Testing the efficacy of river restoration across multiple levels of biological organisation

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Statement of originality

I, Joseph Huddart, confirm that the research presented within this thesis is my own, with the following acknowledgement:

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Abstract

As we start to count the cost of unprecedented biodiversity loss in terms of impaired provisional, supporting and cultural ecosystem goods and services, so to are we increasingly implementing measures to halt and reverse these impacts. A major focus of these efforts has been the restoration river habitats, which rank among the most degraded globally. However, while river restoration has become a global enterprise, biomonitoring to test the ecological effectiveness of these activities remains exceptional and even then typically lacking the rigour necessary for detecting and tracking ecological responses across space and time.

Here I use standardised and quantitative biomonitoring techniques to measure the ecological response to replicated, experimental, reach-scale large wood installations in heavily modified calcareous system. In Chapters 3-5, I used biannual biomonitoring to investigate the response of a target fish species and the wider fish assemblage to restoration and found strong, rapid responses in the target species' predators (Chapter 3). In Chapter 4, I build food webs revealing changes to the food web structure that indicate enhanced energy transfer between predators and prey following restoration. In Chapter 5 I investigate the effect of restoration on ecosystem functioning, by comparing leaf-litter breakdown rates and colonisation in restored and unrestored reaches. In Chapter 6, I discuss how engaging river users as citizen scientists could advance the ecological success of their interventions and restoration science.

The findings presented here highlight the importance of robust biomonitoring methods for revealing, measuring and characterising the response of ecological communities to habitat interventions. Repairing degraded ecosystems is among the most necessary and exciting challenges we have undertaken as a species, and only by advancing our understanding the factors that influence restoration success and failure will we be able to advance the practice of restoration towards an ever more efficient and ecologically effective management practice.

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Chapter 1 | General Introduction

1.1.1 River degradation

Our activities as a species have triggered the beginning of the 6th mass extinction event, with rivers at the forefront of species decline. Freshwater ecosystems are disproportionately biodiverse; despite covering less than 1% of the earth's surface, they are estimated to contain 6% - 10% of all species and one third of all vertebrate species globally (including >40% of all known fish species) (Dudgeon et al 2006, Groombridge 1992). However, extensive physical modifications to provide goods and services of value to human societies, such as water provision, transportation and food, and to reduce flooding, have made streams and rivers objects of human modification and exploitation for centuries (Brookes et al 1983, Vorosmarty et al 2010). Pollution from the on-going global intensification of agriculture and increased urbanisation, coupled with increased abstraction to meet growing human demand, continues to degrade river systems globally (Allan 2004, Walsh et al 2005). As a result, riverine ecosystems are among the most altered and threatened on Earth, and the species they support are disproportionately threatened (Dudgeon et al 2006, Sala et al 2000, Vorosmarty et al 2010); this is supported by a recent report which found that populations of freshwater species have declined by 81% between 1970 and 2012, compared to 38% and 36% for marine and terrestrial species respectively (McLellan et al 2014).

Many factors contribute to degraded environmental conditions in rivers; direct chemical pollution, such as that from industrial effluent or wastewater treatment plants, alongside indirect pollution, via agricultural and urban run-off of pesticides and nutrients, and atmospheric 'dumping' of emissions, can have severe impacts on

both biological communities and functioning (Dudgeon et al 2006, Layer et al 2010a). Serious declines in water quality across Europe and the US in the 1970's led to massive expenditure to establish, implement and enforce regulatory legislation to improve water quality, which have been largely successful (Jenkins et al 2013). These include the introduction of standards for acceptable concentrations of chemicals in effluent and surface waters. However, even after the reduction or cessation of harmful activities and measurable improvement to water chemistry, biological recovery has often been more modest than expected, if at all (Layer et al 2010a, Monteith et al 2005).

This has led to a focus on degraded physical habitat; physical modifications over centuries and even millennia to straighten, divert, impound and control river channels and flows have dramatically altered the profile and hydromorphology of rivers on a global scale (Brookes 1988, Brookes et al 1983). These channelisation activities, coupled with maintenance practices such as dredging, reduce habitat complexity in terms of flow, depth and substrate diversity and associated features such as pools and riffles (Brookes 1988, Brookes et al 1983).

1.1.2 Habitat restoration in the 21st Century

Researchers have extensively grappled with defining river restoration. Fluvial geomorphologists may define it as the need to return physical processes such as natural flow and erosion regimes and physical structure (Sear 1994), whereas ecologists will typically focus on the recovery of biodiversity, i.e. the recovery of species diversity and biomass (Feld et al 2011b). River restoration may also be used to describe actions aimed at enhancing the amenity and aesthetic value of a river and its riparian zone for the local population (Dufour & Piegay 2009). For the purpose of this dissertation, I define river restoration as habitat measures aimed at assisting the recovery of biodiversity and ecological functioning in a degraded system towards a more natural state (Beechie et al 2010, Lake 2013).

Interventions to enhance habitats for riverine species are not new (Tarzwell 1937), however over the last 50 years the rate of implementation has risen exponentially (Feld et al 2011b). This is in part due to shifts in statutory policy, which have placed

increasing emphasis on conserving riverine biodiversity as well as water quality (Huddart et al 2016a). For instance, the European Water Framework Directive (WFD) uses ecological components alongside water chemistry and hydromorphological components to assess the status of rivers (Hering et al 2010). This, accompanied with the risk of punitive fines (EC 2000) and the use of catchment specific "River Basin Management Plans" to target those ecological elements that fall below 'good' status within a given catchment, has encouraged statutory implementation of river restoration measures in Europe (Hering et al 2010, Morandi et al 2014a). In addition, national and international biodiversity strategies such as the Millennium Ecosystem Assessment report and Convention on Biological Diversities Aichi Biodiversity's Targets 11, 14 and 15 (https://www.cbd.int/sp/targets/) have also prioritised and encouraged the restoration of freshwater ecosystems on a global scale (Bernhardt et al 2005b, Huddart et al 2016c, Ormerod 2003, Palmer et al 2014b).

River restoration is not, however, exclusively government funded or driven. Diverse stakeholders operating at various levels of organisation, ranging from reach-scale landowners, catchment-scale (e.g. Action for the River Kennet (http://www.riverkennet.org)) to national (e.g. the Wild Trout Trust (http://www.wildtrout.org) and international organisations (e.g. the World Wide Fund for Nature (wwf.panda.org)) and angling communities have had an important role in the river restoration landscape for centuries (Bernhardt et al 2007, Conrad & Hilchey 2011, Roni et al 2015). These groups have historically been the first to detect declines in biodiversity, and continue to support, fund and implement habitat restorations specifically aimed at improving biodiversity (Figure 1.1).

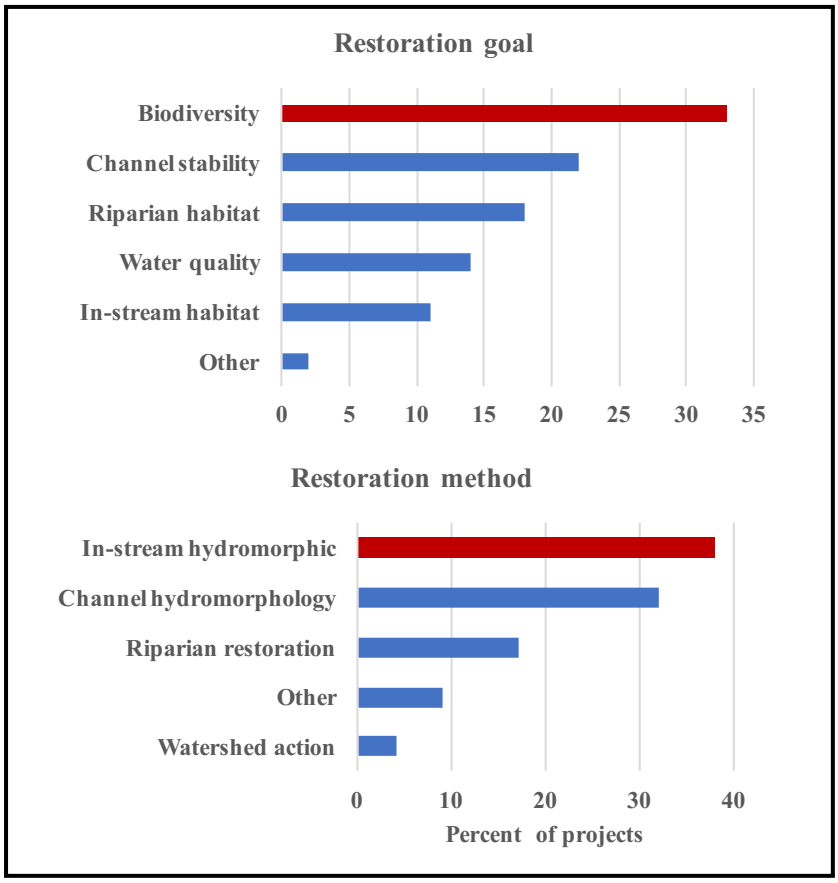


Figure 1.1 Restoration goals and methods derived from collated information on 644 restoration projects in 149 published studies from around the world in which quantitative information on the effectiveness of the restoration was taken (Palmer et al 2014a).

The majority of river restorations are implemented with the aim of restoring biodiversity (Figure 1.1; Top). Habitat restoration measures range from the removal of barriers to increase connectivity (De Leaniz 2008, Fjeldstad et al 2012), to larger catchment-scale interventions to re-instate natural profiles and processes such as erosion and sedimentation that are necessary for sustaining the processes that drive in-stream habitat heterogeneity (Figure 1.1; Bottom). An exceptional example of catchment scale project is the River Skjern in Denmark (Feld et al 2011b), where 19 km of channelised river was restored to its original meandering profile and 22 km^2 of neighbouring agricultural land returned to wetlands and water meadows.

However, in the culturally congested landscapes of lowland Western Europe, where land-use changes and high population densities have degraded natural habitats and altered flow regimes for centuries (Feld et al 2011b), the spatial scale of restorations

is severely restricted. Thus, the vast majority of projects are implemented at the more economically and practicable 'reach-scale' (*i.e.* <60 bank-full width (Miller et al 2010a) within the riparian zone (Lake et al 2007, Palmer et al 2014b). These reach-scale projects typically use in-stream hydromorphic or river channel profiling methods (Figure 1.1 Bottom) (Kail et al 2015, Palmer et al 2014b). These aim to increase local habitat diversity in reaches in simplified channels by creating pools and riffles or introducing missing elements such as boulders and large woody debris, which help to create and maintain these habitats (Kail et al 2007, Lorenz et al 2013, Roni et al 2015, Roni et al 2008).

1.1.3 Habitat restoration theory

Habitat restoration theory is largely based on the assumption that restoring habitat in degraded systems towards a more natural condition will facilitate the recovery of the original biological community. This tenet, known as the 'Field of Dreams' hypothesis, i.e., "if you build it, they will come" (Miller et al 2010a, Palmer et al 1997), has been used to support these interventions since the 1930s (Roni et al 2014).

However, the evidence-base linking habitat restoration to biodiversity remains equivocal. Whereas some studies have demonstrated biodiversity recovery (Brown 2003, Li et al 2001, Whiteway et al 2010a), others have shown differences in effects between species richness and abundance (Kail et al 2015, Miller et al 2010a, Palmer et al 2010). Worryingly, many have found biotic responses to be negligible even where hydromorphology has been substantially altered, implying an uncoupling between structural and biological diversity (Pretty et al 2003, Rosi-Marshall et al 2006, Stewart et al 2009). Even negative biological effects have been recorded (Roni et al 2015). For instance, in their review, Palmer et al. (2010) collated research from 78 independent stream restoration projects and found that only two demonstrated a positive relationship between habitat and taxa richness; no more than you would expect by chance if using the $P < 0.05$ criterion.

Inconclusive results from such studies suggest that, similar to sluggish or unexpected biological responses to chemical amelioration (Layer et al 2011), other, often larger-

scale, environmental and biological factors may override the immediate ecological benefits of habitat restoration to block biological recovery (Palmer et al 2010, Poff 1997, Stoll et al 2016, Tonkin et al 2014). Selective forces such as the regional species pool, hydrological regime and water quality, determine community composition (Poff 1997, Stoll et al 2016). These environmental factors often act like filters operating at hierarchical scales from catchment to microhabitat, in that in order to become established, species must possess the necessary traits to pass through. For instance, in order to recolonise a restored reach, there must be a species pool within proximity to propogate the site, in addition, water quality must also meet the species requirements, and finally, the habitat must be able to sustain the species throughout its life cycle (Poff 1997, Stoll et al 2016).

This theory is supported by the lack of response to expensive habitat measures in urban streams, where chronic stressors outweigh the benefits conferred by habitat interventions (i.e. "urban stream syndrome") (Violin et al 2011, Walsh et al 2005). Such systems typically fail to respond to habitat enhancement efforts and continue to remain dominated by tolerant species, suggesting that other pressures need to be addressed prior to reach-scale habitat restoration efforts (Palmer et al 2010, Violin et al 2011, Walsh et al 2005).

1.1.4 Restoring with large wood

The re-introduction of large wood to stream channels to create habitat is an enduring, widespread and frequently applied techniques for improving stream hydromorphology and ecology (Roni et al 2014). Wood placement in streams for the purpose of improving habitat for fish has been recorded as early as the 1890s in the US, UK and Western Europe (Thompson & Stull 2002, White 2002), and is a core restoration practice in these countries and others, including Japan and Australia (Brooks et al 2006, Nagayama & Nakamura 2010, Reich et al 2003, Roni et al 2014).

Studies throughout the world have demonstrated the importance of naturally occurring large wood to stream ecology and functioning (de Paula et al 2011, Gregory et al 2003, Roni et al 2014, Ruiz-Villanueva et al 2014). Here, wood initiates fluvial

processes, driving and maintaining the formation of hydromorphological features such as pools, riffles and islands (Beechie & Sibley 1997, Montgomery et al 2003, Nagayama & Nakamura 2010). These morphological features have been found to positively correlate with greater fish abundances, and are thought to provide critical habitat for spawning and refugia from predation and high-flows (Angermeier & Karr 1984, Crook & Robertson 1999, Dolloff & Warren Jr 2003, Zalewski et al 2003). In addition to physical habitat, large wood has been shown to enhance biological functions such as nutrient retention via increased accumulation of organic matter (Bilby 1981), and provide additional surface area for processes such as primary and secondary production (Benke et al 1985, Coe et al 2009, Spanhoff et al 2000).

Large wood is naturally recruited to instream channels from the riparian zone and surrounding floodplain via processes such as tree-fall, erosion and flooding, as well as longitudinal transport from upstream reaches (e.g., Gregory et al 2003, Martin & Benda 2001, Ruiz-Villanueva et al 2014). However, large wood has been depleted from many systems often over centuries, via management policies that actively remove wood from channels (*e.g.*, 'snagging') for channelisation, recreation (*e.g.* fishing), flood prevention and aesthetic purposes (Benke et al 1985). Additionally, degraded riparian zones and the loss of horizontal connectivity to floodplains (*i.e.,* seasonal flooding) due to intensified land-use have altered the natural mechanisms that naturally recruit wood into the river channel (Kail & Hering 2005).

Management policies are increasingly encouraging the implementation of artificial wood additions as an economically viable method of harnessing the hydromorphological and biological benefits of naturally occurring wood (Abbe et al 2003, Zalewski et al 2003). Techniques have evolved from heavily engineered structures (e.g. deflectors- using shaped logs e.g. Pretty et al., 2003) to designs that seek to emulate the stochastic accumulations more commonly found in natural systems (Collins et al 2002, Kail et al 2007, Roni & Beechie 2012, White 2002). For instance, felling entire trees into rivers to mimic natural tree-fall, or constructing artificial logjams to mimic natural accumulations of wood (Abbe et al 2003, Reich et al 2003), and there is evidence that these are more effective than their modified counterparts (Kail et al 2007, Pretty et al 2003).

Reviews combining quantitative habitat data from multiple studies have found largely consistent improvements to hydromorphology following restoration with large wood (Jones et al 2014, Kail 2003, Roni et al 2008). These include increased pool area, cover, and increased depth and flow diversity, habitat heterogeneity, organic matter retention and changes in gravel dynamics (Gerhard & Reich 2000, Kail 2003, Laitung et al 2002, Reich et al 2003, Zika & Peter 2002). In a recent review by Roni *et al* (2015), of 83 studies that monitored some type of physical response, 77 reported a positive response in at least one habitat metric.

However, the biological response to wood additions has been more equivocal. While studies have reported improved fish production, especially for salmonids (Binns 1994, Roni et al 2008, Sievers et al 2017, Tarzwell 1937, Whiteway et al 2010b, Zika & Peter 2002), others have reported no detectable changes (Pretty et al 2003, Rosi-Marshall et al 2006, Stewart et al 2009, Thompson 2006). A recent review by Roni et al. (2015), reported that out of 81 studies examining fish response, 68 found positive response in fish abundance, biomass, or survival for at least one fish species and life stage (juvenile or adult), 27 reported no increase for one or more species or life stage, and seven reported a negative response.

Other assemblages have also been less than consistent; with macroinvertebrates displaying both positive (Kail et al 2015, Miller et al 2010a), and weak or negligible responses (*e.g.*, (Haase et al 2013, Louhi et al 2011). In Roni et al's (2015) review, out of 21 studies monitoring macroinvertebrate response (using diversity and density metrics) 14 showed increased macroinvertebrate diversity or density following wood placement for at least one family or functional feeding group. Yet, nine showed no response, and alarmingly, five studies found negative responses. In another meta-analysis comparing wood to boulder additions, wood was more effective for improving species richness rather than density (Miller et al 2010a). These inconsistent responses highlight our limited understanding of the environmental factors that influence the ecological outcome of projects, and there is therefore a real need to better understand the factors that drive ecologically responses.

1.1.5 Biomonitoring and validation: the key to advancing river restoration science and practice

At a global scale, river restoration can be regarded as one of the most ambitious yet poorly designed ecological experiments ever undertaken: the advance of the comparatively new science of restoration has failed to keep pace with the scale of implementation, and most interventions continue to lacking quantitative appraisal (Bernhardt et al 2005a). This is frequently attributed to a widespread lack of adequate project biomonitoring within the practice. Calls for robust project biomonitoring date back to the 1930's (Tarzwell 1937), yet the vast majority of projects are still not monitored (Figure 1.2) and most restoration projects are not designed as experiments with testable hypotheses (Bernhardt et al., 2005; Kail et al., 2007). A seminal study by Bernhardt et al. (2005) highlighted the dearth of empirical knowledge gained from > 37,000 restoration projects in the US at the cost of billions of dollars. While the number of monitored restorations increased from about 1% in the 1980s to 6% in the 1990s, only 10% of more recent projects indicate any biomonitoring had taken place (Bernhardt et al 2005a). Similar findings have been reported across the world in Europe and Australia (Bernhardt et al 2005b, Bernhardt et al 2007, Brooks & Lake 2007, Morandi et al 2014b).

The failure to biomonitor has been linked to resource constraints, as in many cases these are prioritised for implementing measures rather than biomonitoring. In their paper, Bash et al. (2002) found that the most frequently given reasons by practitioners were a lack of funding (34%), time constraints (14%) and a lack of personnel (13%). However, quantitative biomonitoring is essential for sound scientific appraisal of the ecological effectiveness of these actions (Bernhardt et al 2005a, Lake et al 2007, Palmer et al 2007). Additionally, project assessments continue to be dominated by anecdotal, speculative estimations of perceived ecological responses (Morandi et al 2014b, Palmer et al 2007). These not only lack any scientifically meaningful context but also are prone to expectation bias and so inclined to report success over failure (Jahnig et al 2011, Morandi et al 2014a).

For instance, in a study by Jahnig et al. (2011), while 24 practitioners were convinced of the ecological success of their projects, only one was found to have achieved the

desired "good ecological status" as defined by the WFD (Haase et al 2013, Jahnig et al 2011). This highlights the need for quantitative, standardised biomonitoring to reduce the risk of reporting false positives that might encourage the repetition of ecologically ineffective practices (Bernhardt et al 2005a, Palmer et al 2007). Additionally, studies that empirically demonstrate positive responses in ecology can be used to guide future projects and drive adaptive restoration strategies towards ever more ecologically effective outcomes.

Monitoring design is crucial for clearly linking ecological responses to restoration measures across space and time, this can be done effectively by using the commonly applied multiple before–after control-impact (BACI) design. These require that restored ('impact') sites be sampled pre-restoration to provide a baseline for comparison post-restoration (*i.e.*, a spatial control) alongside nearby 'control' (*i.e.*, unrestored) sites. This approach is best for separating responses to restoration from environmental noise- ruling out other confounding variables in space and time, such as wider spatial or temporal variation in the metrics used, for instance natural variation in species abundances between restored and unrestored sites or species abundances over time (Feld et al 2011b). However, studies meeting these robust standards for assessment are staggeringly few (Palmer et al 2005). For instance, in a recent review, only 69 out of 316 studies assessing river restoration employed a BACI design, quantitatively monitored at least one biological organism group and provided background environmental data for the project site (Kail et al 2015).

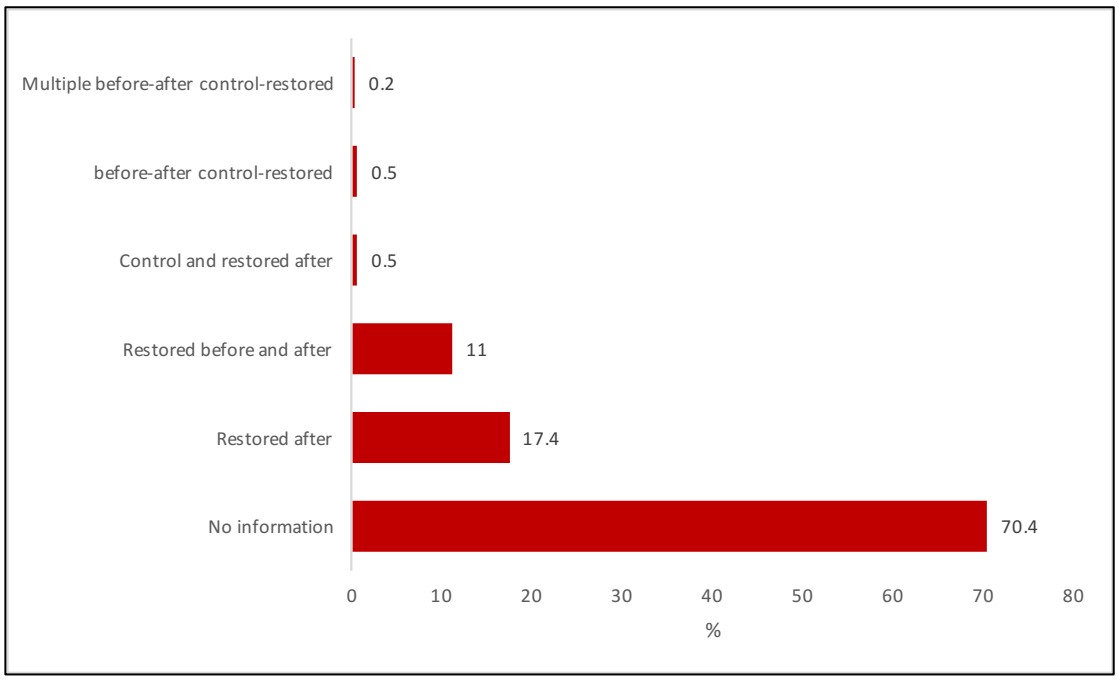


Figure 1. 2 The percentage of the restoration projects recorded on the National River Restoration Inventory (NRRI) and RESTORE databases combined which employ ecological monitoring (from data collated by Dr Murray Thompson, 2013).

The measures used to assess restoration can also influence the project appraisal. Species richness and abundance metrics are frequently used for gauging success, however, studies have observed that these can respond differently to restoration (Kail et al 2015, Miller et al 2010a). For instance, where dispersal or higher ecological filters continue to block the recolonisation of sensitive species and so the recovery of species richness, enhanced habitat and processes (*e.g.* production) may facilitate higher abundances of extant (*e.g.* tolerant) taxa (Sundermann et al 2013). Quantitative, standardised measures that can produce replicated density (i.e. m^2) estimates are crucial for detecting these important changes in abundance and biomass. As these metrics may respond rapidly to environmental change and are strongly linked to ecological functioning (Huddart et al 2016b, Thompson et al 2016, Woodward et al 2012).

The influence of the species groups used to assess ecological restoration also needs to be considered. Fishes are popular indicators of success, particularly salmonid species which have been the primary target of thousands of restoration projects, reflecting their role in driving private and statutory investment in restoration for over a century

(Lepori et al 2005, Whiteway et al 2010b). Benthic macroinvertebrates, aquatic macrophytes (macrophytes from here on) and periphyton (*i.e.*, diatoms) are also routinely used in restoration assessment (Coe et al 2009, Lorenz et al 2012, Miller et al 2010b). These assemblages have exhibited variable responses both to similar restoration practices and to each other (Kail et al 2015, Roni et al 2015, Trexler 1995). For instance, Trexler (1995) estimated the recovery of organism groups to be 3-8 years for aquatic plants, 10-12 years for benthic invertebrates and 12-20 years for fish (Louhi et al 2016, Trexler 1995). As the restoration monitoring timespan, if it is even attempted, for most studies is between 1-7 years (Feld et al 2011a), it is unsurprising that some restoration projects have found macrophytes to exhibit the strongest response to restoration (Kail et al 2015). Standardised and quantitative approaches are therefore crucial for detecting early signs of recovery and its trajectory in those assemblages with slower responses within the typically short monitoring timescale.

Interspecific time lags in recovery makes comparisons between studies that use differing biotic indices challenging (Feld et al 2011b). Additionally, by focusing on bioindicators (*e.g.* fish (Growns et al 2004, Zika & Peter 2002)), changes to more responsive groups (*e.g.,* benthic macroinvertebrates and diatoms (Trexler 1995)) may be missed, leading to false negatives (i.e. reporting no response when there was one). Widening the scope of biomonitoring to assemblages therefore increases the capacity for detecting changes that might help to advance our understanding of how restoration works. This provides a compelling case for trying to characterise as much of the animal community as possible (e.g. Haase et al., 2013 and Kail et al., 2015).

1.1.6 Food web theory: linking restoration to ecosystem functioning

How biodiversity is maintained in systems where species are constantly consuming and competing with one another for resources has perplexed ecologists since Darwin's 'tangled bank' (Pimm et al 1991). How biodiversity recovery is facilitated in the degraded systems of the 21st century in the midst these interactions is a relevant question for restoration ecologists. Complex top-down and bottom-up interactions

govern species populations in aquatic systems and how restoring physical habitat interacts with these to facilitate changes across multiple scales of biological organization (e.g. individuals, populations, communities, food webs, ecosystems) is little understood. More recently there have been calls from within the literature for the incorporation of food web approaches into biomonitoring protocols to better understand how communities function and the potential indirect effects of management actions and environmental changes (Bellmore et al 2017, Feld et al 2011b, Friberg et al 2011, Naiman et al 2012, Pander & Geist 2013).

Food webs are models of ecological interactions; 'trophic links' (i.e. consumer-resource relationships) are established between trophic components or 'nodes' (e.g. species), which can then be scaled up to build complex networks representing entire communities or ecosystems (Pimm et al 1991). These can shed light on the energy pathways through a community from basal nutrient resources, through primary and secondary producers on to top predators (Kiffney et al 2014, Woodward et al 2008).

Food web theory has been applied across a range of freshwater systems, providing insight and advancing our understanding into how community structure and functioning is both maintained and also affected by perturbations such as warming, acidification, species invasion, overharvesting and eutrophication (Layer et al 2010b, O'Gorman et al 2012, Petchey et al 1999, Thompson et al 2016, Woodward 2009). The importance of top-down and bottom-up processes are widely acknowledged in freshwater systems (Carpenter et al 1985). In flowing waters, predatory fish can produce powerful top-down effects, known as 'cascades', substantially reducing the density of grazing prey (i.e. herbivores) and pushing the system towards autotrophy (Jones & Sayer 2003, Persson 2001, Woodward et al 2008).

Food webs have revealed patterns in consumer-resource relationships, such as body-size. Aquatic communities are typically 'size-structured' with energy flowing from smaller resources to larger consumers (Woodward et al 2005). Incorporating species mean individual body mass (log M) and numerical abundance (log N) biomass in 'trivariate food webs' allows this biomass flux through ecosystems to be both visualized and analyzed. This information, alongside feeding links can be used

Despite their demonstrated importance in explaining community structure and function in lakes, food web approaches have rarely been applied to rivers, and even less so river restoration (Lake et al 2007). This probably reflects the challenges of effectively monitoring systems that are both highly dynamic and 'open': with highly mobile species able to move (or be transported) into, or out of, study areas. The effective characterisation and quantification of food webs is also challenging, with substantial terrestrial subsidies and diverse assemblages. Additionally, pain-staking analysis of many hundreds or thousands of individuals of each species is often necessary in order to gain the full set of feeding links within a food web (e.g. Ings et al., 2009). This is rarely practical given financial and time restraints of research funding (Grey et al 2015). As a consequence, many of the most highly resolved food webs to date describe comparatively simple communities in headwater systems, or pelagic zones in lakes, noticeable examples including the Broadstone stream in England, the Breitenbach in Germany and Tuesday Lake in the USA (Carpenter et al 1987, Layer et al 2011, Schmid-Araya et al 2002).

However, ecological networks are also constructed by incorporating species interactions from the published literature (Cohen et al 1985, Strong & Leroux 2014), or by blending observational and extrapolated data, providing a compromise based on both empirical and inferred feeding links (Gray et al 2015, Layer et al 2013, Pocock et al 2012). These methods alongside advances in computational power facilitate the construction of food webs for more complex systems and in this thesis I draw on these to construct and analyse the faunal assemblage of a diverse and complex lowland river.

1.2 Aims and thesis structure

The primary objective of this study was to measure the ecological impact of reach-scale river habitat restoration using large wood and frame this in the context of gauging its efficacy for recovering faunal biodiversity. I specifically wanted to reveal new insight into the mechanisms and factors that wood influences to drive changes in the macroinvertebrate and fish assemblages. In order to do this, I use standardised and quantitative biomonitoring throughout the project, complimented by BACI methodology to mitigate potentially confounding environmental noise.

The River Great Stour, a productive chalk river with a valuable trout fishery in South East England, provides a model system for Chapters 3-5 facilitating comparison of the results from these chapters to draw general overview and summary of the effect of the large wood restorations on the stream ecology. The partnership with a fisheries association provides a real world context for the study.

Chapter 2 – 'General Methods and Hydromorphological Response'
Here I provide details on the site location, the restoration design, as well as biomonitoring, sample processing and data analysis methods consistent throughout Chapters 3-5. I then describe the response of the stream hydromorphology in terms of flow, depth and substrate.

Chapter 3 – 'Not the only fish in the river: interspecific responses to a species-led conservation measure'
Here I undertook biannual fish surveys in spring and autumn before restoration and up to 14 months after restoration to investigate the impact of large wood on the fish assemblage. Alongside more general assemblage metrics, I specifically investigated the response of a target species and two of its predators.

Chapter 4 – 'Restoration of stream networks: investigating the effect of large wood addition on food web structure'
In this study I apply network methods to macroinvertebrate and fish biomonitoring data to construct food webs, using both gut contents analysis and inferred feeding interactions derived from published studies.

Chapter 5 – 'River restoration and ecosystem functioning: investigating the impact of reach scale restoration on leaf-litter breakdown'
Here I present a study in which I investigated the effect of large wood on macroinvertebrate mediated detrital breakdown, a fundamental ecosystem process often assumed to be enhanced by restoration with large wood.

Chapter 6 – 'River restoration and volunteer engagement: advancing the role of citizen stakeholders from advocate to evaluator'
Here I discuss how through engaging river users and restoration stakeholders and providing a standardised protocol for detecting community change, they can not only assess their efforts but also contribute to the restoration evidence base.

