it displayed the feeding traits. Genus affinities for each feeding trait (group) were fuzzy coded from zero (no affinity) to three (strong affinity). Genus-specific secondary production values and trait values were multiplied to calculate FFG production values. Total secondary production and FFG production (mgDM m-2 year-1) were calculated separately for each study reach. More information is available in the Supplementary Information File; Section 2.

### Data analysis

Due to the absence of pre-rehabilitation values of secondary production in this study we could not compare directly the status of the reaches before and after rehabilitation. To address this problem, we used a control-reference-rehabilitated experiment design in which the control reach represented the pre-rehabilitation physically degraded condition, while the reference reach represented a minimally disturbed condition, which served as the target goal for the rehabilitated reach.

The number of in-stream biotopes, SWI-biotope and biotope composition (biotope coverage area relative percentages) were normalised, Euclidean distance matrices were then calculated and used in a two-way PERMANOVA (Anderson *et al.*, 2008). This tested for morphological differences among the study reaches. Two-way PERMANOVA with *Reach type* (fixed factor, three levels: control, reference, rehabilitated), and *Period* (fixed factor, two levels: 2015, 2016) was used to run tests on the collected data and all possible pair-wise tests. Principal Component Analysis (PCA) was conducted to visualise which 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).

We evaluated differences in mean macroinvertebrates total production, taxonomic group production and functional feeding group production between the control, reference and rehabilitated reaches using two-way PERMANOVA (Anderson *et al.*, 2008). Reaches were compared across the first (2015) and second (2016) post-rehabilitation years. Euclidean distance matrices were first used for each of total production, taxonomic group production and FFG production values separately to calculate distances between samples. Production values were log(*x*) transformed prior to the analysis to improve the normality of the data distribution and satisfy the test requirements, where applicable. Two-way PERMANOVA with *Reach type* (fixed factor, three levels: control, reference, rehabilitated), and *Period* (fixed factor, two levels: 2015, 2016) was used to run tests on the collected data. 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). Spatial and temporal differences in total production were visualised using box plots.

When a PERMANOVA gave a significant overall interaction (Reach × Period), all pairwise comparisons were made to examine which elements contributed to the overall interaction. 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.

The relationships between channel morphological variables and macroinvertebrate production values were analysed using distance-based linear modelling (DISTLM) (following Eddy & Roman, 2016; Heerhartz *et al.*, 2016). These analyses were performed after standardisation and normalisation of morphological variables. Euclidean distance matrices of all metrics used for the previously described PERMANOVA analyses were used separately. Sequential tests were used to determine which combinations of morphological variables best explained variability in the response variable. Each sequential test was performed with a step-wise selection procedure using Akaike’s information criterion (AIC). The relationship between morphological variables and biological metrics was determined using Spearman’s rank correlation (ρ).

All analyses were carried out using PRIMER v.7 software (Clarke & Gorley, 2015) and the PERMANOVA+ add-on package (Anderson *et al.*, 2008).

## Results

### Channel morphological variables

There were statistically significant interactions between Period and Reach for channel morphological variables (PERMANOVA, *Pseudo-F* = 36.19*, P*<0.0001) (Table S3). During the first and second post-rehabilitation years, the study reaches remained significantly different from each other according to their measured morphological variables (Table S4). 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 SWI-biotope than either the control reach or the reference reach (Table 1). Coarse biotopes (cobbles and gravel) had a very low embeddedness compared to that in the control reach (i.e. less of the surface area of the riffles was covered by silt). There were significant temporal changes in the rehabilitated reach instream biotope diversity and biotope heterogeneity (post-hoc Student’s *t* test, *t* = 7.64, *P*<0.001) (Table S5). SWI-biotope had increased in the second post-rehabilitation year (Table 1). Principal Component Analysis (PCA) showed that both rehabilitated and reference reaches were separated from the control reach along the first axis (PC1 in Figure 2). PC1 described 60.2% of the differences between the control reach (which lay towards the left of PC1) and rehabilitated and reference reaches (towards the right; Figure 2). This separation was driven by higher silt percentages in the control (ρ > 0.5), than the rehabilitated or reference reaches. The rehabilitated and reference reaches had a higher proportion of gravel, marginal plants, leaf-letter and SWI-biotope (ρ > 0.5) than the control reach (Table S6).

### Total secondary production

During thefirst post-rehabilitation year, total macroinvertebrate secondary production (TP) was about 3× higher in the reference reach than in the other two reaches. TP estimates ranged from 3591 mgDM.m-2.time-1 at the control reach to 3622 mgDM.m-2.time-1 at the rehabilitated reach and 11337 mgDM.m-2.time-1 at the reference reach (Table 2; Figure 3). There were significant interactions between Reach and Period (PERMANOVA, *Pseudo-F* = 30.51*, P* = 0.0001; Table S7) for TP, and the reference reach differed significantly from the control reach (*t* = 12.34, *P* = 0.0002; Table S5) and the rehabilitated reach (*t* = 17.99, *P* = 0.0001; Table S8). The rehabilitated reach TP was similar to that of the control reach (*t* = 0.119, *P* = 0.9134; Table S8). In the second post-rehabilitation year, the rehabilitated reach’s TP value had tripled compared to its the first post-rehabilitation year to become 9098 mgDM (*t* = 7.969, *P* = 0.0011; Table 2& Table S9). Thus, TP became about 3× higher in the rehabilitated than in the control reach (*t* = 7.859, *P* = 0.0018; Table S8), whereas they had been similar to each other during the first post-rehabilitation year. The rehabilitated reach’s TP became similar to that of the reference reach (*t* = 2.665, *P* = 0.0574; Table S8).

### Taxonomic group secondary production

During the first post-rehabilitation year, the reference reach differed significantly (*P* < 0.05; Table S8) from the control reach and the rehabilitated reach for most of the taxonomic groups recorded in Table 2. The reference reach was dominated by Gastropoda, EPT, Bivalvia and Diptera, while the other two reaches were dominated by Gastropoda, Chironomidae and Hirudinea (Table 2).

Gastropoda were the largest relative contributor to TP in all three of the study reaches, with the highest proportion in the reference reach (52%) and smaller proportions in the control (49%) and rehabilitated (48%) reaches (Table S10). EPT production was the second largest relative contributor to TP in the reference reach (20%), while it contributed to only 2% of the other two reaches’ TP. Chironomidae were the second highest relative contributors to the control and rehabilitated reach’s TP (20%), but they were less dominant in the reference reach (3%). Hirudinea were the third highest relative contributors to the control and rehabilitated reach’s TP (17% and 13% respectively), but they were less dominant in the reference reach (3%).

In the second post-rehabilitation year, the rehabilitated reach’s Gastropoda, EPT, Bivalvia, Malacostraca, Odonata and Arachnida productions were increased significantly (*P* < 0.05; Tables S8 & S9) compared with their values either in the first post rehabilitation year or their values in the control reach (Table 2). However, Chironomidae production decreased significantly (*P* < 0.005; Tables S8 & S9) to contribute only 2% of the TP (Table S10). The rehabilitated reach was similar (*P* > 0.05) to the reference reach according to Gastropoda, Bivalvia, Hirudinea, Oligochaeta, Coleoptera and Megaloptera (Table S8).

### Functional feeding group secondary production

During the first post-rehabilitation year, Shredder and Scraper secondary production was 5× higher in the reference reach than in the other two reaches (*P* < 0.0005; Table 3& Table S8). Shredders (43%) and Scrapers (35%) constituted the largest percentages of macroinvertebrate production in the reference reach, whereas Deposit-feeder, Filter-feeder, Piercer, Predator, and Parasite groups constituted the largest percentages of production in other two reaches (Table S11).

In the second post-rehabilitation year, Shredder, Scraper, Filter-feeder and Predator production were increased significantly (*P* < 0.05; Table 3 & Table S9) compared to their values in the first post-rehabilitation year or their values in the control reach. Shredders (36%) and Scrapers (30%) constituted the largest percentages of macroinvertebrate production in the rehabilitated reach (Table S11). The rehabilitated reach was similar to the reference reach for Absorber, Shredder, Scraper, Filter-feeder, Predator and Parasite functional feeding groups (*P* > 0.05; Table S8).

### Relationships between morphological variables and production values

Post-rehabilitation increases of marginal plant coverage were related positively to significant increases in gastropoda, malacostraca, arachnida, shredder and macroinvertebrate total secondary production. Increases in cobble percentage were related positively to significant increases in EPT, bivalvia and odonata production. Increases in leaf-litter percentage were related positively to significant increases in shredder and predator production. However, changes in gravel percentage were related negatively to changes in filter-feeder production. A significant decrease in Chironomidae production was related to a decreases in silt percentage (Table 4).

## Discussion

River rehabilitation has been based on the belief that habitat heterogeneity promotes biodiversity (Palmer *et al.*, 2010) and enhances ecological functioning (Feld *et al.*, 2011). Its success depends on whether population, community and ecological functions recover and attain the characteristics typical of non-degraded ‘reference’ rivers (Ormerod, 2003). Understanding the effectiveness of river rehabilitation techniques is critical for directing future rehabilitation projects, planning and design (Roni & Quimby, 2005). The need for monitoring to achieve this has been acknowledged (Roni & Beechie, 2013; Al-Zankana *et al.*, 2020), but such monitoring and evaluation is still rare (Bernhardt *et al.*, 2005; Palmer *et al.*, 2010; Wolter *et al.*, 2013; Kail *et al.*, 2015; Al-Zankana *et al.*, 2020). Most river rehabilitation schemes fail to assess outcomes and effectiveness (Cowx *et al.*, 2013; Thompson, 2015), or use inadequate statistical designs, or inappropriate biological methods, which hamper rehabilitation ecologists’ ability to detect changes (Friberg *et al.*, 2016). Despite the increasing number of rehabilitation interventions and an increased social drive to identify effective solutions that have economic benefits (Everard, 2012; Smith *et al.*, 2014; Reichert *et al.*, 2015), evidence for strong and long-term positive ecological effects of hydromorphological rehabilitation – particularly on macroinvertebrates - is generally limited (Palmer *et al.*, 2010; Feld *et al.*, 2011; Friberg *et al.*, 2014; Al-Zankana *et al.*, 2020), with few notable exceptions (Miller *et al.*, 2010; Kail *et al.*, 2015). These findings partly reflect the lack of robust scientific assessments of rehabilitation measures (Verdonschot *et al.*, 2015). The conflicting results together with the relative infancy of stream rehabilitation science (Palmer *et al.*, 2014) indicate the urgent need for more and better studies to address the links between hydromorphology rehabilitation and stream biota (Louhi *et al.*, 2011; Wolter *et al.*, 2013).

Forty-four rivers in England, extending some 2,500 km, are legally protected as Riverine Sites of Special Scientific Interest (SSSI) (Wheeldon et al., 2015). These SSSIs provide opportunities for demonstrating large scale strategic approaches to river conservation (Mainstone, 2008). The EU Habitat Directive (Council of the European Communities, 1992) designates approximately 1,684 km of SSSI rivers as Special Areas of Conservation (SAC) and these therefore require concentrated action under European law. There are also domestic UK objectives to rehabilitate the condition of SSSIs, most recently as part of the UK Government’s Biodiversity 2020 agenda (Defra, 2011). Rehabilitation of SSSIs is assigned to relevant parties and implementation is tracked by Natural England - the government’s advisory body for the natural environment (Mainstone & Wheeldon, 2016).

In-stream ‘biotopes’ with distinct macroinvertebrate assemblages provide a useful way of linking macroinvertebrate ecology and stream hydromorphological rehabilitation, and can be used as a tool to assess the hydro-morphological status of rivers (Harper *et al.*, 1992; Demars *et al.*, 2012). The consideration of stream ecology at this scale has proved to be useful in the UK river habitat survey (RHS) (Environment Agency, 2003), and in river management (Harper & Everard, 1998), because in-stream biotopes can be used in a simple building-block approach to rehabilitation (Harper *et al.*, 1992; Petersen *et al.*, 1992; Kemp *et al.*, 1999). They provide the interface between stream biota and the physical processes of a river. The in-stream biotope approach treats streams as being composed of distinct habitat units, recognisable and classifiable on the basis of both their physical and biological attributes (Buffagni *et al.*, 2000). They are a useful unit of study in river channels, providing a rapid and effective way to assess river condition. UK conservation agencies recognise the importance of physical habitat in underpinning biodiversity richness and ecosystem function through their use of broad habitat divisions, such as ‘backwaters’, ‘aquatic macrophyte beds’, ‘tree roots’ and ‘in-stream woody material’. They do not, however, describe habitats covering the entire channel, despite using the term ‘building blocks’ after (Harper *et al.*, 1992) and describing rivers as “a patchwork of linked habitats called a ‘habitat mosaic’” (Addy *et al.*, 2016). We show that the assessment of all in-stream biotopes in a river (as illustrated in Demars *et al.* (2012) can clearly measure rehabilitation effectiveness. The full inclusion of biotopes, at reach level, would add a hierarchical layer that is presently missing in recommendations for conservation and rehabilitation of rivers (Mainstone & Wheeldon, 2016). For example, the Wensum, in East Anglia (England), one of the country’s most important chalk streams, was hailed as a case study of successful rehabilitation brought about by many activities such as re-meandering and gravel re-instatement (Mainstone & Wheeldon, 2016). However, no evidence been produced for these claimed successes, anywhere along the length of the river; biotope level is the simplest.

The inclusion of functional traits - such as feeding traits - could provide a cornerstone in the development of new metrics sensitive to subtle changes following hydromorphological modification (Friberg *et al.*, 2009) and thus provide an alternative method to evaluate the effects of stream rehabilitation (Friberg *et al.*, 2016). Accurate assessment of invertebrate production would include measures of both their structure and function (Dolbeth *et al.*, 2012), and is additionally a fundamental requirement for understanding and quantifying energy flow in lotic systems (Benke, 1993). Maintaining functional redundancy through taxonomic biodiversity is the main rehabilitation target (Palmer *et al.*, 1997). In addition, most invertebrates are sedentary and confined to specific ecological conditions (Cook, 1976). The use of empirical models provides reliable estimates of macroinvertebrate community secondary production when applied to multispecies communities using monthly body mass and density data (Morin & Dumont, 1994; Morin, 1997). The results of the present study were therefore robust for the purposes of relative comparison between the study reaches.