The flow diagram in Figure 1.3 provides an overview of the thesis structure:

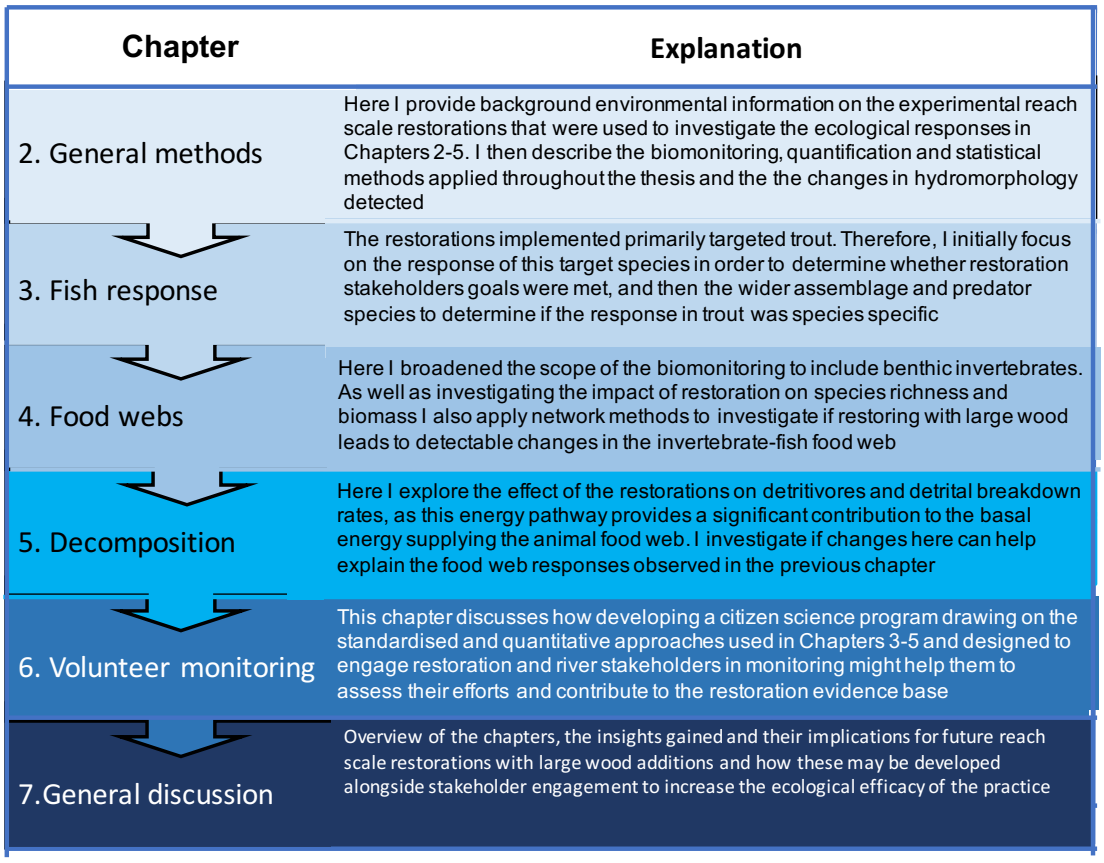


Figure 1.3: Flow diagram of the thesis structure with abbreviated chapter titles and an explanation as to the chosen order.

Chapter 2 | General methods and hydromorphological response

2.1 General methods



Cover image 1 Positioning the large wood in the River Great Stour, spring 2014, showing the fixed bank design approved by the environment agency.

2.1.1 The chalk stream environment

Chalk streams are the product of rare geological conditions and systems of global significance, 85% of which are found in England. These are supplied by groundwater aquifers formed from the gradual percolation of rainwater through highly porous and permeable calcareous chalk rock ($CaCO_3$). This process enriches the water with minerals such as calcium and buffers pH levels to between 7.4 – 8.0 (Berrie 1992). Combined with high water clarity, stable flows and temperatures, this leads to high rates of primary production made possible in these shallow, nutrient rich waters (Dawson 1976). These conditions support high species richness, and the abundance and biomass of the macroinvertebrate and fish assemblages can be exceptional

(Wright 1992). These unique characteristics also provide optimum conditions for salmonid production and growth (Mann et al 1989, Pulg et al 2013)

Chalk streams are located in some of the most intensively managed and densely populated landscapes in the world. These systems are therefore rarely in a natural state (Berrie 1992). Human activities such as abstraction, agriculture, pollution and physical modifications have had wide-ranging impacts on hydromorphology and water quality in these systems, with deleterious effects on ecology (Berrie 1992). For instance, increased nutrient loading via agricultural run-off and wastewater treatment effluent can result in declines in macrophyte diversity and eutrophication. Similar de-oxygenating effects may be caused by heightened siltation, resulting in the loss of sensitive fish and benthic macroinvertebrate species (Berrie 1992). Additionally, abstraction for agriculture and domestic water supply can disrupt natural flow regimes; reduced water levels can exacerbate anoxic conditions by elevating temperatures and even lead to dry river beds (Wright 1992).

The distinct biodiversity of chalk streams has both high amenity and recreational value, especially to anglers, and the intensive surrounding land-uses mean that these systems are typically chosen for reach-scale restoration. Their potential to support high biodiversity coupled with suites of globally widespread stressors therefore provides an ideal setting for testing the efficacy of restoration in the real world.

2.1.2 Study site

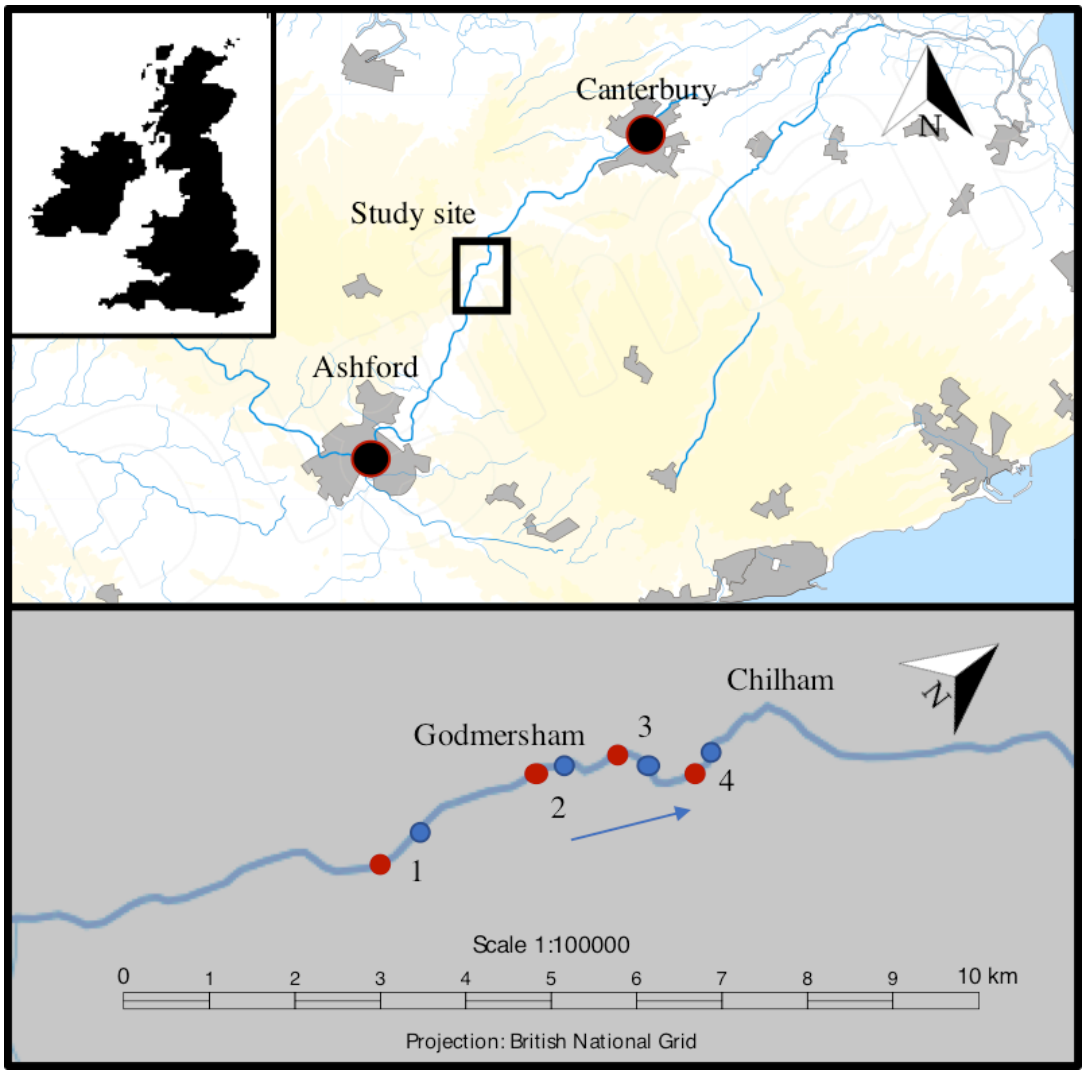


Figure 2.1 A map of the study sites on the River Great Stour, showing the four study sites with paired upstream control (red) and downstream restored (blue) reaches, as well as the two urban centres of Ashford and Canterbury. The light yellow shading illustrates the chalk aquifer, which is charges the river at after the confluence of the tributaries in Ashford.

The studies in Chapters 3 -5 were conducted on the River Great Stour (henceforth Stour), a third-order lowland river in Kent, UK (51 13' 1626" N, 0 57' 2370" E) (Figure). The study area was situated along 4.5 km of river almost equidistant between the urban centres of Ashford, 7 km upstream (population > 74,000) and Canterbury 8 km downstream (population > 55,000) of the study area midpoint (Figure 2.1). The river is fed by a combination of surface water run-off and groundwater, draining greensands and Weald clay in the headwaters prior to their

confluence at Ashford, and charged by the North Downs chalk aquifer downstream of Ashford and in the study area. This unique geology means that the river exhibits a 'flashy' hydrological regime, with rapid rises in water levels following rainfall, supported by more stable baseline flows from the chalk aquifer. Mixed arable and pasture agriculture is the predominant land use in the catchment.

The system has a long history of extensive modification; reach-scale influences include extensive channelization for historic navigational purposes, dating back to 1515. This included a number of canals and locks built to facilitate trade between the town of Ashford, Canterbury and Europe (Hadfield 1969). While their use has long been abandoned, flood alleviation measures have meant that some straightened sections have been maintained via dredging (EA 2009). Ashford has been marked since the 1960's as a place for expansion, and abstraction and urbanisation have been associated with declines in water quality, with nitrate and phosphate pollution historically contributing to algal blooms of *Cladophera glomerata* during summer low flows (Bolas & Lund 1974). In addition, in 2006 the Environment Agency discovered that "feminisation" of 25% of the male roach (*Rutilus rutilis*) population had occurred in close proximity to a wastewater treatment discharge at Bybrook in Ashford. The recent improvement of wastewater treatment works prior to the study (early 2013) has led to considerable improvement in water quality since, however, nitrate pollution continues to be considerably higher than the majority of European rivers and English chalk streams, and moderately enriched with soluble reactive phosphorous and both are deemed "poor" by WFD standards (Figure 2.2).

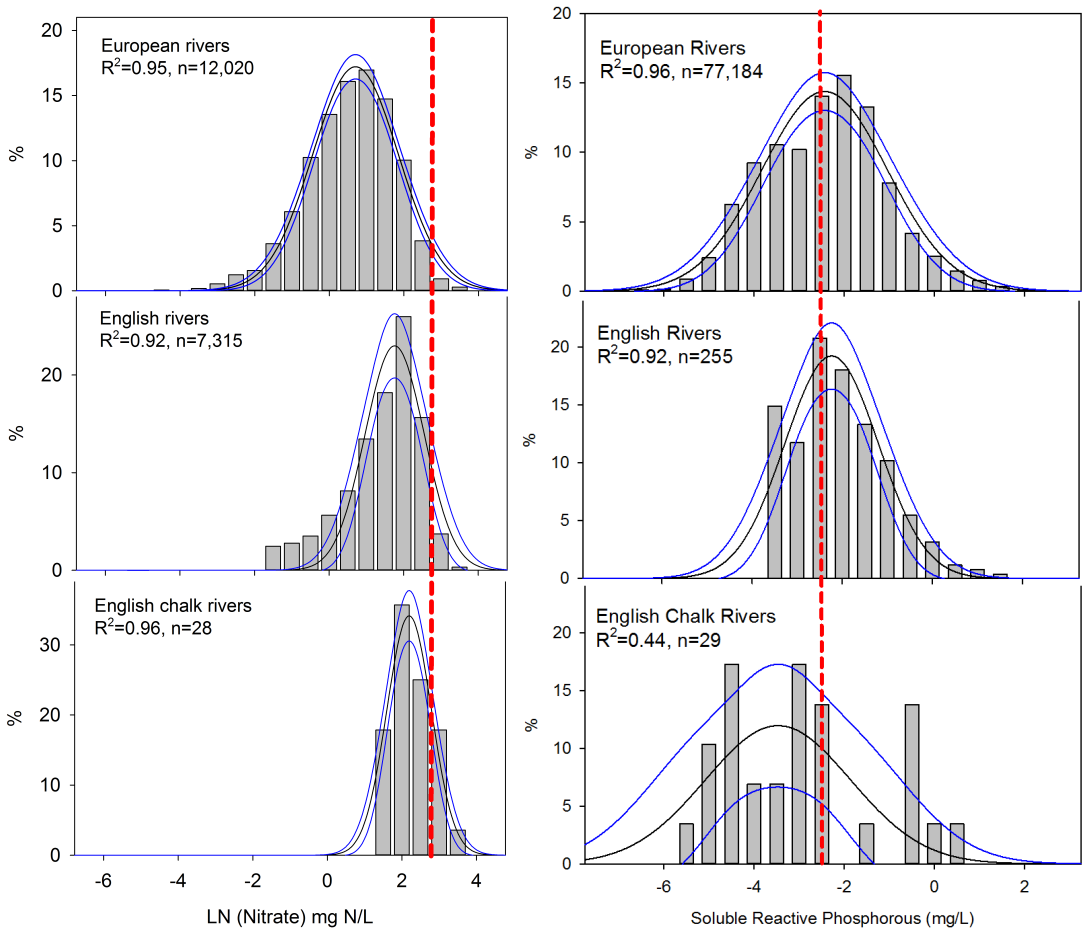


Figure 2.2 Surface water nitrate concentration (natural log transformed) and soluble reactive phosphorous surface concentration in rivers across Europe (EEA Database), across England (EA database) and across lowland chalk rivers, plotted as frequency histograms with Gaussian regression curves (black line) fitted and 95% confidence intervals (blue) and the River Stour marked by the red dashed line (figures made in collaboration with Felicity Shelley).

2.1.3 Restoration Design

Four x100m reaches were selected for restoration along 4.5 km river managed by the Stour Fisheries Association (SFA), a local angling organisation (coordinates provided in Table 2.1). Sites were selected using the following hierarchical criteria: permission from landowners and Environment Agency for the proposed restoration works, ease of access to the sites for implementing works, no nearby potential point source pollution hazards, similar hydromorphology and no natural large wood, a perceived need for habitat enhancement measures (i.e. reaches that appeared to be physically degraded/ simplified) and a comparable upstream (between 100m - 300m) control site. Site selection was a collaborative process with members of the SFA in an effort to ensure that they were representative of those typically chosen for reach-scale habitat interventions. Additionally, an effort was made to select sites that had similar

riparian and morphological characteristics to reduce the impact of potentially confounding environmental factors influencing restoration response and so comparisons between sites.

Table 2.1 Reach characteristics, mean width and average depth of wetted channel for the 50m sampling sites. Surface area was estimated by measuring channel width at 10-meter intervals in spring 2014.

Site	Width	Depth	Surface area	Site coordinates
C1	12.4	0.45	807	51 13' 4374" N, 0 58' 1074" E
I1	10.9	0.53	650	51 13' 5535" N, 0 58' 1074" E
C2	11.3	0.47	785	51 13' 3600" N, 0 57' 2728" E
I2	11.2	0.52	754	51 13' 3774" N, 0 57' 54387" E
C3	12.6	0.53	758	51 13' 2294" N, 0 57' 2748" E
I3	10.5	0.38	694	51 13' 302" N, 0 57' 2994" E
C4	9.7	0.43	580	51 12' 2449" N, 0 56' 5377" E
I4	9.6	0.47	571	51 12' 9873" N, 0 57' 2494" E

Riparian zones ranging from 5- 10 m bordered all sites. The riparian vegetation neighbouring the study reaches was largely dominated by willow (*Salix spp.*), and alder (*Alnus glutinosa*) and is often associated with ash (*Fraxinus excelsior*) oak (*Quercus spp.*) and to a lesser extent hazel (*Corylus avellana*), the understory was dominated by nettle (*Urtica dioica*), bramble (*Rubus fruticosus*) and the invasive species Himalayan balsam (*Impatiens glandulifera*). Pathways have been maintained on at least one bank to maintain access for anglers, however these are separated from the river wetted channel by approximately 3m of dense low lying vegetation.

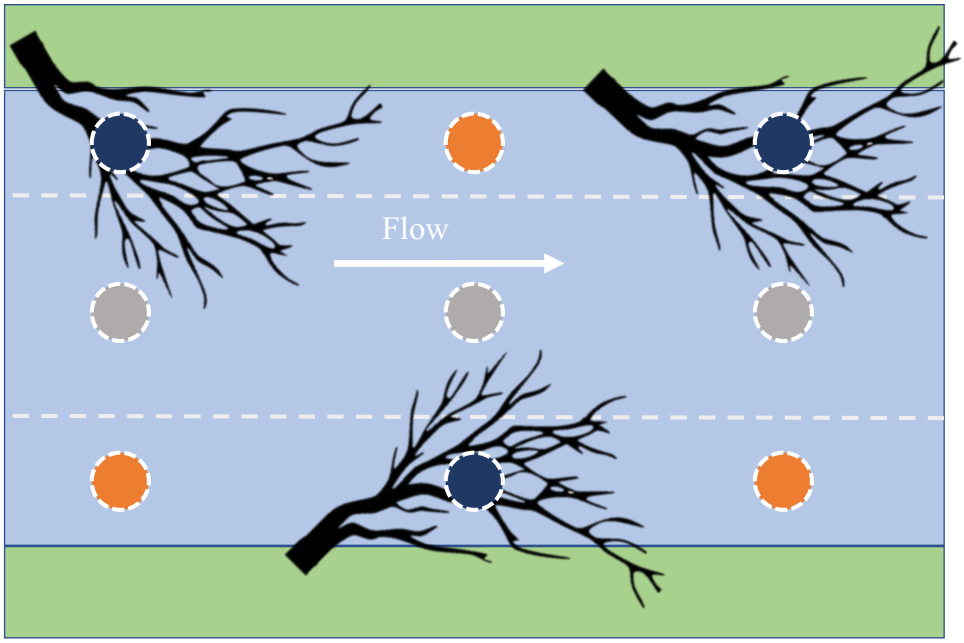


Figure 2.3 Plan view schematic of the restoration and invertebrate sampling design, 3 Hess sample technical replicates were taken for each habitat type midstream (grey), margin (orange) and large wood (dark blue).

2.1.4 Invertebrate sampling

Invertebrate sampling methods, which are consistent throughout the study, are presented here. A bespoke 152.44mm diameter aluminium Hess sampler with 335 microns mesh was used to collect invertebrates. Hess sampling was chosen over a Surber sampling as the design allows for sampling in ponded and/ or deeper areas. Additionally, rows of "teeth" were fitted to the Hess sampler to cut through smaller branches associated with large wood habitat at a depth of up to 50mm of the sediment. Samples were immediately immersed in either ethanol 90%, preserving contents for later identification in the laboratory. After separation from debris, individuals were identified using a 40-100x magnification microscope to the highest possible taxon (usually species) in the laboratory and counted.

2.1.5 Fish Sampling

Quantitative depletion electrofishing was performed on each 50m reach enclosed with 10-mm mesh aperture nets at both upstream and downstream reach limits. Fish were captured using a boat-mounted Easyfisher EFU-1 Electric Fishing unit using minimum 3-pass depletion methods (Carle & Strub 1978). Each pass consisted of one

run starting at the downstream end and moving upstream zigzagging laterally in a bank-to-bank fashion to ensure all habitats were thoroughly covered by the electrical pulse (Thompson et al 2016). This required a minimum of four participants, 2 operating the anodes and 2 capturing stunned fish and placing them in aerated buckets for later processing. The maximum number of passes was based on the rate of depletion in successive fishing with a minimum of three passes, further passes were used in instances where depletion had not been sufficient. Fish captured were anaesthetized with clove oil to reduce handling stress. All individuals were identified to species level and fork length measured to the nearest mm and mass to the nearest 100 mg recorded. After measurement, fishes were placed in a bucket and released back into the river after they had sufficiently recovered.

2.1.6 LWD restoration

The large wood restorations were installed simultaneously in late March 2014. In keeping with recreating natural tree fall and natural loading, native trees commonly found in riparian zones were chosen and selected based on their proximity to the river. The primary species used was alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*) and willow (*Salix spp.*), only dead wood (diameter > 0·1 m and a length > 1 m, (Gregory et al 2003) was used in order to prevent regrowth, and so meeting statutory flood consent conditions. These conditions also demanded more conservative bank-fixed structures extending no more than three meters into the channel, instead of cross channel wood installations (Figure 2.4). Dead wood was left largely unmodified (some branches protruding from the water were removed so that fishing was not obstructed) in order to better emulate natural large wood loading (Roni et al 2015). The wood was then pinned into position using chestnut (*Castanea spp.*) stakes driven into the sediment (at least 0.8 m), and fastened using galvanised wire, this was also part of the statutory flood consent conditions and necessary to minimise the risk of downstream transport and flooding. Structures were staggered from bank-to-bank in order to encourage sinuous flow (Figure 2.4). Each 100m restored reach had approximately 10 structures (5 on each bank).

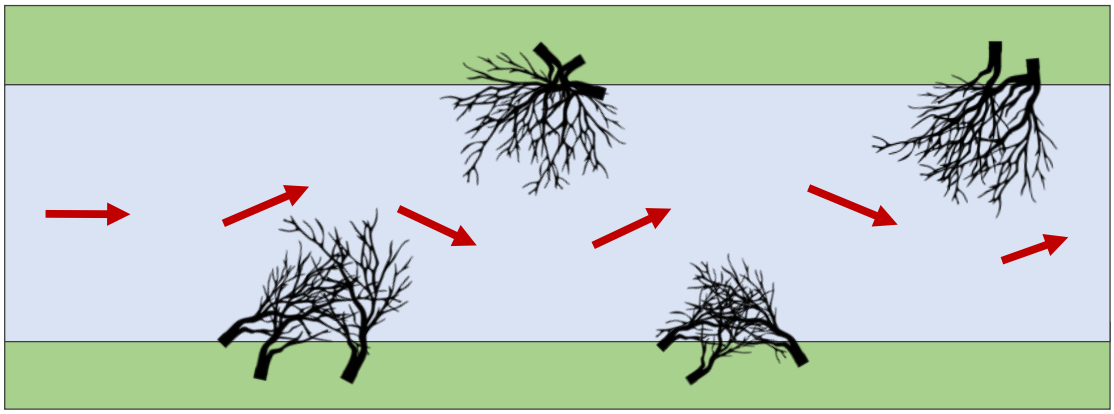


Figure 2.4 Plan view schematic of the restoration design, showing bank-fixed woody debris structures staggered from bank to bank, and anticipated shifting of flow (red arrows).

2.1.7 Hydromorphological profiling

Habitat variables were sampled using bathyscope surveys and a 1m^2 quadrat for each habitat type at all sites in early spring (n = 5, per habitat per reach), prior to restoration in 2014 and after restoration in 2015 and 2016. River reaches were split into midstream (Mid) and margin, i.e. within 1 meter of riverbank and permanently wetted channel (Edge) habitats. Substrate composition was recorded to the nearest 5 % surface area of each type covered and depth was measured. Flow was measured using a VALEPORT BFM002 flow meter with impellor. Readings were taken at 60% depth at each quadrat. Annual averages of water chemistry data collated from the nearest Environment Agency monitoring station at Wye Bridge (51 10' 5485" N, 0 56' 1637" E) were used alongside point measures of temperature, dissolved oxygen and pH (Table 2.2).

Table 2.2 Mean annual River Stour water chemistry data from Environment Agency monitoring station at Wye Bridge ± standard errors.

Factor		2014		2015		2016	
	Unit	Mean	±	Mean	±	Mean	±
Alkalinity	mg/l	176.50	14.12	184.75	8.43	188.50	8.03
Ammoniacal Nitrogen	mg/l	0.05	0.01	0.22	0.14	0.06	0.01
Conductivity at 25 °C	us/cm	677.00	63.88	800.50	35.42	781.50	57.20
Nitrate	mg/l	11.93	2.65	13.60	3.00	16.00	3.29
Nitrite	mg/l	0.04	0.01	0.05	0.01	0.03	0.01

Orthophosphate	mg/l	0.25	0.04	0.39	0.12	0.29	0.05
Dissolved O_2	mg/l	8.50	0.48	8.72	1.36	10.09	0.62
O_2 % Saturation	%	80.13	5.25	79.03	8.38	89.80	2.70
pH		7.91	0.06	7.84	0.05	7.90	0.05
Temperature	°C	11.26	1.83	12.08	3.21	10.70	3.40

2.2 Hydromorphological response

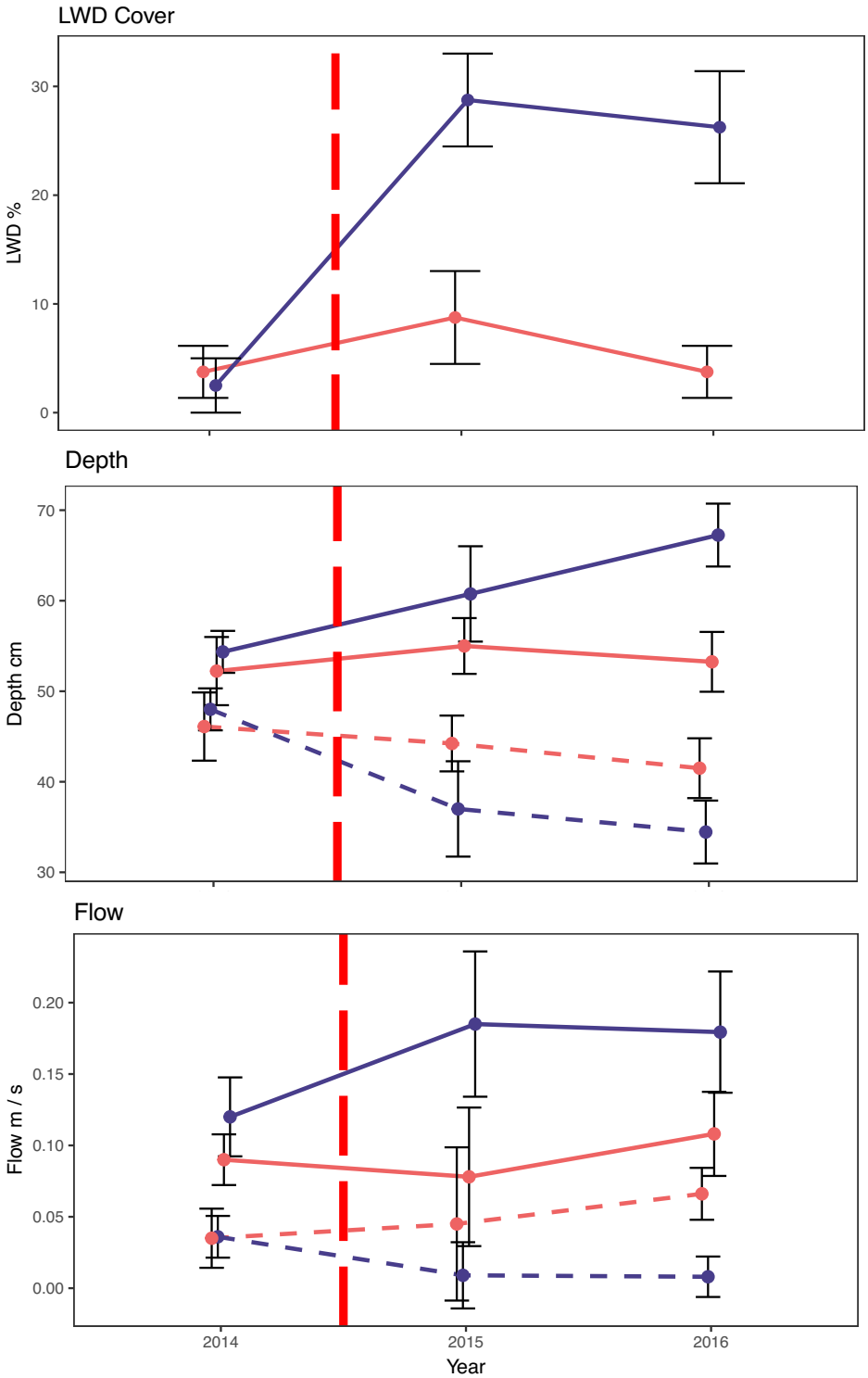


Figure 2.5: Annual recordings control in red and restored reaches in blue, the time of restoration is marked by a dashed red line, all with ± standard error bars. Top: large woody debris (LWD) cover as a percentage of the reach total; Middle: the average reach depth, with midstream as solid line and margin (1 m from bank) as dashed line; Bottom: flow in meters per second, again with midstream as a solid line and margins as dashed.

Prior to restoration, wood cover (i.e. naturally occurring large wood) as a percentage of total reach surface area was < 5% for both impact (i.e. to be restored) and control treatments (Top: Figure 2.5). Following restoration in 2015 this increased to an average of 28.5% in the restored reaches, there was a slight increase in the control reaches to below 7.5%. In 2016 there was a decrease in wood cover as high winter flows transported wood out of both reaches and washed out three of the restoration structures. This occurred in the upstream reaches where the substrate was finer. The bank-fixed wood additions led to an increase in flow in the midstream and decrease in the margin (Bottom: Figure 2.5), which increased the depth in the midstream and led to deposition in the margins (Middle: Figure 2.5), this change in flow was expected (Figure 2.4).

The higher velocity in the midstream of restored reaches led to substrate sorting, with gravel and cobble substrate switching to heavier cobble dominated substrate as gravels were transported downstream by higher flows (Figure 2.6). The slower flows in the margin habitat led to depositional areas immediately downstream of the structures, and a fine layer of silt was observed soon after restoration, which accumulated over time. Silt and sand become the dominant substrates in the margin habitat following restoration with large wood (Figure 2.6).

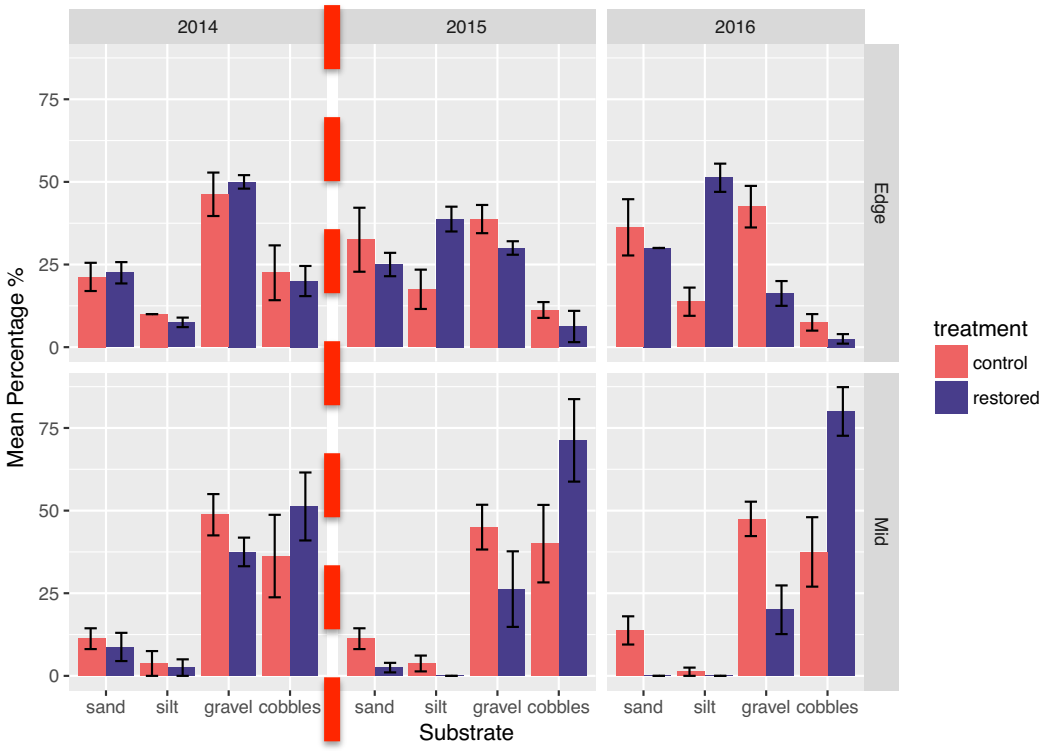


Figure 2.6: Mean percentage substrate composition with standard error bars in both margin (edge) and midstream (Mid) habitats, with control in red and restored in blue, recorded using bathyscope surveys. The time of restoration is represented by the dashed red line.

Chapter 3 | Not the only fish in the river: interspecific responses to a species-led conservation measure



Cover photograph 2: Electrofishing on the River Great Stour in Autumn 2015, with the stop net displayed in the fore ground for *k*-pass depletion electrofishing.