The present study highlights the importance of rehabilitating in-stream biotope conditions that are ecologically relevant for diverse species of macroinvertebrates. It also highlights the importance of using a monitoring design that can measure both structural and functional outcomes. In-stream biotopes represent the building blocks of river rehabilitation and should become the prime focus of river managers (Harper *et al.*, 1992; Harper & Everard, 1998; Newson *et al.*, 1998). The significant increase in macroinvertebrate total secondary production in the rehabilitated reach during the second post-rehabilitation year was associated with increased stability of coarse mineral biotopes (cobbles and gravel) and resource availability of organic biotopes (marginal plants, and leaf-litter) for macroinvertebrates (Table 1). Reduced embeddedness of cobbles and gravel biotope improved the suitability of those substrates for many taxa because of increased substrate stability, reduced deposition of fine sediments, and increased availability of food in epilithic biofilms (Wood & Armitage, 1997). Organic biotopes (especially marginal plants and leaf-litter) support higher taxon richness and diversity (Friberg *et al.*, 1994; Friberg *et al.*, 1998; Harrison *et al.*, 2004; Friberg *et al.*, 2013; Verdonschot *et al.*, 2015). Our study suggests that these beneficial effects of rehabilitation take at least a year to manifest, presumably as substrates settle down and biofilms form, and macroalgae and plants grow. The failure of some rehabilitation projects to have an effect on biotope composition and diversity can explain a consequent lack of positive responses by macroinvertebrates (e.g. Jähnig & Lorenz, 2008; Verdonschot *et al.*, 2015). Macroinvertebrate species often have different specific biotope requirements at different stages of their life, requiring that all these biotopes must be present and of sufficient quality to guarantee re-colonisation 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 *et al.*, 2009).

Higher estimates of EPT production in the rehabilitated reach than in the control reach also indicate that environmental conditions, particularly oxygen concentrations, were improved by rehabilitation. EPT taxa are considered sensitive to a wide array of environmental stressors on multiple scales (Downes *et al.*, 1998), including in-stream biotope quality and water quality, and have been widely used as a measure of stream biotic condition (Richards *et al.*, 1993; Sponseller *et al.*, 2001). Chironomids are generally tolerant of pollution and silt so they are not a good target indicator for rehabilitation (Thompson, 2015), but their secondary production responded uniquely to in-stream biotope changes. Critically, Chironomids are a robust indicator of changes in fine sediment. Significant decreases in their secondary production during the second post-rehabilitation year were related to decreases in silt percentage.

Higher estimates of shredder production in the rehabilitated reach relative to the control reach indicate greater in-stream complexity, as these taxa are dependent on the availability of coarse particulate organic matter being deposited in pool areas (Smock *et al.*, 1989; Fenoglio *et al.*, 2005). Conversely, the increased areas of higher water velocities and larger, more stable substratum particles of riffles (cobbles and gravel) offer more profitable foraging areas for scrapers (algal grazers) (e.g. Benke *et al.*, 1992; Benke & Wallace, 2003), and more suitable attachment sites for filter-feeders (Williams & Moore, 1986; Allan, 1995). Larger interstitial pores increase retention of particulate organic food and act as refugia from diverse flow conditions (Gee, 1982; Culp *et al.*, 1983). The significant increase in shredder production in the Welland also reflects the ecological effects of increased trapped leaf-litter in the rehabilitated reach, especially in the second post-rehabilitation year. This provides suitable in-stream biotopes for shredder colonization, and also serves as a food resource. Low retention of leaf-litter limits shredder production in headwater streams (Roeding & Smock, 1989; Jones Jr & Smock, 1991).

There are relatively few comparable secondary production case studies available in the literature. The present study examines entire-channel rehabilitation in an urbanised stream which had the objective of reinstating lost in-stream biotopes. Dolph *et al.* (2015) assessed effects of stream rehabilitation activities limited to riparian revegetation and installation of boulder weirs and LWM in highly modified agricultural regions, in three streams in Southern Minnesota, USA. These studies aimed to: a) stabilise the stream channel by preventing bank erosion and habitat loss, and b) increase availability and heterogeneity of in-stream biotopes and food resources by increasing the availability of overhanging vegetation and boulder and wood surfaces. After rehabilitation, TP increased significantly so that it was two to three times higher in rehabilitated than non-rehabilitated reaches. Higher productivity in the rehabilitated reaches was largely a result of the disproportionate success of a few dominant, tolerant taxa (e.g. Hydropsychidae caddisflies and Simuliidae black flies). This outcome is thus somewhat different to that observed in the Welland, where most macroinvertebrates taxonomic groups and FFGs production values responded significantly. This was because the Welland rehabilitation actively affected the whole study reach’s in-stream biotope heterogeneity. Macroinvertebrate species often have different specific biotope requirements at different stages of their life, requiring that all these biotopes must be present and of sufficient quality to guarantee re-colonisation and development of sustainable populations (Verdonschot *et al.*, 2015). The way in which macroinvertebrate samples were collected in the study of Dolph *et al.* (2015) may have failed to record any positive effects on most macroinvertebrate taxa, because samples were not collected from all available biotopes: they collected only five samples in total from five habitat types (riffle, overhanging banks, emerged vegetation, woody material and wood dam) with no replication in each visit.

In an earlier study, Wallace *et al.* (1995) assessed the effects of LWM installation in a second order, forested stream in North Carolina, USA where there was an increase in detritivore production after LWM was installed. The installed woody dams, which spanned the entire channel, changed riffle habitats to depositional habitats; and longer-lived taxa were replaced by Chironomidae. This suggests that the approach was not particularly successful. By contrast, Entrekin *et al.* (2009) reported an increase in Scraper production, and little change in detritivore production after LWM installation in three first-order, forested systems in the Ontonagon River basin in Michigan, USA. This better outcome was attributed to the way in which the LWM had been installed (Entrekin *et al.*, 2009). In the Michigan streams, LWM was placed haphazardly within the streams, with part of each log resting on the stream bank, and never spanned the entire channel. This did not create extensive depositional habitat that would increase detritivore production at the expense of other FFGs. In the present study, there was a significant decrease in Chironomidae production in the rehabilitated reach, suggesting that the project was successful in creating suitable habitat for other macroinvertebrate taxa to return to the reach and recolonise. Neither of the two studies collected macroinvertebrate samples to represent all available biotopes. Wallace *et al.* (1995) depended on riffle and woody material habitat samples, with three replicate samples from each habitat per sampling visit, whereas Entrekin *et al.* (2009) depended on five randomly taken benthic samples as noted earlier.

Entrekin *et al.* (2009) found much greater TP in “woody accumulation” (small woody material and leaf-litter) samples than in the main channel “mineral” samples. This indicates that increased retention of small woody material and leaf-litter can increase macroinvertebrate production. Entrekin *et al.* (2009) argued that it is likely to take years for measurable changes in in-stream morphology, organic matter retention or macroinvertebrate production to become apparent; and that monitoring should span more than five years after LWM installation. The present study nevertheless shows that changes in macroinvertebrate production can become apparent within two years if the rehabilitation more effectively increases in-stream biotope number and diversity (SWI-biotope).