3.1 Abstract

The restoration of degraded habitat in physically modified rivers has become a core practice for conserving and recovering fish populations globally, particularly economically important salmonids. However, rigorous quantitative biomonitoring to assess the efficacy of these measures, in terms of achieving their desired effect on target species, remains scarce. In addition, the tendency to only biomonitor target taxa means the response of other species and the wider fish community are often missed. Given evidence of interspecific responses to such measures recorded in literature and the prevalence for strong density-dependent top-down control within aquatic systems, restoration may indirectly impact target species, by facilitating strong responses in predators. Therefore, there is a clear need to better understand the response of non-target species to restoration, especially predators of target species.

I used standardised, quantitative, biannual biomonitoring and a robust replicated before-after control-impact (BACI) design to capture the response of a diverse fish community to experimental large wood installation over a three-year period. The target species, *Salmo trutta*- a species of salmonid, drives significant investment in species-led habitat restoration. While the population response of this species was negligible, total fish biomass responded positively and was attributed to strong and rapid increases in piscivorous *Esox lucius* and *Perca fluviatilis* abundance and *E. lucius* biomass in reaches restored with large wood. We also captured positive responses to restoration in other fishes, as well as negative responses in smaller benthic species.

The differing interspecific responses of the fish assemblage to restoration demonstrates the importance of broadening biomonitoring beyond target species. The significant changes in predatory fish populations suggest that the benefits of species-led restoration measures to target species may be outweighed by increased top-down predation. This has important implications for the future of large wood as a salmonid management practice in systems where target species and predators co-exist and calls for more studies investigating the impact of restoration on trophic dynamics.

3.2 Introduction

In Europe, it is estimated that 64% of rivers have not achieved good ecological status as defined by the EU Water Framework Directive (WFD) (Kristensen, 2012). Halting and reversing these declines in river biodiversity has become a commonly accepted societal goal in many developed nations (Bernhardt & Palmer, 2011; Bernhardt et al., 2005; Kail, Brabec, Poppe, & Januschke, 2015). It is widely assumed that in-stream habitat plays a crucial role in structuring riverine communities, particularly fish species, and that the physical degradation of habitat via channelisation practices, such as dredging- that remove natural hydromorphological features and channel complexity, has contributed to declines in fish populations (Howson, Robson, Matthews, & Mitchell, 2012; Pander & Geist, 2013; Schinegger, Trautwein, Melcher, & Schmutz, 2012). This has led to the assumption that by restoring habitat heterogeneity in physically degraded, homogenised systems, salmonids and other fish populations will recover (Margaret A Palmer, Ambrose, & Poff, 1997). This has established the installation of in-stream structures such as boulders, deflectors and large woody material (henceforth large wood) as a global fisheries management practice to assist the recovery of declining fish populations (P. Roni, Beechie, Pess, & Hanson, 2015; Thompson, 2006).

The installation of large wood for restoring salmonid fish habitat is over three centuries old (Van Cleef, 1885), with various books and technical manuals published aimed at guiding practitioners and anglers on the most effective designs (e.g. Hunt, 1976; P. Roni et al., 2015). Yet, of the estimated tiny proportion (<10%) of restoration projects that have any form of assessment (Bernhardt et al., 2005), the majority are anecdotal qualitative reviews incapable of measuring the strength of responses or providing the statistical power necessary for drawing firm conclusions (Morandi, Piegay, Lamouroux, & Vaudor, 2014). Of those that do use quantitative approaches, the failure to apply robust monitoring designs can mean results are spatially and temporally confounded, with less than 0.2% of restoration projects monitored effectively using before-after control-impact (BACI) designs (Christian K Feld et al., 2011).

Restoring with large wood has been found to lead to largely predictable improvements in fish habitat metrics including: pool frequency, pool depth, woody debris, habitat heterogeneity, complexity, spawning gravels, or sediment and organic matter retention following large wood installation (Cederholm et al., 1997; Haase et al., 2013; Kail et al., 2015; Larson, Booth, & Morley, 2001; P. Roni et al., 2015). However, while studies have detected positive responses in fish populations to restoration (Sievers, Hale, & Morrongiello, 2017; Whiteway, Biron, Zimmermann, Venter, & Grant, 2010), others have found the response of fish populations has been weak (Jahnig et al., 2011; Miller et al., 2010; Margaret A. Palmer, Menninger, & Bernhardt, 2010), negligible (Pretty et al., 2003; Stewart, Bayliss, Showler, Sutherland, & Pullin, 2009; Thompson, 2006), and in some cases, negative (P. Roni et al., 2015), even where substantial improvement to physical habitat has been recorded. The lack of consistent responses to restoration measures across space and time suggests that habitat restoration may not always be effective for restoring fish populations in rivers. There is therefore a clear need to biomonitor restoration on individual systems using replicated, quantitative approaches to gauge the efficacy of these measures and prevent the wasteful repetition of ineffective restoration measures (Bernhardt et al., 2005).

The disproportionate focus on salmonids as the primary target of such measures reflects their cultural, recreational and economic value. These species generate significant income to public statutory environmental protection agencies and other river stakeholders (such as landowners and angling associations), through the sale of rod licences and fishing permits (Kemp et al., 2017; Mawle & Peirson, 2009; P. Roni et al., 2015). However, the identification of fish assemblages as indicators of restoration success, and their more recent inclusion as a 'biological quality element' for assessing the ecological state of rivers in the WFD (WFD; 2000/60/EC), has led to increasing calls to broaden the focus of restoration from single species to the wider fish community (Haase, Hering, Jahnig, Lorenz, & Sundermann, 2013; S. Schmutz et al., 2016).

Another factor commonly overlooked is interspecific responses to restoration measures, as no species exists in a vacuum, measures are likely to affect other species

within the community (Lorenz et al., 2013; S. Schmutz et al., 2016; Vander Zanden, Olden, & Gratton, 2006). Studies have found variable interspecific responses to restoration measures in fish species (Lorenz et al., 2013; S. Schmutz et al., 2016). For instance, a study by Lorenz et al. (2013), found that out of 21 species monitored, piscivorous pike (*Esox Lucius*) populations were negatively impacted by river restoration measures, and another found that pike were extirpated from the system entirely following weir removal to restore flow (Fjeldstad et al., 2012). Thus, restoration measures may directly alter the community composition by changing abiotic conditions.

As well as direct responses to altered habitat, biotic interactions might also indirectly impact restoration success. Strong density-dependent effects of top predators are common in aquatic systems, thus by favouring a predator, restoration measures may alter the strength of predator-prey interactions and so indirectly impact target species (Diehl, 1992; Fjeldstad, Barlaup, Stickler, Gabrielsen, & Alfredsen, 2012; Klecka & (Diehl, 1992; Mittelbach & Persson, 1998; Persson, 2001; Power, 1990) . For instance, a study by Boss and Richardson (2002) found that restoring with large wood reduced predation related mortality by up to 50% in salmonids (Boss & Richardson, 2002). However, the impact of restoration measures in terms of altering biological interactions is rarely considered in river-restoration designs despite their potential for explaining the variable biotic responses of target species to restoration measures (Bellmore, Benjamin, Newsom, Bountry, & Dombroski, 2017; Naiman et al., 2012).

This is especially relevant in lowland calcareous rivers with diverse fish assemblages, here brown trout (*Salmo trutta*), a salmonid, rank among the most recognisable and distinctive fish species associated with these globally rare systems (Berrie, 1992; R. H. K. Mann, Blackburn, & Beaumont, 1989). The unique geological and physical characteristics of chalk rivers, such as aerated gravel necessary for spawning (Pulg et al., 2013), high secondary production, stable temperatures and stable flow, provide optimum conditions for salmonids (R. H. K. Mann et al., 1989). Salmonids grow faster, larger and reach greater abundances in these diverse systems than in other, oligotrophic and less species-rich surface waters where they are more commonly found (Kemp et al., 2017; R. H. K. Mann et al., 1989).

This attracts recreational anglers who pay to fish these waters at substantially higher cost compared to other inland fisheries, in turn driving investment in river management activities to conserve and restore this species. A report by the UK Environment Agency found that trout angling supports an estimated 6,000 jobs and generates £150 million in household incomes in England and Wales, with trout fishing in the southeast of England (where 80% of chalkstreams globally are located) contributing disproportionately more to the economy than other inland fishing practices (Mawle & Peirson, 2009).

However, nearly all lowland calcareous rivers are heavily impacted; widespread physical modifications associated with agricultural, domestic and industrial practices have altered river conditions threatening wild stocks of brown trout (Berrie, 1992; R. H. K. Mann et al., 1989). Channelisation has removed hydromorphological features such as islands, riffles, pools and woody debris, destroying and disrupting the processes responsible for creating habitats key to trout, such as aerated spawning gravels, refugia and riffles (Greig et al., 2007; Gurnell, Gregory, & Petts, 1995; R. H. K. Mann et al., 1989; Pulg et al., 2013; P. Roni et al., 2015). In these systems, as in much of culturally congested landscapes of lowland Western Europe, land availability and so the spatial extent of restoration is limited (Christian K Feld et al., 2011). Therefore, there is a strong demand for simple, cost effective, reach-scale restoration measures, to assist salmonid population recovery, such as instream additions or large wood (Kail et al., 2007).

Pike are known predators of brown trout and top-down control is of major concern for brown trout fishery stakeholders, and the practice of systematically removing this species from chalk streams by some river managers is widespread (R. Mann, 1985). I therefore investigated the response of this species, as well as another piscivore, perch (*Perca fluviatilis*), alongside the wider fish assemblage to estimate the impact of large wood additions on predator populations and so potential indirect benefits or disadvantages to trout.

Here I investigate the assemblage and population response of a diverse fish community to replicated reach-scale large wood restoration using the following specific hypotheses:

1) Restoration will increase total fish abundance, predator and species abundances per reach, including the target species *S. trutta*.
2) This will result in increased total WBM, predator WBM and species WBM in restored reaches.
3) The strength of response will vary between fishes.
4) Restoration will alter both the community abundance composition and WBM composition

3.3 Methods

Locations

Four sites were sampled on the River Stour. Each site had a 'restoration' reach, designated for large woody debris restoration, and an unrestored 'control' reach, which closely resembled the (pre) restoration reach in terms of channel form and riparian characteristics. These provided the four 'impact' (restored) and four 'control' sites necessary for our MBACI design (4x restored + 4 x control, $N = 8$). Reaches were 100 m in length, and at least 200 m apart in order to maintain independence (Harrison *et al.* 2004, Murray et al., 2017). While the use of 'reference' reaches to provide benchmark target conditions is often mentioned in studies, in many cases, such as in this experiment, such reference conditions are not available (Bernhardt et al., 2005). However, it should be noted that distances between reaches were within the home-range and migration of all species**,** so our results should be viewed as a conservative estimate of fish effects and differences among fish. At each restoration reach, LWD installations were undertaken in early February 2015, as described in detail Chapter 2.

Fish surveys

Fish surveys were undertaken using quantitative depletion electrofishing at each control and restoration site blocked at both ends with 5-mm mesh nets, as described in the General Methods Chapter 2 (See Cover Photograph 2). Biannual, rather than annual surveys were chosen to increase the temporal resolution and help track responses to restoration measures through time. Each site was surveyed a total of five times, twice prior to restoration in late-April and mid-October before restoration in 2014 and three times after the restorations took place in February 2015, at the same time intervals up to 2016 (8 reaches x 5 time points, i.e. total number of surveys $N = 40$). Fish from each pass were identified to species level, apart from roach (*Rutilus rutilus*) and dace (*Leuciscus leuciscus*) which are known to hybridize in this system and were therefore grouped together in their subfamily Leuciscinae. Fish were

measured for length (fork length in mm) and mass (g), and then returned to the reach.

Assemblage and population abundance and biomass estimation

All fish except stocked brown trout were included in the analysis. For each reach, total fish abundance (per 100 m bank-length of river) was estimated using iterative multiple-pass method Maximum Weighted Likelihood statistics (Carle & Strub, 1978). Species average wet-mass (g) was estimated for each species by dividing total recorded wet mass for each species by the actual abundance (Table 1). Fish wet biomass mass (WBM per 100m reach) was then estimated by multiplying average wet-mass by the estimated reach abundance, the sum of which was used to estimate total wet biomass per reach.

Data analysis

Models were used to test the effect of the restoration on the abundance and WBM (per reach) of the total fish assemblage, 'predators' (the piscivorous *E. Lucius* and *P. fluviatilis* species combined) and species populations. For abundance, generalized linear mixed effects models (GLMMs) were fitted using a Poisson distribution were used. For biomass, data was log+1 transformed and linear mixed effects models (LMMs) were used to meet test assumptions and the incidence of 0 catches. Rare species (abundance < 10) (*A. brama, B. barbus, G. aculeatus*) were not analyzed at the species level but were included in total abundance and biomass estimates.

The effect of factors Period (before restoration and after restoration) and Treatment (restored and control/unrestored) and the interaction between the two (i.e. Period * Treatment = BACI effect) were tested. Site (one of the four locations with control and impact reaches, $N = 4$), *Reach* (control and restored study reaches, $N = 8$) and Season (spring and autumn, N = 2) were treated as having a random effect on the intercept of the linear relationship. Models were simplified using AIC values to drop random variables that did not reduce the AIC value (Crawley, 2012). All LMMs and GLMs were performed using the lme4 package in R (Bates, 2018).

In order to control for any temporary disturbance impacts of restoration the third sampling point, spring 2015 (2 weeks after the large wood installation) was not included in the LMMs or GLMMs, only four sampling points: spring and autumn 2014 (before restoration 'Before'); autumn 2015 and spring 2016 (after restoration 'After'), this also balanced the model (16 x Before + 16 x After, $N = 32$).

Non-metric Multidimensional Scaling (NMDS) was used to visualize changes in assemblage abundance and biomass compositions between treatments. These were then tested using permutational multivariate analysis of variance (PERMANOVA) with 999 permutations and pairwise PERMANOVA (pair-PERMS) contrasts to look for differences between treatments at each sampling date.

This assessed the explanatory power of restoration on the fish assemblages' composition and biomass and treated each Reach as random effect. Again, spring 2015 was excluded from this analysis, with Period and Treatment grouped to create a Factor variable consisting of four levels: CB = Control Before, RB= Restored Before, CA= Control After and RA = Restored After ($N = 32$). The samples were also split into spring ($N = 32$) and autumn ($N = 16$) and tested using PERMANOVA and pair-PERM to remove any confounding seasonal effects, with spring 2015 included. All NMDS plots and PERMANOVAs were performed using the vegan package in R (Oksanen et al. 2013), pair-PERMS were conducted using the pairwise-adonis function also in R (Martinez Arbizu, 2019).

3.4 Results

Table 3. 1 Species abundances for captured fish and depletion estimates with average mass for each species, fish in bold were not included in analysis.

Species	Captured	Estimate	Average mass
Abramis brama	1	1	15.8
Anguilla anguilla	527	600	136.9
Barbatula barbatula	1361	1724	4.9
Barbus barbus	9	9	54.5
Cottus gobio	781	965	3.3
Esox lucius	159	162	121.5
Gasterosteus aculeatus	5	5	1.4
Gobio gobio	626	739	13.4
Lampetra planeri	47	68	8.2
Leuciscinae	827	995	22.3
Perca fluviatilis	110	114	96.2
Phoxinus phoxinus	133	148	2.8
Squalius cephalus	34	34	327.4
Salmo trutta (Wild)	114	120	176.4
Salmo trutta (Stocked)	52	52	382.3
Total	4734	5684	

A total of 4734 fish were captured giving an estimated abundance of 5684 fish, from 14 species on five sampling dates (Table 3. 1). There were significant period x treatment interactions for abundance and biomass variables, however not in the target species *S. trutta* (Table 3.2, Table 3.3). Total abundance of fish did not respond to restoration, however there was a significant effect of period, with more fish in both treatments after restoration (Figure 3. 1a, Table 3.2). Total WBM did respond to restoration, increasing in restored sites (Figure 3. 1 b, Table 3.3). Conversely, piscivores increased in abundance following restoration (Figure 3. 1c; Table 3.2), but their biomass did not change significantly between treatments but was higher in both treatments after restoration (Figure 3. 1c, Table 3.3).

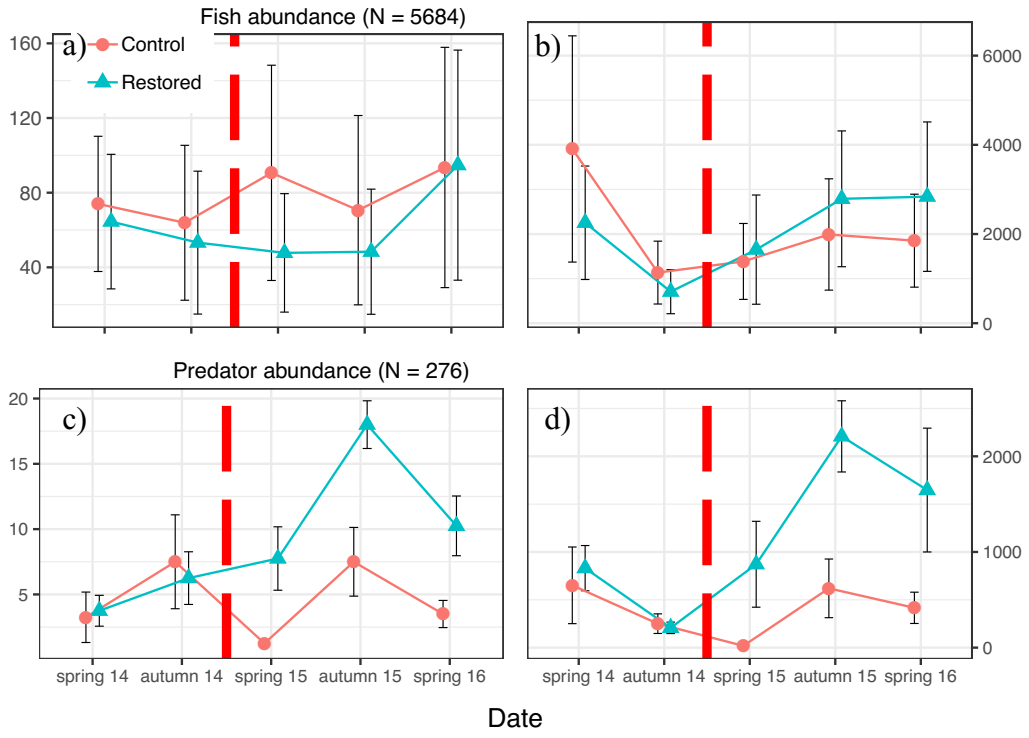


Figure 3. 1 The abundance and biomass per reach of total fish (a, b) and piscivores (c, d) over time in restored (blue triangles) and control (red circles). Points show mean values, ± s.e.m. The red dashed line representing the introduction of large wood.

Both piscivore species, *E. lucius* and *P. fluviatilis*, increased in abundance following restoration (Figure 3.2c, 3.2e, Table 3.2), however, only *E. lucius* increased in WBM (Figure 3.2d, Table 3.3). The target species, *S. trutta*, failed to show and response to restoration in terms of abundance and WBM (Figure 3.2a, Figure 3.2b, Table 3.2, Table 3.3), however there was a spike in abundance and WBM in both treatments in autumn 2015 (Figure 3.2a, 3.2b).

Table 3.2 Statistics of fit for the generalized linear mixed effects models on fish abundance data (*N* = 32). All models include a main effect of treatment, period and the interaction between the two (BACI), and optimized using the random effects of reach, season and sample date on the intercept of the linear relationship depending on lowest AIC values. Significance stars; * = p = 0.05 to 0.01, ** = p = 0.01 to 0.001, *** = p <= 0.001 = *.**

Response variable	Source	df	Estimate	SE	Z	P	
Total	Treatment	26	-0.318	0.298	-1.069	0.285	
	Period		0.032	0.012	2.631	**0.009**	**
	Treatment:Period		0.046	0.018	2.560	0.095	
Predator	Treatment	26	-0.469	0.453	-1.035	0.301	
	Period		0.012	0.075	0.153	0.878	
	Treatment:Period		0.331	0.099	3.354	**0.001**	***
S. trutta	Treatment	26	-0.116	0.798	-0.145	0.885	
	Period		-0.038	0.227	-0.169	0.866	
	Treatment:Period		0.146	0.144	1.015	0.310	
E. lucius	Treatment	27	-0.405	0.430	-0.942	0.346	
	Period		-0.054	0.149	-0.365	0.715	
	Treatment:Period		0.311	0.124	2.507	**0.012**	*
P. fluviatilis	Treatment	25	-0.260	0.854	-0.305	0.761	
	Period		0.082	0.115	0.714	0.476	
	Treatment:Period		0.353	0.157	2.243	**0.025**	*
A. anguilla	Treatment	25	-0.668	0.272	-2.460	**0.014**	*
	Period		-0.218	0.036	-6.015	**0.000**	***
	Treatment:Period		0.111	0.056	2.001	**0.045**	*
B. barbatula	Treatment	25	-0.047	0.260	-0.181	0.856	
	Period		-0.008	0.068	-0.124	0.902	
	Treatment:Period		-0.096	0.032	-3.003	**0.003**	**
C gobio	Treatment	25	0.440	0.528	0.833	0.405	
	Period		0.336	0.031	10.864	**0.000**	***
	Treatment:Period		-0.248	0.046	-5.428	**0.000**	***
G gobio	Treatment	25	-0.262	0.588	-0.446	0.656	
	Period		-0.228	0.065	-3.530	**0.000**	***
	Treatment:Period		0.031	0.053	0.581	0.561	
L. planeri	Treatment	25	1.333	1.338	0.996	0.319	
	Period		0.318	0.173	1.841	0.066	
	Treatment:Period		-0.033	0.190	-0.171	0.864	
Leuciscinae	Treatment	26	-1.929	0.957	-2.016	**0.044**	*
	Period		0.403	0.388	1.038	0.300	
	Treatment:Period		0.449	0.055	8.151	**0.000**	***
P. phoxinus	Treatment	26	-8.292	1.961	-4.228	**0.000**	***
	Period		0.798	0.174	4.581	**0.000**	***
	Treatment:Period		1.836	0.375	4.891	**0.000**	***
S. cephalus	Treatment	26	-1.929	0.957	-2.016	**0.044**	*
	Period		0.403	0.388	1.038	0.300	
	Treatment:Period		0.449	0.055	8.151	**0.000**	***

Table 3.3 Statistics of fit for the linear mixed effects models on log+1 transformed biomass data (*N* = 32). All models include a main effect of treatment, period and the interaction between the two (BACI), and optimized using the random effects of reach, season and sample date on the intercept of the linear relationship depending on lowest AIC values. Significance stars; * = p = 0.05 to 0.01, ** = p = 0.01 to 0.001, *** = p <= 0.001 = *.**

Response variable	Source	*SS*	*df*	*F*	*P*	
All	Treatment	0.069	27	0.215	0.646	
	Period	1.115	27	3.470	0.073	.
	Treatment:Period	2.080	27	6.473	**0.017**	*
Predator	Treatment	0.230	6	3.674	0.104	
	Period	1.209	22	19.317	**0.000**	***
	Treatment:Period	0.090	22	1.443	0.242	
S. trutta	Treatment	0.287	6	0.059	0.816	
	Period	3.066	2	0.627	0.511	
	Treatment:Period	4.764	20	0.975	0.335	
E. lucius	Treatment	4.029	6	1.746	0.235	
	Period	4.670	22	2.024	0.169	
	Treatment:Period	15.019	22	6.507	**0.018**	*
P. fluviatilis	Treatment	7.339	6	2.145	0.193	
	Period	57.844	22	16.908	**0.000**	***
	Treatment:Period	0.145	22	0.042	0.839	
A. anguilla	Treatment	0.244	6	1.721	0.238	
	Period	0.005	2	0.037	0.865	
	Treatment:Period	1.701	20	11.985	**0.002**	**
B. barbatula	SiteClass	0.608	26	0.486	0.492	
	Period	0.040	2	0.032	0.874	
	SiteClass:Period	0.082	26	0.065	0.800	
G. gobio	Treatment	0.651	6	0.375	0.563	
	Period	0.286	2	0.165	0.724	
	Treatment:Period	0.024	20	0.014	0.908	
C. gobio	Treatment	1.772	26	0.890	0.354	
	Period	0.549	2	0.276	0.652	
	Treatment:Period	2.696	26	1.354	0.255	
L. planeri	Treatment	0.062	26	0.031	0.861	
	Period	1.673	2	0.844	0.455	
	Treatment:Period	0.264	26	0.133	0.718	
Leuciscinae	Treatment	0.922	6	0.327	0.588	
	Period	1.571	2	0.557	0.533	
	Treatment:Period	4.289	20	1.522	0.232	
P. phoxinus	Treatment	1.246	6	1.046	0.346	
	Period	15.205	22	12.763	**0.002**	**
	Treatment:Period	0.131	22	0.110	0.743	
S. cephalus	Treatment	2.026	6	0.399	0.551	
	Period	1.719	22	0.339	0.566	
	Treatment:Period	85.457	22	16.844	**0.000**	***

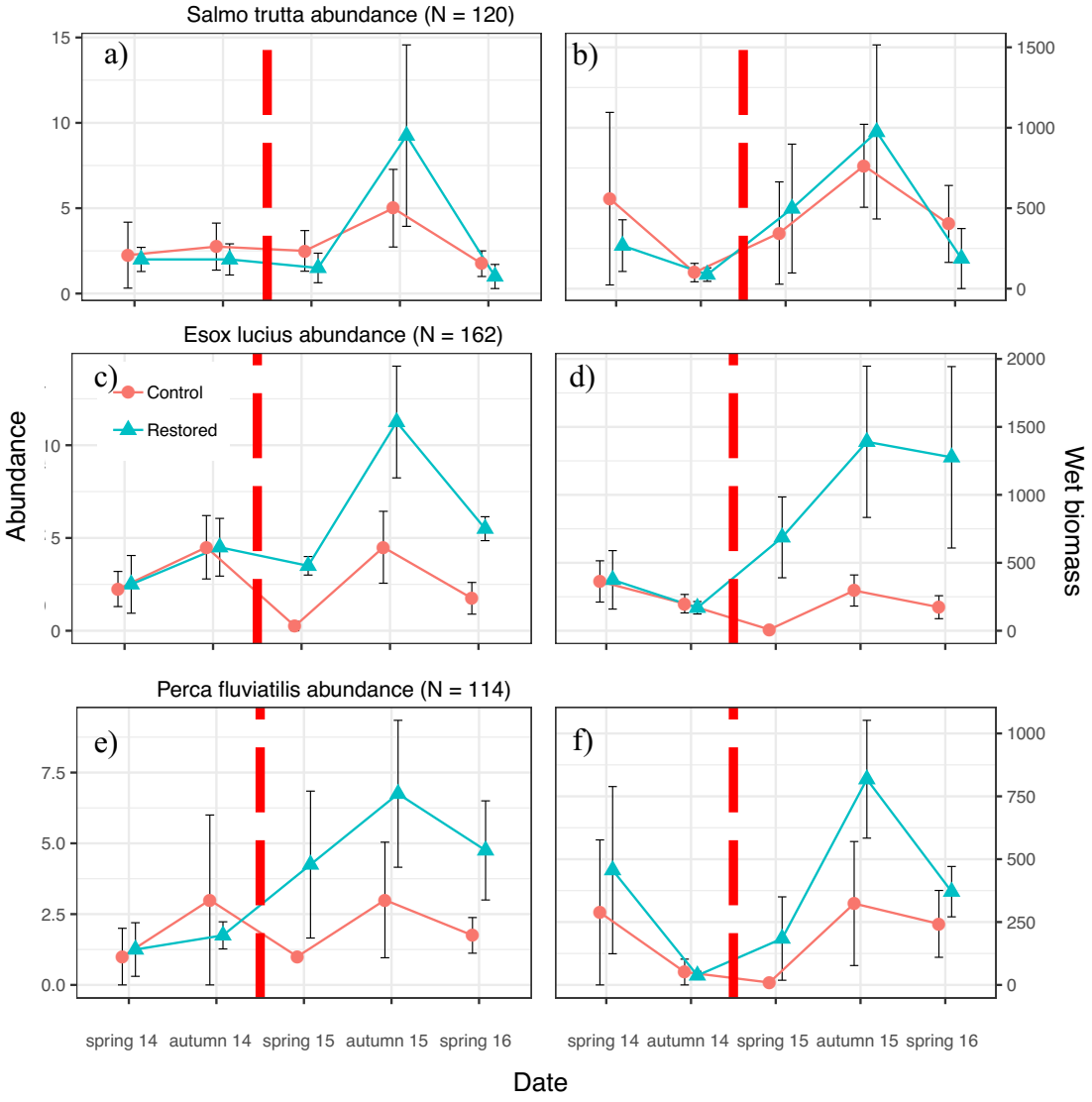


Figure 3.2 The abundance and biomass per reach of the fish species *S. trutta* (a, b), the piscivores *E. lucius* (c, d) and *P. fluviatilis* over time in restored (blue triangles) and control (red circles). Points show mean values, ± s.e.m. The red dashed line representing the point of restoration.

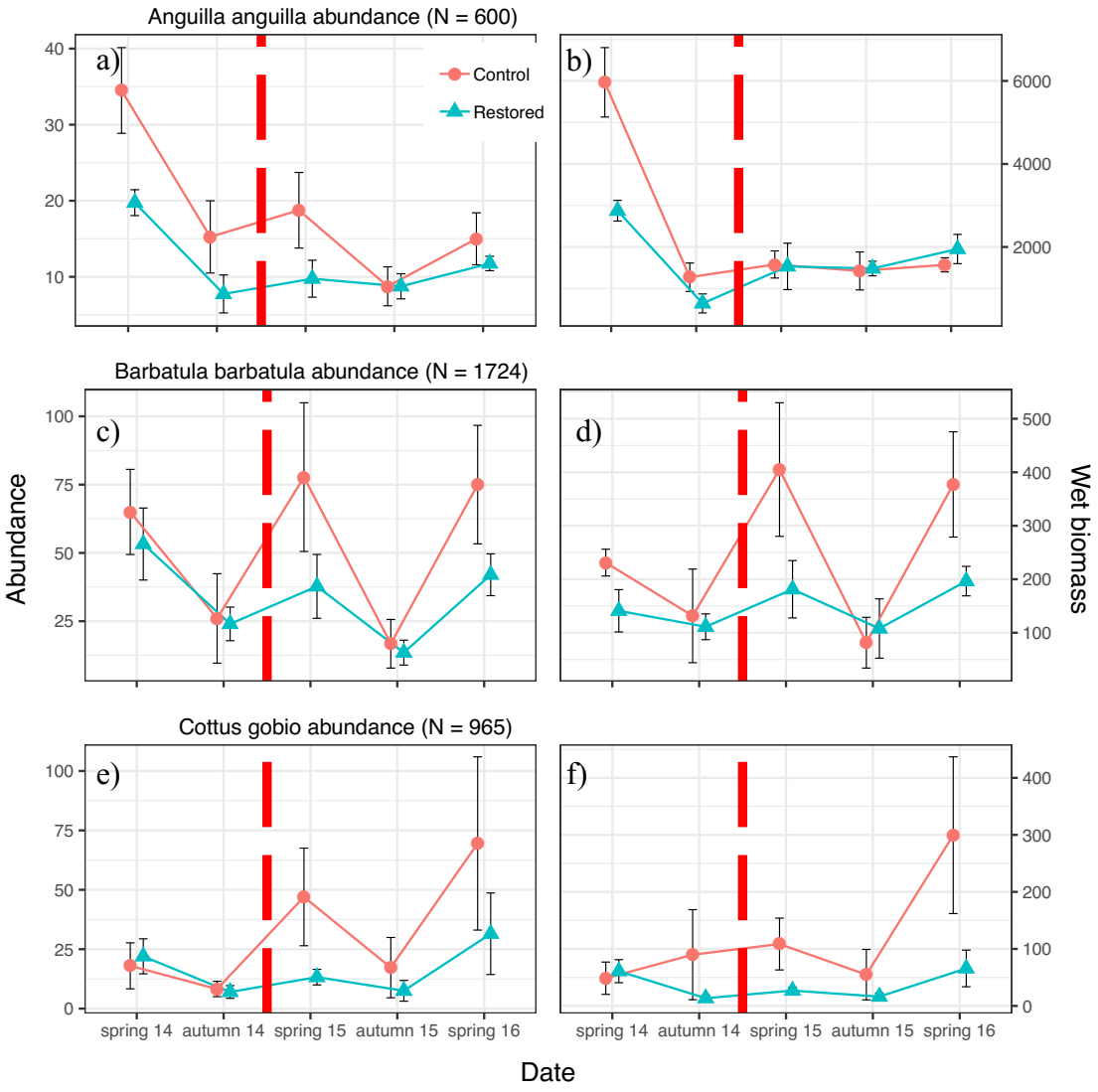


Figure 3. 3 The abundance and wet biomass per reach of the fish species *A. anguilla* (a, b), *B. barbatula* (c, d) and *C. gobio* over time in restored (blue triangles) and control (red circles). Points show mean values, ± s.e.m. The red dashed line representing the point of restoration.