The temporal scale of the present study was relatively short, as it included just two successive years following the rehabilitation project, and this limited the ability of the study to detect responses in some taxa, or longer-term trends. Importantly, however, it did show how rapidly macroinvertebrate secondary production improvements can begin. This latter result provides an important guide to structuring post-project monitoring, shown by a recent review to be necessary but infrequently implemented (Al-Zankana et al., 2020). In particular, early regular sampling can detect rapid changes, and should not be discarded in favour of less frequent but longer-term approaches. This study has demonstrated that rehabilitation of the River Welland had clear beneficial effects on the rehabilitated reach’s functionality. The significant increase of the rehabilitated reach’s secondary production during the second post-rehabilitation year so that it became more similar to that of that reference reach, provides a clear message to river rehabilitation practitioners: rehabilitation of the function of a physically degraded river ecosystem is possible if the rehabilitation actively returns the lost in-stream biotope diversity. The relationship between this kind of river rehabilitation process and ecological processes may require a nuanced interpretation, however, because the effect was not on a particular macroinvertebrate taxonomic group, or a functional feeding group. The rehabilitated reach of the River Welland yielded higher production estimates for Malacostraca, Gastropoda, Bivalvia, EPT, Odonata and Arachnida, and a lower estimate for Chironomidae than did the control reach. The rehabilitated reach also had a higher estimate of production for Shredder, Scraper, Filter-feeder and Predator feeding groups than did the control reach. These outcomes demonstrate recovery of the reach’s entire macroinvertebrate community structure and function after rehabilitation.

The River Welland rehabilitation project used in-stream biotopes as the natural ‘jigsaw’ pieces that needed to be returned back to the degraded river channel, in order to increase its heterogeneity. River rehabilitation through increasing in-stream biotope heterogeneity can be achieved by designing a channel that mimics the natural physical state. This involves creating appropriately spaced meanders and pool and riffle sequences using woody material installation, with the design informed by hydromorphological data from upstream or nearby reference reaches to guide the channel dimensions, pattern, and profile (Rosgen, 1994; 1996; Doll *et al.*, 2003). The river responds by creating the diversity of current velocity, erosion-deposition processes, and marginal berms that together maintain the biotopes. Thus, the rehabilitated channel planform, cross-section, and longitudinal profile are sustainable over time, and in-stream biotope heterogeneity and refuges can increase further after the rehabilitated channel’s design has become more natural (Townsend & Hildrew, 1994; Klein *et al.*, 2007; Ernst *et al.*, 2010).

The rehabilitation measures performed in the Welland Park reach of River Welland demonstrate that active return of the entire lost in-stream biotope heterogeneity could induce measurable changes in macroinvertebrate production relatively quickly and decrease the recovery time (Entrekin *et al.*, 2009). Recommended future restoration needs to increase intensity of the in-stream rehabilitation measures. Understanding how macroinvertebrate community production responds to hydromorphological rehabilitation processes can provide a valuable framework with which to monitor the success of stream rehabilitation projects in enhancing the functioning of a rehabilitated reach’s ecosystem. Further study is nevertheless needed to evaluate the long-term trends in total production of the macroinvertebrate community of the rehabilitated reach of the River Welland, as the in-stream biotope composition and heterogeneity are continuously changing.

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**Data availability statement**

The authors confirm that the data supporting the findings of this study are available within the article and its supplementary materials.

**References**

Addy, S., Cooksley, S., Dodd, N., Waylen, K., Stockan, J., Byg, A. & Holstead, K. (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](file:///G:\WORK\STUDENTS\Ahmed%20Al-Zankana\Paper-4-Welland-II\Revised-2020-10-26\As-accepted\www.crew.ac.uk\publications)

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:10.1016/j.ecohyd.2019.11.001

Allan, J. D. (1995). *Stream Ecology: Structure and Function of Running Waters*. London: Chapman and Hall.

Allan, J. D. & Flecker, A. S. (1993). Biodiversity conservation in running waters. *BioScience, 43*(1), 32-43.

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.

Barnes, J. B., Vaughan, I. P. & Ormerod, S. J. (2013). Reappraising the effects of habitat structure on river macroinvertebrates. *Freshwater Biology, 58*(10), 2154-2167.

Benke, A. C. (1993). Concepts and patterns of invertebrate production in running waters. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie, 25*(1), 15-38.

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.

Benke, A. C., Richard, H. F., Stites, D. L., Meyer, J. L. & Edwards, R. T. (1992). Growth of snag-dwelling mayflies in a blackwater river: the influence of temperature and food. *Archiv für Hydrobiologie, 125*(1), 63-81.

Benke, A. C. & Wallace, J. B. (2003). Influence of wood on invertebrate communities in streams and rivers. *American Fisheries Society, 37*, 149-177.

Bernhardt, E. S., Palmer, M., Allan, J., Alexander, G., Barnas, K., Brooks, S., Carr, J., Clayton, S., Dahm, C. & Follstad-Shah, J. (2005). Synthesizing U.S. river restoration efforts. *Science, 308*(5722), 636-637.

Brinkhurst, R. O. (1971). *A Auide for the Identification of British Aquatic Oligochaeta* (2nd ed.). Kendal: Freshwater Biological Association (FBA).

Buffagni, A., Crosa, G. A., Harper, D. M. & Kemp, J. L. (2000). Using macroinvertebrate species assemblages to identify river channel habitat units: an application of the functional habitats concept to a large, unpolluted Italian river (River Ticino, northern Italy). *Hydrobiologia, 435*(1-3), 213-225. doi:10.1023/A:1004124717508

Bunn, S. E. & Davies, P. M. (2000). Biological processes in running waters and their implications for the assessment of ecological integrity. *Hydrobiologia, 422*, 61-70.

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.

Cook, S. E. K. (1976). Quest for an index of community structure sensitive to water-pollution. *Environmental Pollution, 11*(4), 269-288. doi:Doi 10.1016/0013-9327(76)90067-7

Council of the European Communities. (1992). Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Official Journal of the European Union, L206*, 7-50.

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>

Cranston, P. S. (1982). *A Key to the Larvae of the British Orthocladiinae (Chironomidae)*. Ambleside: Freshwater Biological Association (FBA).

Croft, P. S. (1986). *A Key to the Major Groups of British Freshwater Invertebrates* (Vol. 6): Field Studies Council.

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.

Defra. (2011). Biodiversity 2020: a strategy for England's wildlife and ecosystem services. In: Department for Environment, Food and Rural Affairs London.

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

Dobson, M., Pawley, S., Fletcher, M. & Powell, A. (2012). *Guide to Freshwater Invertebrates*: Freshwater Biological Association (FBA).

Dolbeth, M., Cusson, M., Sousa, R. & Pardal, M. A. (2012). Secondary production as a tool for better understanding of aquatic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences, 69*(7), 1230-1253. doi:10.1139/f2012-050

Doll, B. A., Grabow, G. L., Hall, K. R., Halley, J., Harman, W. A., Jennings, G. D. & Wise, D. E. (2003). Stream restoration: a natural channel design handbook. *NC Stream Restoration Institute, NC State University*.

Dolph, C. L., Eggert, S. L., Magner, J., Ferrington Jr, L. C. & Vondracek, B. (2015). Reach-scale stream restoration in agricultural streams of southern Minnesota alters structural and functional responses of macroinvertebrates. *Freshwater Science, 34*(2), 535-546.

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

Edington, J. M. & Hildrew, A. G. (1995). *A Revised Key to the Caseless Caddis Larvae of the British Isles with Notes on Their Ecology*: Freshwater Biological Association (FBA).

Elliott, J. M. (2009). *Freshwater Megaloptera and Neuroptera of Britain and Ireland: Keys to Adults and Larvae, and a Review of Their Ecology*: Freshwater Biological Association (FBA).

Elliott, J. M. & Humpesch, U. (2010). *Mayfly Larvae (Ephemeroptera) of Britain and Ireland: Keys and a Review of Their Ecology*: Freshwater Biological Association (FBA).

Elliott, J. M., Humpesch, U. H. & Macan, T. T. (1988). *Larvae of the British Ephemeroptera: a Key with Ecological Notes*: Freshwater Biological Association (FBA).

Elliott, J. M. & Mann, K. H. (1979). *A Key to the British Freshwater Leeches: with Notes on Their Life Cycles and Ecology*: Freshwater Biological Association (FBA).

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., Baldigo, B. P., Mulvihill, C. I. & Vian, M. (2010). Effects of natural-channel-design restoration on habitat quality in Catskill Mountain streams, New York. *Transactions of the American Fisheries Society, 139*(2), 468-482.

Esdar, L. C. R. (2019). *Spatial variation in benthic macroinvertebrate community structures in tributaries of Verdal river: effects of biotic and abiotic environmental factors and restoration measures.* (Master Thesis). Norwegian University of Life Sciences,

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

Feeley, H. B., Woods, M., Baars, J.-R. & Kelly-Quinn, M. (2012). Refining a kick sampling strategy for the bioassessment of benthic macroinvertebrates in headwater streams. *Hydrobiologia, 683*(1), 53-68.

Feld, C. K., Birk, S., Bradley, D. C., Hering, D., Kail, J., Marzin, A., Melcher, A., Nemitz, D., Pedersen, M. L., Pletterbauer, F., Pont, D., Verdonschot, P. F. M. & Friberg, N. (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., Moir, H., O’Hare, M. T., Verdonschot, P. F. M. & Wolter, C. (2016). Chapter Eleven: Effective river restoration in the 21st century: From trial and error to novel evidence-based approaches. In A. J. Dumbrell, R. L. Kordas, & G. Woodward (Eds.), *Advances in Ecological Research* (Vol. 55, pp. 535-611): Academic Press.

Friberg, N., Baattrup-Pedersen, A., Kristensen, E. A., Kronvang, B., Larsen, S. E., Pedersen, M. L., Skriver, J., Thodsen, H. & Wiberg-Larsen, P. (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.

Friberg, N., Baattrup-Pedersen, A., Kristensen, E. A., Kronvang, B., S.E. Larsen, Pedersen, M. L., Skriver, J., Thodsen, H. & Wiberg-Larsen, P. (2013). The River Gelså restoration revisited: Habitat specific assemblages and persistence of the macroinvertebrate community over an 11-year period. *Ecological Engineering, 66*, 150-157.

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

Friberg, N., Sandin, L. & Pedersen, M. L. (2009). Assessing the effects of hydromorphological degradation on macroinvertebrate indicators in rivers: examples, constraints, and outlook. *Integrated Environmental Assessment and Management, 5*(1), 86-96.

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.

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

Gledhill, T., Sutcliffe, D. W. & Williams, W. D. (1976). *A Revised Key to the British Species of Crustacea: Malacostraca Cccurring in Fresh Water: With Notes on Their Ecology and Distribution*: Freshwater Biological Association (FBA).

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.

Greenhalgh, M. & Ovenden, D. (2007). *Freshwater Life: Britain and Northern Europe*: Collins.

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., Barham, P. & Howell, R. (1995). The ecological basis for the management of the natural river environment. In D. M. Harper & A. J. D. Ferguson (Eds.), *The Ecological Basis for River Management* (pp. 219–238). Chichester: John Wiley & Sons.

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

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

Hilderbrand, R., Watts, A. & Randle, A. (2005). The myths of restoration ecology. *Ecology and Society, 10*(1).

Hynes, H. B. N. (1977). *A Key to the Adults and Nymphs of British Stoneflies (Plecoptera) with Notes on Their Ecology and Distribution*: Freshwater Biological Association (FBA).

Hynes, H. B. N., Macan, T. T. & Williams, W. D. (1960). *A Key to the British Species of Crustacea: Malacostraca Occurring in Fresh Water: With Notes on Their Ecology and Distribution*: Freshwater Biological Association (FBA).

Jähnig, S. C., Brabec, K., Buffagni, A., Erba, S., Lorenz, A. W., Ofenböck, T., Verdonschot, P. F. & Hering, D. (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.

Johnson, L. B., Breneman, D. H. & Richards, C. (2003). Macroinvertebrate community structure and function associated with large wood in low gradient streams. *River Research and Applications, 19*(3), 199-218.

Jones Jr, J. B. & Smock, L. A. (1991). Transport and retention of particulate organic matter in two low-gradient headwater streams. *Journal of the North American Benthological Society, 10*(2), 115-126.

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

Killeen, I. J., Aldridge, D. & Oliver, G. (2004). *Freshwater Bivalves of Britain and Ireland* (Vol. 82). Preston Montfort/National Museums of Wales: Field Studies Council.

Klein, L. R., Clayton, S. R., Alldredge, J. R. & Goodwin, P. (2007). Long‐term monitoring and evaluation of the Lower Red River meadow restoration project, Idaho, USA. *Restoration Ecology, 15*(2), 223-239.

Lemly, A. D. & Hilderbrand, R. H. (2000). Influence of large woody debris on stream insect communities and benthic detritus. *Hydrobiologia, 421*(1), 179-185.

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., 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. & Muotka, T. (2011). Twenty years of stream restoration in Finland: little response by benthic macroinvertebrate communities. *Ecological Applications, 21*(6), 1950-1961.

Macan, T. T. & Cooper, R. D. (1977). *A Key to the British Fresh-and Brackish-Water Gastropods: With Notes on Their Ecology*: Freshwater Biological Association (FBA).

Mainstone, C. P. (2008). The role of specially designated wildlife sites in freshwater conservation—an English perspective. *Freshwater Reviews, 1*(1), 89-98.

Mainstone, C. P. & Wheeldon, J. (2016). The physical restoration of English rivers with special designations for wildlife: from concepts to strategic planning and implementation. *Freshwater Reviews, 8*(1), 1-25.

Mann, K. H. & Watson, E. (1954). *A Key to the British Freshwater Leeches with Notes on Their Ecology*: Freshwater Biological Association (FBA).

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.

Morin, A. (1997). Empirical models predicting population abundance and productivity in lotic systems. *Journal of the North American Benthological Society, 16*(2), 319-337. doi:10.2307/1468021

Morin, A. & Dumont, P. (1994). A simple model to estimate growth rate of lotic insect larvae and its value for estimating population and community production. *Journal of the North American Benthological Society, 13*(3), 357-367.

Naeem, S., Bunker, D. E., Hector, A., Loreau, M. & Perrings, C. (2009). *Biodiversity, Ecosystem Functioning, and Human Wellbeing: an Ecological and Economic Perspective*: Oxford University Press.

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

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., 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*, 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, 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

Petersen, R. C., Petersen, L. B. M. & Lacoursiere, J. (1992). A building-block model for stream restoration. *River Conservation and Management, 19*(4), 378-379.

Pilotto, F., Harvey, G. L., Wharton, G. & Pusch, M. T. (2016). Simple large wood structures promote hydromorphological heterogeneity and benthic macroinvertebrate diversity in low-gradient rivers. *Aquatic Sciences, 78*(4), 755-766. doi:10.1007/s00027-016-0467-2

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.

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

Richards, C., Host, G. E. & Arthur, J. W. (1993). Identification of predominant environmental factors structuring stream macroinvertebrate communities within a large agricultural catchment. *Freshwater Biology, 29*(2), 285-294. doi:10.1111/j.1365-2427.1993.tb00764.x

Roeding, C. E. & Smock, L. A. (1989). Ecology of macroinvertebrate shredders in a low-gradient sandy-bottomed stream. *Journal of the North American Benthological Society, 8*(2), 149-161.