Other species that showed significant period x treatment interactions by increasing in abundance include *A. anguilla*, Leuciscinae, *P. phoxinus* and *S. cephalus* (Figure 3. 3a, 3.4e, 3.5a, 3.5c; Table 3.2). With *A. anguilla* and *S. cephalus* also increasing in WBM in restored sites (Figure 3.3b, 3.5d; Table 3.3). However, restoration with large wood also negatively impacted fish species, decreasing the abundances of the smaller benthic species *C. gobio* and *B. barbatula* (Figure 3.3c, 3.3e, Table 3.2).

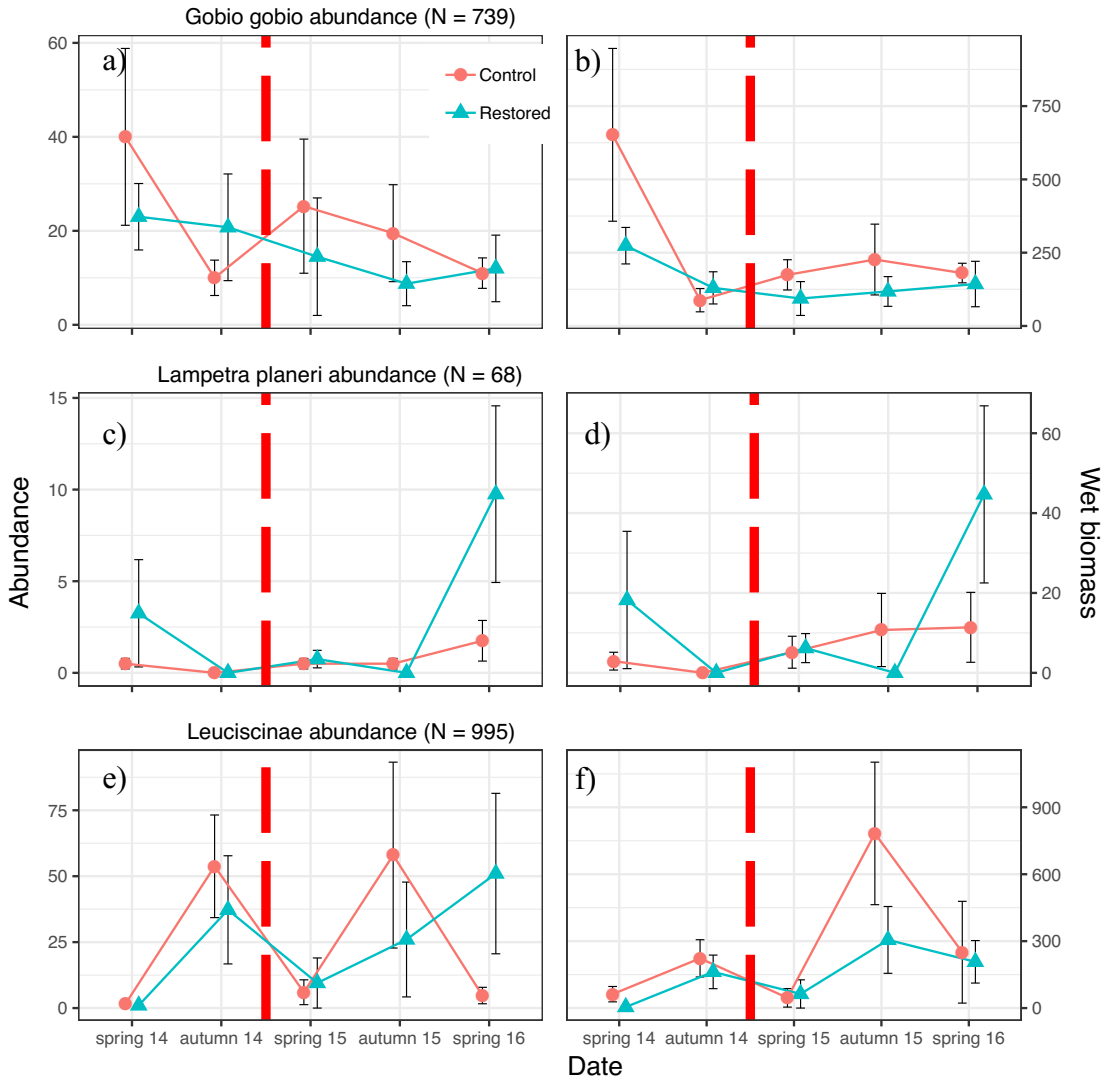


Figure 3.4 The abundance and wet biomass per reach of the fish species *G. gobio* (a, b), *L. planeri* (c, d) and Leuciscinae over time in restored (blue triangles) and control (red circles). Points show mean values, ± s.e.m. The red dashed line representing the point of restoration.

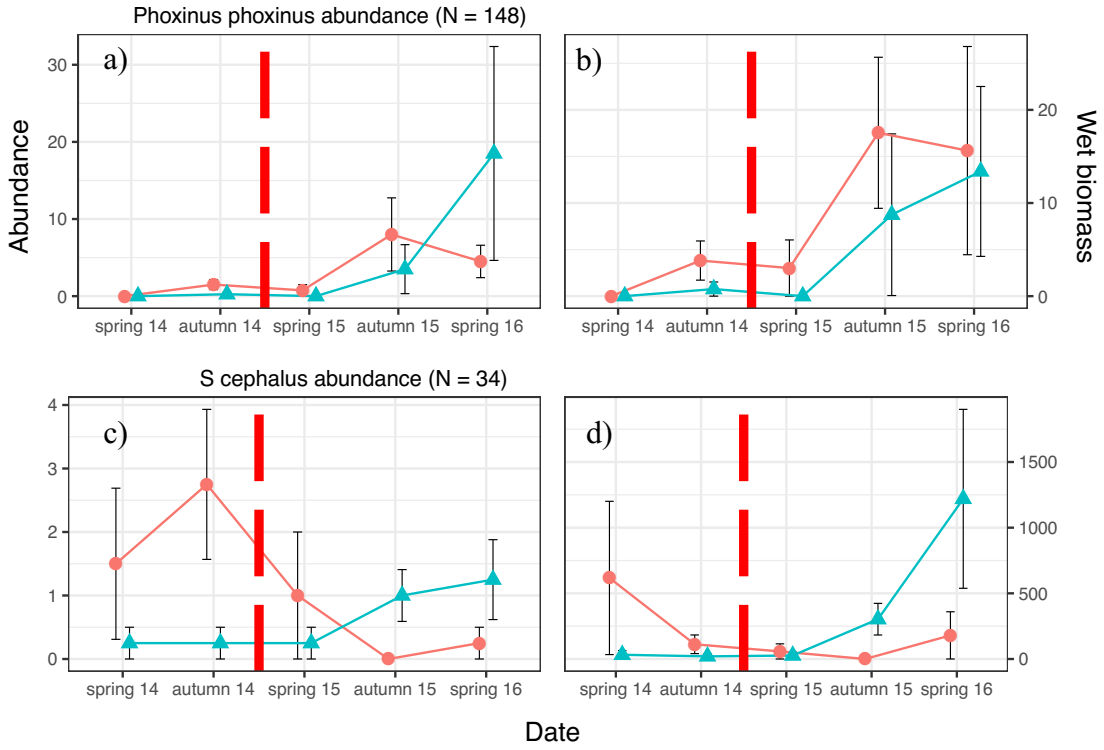


Figure 3.5 The abundance and wet biomass per reach of the fish species *P. phoxinus* (a, b) and *S. cephalus* (c, d) over time in restored (blue triangles) and control (red circles). Points show mean values, ± s.e.m. The red dashed line representing the point of restoration.

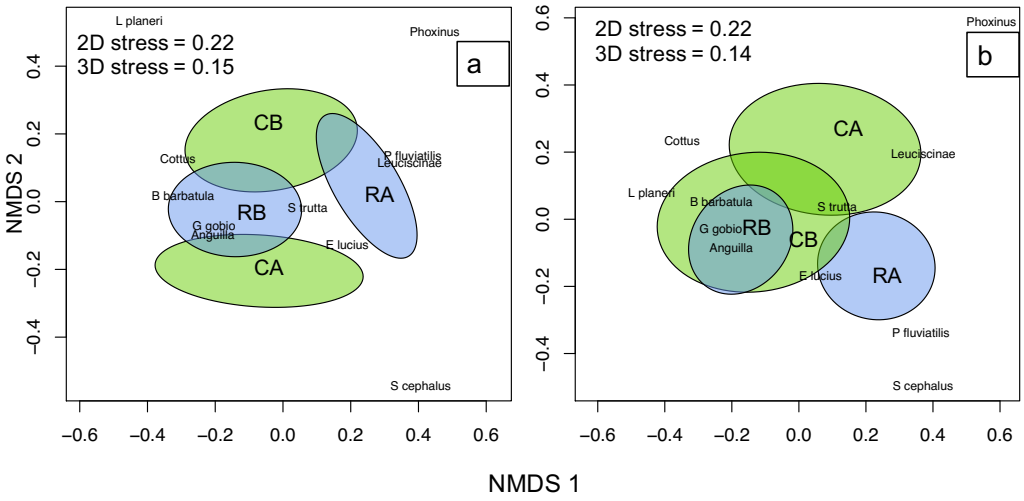


Figure 3.6 NMDS of fish species abundances (a) and biomass (b) with the spring 2015 excluded (*N* = 32). 'C' and 'R' denoting the treatments control (green) and restored (blue), and B and A the period before or after restoration, e.g. CB = Control Before.

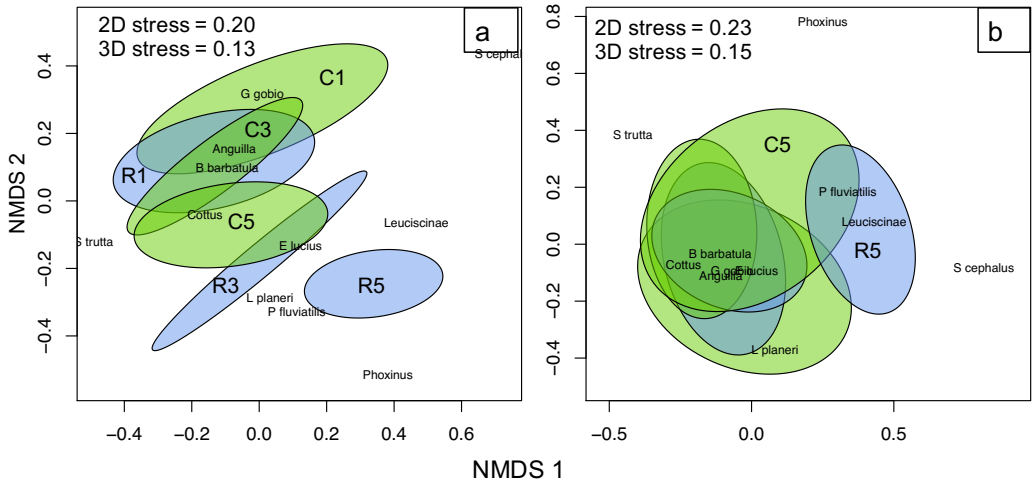


Figure 3.7 NMDS of fish species abundances (a) and biomass (b) only including spring sampling and including spring 2015 (*N* = 24). 'C' and 'R' denoting control (green) and restored (blue) and 1, 3 and 5 the sampling round, e.g. C4 = Control 4.

NMDS of the BACI data suggested that CA and RA samples might differ significantly in both abundance and biomass composition as the standard error ellipses did not overlap (Figure 3.6). In the spring samples, the ellipse for R5 (i.e. restored 3.5) also appeared to be isolated from the other Treatment: Sample round combinations Figure 3.7.

However, PERMANOVAS revealed significant Period x Treatment effects in mass composition for BACI biomass and spring biomass, but did not detect changes in the composition species abundance (Table 3.4). Pair-PERM comparisons of both spring biomass found that restored before was significantly different from restored after (F = 3.556, P = 0.018, N = 16) and control after differed significantly from control before (F = 2.675, P = 0.007, N = 16, **Error! Reference source not found.**), but no significant differences between the *Treatment:sample round* interaction (**Error! Reference source not found.**).

Table 3.4 Effect of treatment, period and the interaction between the two (i.e. BACI) on community and biomass structure using PERMANOVA with 999 permutations, Bray-Curtis dissimilarity and *Reach* as a random effect.

Variable	Source	*R2*	*P*	
Abundance composition BACI	Period	0.052	0.089	.
(N = 32)	Treatment	0.021	0.220	
	Period x Treatment	0.020	0.642	
Mass composition BACI	Period	0.103	**0.006**	**
(N = 32)	Treatment	0.036	**0.002**	**
	Period x Treatment	0.060	**0.048**	*
Abundance composition spring	Period	0.084	**0.006**	**
(N = 24)	Treatment	0.102	**0.001**	***
	Period x Treatment	0.035	0.286	
Mass composition spring	Period	0.069	**0.005**	**
(N = 24)	Treatment	0.140	**0.003**	**
	Period x Treatment	0.081	**0.035**	*
Abundance composition autumn	Period	0.050	0.359	
(N = 16)	Treatment	0.071	0.164	
	Period x Treatment	0.033	0.852	
Mass composition autumn	Period	0.051	**0.016**	*
(N = 16)	Treatment	0.266	**0.008**	**
	Period x Treatment	0.100	0.164	

3.5 Discussion

Studies using standardised, replicated, reach-scale interventions are seldom found in the restoration literature. My findings provide no compelling evidence to support the use of reach-scale large wood as a measure for conserving and recovering trout populations, with the large wood restorations failing to produce any detectable changes in their population over the duration of the study. These findings provide a robust BACI study that joins the already equivocal evidence base supporting wood and other in-stream installations as a means to restoring salmonid populations (De Jong, Cowx, & Scruton, 1997; Pretty et al., 2003; Stewart et al., 2009), and run contrary to the positive results reported in other studies (Kail et al., 2007; Nagayama & Nakamura, 2010; Sievers et al., 2017). Increasing *S. trutta* abundance by reducing mortality is often a goal of restoration measures and species management in general (Pulg et al., 2013), and my results do not suggest that large wood lifted these constraints.

Given the negligible response of the target species to large wood restoration, the strong BACI response found for the piscivore populations are striking. This not only demonstrates that the restorations did produced a detectable ecological response, but also demonstrated the highly variable interspecific responses to interventions (Lorenz et al., 2013). This provides more evidence that species led interventions are likely to transcend target species and have wider impacts on the community of which they are a part (Naiman et al., 2012). The significant responses measured in piscivorous fish species, which are known predators of the target species, (especially juvenile) trout (R. Mann, 1985), provides an interesting factor that is routinely ignored in such studies.

Pike responded contrary to expectations inferred from other studies (Fjeldstad et al., 2012; Lorenz et al., 2013), evidently favouring reaches restored with large wood. The more conservative design of the large wood installations, necessary to meet flood consent conditions, had the opposite effect to a project in Norway, in which weir removal resulted in higher flow rates that extirpated pike from the system and

switched the community back to one dominated by salmonids (Fjeldstad et al., 2012). This may be due to the specific changes in the rivers hydromorphology detected in Chapter 2; in which while velocity increased in the midstream, the woody structures created slower flowing marginal habitat. This may have benefitted these piscivores, by improving their hunting success by providing cover, and/ or concentrating prey resources (Diehl, 1992; Horinouchi et al., 2009).

The predation-refuge hypothesis is one of the key theories underpinning the use of large wood as a salmonid and fish conservation measure (Boss & Richardson, 2002; Diehl, 1992), and a study on the closely related salmonid, cutthroat trout (*Oncorhynchus clarki*), indicated that the addition of wood cover reduced predation mortality by as much as a half (Boss & Richardson, 2002). My findings suggest that in this case the opposite may be true, as predation pressure is often density dependent and therefore increased predator abundance following restoration may strengthen top-down control of trout populations in restored reaches. This opens up the possibility that in systems heavily managed for salmonids where these piscivores are found, habitat restoration may have a facilitative effect on their predators and so a net-negative effect on the target species. This may also explain the perception among anglers that routine controlling of *E. lucius* populations is necessary in these systems (R. Mann, 1985).

However, it should also be highlighted that no negative effects of large wood were detected on *S. trutta*, indicating a neutral effect, as benefits from improved habitat quality (if any) may be evened out by increased predation pressure. As the fish community on the Stour is diverse with many species are at much higher densities than trout, these may be the primary prey of the piscivorous fish. This is not the case for the smaller benthic species *B. barbatula* and *C. gobio*, who showed negative responses to wood additions as abundances were lower in restored reaches. Gut contents analysis of 55 pike collected in spring 2017 yielded no salmonids, but found these more abundant, smaller benthic species made up the majority of the pike's diet (Chapter 4). In addition, a study on two comparable calcareous streams also found pike predation on salmonids to be negligible (R. H. K. Mann, 1976).

There may also be behavioural factors at play, the stratification of midstream and

marginal habitat into faster flowing deeper cobble substrate (discussed in Chapter 2: Hydromorphological Response) preferred by salmonids, and slower flowing marginal habitat with more cover, preferred by pike (Fjeldstad et al., 2012), may increase the spatial segregation of the two species and reduce predatory interactions. However, the fact that this preferred habitat did not yield higher trout numbers compared to the controls, suggests that trout may actively avoid reaches with higher predator densities, and such avoidance behaviour by salmonids has been observed in laboratory experiments (Keefe, 1992).

Time-scales may explain the lack of response, and these have been demonstrated to be far longer (>10 years) in fish (Trexler, 1995), than this study. Although, in Ireland increases in density and abundance were found to occur 1-2 years after restoration (Lehane, Giller, O'halloran, Smith, & Murphy, 2002), and respondents in Kail et al.,'s (2007) review reported significant increases in abundances 2 years after placement, and a 15-fold increase in number after 3.5 years.

Numerous projects highlight the importance of spatial scale and extent of restorations, with ecological response scaling with size (S. Schmutz et al., 2016; Stefan Schmutz et al., 2014). The large wood installation extent and spatial scale (100m reach) of this project was constrained by flood risk concerns, and were far from the 1.95 km threshold identified by Schmutz et al's (2016) review. Therefore our restorations may not have been extensive enough to re-instate hydromorphological processes necessary for shaping habitat diversity, such as scouring and riffle formation (Bernhardt & Palmer, 2011; S. Schmutz et al., 2016). However, given the intensive land-use practices encroaching chalk streams, the high densities of multiple landowners and flood risk, the feasibility of restoring at these catchment scales in Western Europe is severely limited (C. K. Feld et al., 2011; S. Schmutz et al., 2016). Therefore, cost-effective reach-scale solutions to catchment scale issues must be thoroughly explored.

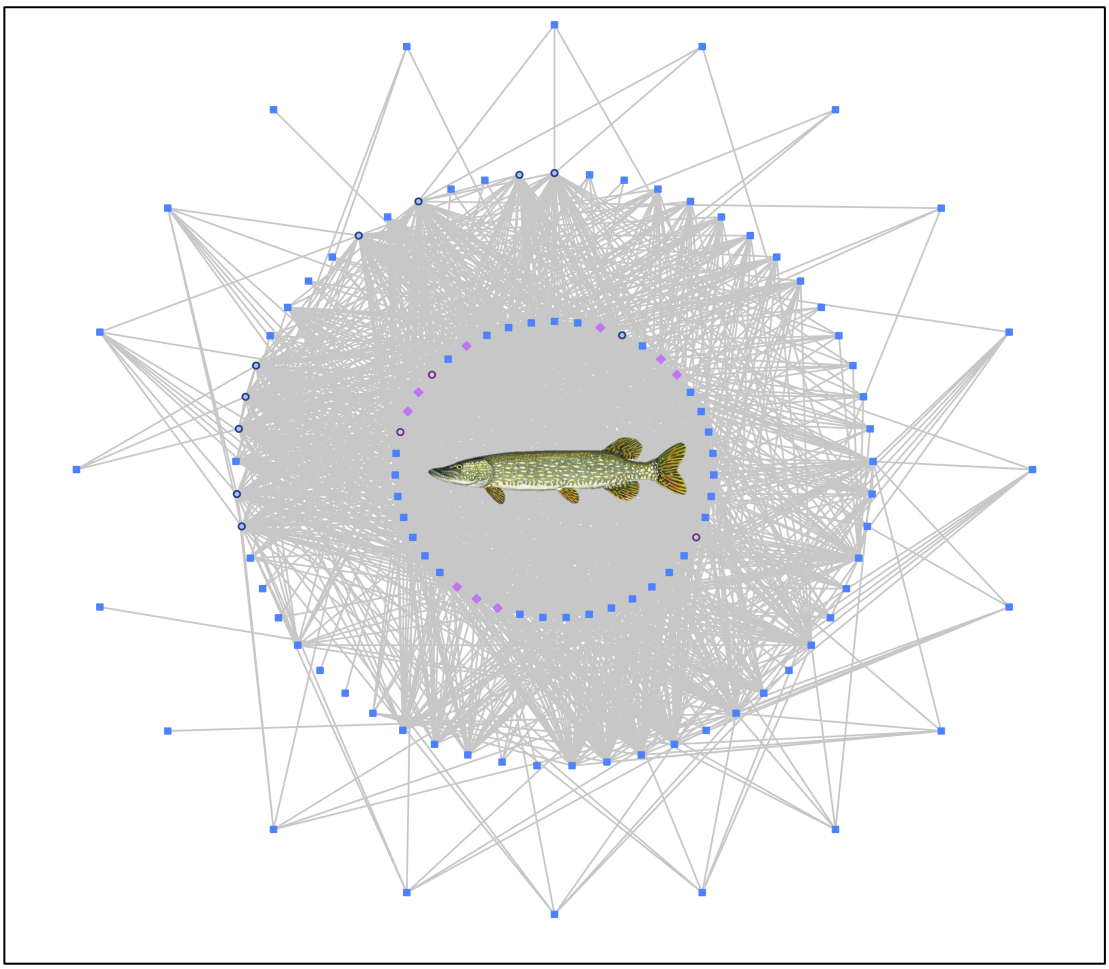
Total fish abundance did not respond to large wood restoration in this study, despite significant increases observed in others. In Lorenz et al.'s (2016) review, which looked at the response of over 20 species in 36 river restoration projects fish abundances increased by over 100 fish per 100 m of river in restored reaches, with

pike the only species to be negatively affected. However, I found that total fish biomass did increase, if only when pike were included, and this has been seen in other large wood restoration studies, although often coupled with increased abundances (Nagayama & Nakamura, 2010).

3.6 Conclusion

The results of this study highlight the importance of broadening the scope of monitoring beyond the target species using robust monitoring designs, which continues to be exceptional. It also suggests that changes in non-target species may provide crucial insight into the variable responses found in target populations. The biannual monitoring meant that even over a short time frame the study provided rare insight into the time-scale and trajectory of responses, an area of river restoration ecology that remains poorly understood. There is little doubt that large wood installation can increase salmonid abundances in some instances, yet the factors that drive these positive outcomes remain largely unknown. This study therefore highlights the need for species-led management measures to consider the responses of predators, as these may alter predator-prey interactions and ultimately outweigh the positive benefits and ultimately have a net-negative effect on target species. While biomonitoring of whole assemblages may be more expensive, known predators of target species should be included as a minimum in order for a more thorough appraisal of the efficacy of restoration and species management, in order to screen for potential indirect effects. The strong response in pike has important implications for the future application of large wood as a management practice for trout conservation in systems where pike are known to coexist.

Chapter 4 | Restoration of stream networks: investigating the effect of large wood addition on food web structure



Cover image 3 The faunal food web of the River Great Stour, centred on the top predator pike (*Esox lucius*). All grey lines linking species are feeding links. Symbols: blue squares = invertebrates; pink diamonds = fish; circles = cannibalistic species.

4.1 Abstract

Restoring river habitat is now a core practice implemented by river managers on a global scale, based on the assumption that recovering structural habitat heterogeneity will facilitate the re-establishment of biodiversity. However, biotic interactions are rarely included in restoration assessment, despite their demonstrated role in regulating biotic communities. Thus our understanding of how restoration alters top-down and bottom-up controls to explain observed population and community composition changes remains weak. Food webs have revealed how, by altering the strength of interactions, changes in environmental conditions can indirectly drive changes to aquatic community structure and biodiversity, for instance via trophic cascades. In the context of restoration, these may help explain the inconsistent responses to similar restoration measures across space and time, enhancing our ability to predict community responses and so what drives successful restoration.

Here I apply food web approaches to investigate how restoring with large wood affects the structure of the macroinvertebrate and fish assemblage and food web. I used replicated and standardised quantitative biomonitoring methods and a before-after control-impact (BACI) design and high taxonomic resolution. Gut contents analysis (GCA) was used to reveal the dietary composition and dominant resources of the most abundant fish species (excluding protected species) and linked to observed changes detected in Chapter 3. These observed feeding links were then grouped with inferred (from literature) feeding links to construct food webs, with both binary (i.e. presence-absence) and trivariate (i.e. incorporating abundance, body-size and biomass) response variables to examine how restoration alters the food web.

Gut contents analysis revealed that piscivore diets were dominated by *C. gobio* and *B. Barbatula*, both species which declined in restored reaches. The majority of invertivore fish diets were made up of comparatively few taxa: Ephemeroptera, Trichoptera and Diptera however these did not respond to restoration. Large wood altered the food web structure with increased species richness of invertebrate and fish ‘nodes’ (i.e. taxa) and feeding links between species over time. In restored reaches fish biomass also increased as found in Chapter 3, and the assemblage mass-abundance scaling relationship became less negative, indicating more efficient energy transfer from resources to predators.

This work demonstrates the insights and explanatory power of incorporating food web measures in to restoration monitoring. Studies able to demonstrate biomass flux, a proxy for energy flow, between species and their resources following habitat restoration are almost entirely lacking in the literature. These findings suggest that even over limited timescales, the restoration of habitat heterogeneity with large wood can facilitate measurable increases in biomass at higher trophic levels, traditional measures of success such as species richness. Therefore, food web approaches can provide both a holistic means verifying that traditional measures of success are accomplished, while advancing our understanding of the processes responsible.

4.2 Introduction

It is widely assumed that the 'biological annihilation', symptomatic of the 6th mass extinction event, is now well underway (Ceballos et al 2017). Rivers rank among the most severely affected ecosystems, with intensifying pressures, such as abstraction to meet the exponential water demand of a rapidly growing human population to widespread channelisation and intensive floodplain uses, continuing to degrade conditions on a global scale (Brookes 1988, Dudgeon 1992, Vorosmarty et al 2010). Thus, while disproportionately biodiverse, riverine species are disproportionately threatened, with greater population declines over the last 50 years compared to marine and terrestrial realms (Dudgeon 1992, McLellan et al 2014, Strayer & Dudgeon 2010).

Over the last 40 years there has been massive and exponential investment in river habitat restoration (henceforth restoration) activities to mitigate and reverse these adverse impacts (Bernhardt et al 2005, Feld et al 2011, Palmer et al 2014). By increasing physical habitat complexity and structure, via practices such as the installation of large wood and/or boulders, interventions are assumed to restore species richness and abundance/ or biomass (Brookes et al 1983, Palmer et al 1997). However, restoration science has failed to keep pace with implementation, largely due to a widespread lack of biomonitoring, with as few as 10% of projects thought to have any form of bioassessment (Bernhardt et al 2005, Morandi et al 2014).

Concerns regarding the metrics commonly used to assess restorations have also been frequently raised within the restoration literature (Feld et al 2011, Morandi et al 2014). While interventions are increasingly part of wider efforts for achieving more comprehensive 'ecosystem restoration': the recovery of as much taxonomic and functional diversity as practically possible while also enhancing ecosystem function (Entrekin et al 2009), this is poorly reflected in much of the biomonitoring that does take place (Feld et al 2011, Friberg et al 2011). The legacy of species-led projects (typically to recover fish populations) has kept the focus on target or indicator species and assemblages (e.g. fishes or macroinvertebrates) (but see Kail et al 2015). Empirical increases in these taxa as a result of restoration serve an important utility for encouraging investment in river habitat restoration (e.g. by fishery stakeholders). However, the full extent of community change is often missed, as are the causal biotic and abiotic processes driving them (Feld et al 2011, Friberg et al 2011).

The equivocal biotic responses to similar restoration measures across time and space, and the use of diverse indicators to assess restoration success has confounded efforts to predict restoration effects (Morandi et al 2017, Palmer et al 2010, Pretty et al 2003, Sievers et al 2017, Whiteway et al 2010). Therefore, despite billions of dollars of investment, hard empirical evidence to support restoration as a practice is lacking, and suggests that restoration or monitoring is failing on a global scale (Lepori et al 2005a, Morandi et al 2014, Palmer et al 2010). There is therefore a real need for more comprehensive quantitative biomonitoring of faunal communities in order to facilitate comparisons between projects (e.g. Kail et al 2015, Miller et al 2010), and advance our understanding of the key environmental and biotic factors influencing ecological outcomes.

This has led to calls from within the field for incorporating network approaches into restoration biomonitoring (Bellmore et al 2017, Friberg et al 2011, Naiman et al 2012, Thompson et al 2012, Tylianakis et al 2010). These provide both a more comprehensive overview for detecting community change and greater mechanistic insight into how these are manifested (Bellmore et al 2017, Naiman et al 2012). Food webs model trophic interactions between taxa, connecting resources (e.g. invertebrates) to their consumers (e.g. fishes). Subtle but important changes in the strength of these interactions due to changes in the environment may help to explain observed changes in ecosystem functioning, stability, and resilience; typically cited goals in ecological restoration that cannot be inferred from studying species

populations in isolation (Bellmore et al 2017, Gray et al 2014, Naiman et al 2012, Thompson et al 2012, Vander Zanden et al 2006).

Food webs have advanced our understanding of how environmental factors such as warming temperatures (O'Gorman et al 2012b), pH (Layer et al 2010b), and nutrient enrichment can influence assemblage structure via biotic interactions (Kiffney et al 2014, Sommer et al 2002). These studies have demonstrating how changes in species populations and/ or environmental conditions can indirectly shift the ecological state of a system due to cascading extinctions or declines and associated severe changes- and even loss of- ecological functioning (Allesina & Bodini 2004, Estrada 2007, Jeppesen et al 2012, Jordan et al 2006, Joseph et al 2009, Persson 2001). For instance, in lake systems the invasion by zoo-planktivorous fish can result in strong top-down control of herbivorous zooplankton, triggering a trophic cascade as declines in zooplankton herbivores reduce the top-down control of phytoplankton (Brett & Goldman 1997, Persson 2001). This can shift the ecological state of the system from macrophyte-dominated to phytoplankton/algal dominated primary production (Persson 2001, Sommer et al 2002). The associated loss of physical habitat structure due to macrophyte loss and declines in water clarity can further alter trophic interactions between predators and prey, reinforcing this trophic cascade and indirectly leading to a restructuring of higher trophic levels (Diehl 1992, Ferreira et al 2014). Food webs may therefore provide a powerful predictive tool for guiding ecosystem management and conservation towards overcoming these issues (Bellmore et al 2017, McDonald-Madden et al 2016, Tylianakis et al 2010).