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

Roni, P. & Quimby, E. (2005). *Monitoring Stream and Watershed Restoration*: CABI.

Rosgen, D. L. (1994). A classification of natural rivers. *Catena, 22*(3), 169-199.

Rosgen, D. L. (1996). *Applied River Morphology*. Colorado: Wildland Hydrology.

Ross, D. H. & Wallace, J. B. (1983). Longitudinal patterns of production, food consumption, and seston utilization by net-spinning caddisflies (Trichoptera) in a Southern Appalachian Stream (USA). *Holarctic Ecology, 6*(3), 270-284. doi:10.2307/3682382

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B. & Kinzig, A. (2000). Global biodiversity scenarios for the year 2100. *Science, 287*(5459), 1770-1774.

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

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

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

Soar, C. D. & Williamson, W. (1925). *The British Hydracarina, Volume I* (Vol. 1). London: The Ray Society.

Soar, C. D. & Williamson, W. (1927). *The British Hydracarina, Volume II* (Vol. 2). London: The Ray Society.

Soar, C. D. & Williamson, W. (1929). *The British Hydracarina, Volume III* (Vol. 3). London: The Ray Society.

Sponseller, R. A., Benfield, E. F. & Valett, H. M. (2001). Relationships between land use, spatial scale and stream macroinvertebrate communities. *Freshwater Biology, 46*(10), 1409-1424. doi:10.1046/j.1365-2427.2001.00758.x

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

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>

Townsend, C. R. & Hildrew, A. G. (1994). Species traits in relation to a habitat templet for river systems. *Freshwater Biology, 31*(3), 265-275.

Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R. & Cushing, C. E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences, 37*(1), 130-137.

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

Wallace, I. D. (2006). *Simple Key to Caddis Larvae*: AIDGAP Field Studies Council.

Wallace, I. D., Wallace, B. & Philipson, G. N. (1990). *A Key to the Case-Bearing Caddis Larvae of Britain and Ireland*: Freshwater Biological Association (FBA).

Wallace, J. B. & Webster, J. R. (1996). The role of macroinvertebrates in stream ecosystem function. *Annual Review of Entomology, 41*(1), 115-139.

Wallace, J. B., Webster, J. R. & Meyer, J. L. (1995). Influence of log additions on physical and biotic characteristics of a mountain stream. *Canadian Journal of Fisheries and Aquatic Sciences, 52*(10), 2120-2137.

Waringer, J. & Graf, W. (2013). Key and bibliography of the genera of European Trichoptera larvae. *Zootaxa, 3640*(2), 101-151.

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.

Wheeldon, J., Mainstone, C., Cathcart, R. & Erian, J. (2015). *River restoration theme plan: A strategic approach to restoring the physical habitat of rivers in England’s Natura 2000 sites*. Retrieved from Peterborough, UK: www. gov.uk/government/publications/improvementprogramme-for-englands-natura-2000-sites-ipens

Wilcove, D. S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. (1998). Quantifying threats to imperiled species in the United States. *BioScience, 48*(8), 607-615.

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

Wolter, C., Lorenz, S., Scheunig, S., Lehmann, N., Schomaker, C., Nastase, A., García de Jalón, D., Marzin, A., Lorenz, A. & Kraková, M. (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.

Table 1. Mean and Standard Deviation (SD) of channel morphological variables of the three study reaches recorded during the first (2015) and second (2016) post-rehabilitation years. SWI-biotope, in-stream biotope diversity.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Morphological variables | Period | Degraded | | Reference | | Rehabilitated | |
| Mean | SD | Mean | SD | Mean | SD |
| Number of biotopes | 2015 | 5 | 0 | 7 | 0 | 8 | 0 |
| 2016 | 5 | 0 | 7 | 0 | 8 | 0 |
| SWI-biotope | 2015 | 0.67 | 0.05 | 0.82 | 0.04 | 0.82 | 0.03 |
| 2016 | 0.67 | 0.04 | 0.81 | 0.06 | 0.94 | 0.03 |
| Cobbles% | 2015 | 0.0 | 0.0 | 10.8 | 0.5 | 3.1 | 0.1 |
| 2016 | 0.0 | 0.0 | 11.2 | 0.5 | 5.5 | 0.1 |
| Gravel% | 2015 | 36.0 | 1.5 | 74.6 | 1.3 | 83.1 | 1.6 |
| 2016 | 35.0 | 1.8 | 75.0 | 1.9 | 59.6 | 1.2 |
| Sand% | 2015 | 5.4 | 0.5 | 4.2 | 1.0 | 2.3 | 0.1 |
| 2016 | 8.5 | 0.9 | 4.9 | 1.2 | 4.0 | 0.4 |
| Silt% | 2015 | 52.0 | 2.3 | 1.0 | 0.1 | 1.0 | 0.1 |
| 2016 | 51.0 | 1.2 | 1.0 | 0.2 | 0.0 | 0.0 |
| Tree-root% | 2015 | 0.0 | 0.0 | 0.0 | 0.0 | 2.8 | 0.2 |
| 2016 | 0.0 | 0.0 | 0.0 | 0.0 | 3.0 | 0.3 |
| Marginal plants% | 2015 | 1.0 | 0.0 | 1.8 | 0.0 | 2.7 | 0.0 |
| 2016 | 1.0 | 0.0 | 2.2 | 0.0 | 9.0 | 0.5 |
| Leaf-letter% | 2015 | 0.0 | 0.0 | 0.0 | 0.0 | 3.0 | 0.0 |
| 2016 | 0.0 | 0.0 | 0.0 | 0.0 | 8.0 | 1.3 |
| Macroalgae% | 2015 | 0.0 | 0.0 | 7.6 | 0.8 | 2.0 | 0.0 |
| 2016 | 0.0 | 0.0 | 5.7 | 0.3 | 5.4 | 0.2 |
| Submerged Fine-leaved Macrophytes% | 2015 | 5.5 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 |
| 2016 | 4.5 | 0.3 | 0.0 | 0.0 | 5.5 | 0.2 |

Table 2. Mean (SD) secondary production (mgDM m-2) for each macroinvertebrate taxonomic group in each study reach for the first and second post-rehabilitation years.

|  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Control  2015 | | Reference  2015 | | Rehabilitated  2015 | | Control  2016 | | Reference  2016 | | Rehabilitated  2016 | |
| Taxonomic groups | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| Malacostraca | 88.6 | 18.2 | 361.1 | 26.0 | 201.2 | 37.3 | 75.2 | 18.9 | 385.7 | 6.5 | 1314.2 | 457.9 |
| Gastropoda | 1746.3 | 330.6 | 5896.9 | 187.7 | 1751.0 | 115.7 | 1501.5 | 266.1 | 5435.8 | 325.9 | 4473.9 | 168.9 |
| Bivalvia | 135.1 | 87.6 | 1052.8 | 65.2 | 233.2 | 106.0 | 91.9 | 76.8 | 1151.7 | 141.6 | 938.4 | 56.8 |
| Hirudinea | 595.9 | 230 | 317.6 | 93.0 | 485.6 | 98.5 | 499.8 | 80.9 | 408.6 | 201.9 | 511.3 | 155.9 |
| Oligochaeta | 74.2 | 9.4 | 32.4 | 4.1 | 43.9 | 1.1 | 41.4 | 5.1 | 25.1 | 2.0 | 29.8 | 2.1 |
| Turbellaria | 2.2 | 0.6 | 0.0 | 0.0 | 3.1 | 1.8 | 0.9 | 0.2 | 0.0 | 0.0 | 2.9 | 0.8 |
| Coleoptera | 0.0 | 0.0 | 0.2 | 0.0 | 0.1 | 0.1 | 0.0 | 0.0 | 0.2 | 0.0 | 0.2 | 0.1 |
| Diptera | 26.7 | 17.6 | 873.2 | 123.9 | 37.0 | 15.2 | 22.0 | 16.5 | 1083.4 | 150.2 | 59.2 | 11.2 |
| Chironomidae | 728.7 | 11.0 | 386.7 | 10.5 | 731.3 | 36.4 | 748.3 | 66.2 | 418.8 | 43.3 | 210.5 | 42.6 |
| EPT | 55.6 | 26.4 | 2315 | 201.2 | 57.5 | 22.9 | 76.1 | 26.4 | 2653.1 | 336.4 | 1254.8 | 82.0 |
| Megaloptera | 41.5 | 41.3 | 16.7 | 10.5 | 0.3 | 0.1 | 19.4 | 18.9 | 10.6 | 9.1 | 1.7 | 2.3 |
| Odonata | 1.0 | 0.3 | 0.2 | 0.3 | 2.4 | 0.8 | 1.2 | 0.0 | 0.0 | 0.0 | 21.1 | 5.4 |
| Arachnida | 95.3 | 21.6 | 84.2 | 16.3 | 75.5 | 10.3 | 100.8 | 5.8 | 118.2 | 27.1 | 280.1 | 17.4 |
| TP | 3591.1 | 583.0 | 11337 | 212.0 | 3622.1 | 537.0 | 3178.5 | 512 | 11691.2 | 311.1 | 9098.4 | 529.0 |

Table 3. Mean (SD) secondary production (mgDM m-2) for each macroinvertebrate feeding group in each study reach for thefirst and second post-rehabilitation years.

|  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Control  2015 | | Reference  2015 | | Rehabilitated  2015 | | Control  2016 | | Reference  2016 | | Rehabilitated  2016 | |
| Feeding groups | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| Absorber | 42.3 | 0.1 | 31.7 | 2.5 | 31.2 | 3.2 | 47.7 | 22 | 32.0 | 4.4 | 36.9 | 3.2 |
| Deposit-feeder | 266.0 | 17.4 | 408.9 | 18.4 | 303.0 | 50.2 | 263.7 | 91.7 | 486.6 | 28.1 | 260.9 | 5.4 |
| Shredders | 849.0 | 212.2 | 4912.7 | 75.2 | 881.7 | 98.6 | 810.7 | 219.9 | 4849.7 | 259.8 | 3276.2 | 152.2 |
| Scraper | 687.6 | 178.3 | 3920.9 | 140.3 | 666.9 | 108.8 | 585.7 | 149.5 | 3679.8 | 196.3 | 2682.6 | 334.8 |
| Filter-feeder | 787.7 | 25.8 | 1150.3 | 43.2 | 712.1 | 76.3 | 686.0 | 136.2 | 1367.6 | 182.5 | 1386.3 | 121.0 |
| Piercer | 167.8 | 61.0 | 42.8 | 35.3 | 194.3 | 39.6 | 139.2 | 13.6 | 46.6 | 42.1 | 204.5 | 47.5 |
| Predator | 534.1 | 45.4 | 836.8 | 130.6 | 566.3 | 46.6 | 413.5 | 96.2 | 1189.8 | 347.7 | 1171.1 | 503.7 |
| Parasite | 256.6 | 16.6 | 32.9 | 9.2 | 261.7 | 25.4 | 231.9 | 71.8 | 39.0 | 11.0 | 80.0 | 11.0 |

Table 4. Summary of sequential tests, obtained from distance-based linear models (DISTLM), seeking relationships between temporal variations in macroinvertebrate production and channel morphological variables. Values displayed are significant at P<0.05 and indicate both the proportion of variability explained by each channel morphological variable and the cumulative variability explained by the models. +/- indicate additions to or subtractions from the model. Correlations were obtained using Spearman’s rank correlation (ρ), ‘positive’ and ‘negative’ indicate positive or negative correlations. SWI-biotope, in-stream biotope diversity.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Macroinvertebrate community data | Morphological variables | Proportion | Cumulative | Relationship |
| Total Production | Marginal plant% | 0.96 | 0.96 | positive |
| Gastropoda | Marginal plant% | 0.86 | 0.86 | positive |
| EPT | Cobbles% | 0.77 | 0.77 | positive |
| Bivalvia | Cobbles% | 0.75 | 0.75 | positive |
| Malacostraca | Marginal plant% | 0.89 | 0.89 | positive |
| Odonata | Cobbles% | 0.95 | 0.95 | positive |
| Arachnida | Marginal plant% | 0.86 | 0.86 | positive |
| Chironomidae | Silt% | 0.94 | 0.94 | positive |
| Shredder | Marginal plant%  +Leaf-litter% | 0.78  0.20 | 0.78  0.98 | positive  positive |
| Filter-feeder | Gravel% | 0.91 | 0.91 | negative |
| Predator | +Leaf-litter% | 0.38 | 0.38 | positive |