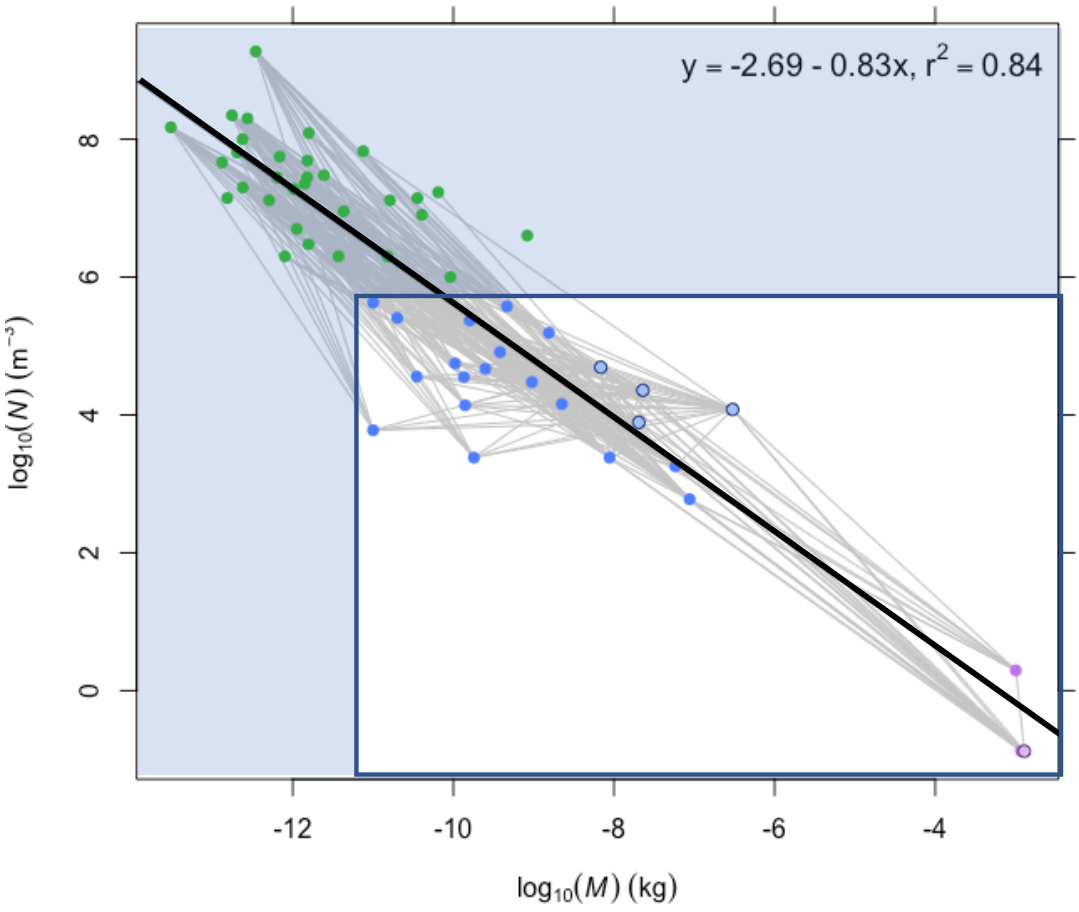


Figure 4.1 Trivariate food web representing the pelagic community of Lake Tuesday (Cohen et al 2003) In each plot the nodes represent the log10-transformed species abundance between the four treatments (*N*) per m^2 plotted against their respective mean log10-transformed body mass (*M*) in mg. Green symbols represent primary producers, blue symbols represent invertebrate taxa and pink symbols represent fish species, cannibalism is indicated by open symbols. The slope is a measure of how efficiently energy is converted from resource to consumer biomass and feeding pathways are shown as grey links between nodes. The clear square represents the faunal community which was the focus of this study.

Traditional food webs use binary networks, where species ('nodes') are linked by prey or consumer interactions ('links'), however, these lack body size and abundance. 'Trivariate' food webs are able to include species average mass *M* and density per m^2 (*N*) in 'trivariate' food webs (Cohen et al 2003). These are more sophisticated than their binary equivalents, and can illustrate the flow of energy through ecological communities from small, more abundant resources, through primary consumers to larger less abundant predators (Cohen et al 2003, Layer et al 2010b, Thompson et al 2016). The overall community mass-abundance (i.e. *N* versus *M*) scaling relationship, indicated by the slope of the fitted line of the feeding

pathways between consumers and their resources, provides an indicator of the proportion of biomass shared between them (Figure 4.1) (Cohen et al 2003).

This approach provides insight into how biomass transfer is mediated through communities and even ecosystems, and has been used to investigate the impact of a range of environmental factors on aquatic communities (Ings et al 2009, O'Gorman et al 2012b, Thompson et al 2016). However, despite calls from within the literature (Bellmore et al 2017, Feld et al 2011, Pander & Geist 2013), these methods are rarely ever used in a habitat restoration context, despite providing unique opportunities to explore the role of habitat on river food webs and biotic interactions in real time. Planned interventions allow for robust before-after control-impact (BACI) designs, frequently cited as the best for disentangling causal change from wider environmental noise (Feld et al 2011, Huddart et al 2016).

The other instances in which food webs have been applied, habitat restoration is likely to transcend target taxa and reverberate through the community in complex, non-linear and indirect ways via species interactions (Bellmore et al 2017, McDonald-Madden et al 2016, Naiman et al 2012, Vander Zanden et al 2006, Wootton 1994). For instance, riverine fish populations are regulated by the availability of resources (e.g. Kiffney et al 2014), competition for shared food resources (e.g. Bellmore et al 2013), and predation by predators (i.e. top-down control) (Boss & Richardson 2002, Woodward et al 2008). Changes in physical habitat structure following restoration can potentially alter the strength of these predator-prey interactions through behaviour and other factors (Boss & Richardson 2002, Diehl 1992). For instance, by hindering the movement of fish predators or their ability to detect prey, large wood may provide refuge from predation for macroinvertebrates and small fish (Alexander et al 2012, Boss & Richardson 2002, Burks et al 2001, Everett & Ruiz 1993).

Such prey refuges can weaken the effect of predators on the prey community with positive effects on local species diversity and abundance (Boss & Richardson 2002, Diehl 1992), and so potentially functioning (Lefcheck et al 2015). Conversely, large wood may benefit predators by providing cover for ambushing prey and improving hunting success, or concentrating prey resources such as juvenile fish and invertebrates (Diehl 1992, Entrekin et al 2009, Horinouchi et al 2009). However, our understanding of how large wood (and habitat restorations generally) affects these biotic interactions to alter the relative strengths of top-down and bottom-up processes remains poorly understood. Therefore, the use of food web

approaches able to clearly link changes in species populations to changes in their consumer or resources largely due to the inability of most biomonitoring metrics to clearly detect and link changes in biotic interactions to changes in species populations.

The practice of installing large wood (defined as logs with a diameter > 0·1 m and a length > 1 m, (Gregory et al 2003)) is now an established tool used by river managers globally to restore biodiversity in physically degraded systems (Kail et al 2007, Roni et al 2015, Tarzwell 1937). Large wood is an important component in river ecosystems; helping to drive the hydromorphological processes responsible for substrate sorting and creating and maintaining habitat diversity by the formation of pools and riffles (Gregory et al 2003, Gurnell et al 1995), and reviews of projects have found the return of these natural channel dynamics following the addition of large wood to be largely consistent (Haase et al 2013, Kail 2003, Morandi et al 2017, Roni et al 2015).

The improved hydromorphology and habitat complexity following large wood installation is thought to both recover species richness and assist the bottom-up recovery of the biological community in rivers (Miller et al 2010). Wood can provide increased surface area for biofilms and the macroinvertebrates that feed on them to grow (Benke & Wallace 2003, Spanhoff et al 2000), can increase the retention of terrestrially derived (allochthonous) organic matter and stability and so enhance the provision of food resources and habitat for detritivore growth (Kupilas et al 2016, Lepori et al 2005b, Muotka & Syrjanen 2007), and may also indirectly enhance resources for primary ‘grazing’ consumers by sorting substrates and exposing gravels and cobbles in the main channel, providing stable habitat for autochthonous algal production (Kail 2003, Tonetto et al 2014). It has also often suggested that large wood provides refugia against environmental perturbations, buffering organisms against high flows and shear stress in times of flood (Borchardt 1993, Roni et al 2008). However, the paucity of empirical evidence to substantiate and quantify these assumed biological benefits, and the inability to link macroinvertebrate production to changes in fish biomass and abundance, means that the efficacy of the practice of habitat restoration remains strongly contested (Feld et al 2011, Lepori et al 2005a, Palmer et al 2010).

Hypotheses

1. Gut contents analysis of fish will reveal the key prey taxa for each of the fish studies analysed; changes in the abundance and biomass of their predator should therefore alter their abundance in restored reaches.
2. Assuming large wood restoration positively relates to species richness, the number of fish and invertebrate nodes will increase as will the number of links in restored reaches.
3. Large wood restoration will increase both fish and invertebrate abundance and biomass, the response will be weaker for invertebrates, inferring increased top-down control by fish.
4. Increases in fish biomass will result in a shallowing of the mass-abundance slope, indicating higher energy transfer efficiency between invertebrates and fish predators.
5. The faunal assemblages will diverge over time, with the greatest difference between before restoration in 2014 and after restoration in 2016, rather than 2014 and 2015, reflecting the timescale of recovery (i.e. species recolonisation) following restoration and the initial disturbance effect of restoration.

4.3 Methods

Details on the study site and habitat responses are described in the General Methods in Chapter 2. Four replicated restorations were carried out on the River Great Stour, a lowland chalk stream, in spring 2015. All annual biomonitoring took place in spring, once before (2014) and twice following restoration (2015-2016). Sampling at this time of year captures invertebrate species that have been able to persist over winter and are in their aquatic life stage prior to emergence in the case of winged insects.

Biomonitoring

The fish data from the spring surveys investigated in Chapter 3 was used here, with all species included except stocked *S. trutta*. To calculate *N*, reach abundance was divided by the wetted surface area (m^2) of its respective reach and *M* by taking the average mass of each species per reach and converting to dry mass using the equations in **Error! Reference source not found.**. Invertebrates were monitored at the habitat-scale 1 week prior to the fish surveys. In order to estimate taxa density ($N\ m^2$), three habitats were identified: mid-stream (Mid), margin (Edge) and large wood in the restored sites after restoration (LWD) (Murray et al. 2017). In control sites and restored sites prior to restoration (2014), 3 x Hess samples were collected in the Mid and Edge habitats per reach (3x Mid, 3 x Edge = 6 replicates). After restoration, 2 x Hess sample replicates were taken from each habitat (2x Mid, 2 x Edge, 2 x LWD = 6 replicates per reach).

All species identified to lowest taxonomic resolution possible. Invertebrate taxa mean body sizes (mg) were estimated for each reach at each year using the relative measurements from at least 30 individuals, or the total number of individuals recorded. The surface area of each habitat was estimated as a percentage of reach total surface area. These were then weighted accordingly to provide dry mass m^2 and abundance m^2 estimates for each reach. This was not necessary for fishes, which were monitored at the reach, rather than habitat, scale (as described in the General Methods section in Chapter 2).

Table 4.1 Fish species examined for GCA with the number of individuals

Fish species	Number of individuals
Barbatula barbatula	12
Esox lucius	37
Gobio gobio	12
Leuciscinae	6
Perca fluviatilis	7
Phoxinus phoxinus	3
Rutilus rutilus	5
Salmo trutta	17
Squalius cephalus	3

Table 4.2 Fish species showing positive responses in abundance to restoration from chapter 3, fish in bold had their gut contents analysed, *A. anguilla* and *C. gobio* are both protected under the Habitats directive and so were not included in the analysis.

Response variable	Source	df	Estimate	SE	z	P	**
E. lucius	Treatment:Period	27	0.311	0.124	2.507	**0.012**	*
P. fluviatilis	Treatment:Period	25	0.353	0.157	2.243	**0.025**	*
A. anguilla	Treatment:Period	25	0.111	0.056	2.001	**0.045**	*
B. barbatula	Treatment:Period	25	-0.096	0.032	-3.003	**0.003**	**
C gobio	Treatment:Period	25	-0.248	0.046	-5.428	**0.000**	***
Leuciscinae	Treatment:Period	26	0.449	0.055	8.151	**0.000**	***
P. phoxinus	Treatment:Period	26	1.836	0.375	4.891	**0.000**	***
S. cephalus	Treatment:Period	26	0.449	0.055	8.151	**0.000**	***

Gut contents analysis

Gut contents analysis (GCA) was performed on the 9 most abundant species (Table 4.1). With at least 5 individuals processed, excluding *P. phoxinus* and *S. cephalus* which were comparatively rare ($N = \geq 3$ for each species). Those that were subject to statutory protection eel (*Anguilla anguilla*), (*Cottus gobio*) and lamprey (*Lampetta planeri*) were not included in the GCA. All stomach samples were extracted from fish captured within the study area, the River Great Stour, in spring 2016. In order to get sufficient sample size an effort was made to use individuals that did not survive or were damaged during fish sampling, with other individuals humanely euthanised. For *S. trutta*, fish removal was not permitted by the angling association so a non-fatal stomach lavage process was used instead to extract gut contents at the study site which were kept in 90% ethanol (Murray et al., 2017).

All other fish specimens were dissected and all diet contents identified in the laboratory. Prey items were identified to at least family level using a dissection microscope (40x magnification and individual body mass (mg) was estimated using body dry mass equations (**Error! Reference source not found.**) (Murray et al., 2017). For each predator, all prey items were pooled and their percentage proportion estimated, those that constituted less than 3% of total diet mass for each species were included as feeding links but not further analysis. The dominant prey orders of the species making up the majority of the fishes diets whose abundance responded to restoration in Chapter 3 (Table 4.2) were tested to see if they also responded to restoration, i.e. suggested a top-down or bottom-up effect.

Food web construction

Building food webs for complex systems based on gut contents analysis (GCA) or first-hand observations is prohibitively challenging and only captures a snapshot of a consumer's diet (Gray et al 2015, Ings et al 2009). Feeding links between species were therefore determined by a combination of the empirical GCA of fish species and published literature (e.g. O'Gorman et al 2012a, Thompson et al 2016). All empirical links were then pooled with links from the literature and a recently collated database of trophic interactions from UK freshwaters (https://sites.google.com/site/foodwebsdatabase/; Gray et al 2015).

Inferred feeding links were added to each network using the *WebBuilder* function (Gray et al 2015), in R (R Core Team 2013). This approach assumes that all feeding links that have been

empirically observed in past literature are realized whenever and wherever both species exist and is widely applied in the literature (Layer et al 2013, Thompson et al 2016). Given that consumers in aquatic systems are typically highly generalist, with prey resources often determined by size, this is deemed more acceptable than underestimating linkage food web links and complexity if only empirically observed food webs were used (Gray et al 2015, Hall & Raffaelli 1991, Layer et al 2010b, Pocock et al 2012).

Network metrics

Quantitative trivariate food webs were constructed, nodes (taxa) are plotted by their Log_{10} average body mass (M) and Log_{10} abundance (N) and linked via their interactions (Figure 4.1). These were constructed for each of the 8 reaches (4 x control, 4 x restored) at each sampling point (2014, 2015 and 2016), producing a total of 24 food webs (8 reaches x 3 sampling dates, $N = 24$). From these a range of binary (presence/ absence) food web metrics was calculated: total number of nodes (S), number of invertebrate nodes, number of fish nodes and total number of feeding links (L).

Trivariate analysis was used to compare the relationship between $Log_{10}N$ and $Log_{10}M$ (NvM) in each reach food web with the slope used to estimate the overall efficiency of energy transfer between resources and their predators (Cohen 2009). Trophic interactions can be viewed as a vector from a resource to its consumer in mass-abundance space, a steepening of this slope indicates less efficient energy transfer and reduced biomass flux (Cohen et al 2003). This can be used to estimate changes in potential biomass flux between prey and predators, with cannibalistic interactions removed (Cohen et al 2009, Thompson et al 2016). All food webs were constructed and metrics estimated using the *Cheddar* package, (described in greater detail in Hudson et al (2013)).

Statistical analysis

Linear mixed effects models (LMMs) were used to test for a significant effects of the fixed effects Time and Treatment and the interaction between the two Time * Treatment (i.e. the BACI effect) on both the dominant dietary compositional taxa of fish species who showed a response to restoration, as well as the food web metrics. In all cases, the spring 2015 sampling round, which was immediately after restoration, was removed, due to (4 control before + 4 restored before + 4 control after + 4 restored after, $N = 16$). Reach was treated as having a random effect on the intercept of the linear relationship in all models. All statistical analysis was done in R (R Core Team 2013).

4.4 Results

Table 4.3 Dominant prey orders of the 1305 individual specimens (> 3% total fish diet mass) identified by GCA of the 7 most abundant fish species (excluding protected species, *N* = 102), those fish species which responded to restoration in Chapter 3 are shown in bold.

Consumer	Prey Order	Sum mass (mg)	Fishes diet % mass
Barbatula barbatula	*Trichoptera*	40.03	45.67
	Diptera	24.20	27.61
	Ephemeroptera	23.42	26.72
Esox lucius	*Barbatula barbatula*	23818.58	51.87
	Cottus gobio	11609.16	25.28
	Leuciscinae	10399.65	22.65
Gobio gobio	*Trichoptera*	81.81	87.96
	Coleoptera	5.73	6.16
	Diptera	2.81	3.02
	Ephemeroptera	2.65	2.84
	Crustacea	0.02	0.02
Perca fluviatilis	*Cottus gobio*	3245.62	78.73
	Leuciscinae	876.84	21.27
Phoxinus phoxinus	*Trichoptera*	1.20	38.59
	Ephemeroptera	1.19	38.07
	Diptera	0.73	23.34
Leuciscinae	*Trichoptera*	35.70	82.63
	Mollusca	6.59	15.24
	Coleoptera	0.19	0.44
	Diptera	0.73	1.69
Salmo trutta	*Cottus gobio*	1141.48	56.23
	Trichoptera	467.34	23.02
	Diptera	199.61	9.83
	Mollusca	116.75	5.75
	Ephemeroptera	50.53	2.49
	Coleoptera	36.79	1.81
Squalius cephalus	*Trichoptera*	0.69	51.77
	Diptera	0.63	47.12
	Coleoptera	0.01	1.11

Empirical gut contents analysis

A total of 42 taxa (*N* = 1305) were recovered from the fish gut contents analysis revealing 88 empirical feeding links (**Error! Reference source not found.**). Of these, 7 were piscivorous interactions by the predators *S. trutta*, *P. fluviatilis* and *E. lucius*. The GCA analysis showed that species *B. barbatula* and *C. gobio*, which responded negatively to restoration in Chapter 3 (Table 4.2)Table 4.2 Fish species showing positive responses in abundance to restoration from chapter 3, fish in bold had their gut contents analysed, *A. anguilla* and *C. gobio* are both protected under the Habitats directive and so were not included in the analysis., are core constituents of the diets of *P. fluviatilis* and *E. lucius*, which increased in abundance following restoration (Table 4.2, Figure 4.2). The majority of diet for *E. lucius* was *B. barbatula* (*N* = 35, 51.87 %), followed by *C. gobio* (*N = 35,* 25.28 %) and Leuciscinae (*N* = 2, 22.65%) (Figure 4.2, Table 4.3**)**. The majority of *P. fluviatilis* diet consisted of C. gobio (*N* = 3, 78.73 %) and Leuciscinae (*N* = 1, 21.27 %) (Figure 4.2, Table 4.3). Invertebrates contributed a small proportion of mass to the piscivore species diet (< 2%) and so were not included in Figure 4.2. Despite showing a positive response to restoration, Leusciscinae were also consumed by *E. lucius* and *P. fluviatilis* (Figure 4.2, Table 4.3).

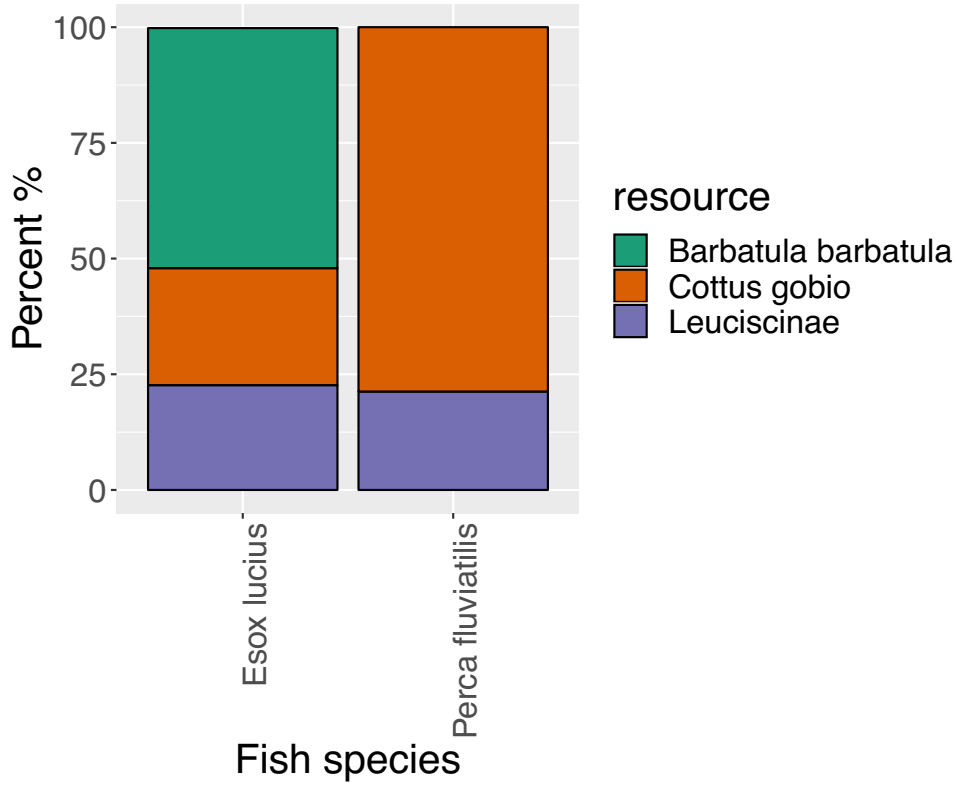


Figure 4.2 Percentage composition of fish prey species in the diets of *E. lucius* (*N* = 37) and *P. fluviatilis* (*N* = 7) identified by GCA.

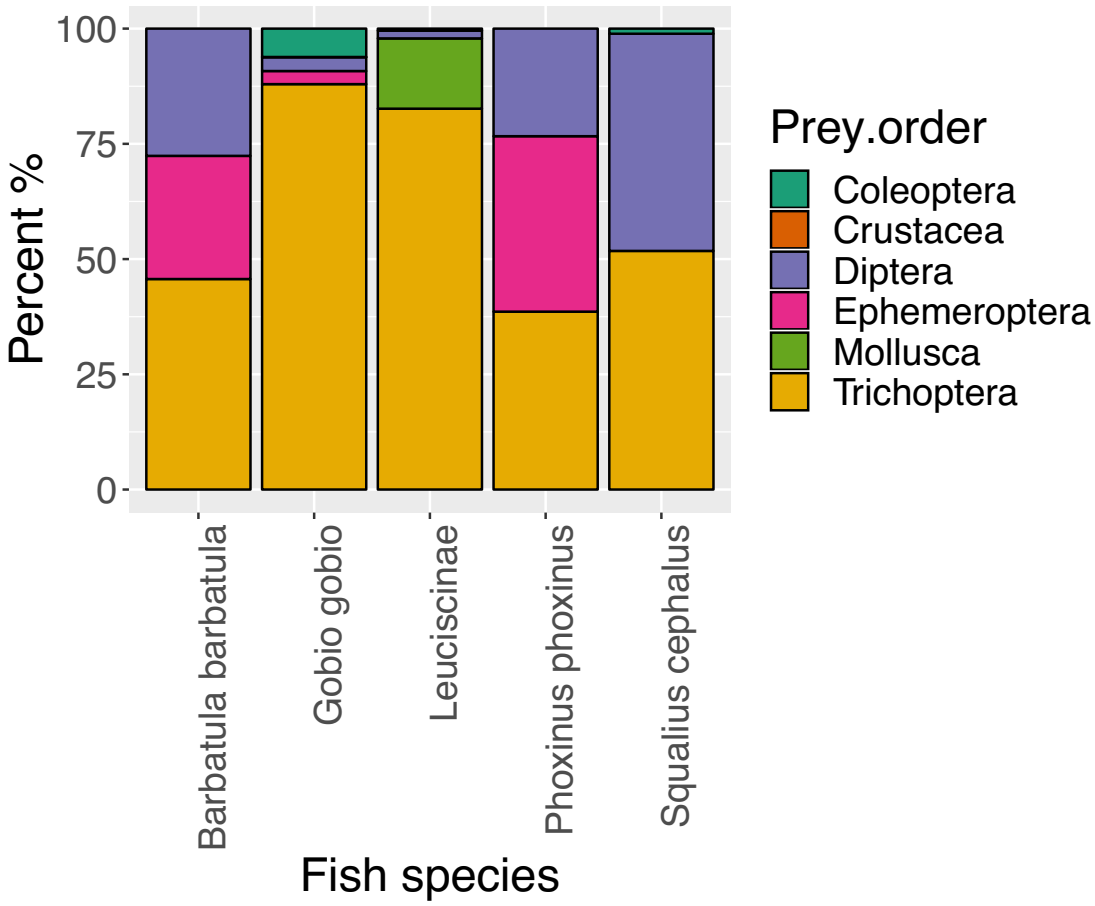


Figure 4.3 Percentage mass composition of invertebrate prey orders (> 3%) in invertivore diets identified by GCA.

Invertivores

Trichopterans made up 66% of all cyprinids diet, with all species found to feed on this group (Figure 4.3, Appendix prey order), 92% of which consisted of the species *Agapetus fuscipes* (*N* = 272) which was therefore identified as a core prey species for this group of fishes (Figure 4.3, Table 4.3). Diptera (N = 225) were also found in all cyprinids (Table 4.3), but were most important for *B. barbatula* (27.61%), *P. phoxinus* (N = 6, 23.34%) and *S. cephalus* (N = 2, 47.12%) (Figure 4.3, Table 4.3). This group were therefore chosen as core prey taxa. Ephemeroptera made up 23.42% (N = 93) and 38.97% (N = 8) of *B. barbatula* and *P. phoxinus* diets respectively (Figure 4.3, Table 4.3), consisting of the taxonomic groups Baetidae (N = 51) and *Seratella ignita* (N = 61) (Error! Reference source not found.).

Brown trout (*Salmo trutta*) were more generalist than other species Figure 4.4, with over 34 taxa recorded (**Error! Reference source not found.**.4) the majority of mass consisted of *C. gobio* (Scorpaeniformes, 56.23%, N = 3) and Trichoptera (23.02, N = 261) (Figure 4.4 , Table 4.3), however there were also terrestrial invertebrates. Unlike the fish prey species, the invertebrate orders Diptera, Ephemeroptera and Trichoptera, LMM's failed to show any detectable response in these orders to restoration in terms of *N* and *M* (**Error! Reference source not found.**.4).

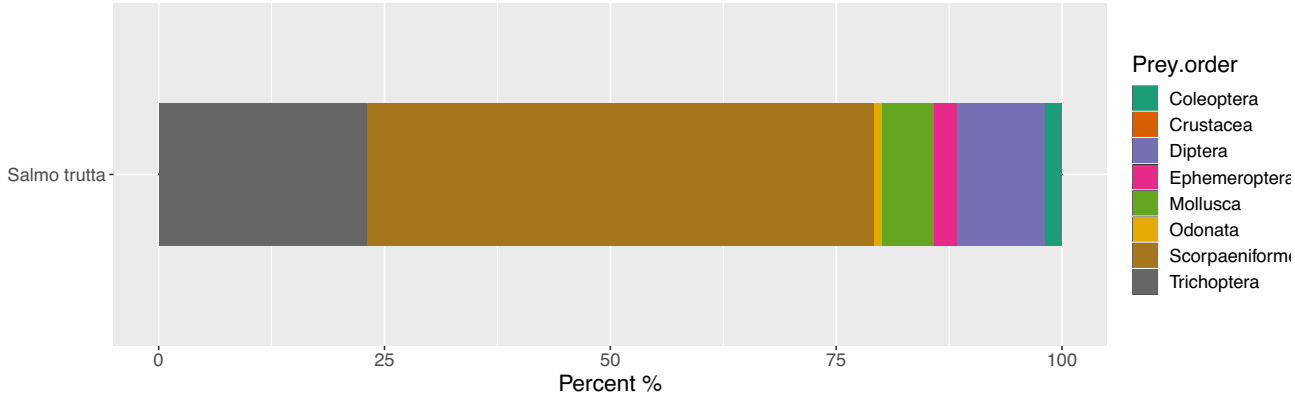


Figure 4.4 *S. trutta* gut contents identified by GCA analysis (*N* = 17).

Food webs

A total of 31,731 individual invertebrates were collected from 122 taxonomic groups. Of these, 120 invertebrate taxa were identified and 13 fish (total 133) species connected by 1651 feeding links. The full binary web of all taxa encountered is shown in the **Error! Reference source not found.**.5 with the taxa in **Error! Reference source not found.**.5. 1570 (95%) of the links were inferred from the database.

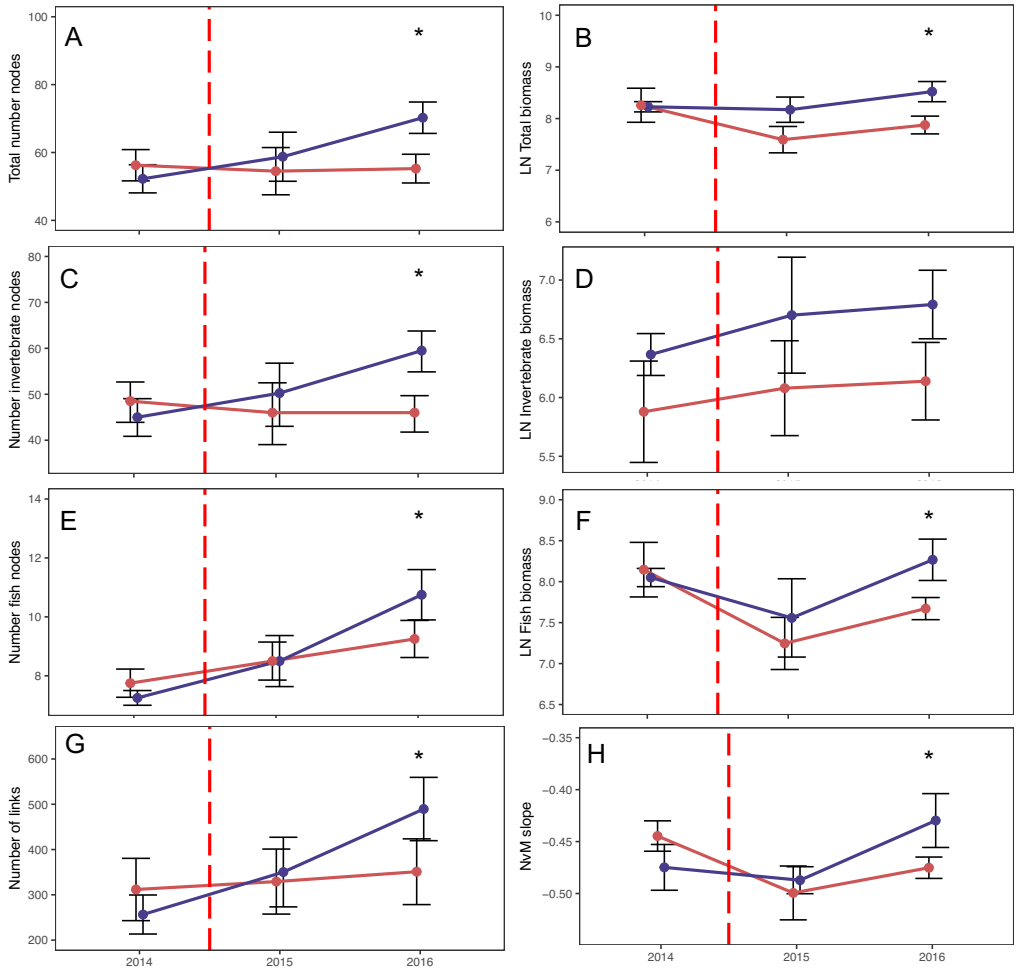


Figure 4.5 Number of nodes and log transformed biomass for total fish and invertebrates (A, B), invertebrates (C, D) and fish (E, F), over time in control (red) and restored (blue) sites. The time of restoration is depicted by the dashed red line and points show mean values, ± standard error.

Large wood led to significant restructuring of the macroinvertebrate and fish food web, with treatments diverging over time (Figure .5). Large wood additions led to a significant increase in invertebrate and fish nodes, supporting hypothesis 1 (Figure A, C, E; Table 4.4). This led to increases in the number of feeding links (Figure G; Table 4.4). The increase the total biomass of the faunal assemblage (Figure B, Table 4.4) was due to the fish population, whose biomass increased significantly in restored reaches diverging from the control treatment in 2016, as detected in Chapter 3 (Figure F, Table 4).

Table 4.4 Statistics of fit for the multiple mixed effects models that responded significantly (N = 16). All models include a main effect of treatment, time nested within treatment, and a random effect of site on the intercept of the linear relationship. Significance: · = *P* < 0.1, * = *P* < 0.5.