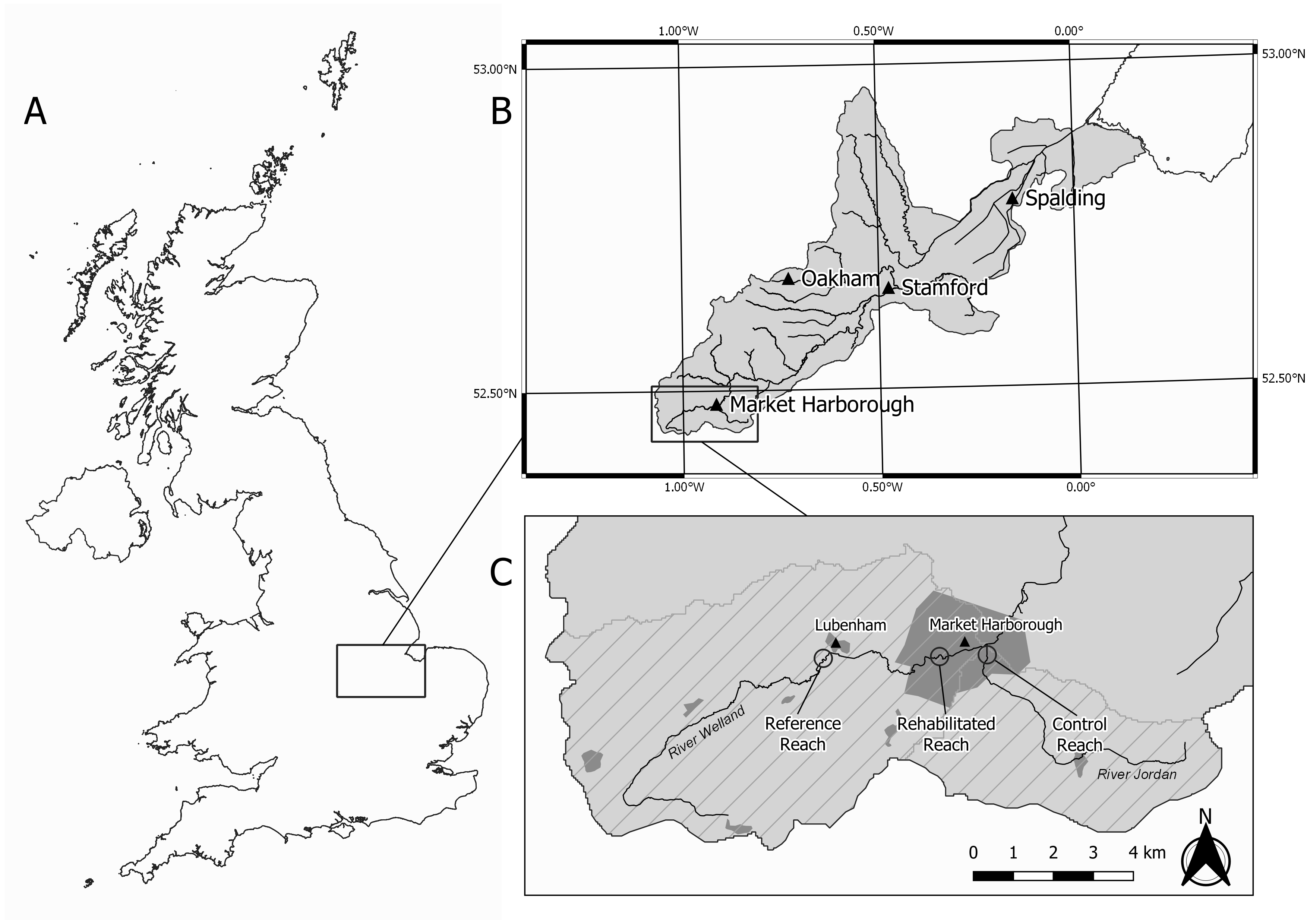


Figure . Map of the study area. A) Outline of the UK. B) Outline of the catchment of the River Welland and the location of Market Harborough. C) The location of the reference reach, the rehabilitated reach and the control reach. Drawn by Mr Chris French, Welland Rivers Trust.

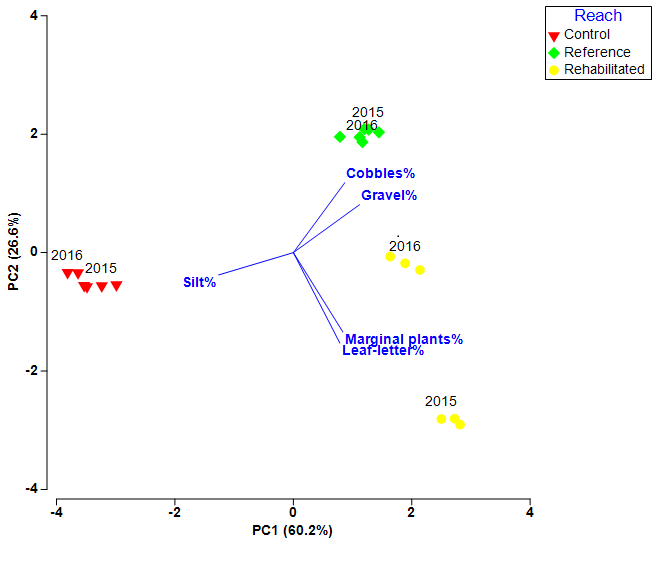


Figure 2. PCA ordination plots showing temporal trends of channel morphological variables, based on reach-level data measured during the first (2015) and second (2016) post-rehabilitation years. Vectors indicate variables correlated at ρ >0.5.

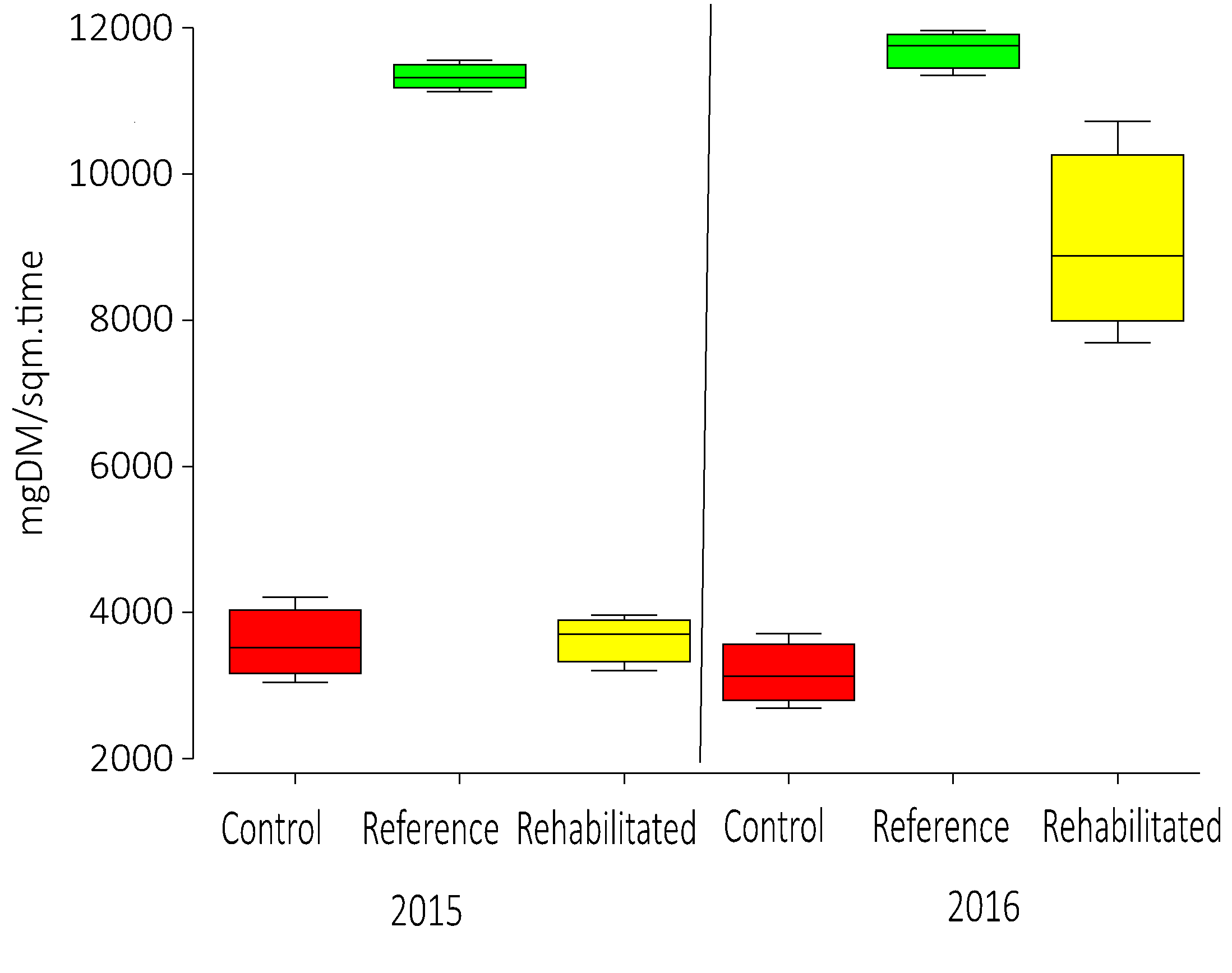


Figure . Total production (mgDM.m-2) of macroinvertebrates according to the study reaches.