Variable	Test	Estimate	*SE*	*df*	*T*	*P*	
Total nodes (log)	Treatment	-4.00	4.58	9.00	-0.87	0.41	
	Year	-1.00	4.58	9.00	-0.22	0.83	
	Treatment: Year	19.00	6.48	9.00	2.93	**0.02**	*
Total biomass (log)	Treatment	-0.03	0.21	9.00	-0.14	0.89	
	Year	-0.38	0.21	9.00	-1.82	0.10	
	Treatment: Year	0.68	0.30	9.00	2.27	**0.05**	*
Invert nodes (log)	Treatment	-0.08	0.10	9.00	-0.80	0.44	
	Year	-0.05	0.10	9.00	-0.54	0.60	
	Treatment: Year	0.34	0.14	9.00	2.47	**0.04**	*
Invert biomass (log)	Treatment	0.49	0.45	12.00	1.07	0.30	
	Year	0.26	0.45	12.00	0.57	0.58	
	Treatment: Year	0.17	0.64	12.00	0.26	0.80	
Fish nodes	Treatment	-0.50	0.65	9.00	-0.78	0.46	
	Year	1.50	0.65	9.00	2.32	**0.05**	*
	Treatment: Year	2.00	0.91	9.00	2.19	0.06	.
Fish biomass (log)	Treatment	-0.10	0.22	9.00	-0.43	0.68	
	Year	-0.48	0.22	9.00	-2.13	0.06	.
	Treatment: Year	0.69	0.32	9.00	2.19	0.06	.
Number of links (log)	Treatment	-55.25	62.97	9.00	-0.88	0.40	
	Year	39.25	62.97	9.00	0.62	0.55	
	Treatment: Year	193.75	89.06	9.00	2.18	**0.05**	*
NvM slope	Treatment	-0.03	0.03	9.00	-1.17	0.27	
	Year	-0.03	0.03	9.00	-1.18	0.27	
	Treatment: Year	0.08	0.04	9.00	2.07	**0.04**	*
Total abundance (log)	Treatment	0.17	0.26	9.00	0.64	0.54	
	Year	0.00	0.26	9.00	-0.02	0.99	
	Treatment: Year	0.13	0.37	9.00	0.35	0.73	
Invertebrate abundance (log)	Treatment	0.17	0.26	9.00	0.64	0.54	
	Year	0.00	0.26	9.00	-0.02	0.99	
	Treatment: Year	0.13	0.37	9.00	0.35	0.73	
Fish abundance (log)	Treatment	-0.02	0.31	9.00	-0.07	0.94	
	Year	0.12	0.31	9.00	0.37	0.72	
	Treatment: Year	0.20	0.44	9.00	0.45	0.66	

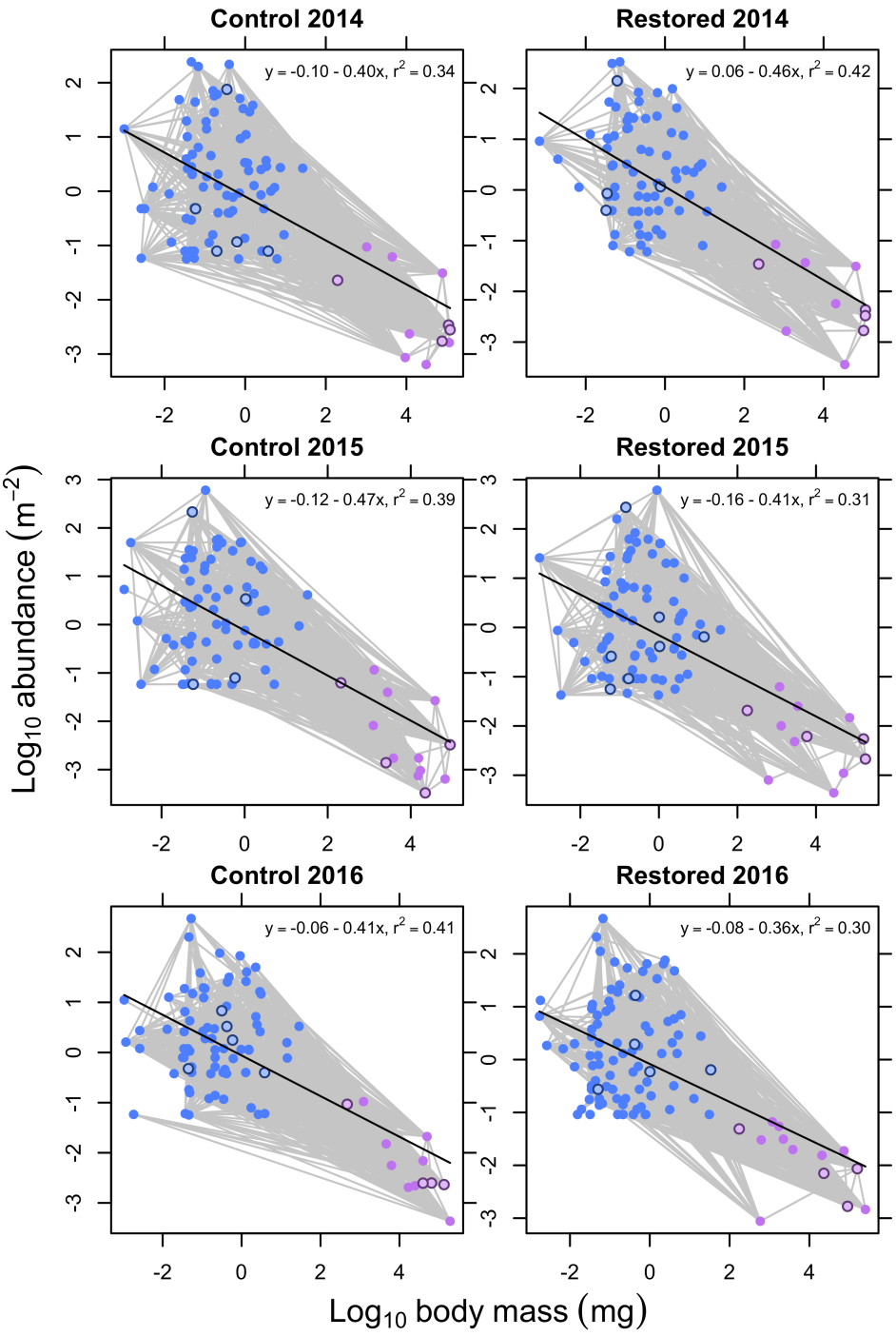


Figure 4.5 Trivariate food webs for each treatment at each year before (i.e. Control 2014, Impact 2014) and after restoration (i.e. Control 2015 and 2016, Impact 2015 and 2016). In each plot the nodes represent the log10-transformed species average abundance between the four treatments (N) m2 plotted against their respective mean log10-transformed body mass in mg. Blue symbols represent invertebrate taxa and pink symbols represent fish species, cannibalism is indicated by open symbols. On each plot the slope is given, which is a measure of how efficiently energy is converted from resource to consumer biomass and feeding pathways are shown as grey links between nodes.

There was a significant change in the mass-abundance scaling relationship in restored communities; as predicted in my third hypothesis, the slope became less negative (i.e. shallower) over time in restored reaches compared to the controls, which remained unchanged (Figure H, Figure 4.5; Table 4). This indicated altered mass-abundance scaling within the food web and suggests increased energy transfer efficiency through the prey-predator pathway to the larger fish species.

4.5 Discussion

Reversing the impacts of degradation to recover biodiversity in impoverished systems is one of the most urgent and challenging activities we have attempted as a species. Despite global implementation, robust data able to clearly demonstrate restoration as the causal agent in changes to the structure of species assemblages are remarkably few. Here, a robust, replicated BACI design has demonstrated that restoring with large wood can lead to significant increases in biodiversity and positive changes to the structure of the faunal food web. Furthermore, the inclusion of trophic theory has uncovered evidence that habitat restoration alters the strength of trophic interactions in fish, as the two species to show decreases in abundances following restoration were also the primary prey of the piscivores which responded by increasing in abundance, explaining the results found in Chapter 3.

These findings support other studies using trivariate food web approaches that incorporate *N* and *M* in aquatic systems, with energy flowing from smaller abundance prey to larger rare predators (Cohen et al 2003, Layer et al 2010b, Thompson et al 2016). The slopes compared well, although were less negative, to those found in other studies (Layer et al 2010b, Thompson et al., 2017). As predicted in hypothesis 3, the negative slope of the mass-abundance relationship, which illustrates the efficiency of energy transfer, became less negative in the restored reaches. In the absence of any change to the biomass of resources this suggests that the efficiency of energy transfer between predators and prey throughout the community was enhanced (Cohen et al 2003, O'Gorman et al 2012b).

The increase in invertebrate diversity but not total abundance supports the findings of a review of large wood additions by Miller et al., (2010). Large wood has been demonstrated to increase macroinvertebrate production in streams (Entrekin et al 2009), however, in this study this was not detected using either abundance or biomass as a proxy, which remained similar across treatments. Changes to the strength of predator-prey interactions between invertebrates and fish may be key here. While fish abundance did not increase, fish biomass did, indicating that fish were on average larger in restored reaches. As resource demands scales with body size (Brown et al. 2004; Emmerson & Raffaelli 2004), it is likely that these larger individuals may have exerted greater top-down control on the invertebrate assemblage, and so making changes to invertebrate production using static standing stock measures challenging. Further experiments could try to disentangle bottom up invertebrate secondary production from the confounding effects of top-down control by using predator exclusion experiments (Woodward et al 2008).

Empirical gut contents analysis was crucial for identifying the keystone prey species within the system that made up the majority of the fishes diets. While mass-abundance provides an illustration of binary nodes and indication of the snapshot of energy flowing through the system, it infers the strengths of predator-prey interactions via body mass. The high amount of diet overlap among the cyprinid species contrasted strongly with the more specialist feeding and resource partitioning displayed by the piscivores. These results suggest the potential for intense competition between particular pairs of cyprinids, such as *B. barbatula* and *P. phoxinus*, and *Gobio gobio* and Leusciscinae, for the same resources.

Importantly, no *S. trutta* were discovered during gut contents analysis of either piscivore species, important given the salmonid fisheries context of this project and many other restorations past and present. This supports findings from other studies investigating pike diets in calcareous streams, which found that pike are more likely to target smaller, more abundant cyprinids (Mann 1976), and raises questions about the perceived need to manage *E. lucius* populations in rivers used for angling (Mann

1985). *S. trutta* were more generalist compared to all other species and their ability to exploit terrestrial macroinvertebrates, aquatic invertebrates and fish is well supported in the literature (Murray Thompson et al., In Press (2017) Bellmore et al 2013, O'Gorman et al 2012a, Thompson et al 2016). This generalism may be advantageous and explain their adaptability; introduced brown trout can quickly establish populations and are considered invasive in many parts of the globe. However, their generalism may also come at a cost, as dietary overlap with both cyprinid species for invertebrates and *P. fliviatilis* for *C. gobio* in this system may explain their comparatively low population as found in Chapter 3. *E. lucius* may facilitate trout populations by reducing competition for resources such as Trichoptera. Despite restoration increasing species richness, these competitive interactions and provide alternative resources for trout to exploit.

The significant increase in invertebrate and fish species richness support hypothesis 1: that species richness increases following large wood additions. This appears to contradict the findings of similar investigations, where changes to richness have been found to have negligible in these assemblages (Lepori et al 2005a, Roni et al 2015). The increase of both invertebrate and fish taxa in the restored reaches led to an increase in the nodes, links and so complexity in the stream food webs. Contrary to earlier food web theories, empirical and theoretical research suggests that increased complexity in stream food webs contributes to their stability, and complexity has been used as a proxy for measuring the resilience of food webs against environmental perturbations (Layer et al 2011).

This suggests that restoring with large wood can achieve the desired structural diversity goals typical of restoration, but also might contribute to building resilience against future perturbations, another typically cited but rarely ever substantiated expectation (Lake 2013). That fish richness responded as well as invertebrates is encouraging, the only other study applying food web approaches to large wood restoration found that positive changes in diversity were chiefly due to the response of Chironomidae taxa (Thompson et al., in Press). While gains in species richness of any taxa is important, the recovery of larger fish species that have higher energy demands and greater habitat requirements than invertebrates suggests that the scale of ecological

change is greater. It may also serve as a powerful incentive for fishery managers who are less focused on trout.

4.6 Conclusions

Here, I have been able to demonstrate that restoring with woody debris at the reach scale increases animal species richness and biomass, frequently cited but rarely substantiated goals of restoration. Additionally, the novel application of food web approaches has revealed insights into how the mechanisms responsible for these changes have enhanced the energy transfer from macroinvertebrate primary consumers through to apex predators, which is rarely achievable using static biomass and abundance measures. The results merit further studies using experimental exclusion of predators and herbivores in order to establish if bottom-up controls (i.e. production) facilitate the greater biomass and to determine which energy flux is responsible.

Chapter 5 | River restoration and ecosystem functioning: investigating the impact of reach scale restoration on leaf-litter breakdown

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5. 1 Abstract

The impact of degraded habitat on biodiversity is well documented; less so are the associated impacts on ecosystem functions, despite their recovery often being included in definitions of successful river restoration. This is also reflected in restoration assessments, as the majority continue to rely solely on structural measures of biodiversity (i.e. species abundance and diversity). As such, the effect of restoration on ecosystem functioning remains poorly understood.

Terrestrial inputs of dead organic matter (allochthonous resources) provide a significant contribution to the basal energy subsidy in aquatic systems, and the assimilation of this resource into the living biomass is dependent on the action of detritivorous microbes and invertebrates. Here I investigate the impact of restoring with large wood on leaf-litter breakdown, as well as the biomass and composition of colonizing detritivorous macroinvertebrates in a modified lowland river. Using replicated before-After control-impact (BACI) methods and standard leaf-litter bag techniques, I monitored the response of microbial-mediated decomposition (MMD) and invertebrate-mediated decomposition (IMD) in the midstream habitat.

Total decomposition was significantly lower in restored reaches following restoration, while colonizing invertebrate abundances and biomass remained unchanged between treatments, as did their composition. Control-impact comparison of mid-channel and margin habitats revealed no significant difference in detrital breakdown both between treatments and between habitats in restored and control reaches. These findings suggest that any change in functioning following large wood installation was limited,

and that despite being included in many definitions of successful river restoration, ecosystem processes may not be as prosaic to repair.

5.2 Introduction

Channelization and the loss of habitat heterogeneity is one of the major causes of habitat degradation in rivers, detrimentally impacting both species (i.e. diversity and abundances) and functioning (Feld et al 2011, Lepori et al 2005b, Muotka & Laasonen 2002, Palmer et al 2014). The implementation of river habitat restorations to reverse these impacts is rising at an exponential scale globally (Bernhardt et al 2005, Palmer et al 1997). It is widely recognised that the majority of river restoration assessments continue to lack any form of quantitative biomonitoring (Bernhardt et al 2005, Friberg et al 2011, Morandi et al 2014). Yet, where biomonitoring does take place, researchers also raise concerns about the effectiveness of the measures used for tracking ecological response (Beechie et al 2010, Palmer et al 1997, Palmer et al 2005, Ruiz-Jaen & Aide 2005).

Many definitions of river restoration success include the recovery of core ecosystem processes and functions, such as primary production and decomposition, which regulate energy within ecological systems (Beechie et al 2010, Palmer et al 1997, Palmer et al 2014, Richardson & Hinch 1998). Yet, the vast majority of projects continue to base restoration assessments solely on changes in parameters of community composition (e.g. species richness) or the populations of various biological groups (Beechie et al 2010, Kupilas et al 2016), such as fish and macroinvertebrate biomass, abundance and diversity (Kail et al 2015, Miller et al 2010, Pretty et al 2003). While these structural parameters are linked to ecosystem functioning (Hooper et al 2005, Thompson et al 2016), their inconsistent responses to restoration has meant that despite decades of restoration and thousands of studies, highly variable and even contradictory ecological outcomes have hampered efforts to characterize biotic responses to most restoration measures (Palmer et al 2010, Roni et al 2015, Thompson 2006, Thompson et al 2016). Therefore, equivocal empirical evidence to support the practice of river restoration is lacking, and our understanding

of what processes and functions drive success or failure, is far from complete (Kupilas et al 2016, Palmer et al 2014, Palmer et al 2010, Pretty et al 2003, Stewart et al 2009).

This has led for calls within the relevant restoration literature for the inclusion of ecosystem processes, such as autochthonous (photosynthetic) production and detrital decomposition, measured as standardized rates in restoration assessments (Beechie et al 2010, Jackson et al 2016). These provide measures of 'functional integrity', that is, how well an ecosystem is functioning, that can be used for comparisons across space and time (Castela et al 2008, Ferreira et al 2016, Gessner & Chauvet 2002, Karr 1991, Woodward et al 2012). This increases our ability to detect trends and patterns, as well as link these to changes in the environment, and so can further our mechanistic understanding of how these changes operate to restore ecosystem functioning and species at higher trophic levels (Beechie et al 2010, Gessner & Chauvet 2002, Jackson et al 2016, Kondolf et al 2006, Lefcheck et al 2015, Woodward et al 2012).

However, high levels of 'functional redundancy' (i.e. many species performing the same functional role) in aquatic systems means that increases in functional measures alone cannot ensure that the structural biodiversity gains typically included as restoration objectives have been achieved (Chauvet et al 2016, Rosenfeld 2002). Thus, functional measures are best used complementary to structural monitoring approaches, such as those providing mechanistic insight into how changes at the community level are manifested (Jackson et al 2016, Monteith et al 2005, Wenger et al 2009, Woodward et al 2012).

Energy within aquatic food webs in derived from two major pathways, primary production of photosynthetic plants and algae and decomposition of dead organic material by microbes and detritivores, these are often referred to as the 'green' and 'brown' energy pathways respectively (Chauvet et al 2016, Cummins et al 1989). These regulate the basal energy that percolates through food webs, driving secondary production in primary consumers (e.g. herbivores and detritivores) and ultimately sustaining predators, such as fish (Wallace et al 1997).

"Brown" resources are often subsidised by external allochthonous detrital inputs (i.e. originating from outside the aquatic system) such as leaf litter, and this can provide an external contribution to the net basal energy within the system from photosynthetic plants and algae (Fisher 1995, Rosi-Marshall et al 2016). In temperate regions, autumn leaf fall provides a predictable and substantial allochthonous subsidy, forming leaf packs within rivers. This is broken down through a combination of abiotic and biotic factors. Abiotic factors include the mechanical fragmentation by water velocity flows (Webster & Benfield 1986). Biotic breakdown involves initial action by microbial decomposers such as fungi and bacteria, i.e. microbial mediated decomposition (MMD). This increases the palatability for further breakdown by macroinvertebrate detritivores, i.e. invertebrate mediated decomposition (IMD).

Leaf packs provide both physical habitat and food for shredding macroinvertebrates ("shredders") such as Trichopterans and gammarid shrimps, which consume coarse particulate organic matter (CPOM) (>1mm), but also break it down into smaller fine particulate organic matter (FPOM) (<1mm). This FPOM is in turn consumed by "gathering collector" macroinvertebrates, such as Caenidae species, or becomes entrained and transported downstream (Ferreira et al 2016, Gessner & Chauvet 2002). That many detritivorous invertebrates have their major growth period in winter, when autochthonous production is limited by reduced sun/ day lengths, yet coinciding with this peak input of well-conditioned leaf detritus (also known as the 'shredder response model' (Cummins et al 1989)), highlights the importance of this seasonal allochthonous subsidy (Kupilas et al 2016). These taxa provide the critical entry point at which this additional organic carbon subsidy is released back into the living food web, increasing net energy within the system and ultimately resources for their predators, such as fish, often the primary target of restoration (Lepori et al 2005b, Muotka & Laasonen 2002, Wallace et al 1997).

Macroinvertebrate and microbial detrital breakdown rates are driven by a combination of biotic and abiotic factors, including resource abundance and quality; the abundance, diversity, and activity of consumers; and environmental factors such as temperature and water chemistry (Gessner & Chauvet 2002, Hladyz et al 2011a, Woodward et al 2012). Decomposition is therefore sensitive many forms of

degradation, such as reduced detritivore abundance, which can restrict the (i.e. bottom-up) flow of allochthonous derived energy to higher trophic levels (Wallace et al 1997, Woodward et al 2012). However, the response of this rate to restoration is poorly understood, and there is therefore a need for studies measuring the impact of such measures on this critical process (Lepori et al 2005b, Smith & Chadwick 2014).

Riparian degradation directly impacts litter input by reducing leaf fall due to reduced riparian cover (Lecerf et al 2005), and resource quality (i.e. due to invasive species) (Hladyz et al 2011b). However, the amount of benthic in-stream organic matter is additionally, and perhaps more importantly, determined by the capacity of streams to retain terrestrial inputs (Cummins et al 1989). Coarse particulate organic matter (CPOM) retentiveness can be considerably reduced by channelization practices such as dredging, channel realignment and the removal of large wood and boulders (Kupilas et al 2016, Lepori et al 2005b, Muotka & Laasonen 2002). Associated higher flow velocities can increase mechanical breakdown by physical fragmentation and the downstream transport of CPOM (Lepori et al 2005b, Webster et al 1994). Thus, channelization directly impacts detritivores both by loss of habitat (Kail 2003), and consequent reductions in their CPOM food (i.e. leaf packs). This can have a bottom-up effect on detritivore invertebrates, a functional group often limited by food availability, and the predators they sustain (Dobson & Hildrew 1992, Wallace et al 1997).

Large wood is a widespread restoration measure implemented on a global scale to provide habitat complexity in channelized rivers, often for the purpose of improving habitat for fish (Kail et al 2015, Roni et al 2015). Large wood has also been demonstrated to increase the retentive capacity of channelized upland streams subject to historic logging practices, and so both habitat stability and availability of food resources for detritivorous invertebrates (Lepori et al 2005b, Muotka & Laasonen 2002). In lowland rivers, while the green to brown energy ratio is more likely to favour green, a significant proportion of the energy flux is still derived from allochthonous resources (Bärlocher 2015, Hladyz et al 2011a). Large wood restoration is expected to increase CPOM accumulation and stabilizing substrate by sorting gravels (Kail 2003), and so increasing the availability of stable habitat and resources for detritivores (Entrekin et al 2009, Gurnell et al 1995).

Here I investigate the impact of large wood installation on the rate of MMD and IMD, as well as the abundance, biomass and composition of colonizing detritivore invertebrates. The increased retention of allochthonous resources in restored reaches is likely increase IMD (Tonetto et al 2014), as more detritivores drive elevated secondary (detritivore) production, and support greater detritivore invertebrate biomass (Lepori et al 2005a). Whereas microbial breakdown is likely to remain consistent, as the environmental factors that affect microbes, such as water chemistry, remains largely unchanged between treatments (Lefcheck et al 2015). With elevated IMD and detritivore production increasing the net transfer of basal energy to secondary consumers and higher trophic levels, such as fish (Lepori et al 2005a).

Hypotheses

The effect of large wood on detrital decomposition was investigated using the following specific hypotheses:

1. There will be a greater biomass and abundance of colonising invertebrate shredders in restored sites, as large wood facilitates the recovery of the shredder community through enhanced habitat and detrital resources.
2. IMD rates in restored reaches will increase compared to controls, this will be due to higher detritivore biomass and elevated levels total breakdown, rather than MMD, which will remain similar in both treatments.
3. Colonising detritivore composition will change in the restored reaches as restoration alters conditions.

5.3 Methods

Study site

Detailed descriptions of the study area and environmental factors are mentioned in detail in the General Methods in Chapter 2. In brief, the study system, the River Great Stour, is a heavily modified calcareous stream, stressors include both agricultural activity within the catchment, urbanization and channelization. Dredging for navigation and current flood alleviation measures has simplified the physical profile of the system reducing its ability to retain allochthonous material. Four reaches were selected for restoration paired with nearby upstream 'control' sites selected based on similar hydromorphological and riparian characteristics.

Leaf litter and bag preparation

A widespread method for measuring the rate of litter breakdown has been the deployment of leaf-litter bags containing allochthonous leaf-litter within the wetted channel, with the abundances and diversity of colonizing invertebrates used to characterize the detritivore community (Smith & Chadwick 2014, Woodward et al 2012). Paired with fine leaf-litter bags that restrict macroinvertebrate access to the leaf litter, these enable the relative contribution of macroinvertebrate mediated and microbial detrital breakdown to be quantified and compared.

Alder (*Alnus glutinosa*) is a tree native to the UK, associated with watercourses and boggy areas, and alongside willow (*Salix sp*) was the dominant riparian tree fringing all reaches and so supplies a large proportion of the leaf litter input. Furthermore, alder leaves decompose faster than those of other tree species and their use in other studies facilitates between project comparisons of results (Lepori et al 2005b, Woodward et al 2012). Senescent alder leaves were collected in October 2014 from within the same 30-m^2 area (e.g., to minimize problems of intra-species variation in breakdown rates – (Gessner & Chauvet 2002)). Fine and coarse mesh bags, of dimensions 160 x100mm were paired. Mesh sizes were coarse (~10 mm) wide enough to permit invertebrate colonization, and fine (~250-µm mesh size) to exclude macroinvertebrate colonization. The bags were loaded with 3.0 ± 0.1 g oven dried alder leaves weighed to 0.01 g; these were pre-wetted with distilled water to avoid

fragmentation before being placed into labeled bags. All bags were then stapled shut, with care taken to ensure fine mesh bags had no openings.

Sampling and deployment

We placed six paired fine and coarse bags along the center of each reach (6 x paired bag replicates per reach x 8 reaches, N = 48 per time point), secured with a metal stake. Six technical replicates allowed for the expected accidental loss of bags within the reaches. Bags were initially deployed in mid-autumn when leaf-fall is greatest. However, high flows in autumn 2014 resulted in the loss of the bags and inability to retrieve them. In order to get the 'before' samples, crucial to the experimental BACI design, bags were again deployed in early spring 2015 (Before 2015), when flows were lower and prior to the implementation of the restoration with large wood. Bags were then deployed after restoration in spring 2016 (After 2016) and 2017 (After 2017), i.e. 6 paired bags x 8 reaches x 3 time points, N = 144. Allochthonous material is still a major resource for stream detritivores at this time of the year while daylight is shorter and so autochthonous production reduced (Hladyz et al 2011a). Of the 144 paired bags deployed, 138 were recovered.

MiniDot Sensors were attached to middle litterbags at each reach; these collected oxygen and temperature data every fifteen minutes. The paired fine and course leaf bags were retrieved after 9 days, this period has been used in other studies and is thought to be a sufficient time scale for both MMD and IMD to take place (Thompson et al 2016). During retrieval, litterbag pairs were carefully removed from the metal stakes and immediately sealed individually in plastic bags. These were then stored at -20°C in order to halt decomposition and humanely euthanize and preserve macroinvertebrates for later processing.

Leaf litter processing

Bags were processed in laboratory conditions. The fragments of alder leaves were retrieved by hand from the litterbags after silt and invertebrates had been thoroughly rinsed off over a 250-µm sieve. Leaves were then oven dried at 80 °C for 48 h to determine dry mass, and macroinvertebrates stored in 70% ethanol for identification (Thompson et al 2016). The leaves were then reweighed to the nearest 0.01g.

Macroinvertebrate processing

Detritivore invertebrates collected from each bag were sorted and identified down to family level; samples were then photographed and the photos imported into *ImageJ*, image-processing program (Abràmoff et al 2004). From these images the necessary measurements, either body length or head capsule width, were extracted in order to determine the body mass of each individual using the equations in Chapter 4: Appendix 4.1. In addition, detritivores were assigned a functional feeding group (FFG); determined by species (if known) or family these were either shredders or gathering collectors (Thompson et al., 2016). Inactive individuals at time of collection, such as pupae, were excluded from analysis.

Estimation of breakdown rates

As temperature is known to have a strong influence on rates of decomposition Degree-days (*dd)* were used (Anderson & Sedell 1979). For each leaf bag, the exponential decay coefficient, k, was calculated in order to compare decomposition rates using the following equation:

$$k = -\frac{\ln\left(\frac{m_1}{m_0 \times c}\right)}{dd}$$

Where: m_0 = dry mass of leaf litter placed in river (g), m_1 = dry mass of leaf, litter After 9 days (g), c = air-dry to oven-dry conversion factor (0.968), dd = degree-days (Thompson et al 2016, Woodward et al 2012). By using this equation on the coarse litterbags, IMD is calculated; however, this equation also gives the decomposition rate attributed to microbe, MMD when applied to the data from the fine litterbags as the aperture excludes invertebrates. Degree-days were calculated by multiplying the mean water temperature during the deployment period by the number of days the leaves were left in the river.

Statistical Analysis

Decomposition rates

All statistical analysis was performed in R (R Core Team 2013). Linear mixed-effect models (LMM) were fitted to the decomposition rates from the midstream samples. In order to estimate the BACI response and measure the effect of restoration through time, LMMs were used to test for BACI responses by comparing Before 2015 data with After 2016 and also Before 2015 with After 2017. The models used the fixed effects of period (i.e. before or after restoration) and treatment (i.e. control or restored) and their interaction. River reach was added as a random effect variable. Outliers where the rate was below 0 or above 0.015 were removed to normalize the data.

Colonizing detritivore abundance and biomass

Total colonizing detritivore, shredder and gathering-collector biomass was log transformed to normalize the data and fitted to LMMs. The abundance data was found to have a negative binomial distribution so generalized linear models (GLMs) were used to test the effect of treatment, period and their interaction using reach as random effects.

Detritivore composition

Differences in the composition of colonizing detritivores were visualized using non-metric multidimensional scaling (NMDS) using Bray-Curtis Index of the family abundance data. To analyse the BACI effect, year and treatment were grouped into a factor. The explanatory power of year, treatment and an interaction between the two was assessed using permutational multivariate analysis of variance (PERMANOVA) with 9999 permutations. Pairwise-PERMANOVAs (Pair-PERMS) were then used to see which factors differed significantly. For the habitat comparison, habitat and treatment were grouped into a factor and tested. Plots and analyses were performed using the Vegan package (Oksanen et al., 2007).

5.4 Results

Midstream habitat BACI responses

There was a significant decrease IMD breakdown rate in restored sites almost a year after restoration in 2016, however in 2017 this was not significantly different from pre-restoration levels (Figure 5.1; Table 5.1). As expected, microbial breakdown did not change significantly between treatments either in 2016 or 2017. 10 families of detritivore were found, 5 shredder and 5 gathering collector the most abundant being the Trichopeteran families Sericostomatidae and Lepidostomatidae (Table 5.2).

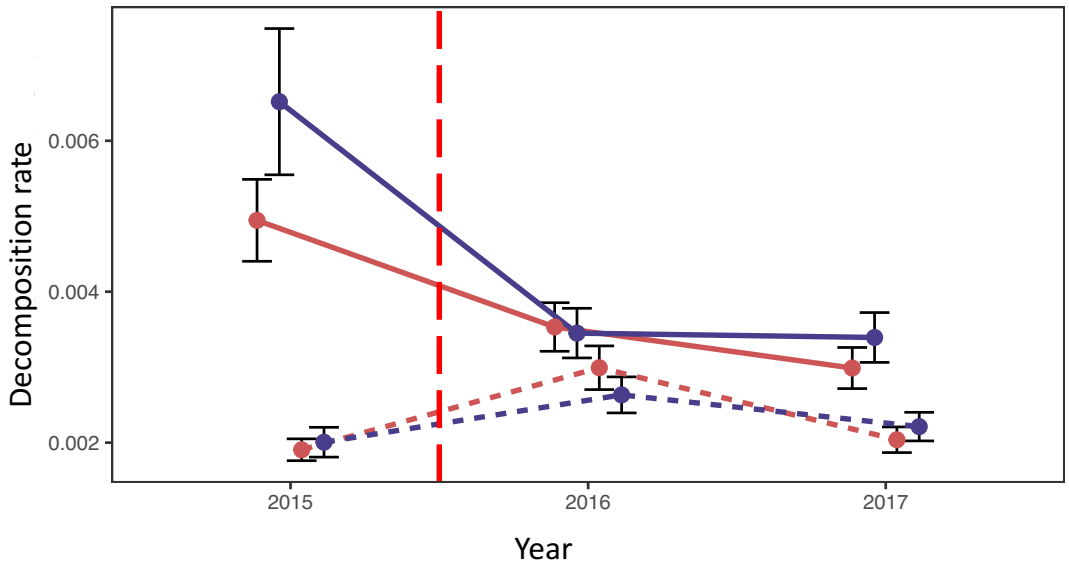


Figure 5.1: The decomposition rate expressed as temperature corrected rate of decomposition, over time in mid-stream habitat for restored (blue) and control sites (red), with the time of restoration shown as a vertical red dashed line. Points show mean values, ± standard errors. The solid lines representing IMD and the dashed lines MMD.

Table 5.1 Statistics of fit for the LMM models for both log transformed invertebrate mediated decomposition (IMD) and microbial mediated decomposition (MMD). All models include a main BACI effect of pre-restoration Before 2015 compared to After 2016 and Before 2015 compared to After 2017, fitted with study reach ($N = 8$) as a random effect. Significance: · = $P < 0.1$, * = $P < 0.5$.

Response variable	BACI comparison		Estimate	*SE*	*Df*	*T*	*P*	
IMD	Before 2015	After 2016	-0.3080	0.1507	85.2	2.04	0.044	*
	Before 2015	After 2017	-0.2688	0.1448	80.5	1.86	0.067	.
MMD	Before 2015	After 2016	0.0001	0.0005	88.7	0.26	0.798	
	Before 2015	After 2017	0.0001	0.0004	75.7	0.18	0.856	

Table 5.2 Colonizing detritivore families and their functional feeding groups with total abundance and total mass estimates.

Order	Family	FFG	Treatment	Abundance	Mass
Amphipoda	Gammaridae	Shredder	Control	590	645.9
Amphipoda	Gammaridae	Shredder	Restored	519	678.0
Ephemeroptera	Baetidae	Gathering.collector	Control	525	680.5
Ephemeroptera	Baetidae	Gathering.collector	Restored	558	466.3
Ephemeroptera	Caenidae	Gathering.collector	Control	145	318.9
Ephemeroptera	Caenidae	Gathering.collector	Restored	135	312.4
Ephemeroptera	Ephemerellidae	Gathering.collector	Control	121	30.9
Ephemeroptera	Ephemerellidae	Gathering.collector	Restored	170	86.8
Isopoda	Asellidae	Shredder	Control	116	689.1
Isopoda	Asellidae	Shredder	Restored	35	252.3
Trichoptera	Glossosomatidae	Gathering.collector	Control	165	11.3
Trichoptera	Glossosomatidae	Gathering.collector	Restored	41	1.9
Trichoptera	Lepidostomatidae	Shredder	Control	163	1096.0
Trichoptera	Lepidostomatidae	Shredder	Restored	196	1405.9
Trichoptera	Limnephilidae	Shredder	Control	17	402.6
Trichoptera	Limnephilidae	Shredder	Restored	55	1460.1
Trichoptera	Sericostomatidae	Gathering.collector	Control	144	1188.8
Trichoptera	Sericostomatidae	Gathering.collector	Restored	224	2370.8
Trichoptera	Psychomyidae	Shredder	Control	70	13.47
Trichoptera	Psychomyidae	Shredder	Restored	56	55.97

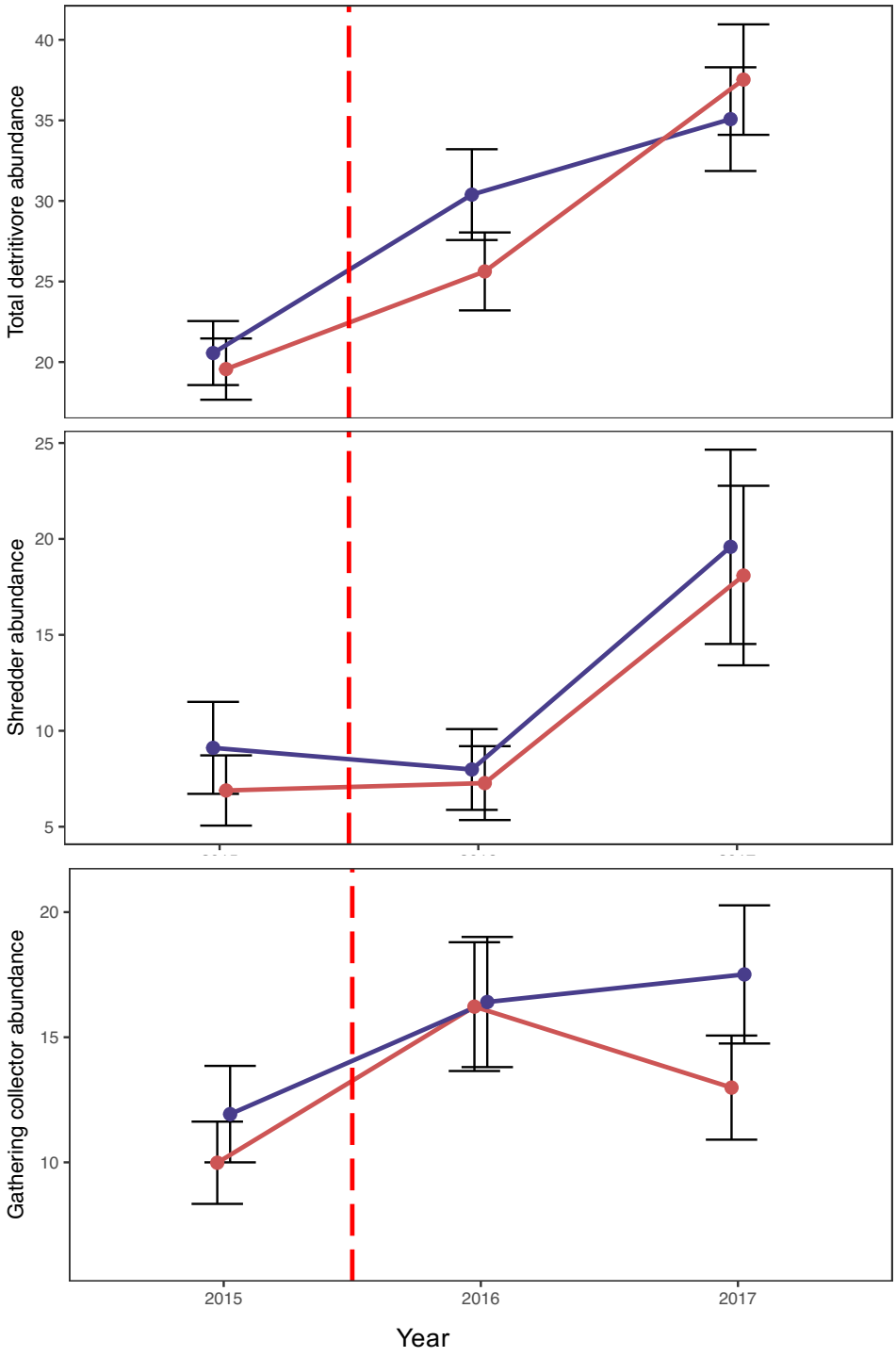


Figure 5.2: Mean colonizing detritivore abundance in the mid-stream habitat per bag at each time point in restored (blue) and control sites (red), with the time of restoration shown as a vertical red dashed line. Points show mean values, ± standard error.

Restoration had no effect on the total abundance of colonizing detritivores, shredders or gathering collectors, with treatments tracking each other through time (top Figure 5.2; Table 5.3). Total detritivore abundance increased through time (Figure 5.2 Top), due to an increase in gathering collectors in 2016 (bottom Figure 5.2 Mid), followed by an increase in shredder abundance in 2017 (bottom Figure 5.2).

Table 5.3 Statistics of fit for the GLMM models for total colonizing detritivore abundance, shredder abundance and gathering collector abundance fitted to a negative binomial distribution. Results show a main BACI effect of pre-restoration Before 2015 samples compared to After 2016 and Before 2015 compared to After 2017 samples, fitted with study reach (*N* = 8) as a random effect.

Response variable	BACI comparison		Estimate	*SE*	*Df*	*Z*	*P*
Total Abundance	Before 2015	After 2016	0.065	0.214	87	0.30	0.762
	Before 2015	After 2017	-0.125	0.209	88	-0.60	0.549
Shredder	Before 2015	After 2016	-0.197	0.223	85	-0.88	0.377
	Before 2015	After 2017	-0.292	0.225	85	-1.30	0.194
Gathering collector	Before 2015	After 2016	0.176	0.324	85	0.54	0.587
	Before 2015	After 2017	-0.218	0.277	86	-0.79	0.431

Restoration was also found to have no effect on the total biomass of colonizing detritivores, shredders or gathering collectors, while there were annual variation, similar to the abundance the treatments tracking each other through time (top Figure 5.3; Table 5.4).

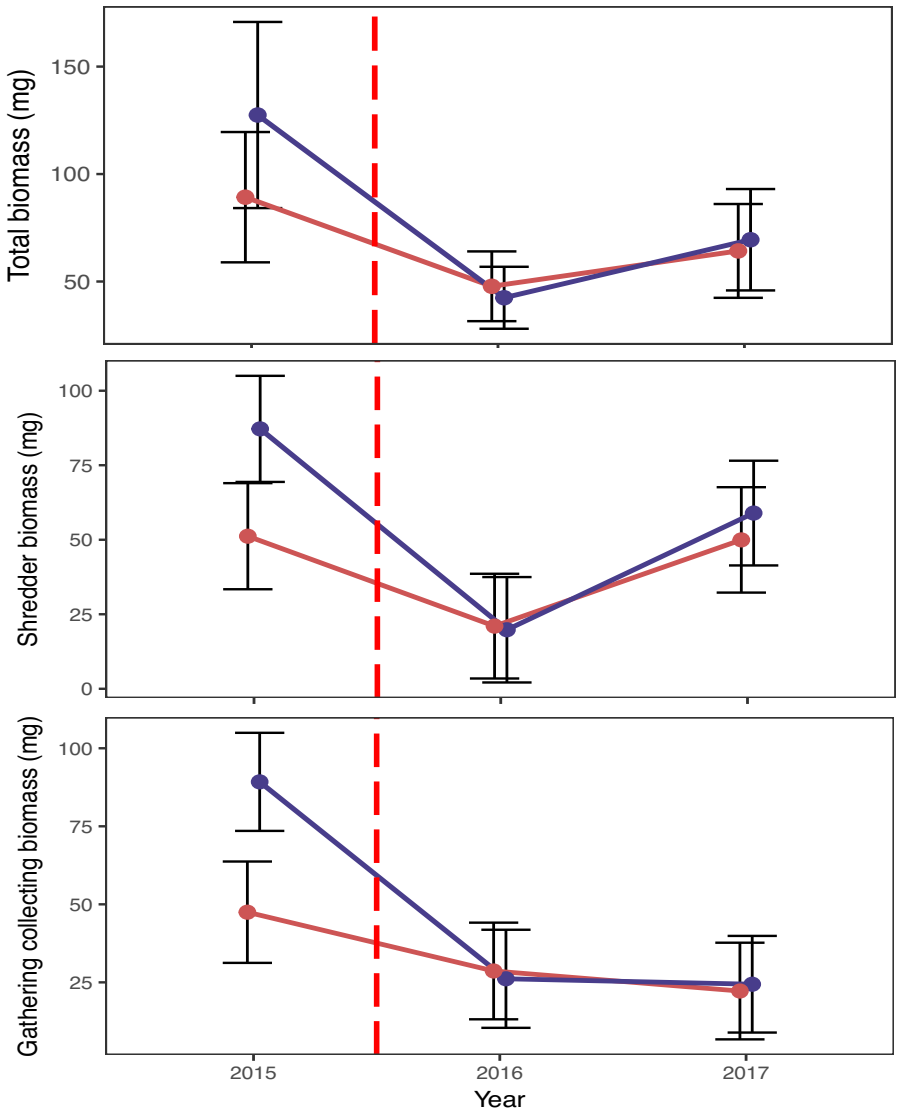


Figure 5.3 Mean colonizing detritivore biomass in the mid-stream habitat per bag at each time point in restored (blue) and control sites (red), with the time of restoration shown as a vertical red dashed line. Points show mean values, ± standard error.

Table 5.4 Statistics of fit for the LMM models for log transformed total colonizing detritivore biomass, shredder biomass and gathering collector biomass. All models include a main BACI effect of pre-restoration Before 2015 samples and After 2016 and After 2017 samples, fitted with study reach ($N = 8$) as a random effect. Significance: · = $P < 0.1$, * = $P < 0.5$.

Response variable	BACI comparison		Estimate	*SE*	*Df*	*T*	*P*
Total biomass	Before 2015	After 2016	0.530	0.381	83	1.39	0.168
	Before 2015	After 2017	0.418	0.341	84	1.23	0.223
Shredder	Before 2015	After 2016	0.509	0.413	84	1.23	0.221
	Before 2015	After 2017	0.272	0.417	81	0.65	0.516
Gathering collector	Before 2015	After 2016	0.186	0.515	81	0.36	0.719
	Before 2015	After 2017	0.140	0.459	82	0.30	0.762

Colonizing detritivore community analysis

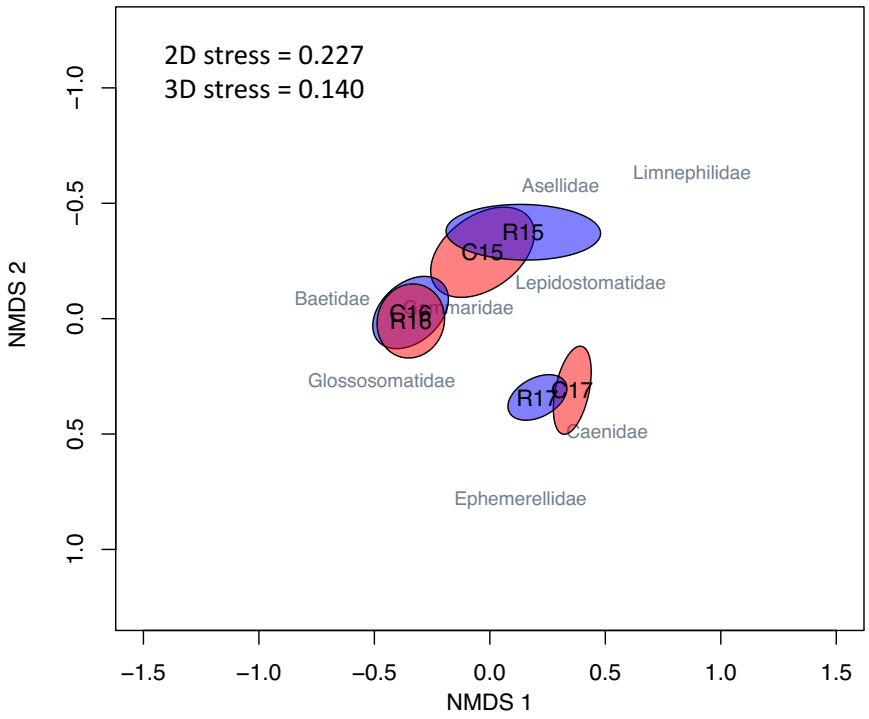


Figure 5.4: NMDS of the colonizing detritivore community. Ellipses represent standard error for each factor with restored reaches (blue) and control reaches (red) at each time point, with centroid labels for each (*N* = 141).

The NMDS of the colonizing macroinvertebrate community suggested that while there was year on year variation in the communities, composition remained similar between treatments (Figure 5.4). This was confirmed by PERMANOVA which found significant differences between treatments but no treatment x year effect (Table 5.5).

Table 5.5 Effect of treatment, time and the interaction on community structure, PERMANOVA with 999 permutations, (*N* = 141). Significance stars; *** = p <= 0.001.

Source	*Df*	*SS*	*Mean S*	*F*	*R2*	*P*	
Treatment	1	0.573	0.573	3.329	0.019	0.001	***
Year	2	6.190	3.095	17.985	0.203	0.001	***
Treatment:Year	2	0.489	0.245	1.422	0.016	0.089	
Residuals	135	23.231	0.172	0.762			
Total	140	30.4831	1				

Further analysis with pair-PERM showed that all pairwise comparisons were significant except between treatments at each time point (Table 5.6 in bold), suggesting that restoration did not alter colonizing detritivore composition between treatments.

Table 5.6 Pair-PERM of treatment-year factors. Significance stars; * = p = 0.05 to 0.01

Source	*Pairs*	*F*	*R2*	*P*	*P adjusted*	
1	**C15 vs. R15**	**2.327**	**0.050**	**0.021**	**0.315**	
2	C15 vs. C16	3.021	0.063	0.005	0.046	*
3	C15 vs. R16	3.872	0.081	0.003	0.045	*
4	C15 vs. C17	8.417	0.158	0.001	0.015	*
5	C15 vs. R17	7.613	0.145	0.001	0.015	*
6	R15 vs. C16	5.256	0.105	0.001	0.015	*
7	R15 vs. R16	6.124	0.122	0.001	0.015	*
8	R15 vs. C17	9.012	0.167	0.001	0.015	*
9	R15 vs. R17	8.250	0.155	0.001	0.015	*
10	**C16 vs. R16**	**0.965**	**0.021**	**0.433**	**1**	
11	C16 vs. C17	9.050	0.164	0.001	0.015	*
12	C16 vs. R17	7.137	0.134	0.001	0.015	*
13	R16 vs. C17	11.527	0.204	0.001	0.015	*
14	R16 vs. R17	7.697	0.146	0.001	0.015	*
15	**C17 vs. R17**	**2.206**	**0.046**	**0.01**	**0.15**	

5.5 Discussion

Large wood restoration was expected to facilitate elevated levels of total decomposition by improving habitat conditions for detritivores. Few studies have attempted to demonstrate this empirically and the results of this study provide little evidence to support this theory, and so hypothesis 1 and 2, that abundance and biomass would increase leading to elevated total breakdown are not supported. IMD responded negatively to restoration in 2016, this suggests that large wood additions may have a negative impact on this fundamental process.

This supports other equivocal studies investigating the effect of restoration on detrital breakdown have also failed to detect any causal changes in breakdown rates or colonising detritivore abundance, biomass and composition, despite extremes in the extent of degradation (Lepori, Palm et al. 2005, Smith and Chadwick 2014). For instance, Smith and Chadwick (2014), found that despite significantly enhanced aesthetics, reach scale restorations in Greater London, UK, failed to produce any measurable responses in either breakdown rate or the invertebrate assemblage. This is also true for Lepori et al (2005), in their investigation on the presumably less impacted River Ume in Northern Sweden, while restoration significantly increased detrital retention there were no measurable effects on decomposition or the colonising invertebrate assemblage. The evidence therefore suggests that reach scale restorations have negligible impacts on decomposition.

There was evidence of a negative relationship between detritivore abundance and breakdown rate. Detritivore biomass may be key here; while there were higher abundances of colonising detritivore invertebrates After the before sampling in 2015, invertebrate biomass fell. Colonising detritivores in the mid-stream habitat in 2015 prior to restoration were therefore larger in both treatments, and replaced by smaller colonizers in 2016 and 2017, which may explain the reduction in breakdown rates for these years. This indicates that the community shifted to more abundant, but smaller colonising detritivores that were less efficient at processing detritus. However, while the rate of IMD decreased significantly in restored reaches after restoration in 2016,

and it should be emphasised that the only other statistical difference between the treatments were annual, catchment-wide effects, rather than treatment related.

It may be that allochthonous material (i.e. bottom-up control) is not the primary constraint regulating detritivore abundance and biomass in this community, but rather top-down predatory control (Leroux and Loreau 2008). Given the increase in fish biomass in restored reaches detected in Chapter 2 and 3, it may be that larger detritivores were subject to increased top-down predation pressure by larger fish, which resulted in the more significant decreases in midstream detrital breakdown rates and invertebrate biomass.

It is worth noting that in many of the studies that have found strong impacts on detritivore-mediated breakdown using these methods have investigated environmental perturbations that are far more likely to severely alter the detritivore community. For instance, Woodward et al's (2012) study was a pan-European experiment investigating nutrient enrichment in 100 streams over a greater-than 1000 fold gradient. Nutrient enrichment in known to drive extensive changes in community structure and functioning via eutrophication and associated biogeochemical changes such as anoxia, and coupled with the extended gradient (from severely impacted to oligotrophic) and replication, this is stressor is far more likely to drive detectable changes in decomposition. Similarly, Thompson et al's (2016) study investigated the impact of a catastrophic pollution spill that extirpated most of the arthropod community in 6km of river.

These stressors can be detected using structural measures of community composition and abundance and biomass, whereas reach scale restorations with wood often have no measurable effect on invertebrate community structure. These stressors are therefore far more likely to drive measurable changes in decomposition than the introduction of reach scale woody debris.

Mechanistic understanding of how large wood restoration operates to increase species abundances and diversity are not well understood; it is thought that bottlenecks in habitat quality and/ or resource availability are potentially alleviated (Miller, Budy et al. 2010). In steep, shaded forested headwaters these two are likely closely entwined, as habitat complexity provides the stability necessary for retaining allochthonous

organic matter, that provides the majority of the energy flux, and stable habitat for detritivore macroinvertebrates to grow, in systems that a subject to regular high flow conditions (Muotka and Laasonen 2002). Our study suggests that in lowland rivers, reach-scale large wood debris restoration does not enhance invertebrate decomposition or other factors regulating litter breakdown.

Another potential biotic factor may be a saturation effect due to the availability of higher quality allochthonous food resources already within the system (Hladyz, Abjornsson et al. 2011). The early action of microbes such as fungi and bacteria has been shown to be important for increasing the palatability of leaf-litter and so later action by detritivores, which feed After conditioning by microbes (Mora-Gomez, Elosegi et al. 2016). The limited timescale (9 days) of the leaf-bag deployment may not have been sufficient for the leaf litter to be conditioned to a level comparable to allochthonous material already present within the system, and so did not attract colonising detritivores away from this higher quality resources.

While allochthonous resource availability has been shown to constrain detritivore populations in headwater streams (Dobson and Hildrew 1992, Muotka and Laasonen 2002), in lowland rivers this may be less important as entrained, well-conditioned material supplied from the headwaters is deposited by the slower flows in the margins, and so available in greater abundances, especially in spring. Future studies could incorporate paired standardised benthic Surber samples to compliment leaf bags and provide direct estimates of the detritivore communities abundance, biomass and composition, as opposed to inferring this from colonizing detritivores (e.g. Thompson, Bankier et al. 2016). Additionally, methodological considerations may also have affected the outcome; the pinning of the bags within the higher flow midstream provides both an artificial flow refuge for shredders, and unnatural availability of their resources in a habitat where it is otherwise limited due to downstream transport by higher velocities, and so selected for smaller detritivores able to withstand flow. This also exposed the bags to higher fish predation pressure, for instance by species such as gudgeon (*Gobio gobio*), which actively forage in faster flowing and exposed midstream habitats (Winkelmann, Worischka et al. 2007). Further advances in this area of research have also applied more standardised detrital resources other than leaf-litter, such as cotton-strips, which may be more effective at

detecting broad patterns across ecological gradients (Jenkins, Woodward et al. 2013), however in their current form these cannot isolate invertebrate mediated breakdown from microbial, and are more centred on water quality, rather than habitat assessments.

5.6 Conclusions

Large wood material is frequently cited as benefitting allochthonous detrital breakdown is stream systems. Studies have shown that while it demonstrably assists the retention of organic CPOM, the anticipated measurable increase in the rate of detrital breakdown is rarely detected using leaf bag methods and colonising macroinvertebrate abundances and biomass rarely differ between restored and impact reaches. This suggests that either the effect of large wood on the allochthonous energy pathway may be negligible, or that the current methodology fails to attract detritivores.

Chapter 6 | River restoration and volunteer engagement: advancing the role of citizen stakeholders from advocate to evaluator

6.1 Abstract

River stakeholders are frequently engaged in planning and implementing reach scale river restorations. However, these self-mobilised efforts are rarely assessed using standardised and quantitative methods. Robust river restoration biomonitoring continues to remain rare and often dependent on either paid third parties or research institutions. As such, the volume of data generated fails to match the rate of implementation, with the vast majority of projects lacking any form of monitoring. Thus, while in-stream habitat restoration is a growing enterprise, driven by statutory targets and local grassroots interest groups such as anglers, conservationists and third-sector charities, monitoring subsequent ecological recovery is scarce and when done rarely standardised or designed to disentangle restoration effects from wider environmental noise.

These same river stakeholders often also volunteer in citizen science water quality monitoring initiatives that help to safeguard their local rivers against pollution. If a standardized restoration monitoring programme were designed adopting a similar model to water quality initiatives, citizen scientists could both pioneer restoration and determine its effectiveness in biodiversity conservation, while also helping develop our understanding of ecological response to it. This would, in turn, inform the design process and could help to prove the effectiveness of ecological river restoration in general, while drive adaptive management cycles towards more ecologically effective outcomes.

6.2 Introduction

Citizen science is a rapidly developing approach to environmental research that aims to engage all members of society in science (Silvertown 2009). Citizen scientists (in this case unpaid members of the public who volunteer their time to contribute towards addressing ecological questions and tackling environmental questions), experts and organisations are collaborating globally to form initiatives that advance ecological knowledge and address problems of global concern (Bonney & Shirk 2007), such as declines in pollinators (Biesmeijer et al 2006), the spread of invasive species (Delaney et al 2008), or monitoring river water quality (Conrad & Hilchey 2011). Typically, the combined observations of hundreds or thousands of citizen scientists over time are used to track broad-scale ecological trends and patterns linked to environmental change (Dickinson et al 2012). For example, the 2014 UK Big Butterfly Count received data on over 560,000 individual moths and butterflies, logged online by over 44,000 participants (2014), or the Secchi Disk project which maps the global distribution of marine phytoplankton (Carling 2013). The steady rise in the annual number of peer-reviewed publications concerning citizen science over the last 15 years is testament to its growing use as a method for environmental research (Figure 6.1) (Dickinson et al 2012).

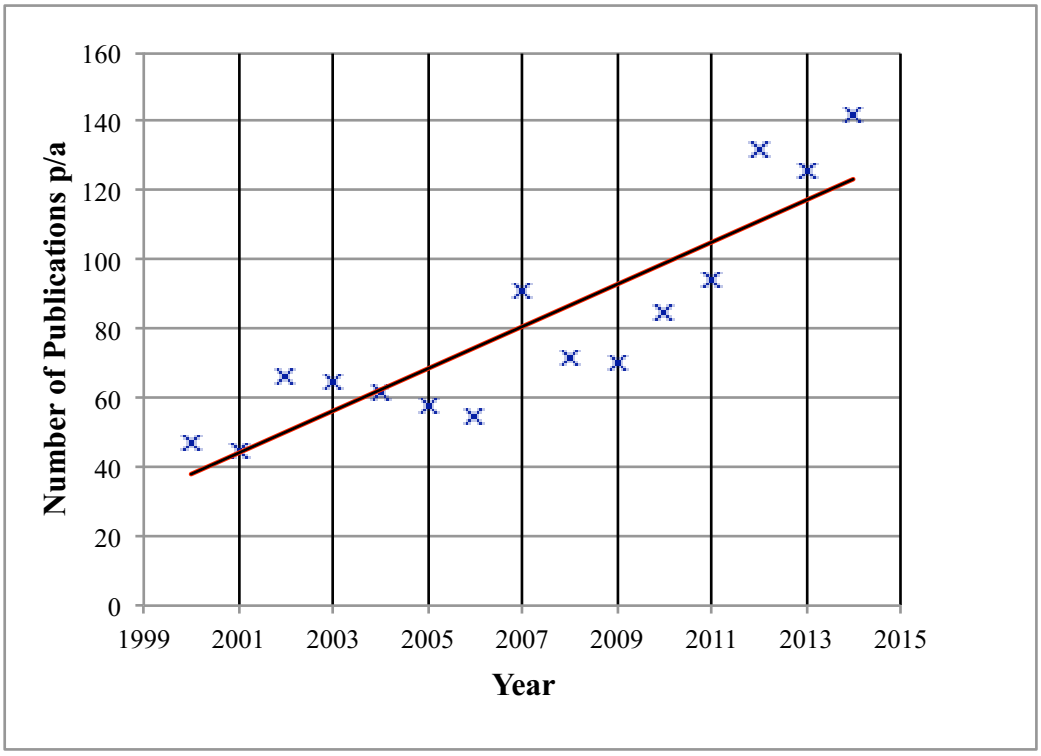


Figure 6.1: Graph showing the per annum increase in peer reviewed papers concerning citizen science from 2000 to 2015, with trend line (R^2 0.78061). 'Citizen science' was searched within the 'Environmental Sciences, Ecology' subsection in Web of Knowledge (https://webofknowledge.com)

River stakeholders, including anglers and conservation groups, value good water quality and the conservation of biodiversity (Conrad & Hilchey 2011, Latimore & Steen 2014). These stakeholders are engaging in citizen science via community-based monitoring initiatives, in which they act as 'environmental sentinels' detecting pollution incidents and alerting statutory agencies to mitigate against pollution (Conrad & Hilchey 2011). These same stakeholders lobby for ecological restoration schemes as a means of restoring biodiversity. Statutory bodies are increasingly encouraging their involvement in statutory project catchment management planning, i.e. mitigating flooding and ecological restoration planning (Orr et al 2007). Despite their increasingly important role in assessing the status of river quality (e.g., citizen scientists in the Riverfly Monitoring Initiative (RMI) sample 750 UK sites monthly), a scheme that enables them to monitor the effectiveness of restoration on local river ecology is currently lacking.

Ecological restoration describes the process of assisting the recovery of both structure and biological function to a degraded system (Palmer et al 2005), and maintain/reinstate ecosystem services and processes, e.g. supply of clean water (MEA 2005), and nutrient cycling (Palmer et al 1997, Palmer et al 2014). Stressors resulting from human activities, e.g.

pollution and homogenisation habitat, have resulted in the widespread degradation of river systems and global declines in freshwater species (Strayer & Dudgeon 2010). Despite widespread improvements to water chemistry, ecological recovery has been comparatively limited.(Brooks et al 2002, Ormerod 2003) Therefore in-stream habitat restoration is widely used to accelerate recovery (Feld et al 2011b, Friberg et al 2011), and is applied under the assumption that improving habitat will drive the recovery of species populations (Palmer et al 1997).

In-stream habitat restoration is a popular practice as it is often logistically, economically and conceptually less challenging than other restoration methods, e.g. reconnecting rivers to floodplains, or mitigating diffuse pollution, which may involve multiple landowners (Feld et al 2011b, Palmer et al 2010). Legislative ecological targets in the USA and Europe (Directive 2000), and stakeholders desire to improve river ecology, has fuelled demand for habitat restoration, stimulating a multi-billion dollar global enterprise (Morandi et al 2014, Palmer et al 2005). However, practitioners consistently fail to budget resources for project monitoring, which remains the exception rather than the rule (Bernhardt et al 2005, Downs et al 2012, Kondolf et al 2007). Thus, post-project appraisals often lack robust monitoring and are subjective (Jähnig et al 2010, Morandi et al 2014). Consequently, the tenet that in-stream habitat restoration increases species biodiversity and abundance lacks scientific evidence (Feld et al 2011b, Tompkins & Kondolf 2007). Confronting this evidence-gap is crucial for advancing restoration science and acquiring objective feedback to guide managers towards more predictable and successful ecological outcomes (Feld et al 2011b, Jenkinson et al 2006, Miller et al 2010).

In this opinion piece, we argue that the high uptake of citizen science water monitoring initiatives by the public demonstrates their motivation to participate in skilled scientific monitoring activities that can benefit their local rivers. We reason that this supports the development of a river restoration monitoring initiative in which citizen scientists track local ecological responses to river restoration, and that citizen science programmes, e.g. the UK RMI, provide a model that could be adjusted to suit restoration monitoring. This could potentially generate large volumes of standardised monitoring data at the spatiotemporal scales necessary to detect the response of river ecosystems to river restoration practices globally; advancing river restoration science and assisting global conservation efforts, whilst elevating both scientific and societal understanding of ecological river restoration.

6.3 Citizen Science and Environmental Monitoring

The Internet has increased citizen sciences' accessibility and facilitated collaborative initiatives that transcend geographic and institutional barriers, providing a global platform for connecting people and collecting data (Dickinson et al 2012, Finholt 2002, Wiggins & Crowston 2010). Web-centred citizen science initiatives have societal and scientific benefits over traditional approaches to scientific research (Dickinson et al 2012, Roy et al 2012). Society benefits from increased scientific literacy (Bonney et al 2009b), and more sympathetic attitudes and behaviour towards the countryside and nature conservation (Toomey & Domroese 2013). Science benefits from gaining large volumes of environmental data on unprecedented scales that are otherwise economically unachievable (Delaney et al 2008, Roy et al 2012, Silvertown 2009). For example, in the UK the British Trust for Ornithology's (BTO) 2013 Breeding Bird Survey had 2,854 volunteers survey 3,619 km^2 (Harris et al 2014). Armed with information at this scale, conservation bodies can make informed management decisions and allocate resources to maximise their conservation efforts (e.g. eBird) (Sullivan et al 2009).

Understanding citizen scientists' motivations for participating in programmes is key to long-term engagement (Grove-White et al 2007, Roy et al 2012). Volunteers engaged in monitoring water quality, such as the RMI and Missouri Stream Teams, often have an emotional connection to project goals and locations, heightening their involvement and leading to long lasting engagement and high output of quality data (Roy et al 2012). Streams and rivers are features of cultural significance in our landscapes that offer a focal point for appreciating nature and for local communities to pursue activities such as fishing, walking and observing wildlife (Pocock et al 2014, Roy et al 2012). These communities are keen to engage in activities that can help conserve and improve biodiversity (Conrad & Hilchey 2011). For example, anglers take an interest in stream and river management. They are often skilled at fish and invertebrate taxonomy, matching baits to seasonal abundances of riverflies for instance (Bate 2002), and many recognise the pivotal role of habitat and water quality in sustaining riverfly and fish populations. Although anglers observe changes in fish populations, noticing declines, their concerns have been historically marginalised from statutory policy and conservation as their observations lack 'hard science'(Bate 2002). The

2012 UK National Angling Survey found that out of >29,000 anglers, 23.3% currently volunteered for an angling organisation and over 26% wanted to volunteer for environmental work (Brown 2012). Citizen science initiatives for detecting pollution, e.g. Missouri Stream Team, provide an opportunity for anglers and other concerned stakeholder communities to substantiate their concerns, safeguard their interests, and stimulate action from statutory bodies; whilst developing a deeper understanding of their local environment.

Community-based water quality monitoring is proliferating across river catchments in North America and Europe (Conrad & Hilchey 2011, Orr et al 2007). Typically, groups of local volunteers, take 'structural' measures, e.g. sampling macroinvertebrates and recording taxon abundance, presence/absence and/or taxonomic diversity, alongside physicochemical measures, e.g. depth and temperature.(Conrad & Hilchey 2011). The advantage to centralised regional and/or national, citizen science programmes like Missouri Stream Team and the RMI, is that they often include statutory bodies, such as the Missouri Department of Conservation in the US or Environment Agency in England, as partners. These wield the resources to mount investigations and authority to prosecute (thus discouraging regular polluters), and can sway management policy to more sympathetic practices (Conrad & Hilchey 2011).

The RMI was launched in 2004, this community-based monitoring initiative uses one-day workshops to train groups of anglers and other interested individuals to sample, count and identify eight invertebrate taxa with varying sensitivities to pollution (e.g. Ephemeroptera, Trichoptera, Plecoptera), using a simple, standardised sampling protocol. This information complements routine monitoring by the Environment Agency, who usually sample biannually in spring and autumn once every two to three years. However, River Monitoring Initiative volunteers sample multiple sites once a month, increasing the likelihood of detecting and sourcing a pollution event. Community-based monitoring therefore supplements Environment Agency monitoring; increasing their spatiotemporal jurisdiction/responsiveness, and also empowers stakeholders with the control to determine the frequency and location of monitoring, ability to produce robust data, and a fast-track response to pollution incidents they detect. The RMI has created a growing network of over 100 local monitoring groups throughout the UK, which monitor the same 750 sites monthly. Volunteers submit geotagged sampling data online to the Riverfly Monitoring Database, if the data falls below 'trigger level' set by the Environment Agency (e.g. Figure 6.2), they 'respond' with a site visit, and if necessary, launch an investigation.

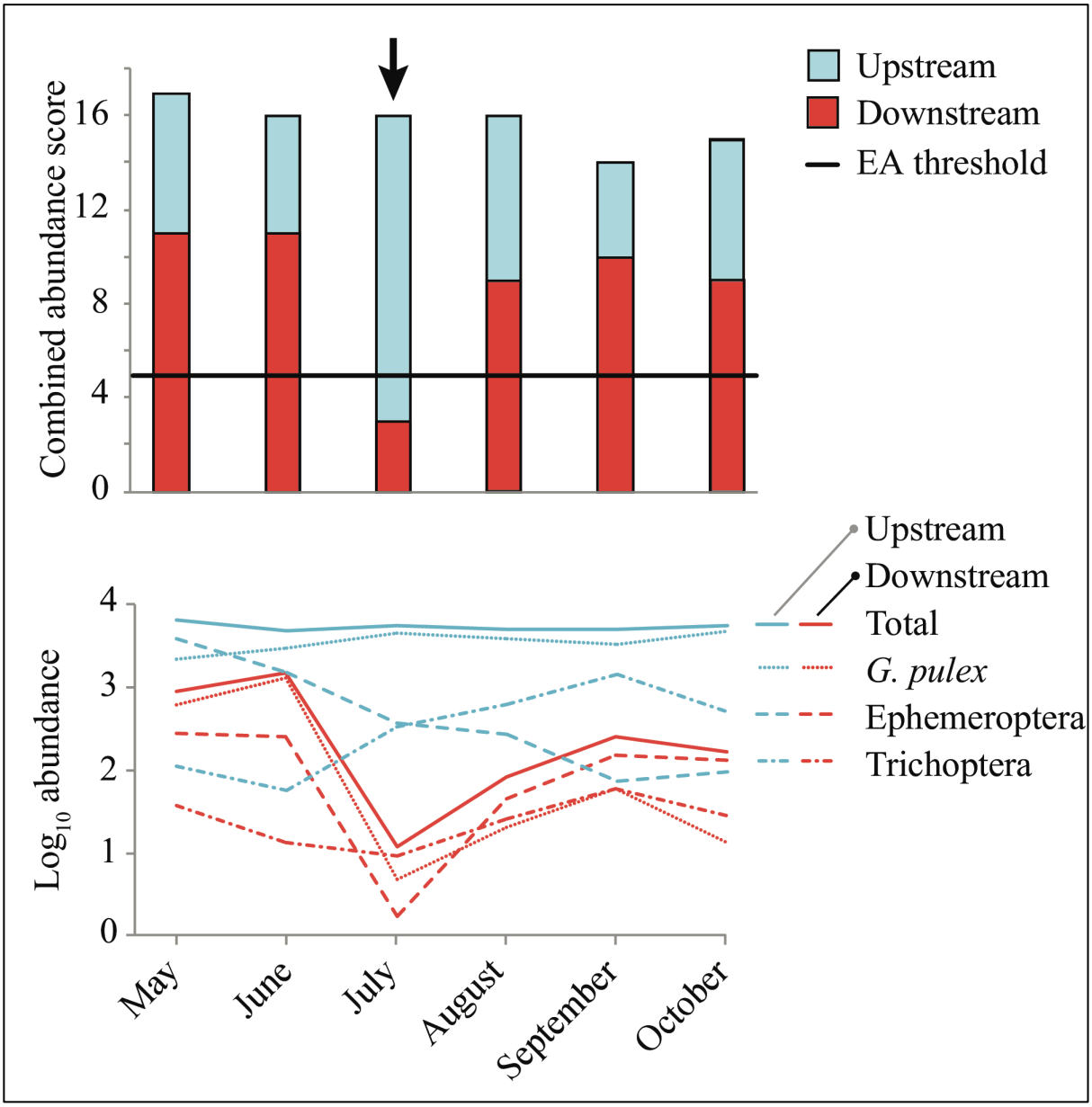


Figure 6.2: Top: ARK routine RMI data show invertebrate scores before and after the spill (red arrows), based on a sum of the abundance of target taxa. The red line represents an Environment Agency 'trigger levels' for substantial ecological degradation. Bottom: abundance of key taxa in relation to scores from an upstream control and downstream impact site respectively.

A recent case-study demonstrating the efficacy of the RMI is provided by the catastrophic pollution event on the River Kennet, a designated Site of Special Scientific Interest. In July 2013, a local conservation group (Action for the River Kennet (ARK)), conducting RMI monitoring detected a severe depletion in macroinvertebrates (Figure 6.2). The insecticide Chlorpyrifos had been discharged into the river via a sewage treatment works in what appeared to be a 'down the drain' incident, extirpating macroinvertebrate populations along a 15km stretch of river downstream of Marlborough, UK. The Environment Agency responded and located the source of the pollution and prevented further release. Subsequently a collaborative project between scientists, ARK, the Environment Agency, the angling community, and other stakeholders, was established to study the effects of the pesticide spill on the river ecosystem and recovery (Thompson et al 2016). This has revealed rare insight into the effects of this pollution incident on the river food web, and provided a case study for future similar perturbations (Thompson et al 2016).

The R. Kennet case study demonstrated that citizen scientists are motivated to track ecological recovery (Figure 6.2). Stakeholder communities engage in activities, such as litter removal and restoration, to enhance local streams, e.g. the Missouri Stream Team volunteers removed 688 tonnes of rubbish from Missouri rivers in 2013.(2013) Statutory bodies are also encouraging their engagement in river management plans (Carr et al 2012), and as a result, these communities are being integrated into the restoration planning process, and as well as beneficiaries to improved ecology, are therefore becoming 'restoration stakeholders'. Yet, they remain reliant on organisations (e.g. conservation organisations, research institutions) to monitor and assess local projects. There is, therefore, an urgent need to establish a citizen science initiative, employing a similar framework to the RMI, but designed to effectively monitor the ecological response of rivers to habitat restoration. Stakeholders could then evaluate ecological restoration and design projects that provide the greatest return on investment (Jenkinson et al 2006). A nationally, or even globally, coordinated approach could also generate high levels of quantitative, reliable, standardised data, which would also be value to river restoration science.

6.4 Current Challenges to River Restoration Science

In-stream habitat restoration projects typically use practices such as large woody debris, boulder or riffle additions, to diversify habitat. These are expected to enhance hydraulic and substrate heterogeneity, production, and food availability, and are thus, assumed to support higher species densities and biomass (Bernhardt et al 2007, Miller et al 2010). However, this assumption remains largely unsupported due to lack of monitoring (Bernhardt et al 2005, Feld et al 2011b, Morandi et al 2014, Palmer et al 2010). For example, Bernhardt et al (2005), found that out of >37,000 river restorations in the US, only 10% showed any form of monitoring or assessment. Monitoring has already demonstrated some practices (e.g. deflectors) have no measureable impact on fish or macroinvertebrate communities (Harrison et al 2004). Although monitoring often demonstrates consistent changes to hydromorphology, the biological response remains largely equivocal following in-stream restoration (Bernhardt & Palmer 2011, Haase et al 2013, Jahnig et al 2011, Palmer et al 2010). This failure to detect biotic change, and therefore substantiate theory with empirical evidence, is frequently ascribed to poor monitoring design, non-standardisation of evaluation criteria and uncertainty as to what constitutes project success (Jahnig et al 2011, Morandi et al 2014, Palmer et al 2005). This is perhaps not surprising, given the varied and often conflicting goals and limited resources of the organisations that typically carry out restoration monitoring (Morandi et al 2014).

Restoration success is often judged on qualitative attributes (e.g., post-project appearance and public opinion) (Bernhardt et al 2007), to the extent that a recent study in France reported that restorations with the poorest scientific evaluation strategies reported the most favourable ecological outcomes (Morandi et al 2014). These subjective evaluations lack scientific credibility and fail to advance restoration science and potentially misguide future ecological restoration projects. In order to isolate changes resulting from restoration, pre- and post-restoration assessment of environmental variables at restoration sites is essential. This approach reflects the robust before-after control-impact (BACI) experimental design widely used in ecology, which accounts for the 'noise' produced by natural variability (e.g. seasonal and annual differences) (Friberg et al 2011). Unfortunately, despite the statistical strength of such designs, BACI-style studies remain rare in restoration monitoring (Feld et al 2011b), e.g. 11% of monitored projects in the US (Bernhardt et al 2007).

The diversity in evaluation methodologies used to assess restorations is problematic as it invariably leads to varying interpretations of ecological success (Palmer et al 2005). Morandi et al. (2014), highlighted the difference in monitoring approaches between organisations, e.g. statutory bodies, fisheries associations, research institutions, with a more recent analysis has found diverse approaches between neighbouring countries (Morandi et al 2017). As ecological restoration is defined as returning both structure and function to a system, monitoring should include functional metrics (e.g. rates of processes such as primary or secondary production and decomposition) as well as structural metrics (e.g. species richness of target taxa), to determine success (Palmer et al 1997). However, structural metrics remain the dominant focus, as changes to communities are often more tangible than the underlying causal processes, e.g. detrital retention (Muotka & Laasonen 2002), or decomposition, using the methods demonstrated in Chapter 5.

The structural metrics chosen to determine success tends to vary between projects (e.g. presence/absence of species vs. absolute abundances)(Jahnig et al 2011, Palmer et al 1997). This can constrain the interpretation of ecological success (Rosi-Marshall et al 2006). Historic 'species-led' conservation has left a legacy where focal taxa and even single species are used as endpoints for measuring ecological outcome (e.g. trout) (Rosi-Marshall et al 2006). However, as demonstrated in Chapters 4 and 5, the response to habitat alterations is unlikely to be confined to just target taxa, and other assemblages (e.g. periphyton), are likely to respond and should be considered in the overall determination of success (Rosi-Marshall et al 2006), because restoring focal taxa often requires restoration of ecosystem functioning and wider community structure in order to be successful (Palmer et al 1997). Similarly, species richness measures may not detect increases in density, abundance and biomass, expected to result from improved ecosystem functioning, e.g. enhanced basal resources for detritivores (Muotka & Laasonen 2002). Recolonisation is also dependent on the availability of colonists that may not even exist or could be obstructed by degraded habitat, delaying/preventing a response (Parkyn & Smith 2011). The timescale of monitoring programmes is also a key factor when tracking population dynamics in aquatic communities (Feld et al 2011a, Jones & Schmitz 2009, Morandi et al 2014, Trexler 1995).

Problems in comparing restoration outcomes are often exacerbated by the contingent, case-by-case approach to restoration monitoring, i.e. *ad hoc* protocols that use varying methods, preventing meaningful comparison between projects (Miller et al 2010, Morandi et al 2014, Palmer et al 2014). These single study evaluations lack replication, and are characterised by

high variability and low statistical power. Robust data, however, would allow meta-analyses to provide more reliable assessments of restoration efficacy (Miller et al 2010). Therefore, restoration scientists repeatedly call for a centralised approach to restoration monitoring (Feld et al 2011b, Jenkinson et al 2006, Palmer et al 2005), even a programme of targeted monitoring on a strategic subset of projects has been suggested to provide a greater perspective on the performance of particular restoration practices and focus resources towards successful project designs (Bernhardt et al 2007, Jenkinson et al 2006). As stated by Palmer et al. (2005), this approach means even unsuccessful projects a partial success if they inform restoration science and prevent repetition of mistakes (i.e. installing deflectors (Harrison et al 2004)). Engaging citizen scientists in monitoring their local projects using a standardised protocol is a novel opportunity to realising this goal.

6.5 A Citizen Science Approach to Monitoring Restoration

The global scale and increased frequency of in-stream habitat restoration means that it is logistically, temporally, and economically impractical to rely on professionals and experts to monitor the majority of projects is. However, volunteers have demonstrated their proficiency in undertaking regular water quality monitoring, via the RMI and Missouri Stream Team. Adapting and expanding the RMI method provides a framework that can be used for monitoring river restorations. This approach could generate higher volumes of standardised, and thus directly comparable, data, than strategic monitoring of subsets of projects (Bernhardt et al 2007). Citizen science participation in restoration monitoring provides an opportunity for citizen scientists to share in scientific methods and discovery, track the progress and effectiveness of their projects and further connect to their local environments, whilst advancing both societal and scientific understanding of the processes enhanced by river restoration. This could produce a cycle, in which stakeholder monitoring accelerates progress in restoration science, in turn informing design towards more ecologically successful outcomes, and rallying further stakeholder engagement (Figure 6.3), whilst better focussing resources.

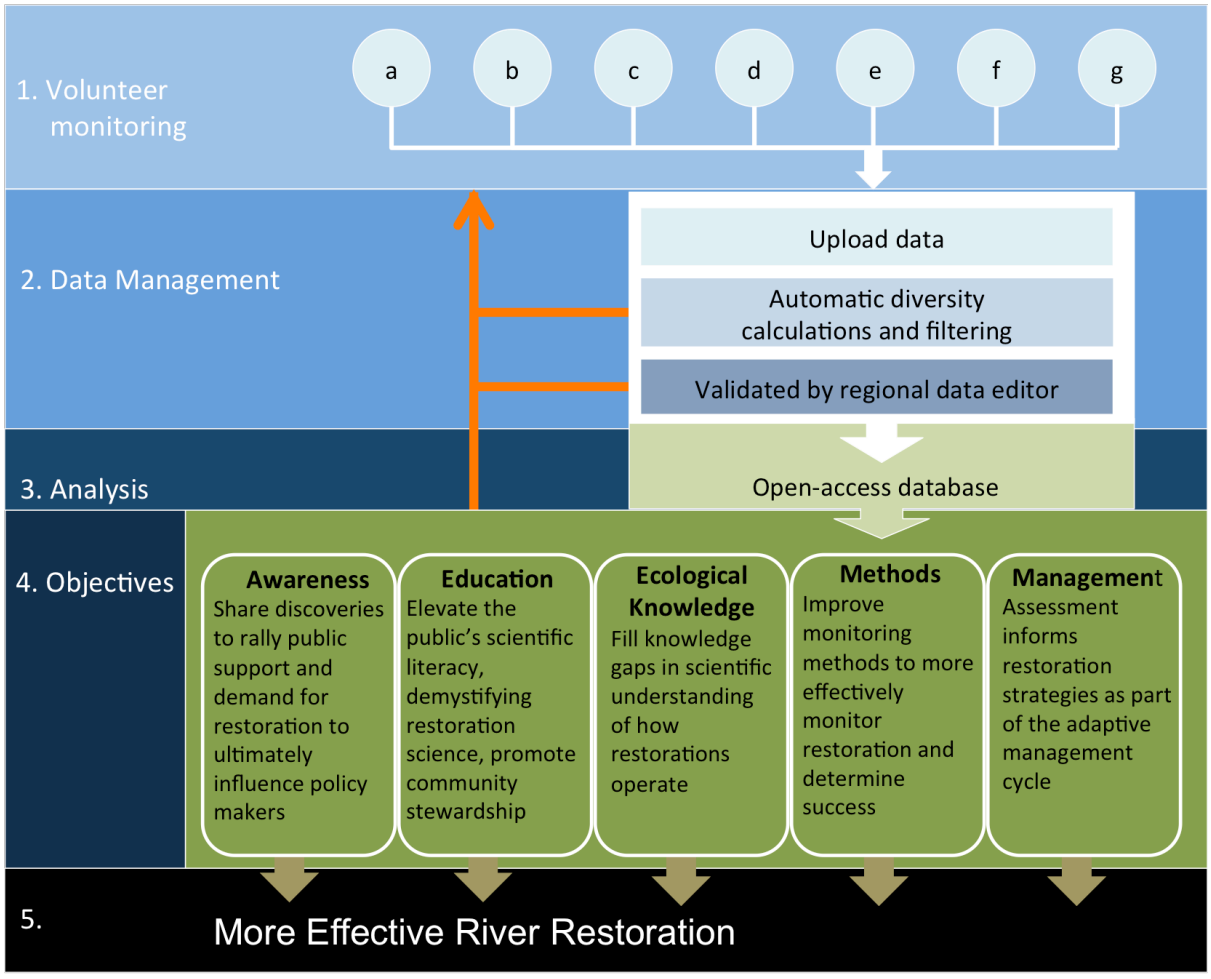


Figure 6.3: Cycle diagram showing the potential for stakeholder engagement in monitoring to advance restoration science, in turn feeding back into the restoration industry and informing design towards more ecologically successful projects. This would in turn attract more stakeholders and motivate increased engagement and therefore monitoring.

Protocols for citizen scientists require careful consideration, as the methodologies often demand a trade-off between scientific rigour and what can be realistically from volunteers. Protocols with long, complex, repetitive methodologies can be challenging and deter participants (Dickinson et al 2010). The status of fish populations is often a focus of in-stream habitat restoration and a popular end-point for assessing ecological response (Miller et al 2010, Rosi-Marshall et al 2006). However, the logistics of sampling (e.g. electrofishing) and the often relatively slow response of fish to restoration(Selego et al 2011) (e.g. 12-20 years(Trexler 1995)), reduces the viability of fish as an suitable indicator for citizen science monitoring programmes. Conversely, benthic macroinvertebrate assemblages are easy to sample and require inexpensive sampling equipment. They can also exhibit rapid recovery rates to restoration (Miller et al 2010). These qualities make them suitable for use to both citizen scientists and as indicators of environmental change. The RMI and other water quality monitoring initiatives use semi-qualitative methods, such as 3-minute kick-net sampling to obtain structural measures and diversity indices, sufficient for detecting decreases in diversity and abundance due to pollution (Godfrey 1978). Yet, replication would be necessary to increase the statistical power of abundance or biomass measures (Miller et al 2010).

The RMI uses eight easily recognisable taxa with different pollution sensitivities. However, expanding the taxonomic scope to include additional identifiable macroinvertebrate families and increasing the resolution to genus or species level, would provide a more detailed insight into the response of the benthic macroinvertebrate community to restoration, such as patterns in succession and recolonisation (Parkyn & Smith 2011). This would require higher levels of taxonomic skill than required for water quality monitoring, however, similar to the RMI and Missouri Stream Team, training workshops would develop volunteer's skills and demonstrate sampling methodology. Although this level of taxonomic resolution demands more skill and time, sampling can be less frequent (i.e., seasonal or biannual, instead of monthly). Also the ability of volunteers to identify species increases as they become familiar with the macroinvertebrate community in the rivers they sample. The data produced could be uploaded online, using a similar submission 'form' to the RMI, i.e. 'geotagged' with volunteer's names, date and site variables such as depth, temperature, flow and pH. Other wildlife observations could also be included, such as invasive species and birds.

Modest biotic responses to habitat restoration has led to an emerging focus on ecological process-based metrics of ecosystem functioning (Palmer et al 2014). Therefore, expanding the scope of citizen science monitoring to incorporate ecosystem processes, in addition to

structural measures, would be a positive step towards elevating public appreciation and understanding of ecosystem functioning. Scientific understanding of the effect of restoration practices on ecosystem processes would also be enhanced. This approach is already used in citizen science via the Leaf Pack Network (http://www.stroudcenter.org/lpn/), which is used throughout the Americas as an educational teaching exercise in schools. The initiative provides 'leaf pack kits' containing all the necessary equipment for deploying leaf packs in local streams (mesh bags), for analysing the invertebrate community (trays, magnifying glasses and sieves) and uploading results online. These measures are easy to implement, requiring little assistance and cheap equipment (i.e. electronic scales, sorting trays and net bags), yet could develop a better understanding of the processes that dictate ecological recovery in rivers and streams.

Traditional structural and functional measures are not the only sampling methods that can be explored for potential use by citizen scientists. 'Environmental DNA' (eDNA) is a rapidly developing cutting edge technology that can produce a static snapshot of ecosystem diversity, from water or benthic samples, simultaneously identifying diversity across the kingdoms of life, i.e. plants, fungi, bacteria, and animals (Bohmann et al 2014, Lallias et al 2014). A recent study trialling eDNA sampling by citizen scientists for conservation found it to be more effective than standard survey methods, and that volunteers were able to successfully collect eDNA samples with very little training (Biggs et al 2015). For restoration monitoring, citizen scientists could take eDNA water/sediment samples, and send them in for scientific analysis, circumventing time consuming observation or sampling methodologies and taxonomic identification. Repetitive eDNA sampling could also create a 'stop-motion eDNA video,'(Bohmann et al 2014) to shed light on changes to ecological processes. However, eDNA requires experts for processing and analysis, and the costs may be prohibitive. eDNA has also been shown to travel up to 12km in aquatic systems, so may not accurately represent study site biota (Deiner & Altermatt 2014). On the other hand, commercial companies are specialising in eDNA processing which could drive down costs (Bohmann et al 2014). Also, eDNA technology could enhance traditional macroinvertebrate monitoring, e.g. provide a list of extant species in a watershed to assist the development of simplified catchment specific keys to aid identification, reducing false positives, i.e. checking recorded species are present. It could also rally volunteer enthusiasm by detecting and raising public awareness of rare or elusive charismatic species, e.g. otters, salmonids, birds.

Citizen science offers exciting possibilities for river restoration, but the effect of volunteer error on researcher interpretation remains a key concern (Dickinson et al 2010, Gardiner et al 2012). As shown by the analysis of Gardiner et al. 2012, in which volunteers overestimated the abundance of rare species and underestimated the abundance of common species. This resulted in citizen scientists reporting significantly greater diversity compared to scientists across three initiatives. However, volunteer skill can be enhanced by investing time and resources into training and materials (Bonney et al 2009a), an approach already adopted by stream monitoring initiatives like the RMI. Additionally the design of high-resolution photographic identification guides specifically tailored to illustrate a catchments extant taxa (simplified by eDNA technology), could also help to develop identification skill.

Volunteers in scientific research suggests a free resource, however, often-substantial initial investment is required to implement citizen science initiatives. Designing a scientifically sound and user-friendly protocol, and creating the online infrastructure for disseminating information and collecting data, often requires the input of professional staff (Roy et al 2012). Additionally, Roy et al. 2012 estimated that annual maintenance of successful citizen science projects cost between £70,000 – 150,000. For example, the River Monitoring Initiative required at least one full time employee for start-up and an additional employee for national coordination once launched. Providing regular workshops to train people can also require professionals, as does data checking and initiative coordination. Training citizen scientists as instructors can circumvent this bottleneck. However, to put expenditure into context, the US has spent $14-15 billion on river restoration since 1990, yet this expenditure cannot be assessed due to the dearth of project monitoring and assessment.(Palmer et al 2005) If just a fraction of this sum was budgeted for monitoring resources (even less if volunteers are used), it could pay dividends, as restoration science is advanced and informs designs towards more efficient, cost-effective designs and effective ecological outcomes. Therefore, restoration decision makers and practitioners should strive to budget for project monitoring as a policy of best practice, as they, in the long-term, stand to benefit.

6.6 Conclusion

In light of the global biodiversity crisis, and our reliance on river ecosystem goods and services, it is crucial that habitat restoration is successful in conserving biodiversity and recovering degraded ecosystems. Standardised monitoring by citizen scientists could play a key role in developing our understanding of how these practices affect ecology and the effectiveness of restorations to mitigate anthropogenic impacts and aid ecological recovery.

Habitat restoration and citizen science are subjects at the fore of environmental research, illustrated by the wealth of literature discussing their application and growing importance in nature conservation. Widespread advances in communication and information technology has accelerated the swift uptake of citizen science, heralding a new era in environmental research in which both scientists and volunteers work in partnership to conserve nature and further ecological knowledge. This relationship not only elevates the public's scientific literacy, but is also enables monitoring at spatiotemporal scales that would otherwise be impossible, but are crucial, for testing hypotheses and detecting patterns in ecology. Developing wider societal engagement in local restoration ecology paves the way for the next generation of citizen scientists to be more active contributors to the scientific evidence base, as opposed to being passive observers and data-gatherers, in the future.

A national or international network of volunteer groups conducting coordinated monitoring on local restoration projects, using a robust standardised protocol would enable a meta-analysis of restorations that could be used to test the efficacy of habitat restoration practices across broad spatiotemporal scales and environmental gradients. This would generate significant advances in ecological restoration and allow scientists to make improved predictions about the efficacy of particular restoration practices. The benefits of involving citizen scientists in restoration monitoring extend beyond purely advancing restoration science, however. The involvement of stakeholders offers an opportunity for outreach, increasing societal awareness of freshwater ecology and project legacy, possibly resulting in increased public demand for restoration. Therefore, investing time and resources into developing such an initiative is likely to be a rewarding process that would pay dividends to both science and society.

7 | General Discussion

The main aim of this project was to apply standardised quantitative biomonitoring to reach scale restorations to capture and measure ecological change called for in the literature (Morandi et al 2017, Morandi et al 2014, Palmer et al 2005). In all three of the data chapters I was able to detect statistically significant responses to restoration, which was only possible due to the replicated design employed. In Chapter 3, significant increases to the abundance of piscivore fish species were observed; in Chapter 4, it was found that the trophic network for benthic invertebrates and fish had also changed significantly, leading to more species and increased energy efficiency; in Chapter 5, there was a significant decrease in rate of detrital breakdown in the midstream habitat of restored sites. Additionally, the BACI design was instrumental for disentangling responses to restoration from wider environmental noise, confirming the calls from the literature for this approach to be more widely adopted (Downes et al 2002, Feld et al 2011). The use of control sites provided a crucial temporal baseline, in which annual and seasonal changes could be disentangled from restoration responses, this was most evident in Chapter 3, where, in the absence of control sites, the significant increase in juvenile trout recorded in autumn 2015 would have been attributed to the restorations, rather than a wider catchment response. This may have encouraged the further implementation of wood as a trout management measure, despite the negligible responses on trout and strong response of their piscivore predators.

Studies tracking changes in fishes following restoration are among the most frequent in the restoration biomonitoring literature (e.g. Stewart et al 2009, Whiteway et al 2010), this is in part due to their significance as charismatic species of high cultural and economic significance, but also because of their highly equivocal responses to interventions. My findings demonstrate that interspecific responses in fishes may be key to understanding this inconsistency (Roni et al 2015), and that the choice of

species chosen for assessing restoration is likely to be among the most important factors influencing ecological outcomes (Friberg et al 2011). This demonstrates the need for widening the scope of fish biomonitoring to the assemblage level, and the potential for interventions and management practices to have indirect effects mediated via biotic interactions (Bellmore et al 2017, Naiman et al 2012). If restorations benefit predators more than target species, the strengthening of density dependent top-down interactions may counter or even outweigh the benefits of restoration to focal species. This in turn may contribute to either a real or perceived need for further follow-up practices such as regular predator control (Mann 1985), similar to the controlling of planktivores to maintain water clarity in lakes (Jeppesen et al 2012), and food web approaches for restoration monitoring have been widely called for in the literature (Bellmore et al 2017, Pander & Geist 2013).

Chapter 4 revealed insights into how the faunal food web was altered by restoration, detecting a significant change in the biomass flux between predators and prey. This suggested that the transfer of biomass, a proxy for energy, became more efficient following restoration, with the conserved energy concentrated as biomass in higher trophic levels. However, my results in Chapter 5 do not support the theory that the observed increase in fish biomass was powered by the increased release of allochthonous energy lifting bottom-up constraints as the rate of detrital breakdown was found to decline significantly following restoration. However, autochthonous production was not assessed, and given the changes in substrate composition following restoration to cobble dominated midstream, similar to other studies (Kail et al 2015), which provide stable habitat facilitating algal growth (Tonetto et al 2014), it may be that this increased secondary production facilitating increased fish biomass.

That the restorations induced detectable changes over a short time scale are further evidence that reach scale habitat restoration can initiate changes to food web structure (Thompson et al In Press). Given the disparity in recovery timespan between both species and also the typically timespan of most monitoring (Feld et al 2011, Trexler 1995), this suggests that food web approaches may be better able to detect responses. Additionally, the comprehensive biomonitoring necessary to effectively characterise the animal assemblage and construct the food web detected significant increases in the species richness of both invertebrates and fish assemblages following restoration.

This supports the widely held assumption that habitat diversity facilitates species diversity by enhancing conditions for recolonisation, which continues to remain highly contentious due to the other inconsistent responses recorded in other projects (Palmer et al 2010). Recent research suggests that this recolonisation is dependent on the regional species pool and the proximity of viable species populations providing propagule strength for recolonisation, in which case reach scale restoration unlikely to be effective (Stoll et al 2016, Tonkin et al 2014). However, this study demonstrates that even in a highly modified river, large wood can lead to detectable increases in both invertebrate and fish species richness.

Reversing the impacts of typically hundreds, and in some cases thousands, of years of extensive river modifications and habitat degradation to recover biodiversity and faunal assemblages is an enormously ambitious challenge. This is made more complex by the concurrent intensifying pressures of land-use change, abstraction and other activities associated with meeting the needs of a growing human population and wider environmental perturbations operating on a planetary scale, such as climate change and pollution (Ceballos et al 2017). Much of what we know about the role of habitat in structuring animal populations and communities has been derived from linking their decline to modifications in their habitat environment. Restoration provides a counter opportunity to track the recovery of biodiversity, and judged on the literature it is becoming widely accepted that the recovery of species populations and assemblages is less consistent and takes longer than expected (Layer et al 2010, Monteith et al 2005).

There are many reasons for why this may be and the disparity in the spatial scales of degradation and restoration ranks among the most frequently cited (Stoll et al 2016). Degradation factors, be they chemical, physical or biological, often operate at catchment if not regional spatial scales, whereas habitat restorations are typically implemented at the reach scale (Feld et al 2011, Stoll et al 2016). This is most likely why the removal of barriers to migration often have such immediate positive effects on ecology (Fjeldstad et al 2012). As this project has demonstrated, with the restrictions on the extent and design of the large wood restorations to meet the strict flood conditions, in cultural landscapes where societal needs are placed well above

those of ecology, the spatial scale of restorations implemented is unlikely to change in the immediate future.

There is therefore a real need to thoroughly test the ecological efficacy of reach scale measures in order to understand what does and does not work, and the reasons why (Palmer et al 2014). This will help to steer us towards identifying the environmental boundaries of the reach scale restoration "Goldilocks zone", where environmental conditions are more likely to permit positive ecological responses (Stoll et al 2016). This does not mean that reach scale restorations in areas that fail to meet these conditions are doomed to failure, but that the case for tackling other hierarchical pressures first, such as water quality, that may be more expensive to mitigate, is that much stronger. However, delineating the "Goldilocks Zone" and advancing our understanding of the factors that influence restoration outcomes requires more rigorous quantitative biomonitoring of more projects. This requires methods that are able to detect the typically modest ecological responses to habitat restoration within the short time frame of most biomonitoring protocols. In Chapter 6 I outline how this might be achieved by engaging restoration stakeholders: local groups who take an active interest in restoration and are keen to participate in activities which help to conserve, restore and safeguard local rivers. If mobilised, these groups could contribute an unprecedented volume of data to the restoration evidence base.

It is with this in mind that while this thesis has focused on a single system, the methods applied and metrics used have been designed so as to be reproducible, universal and most importantly, comparable. While researchers should be mindful of the "genius" of river systems: understanding that each is unique in space and time, this should not be extended to the methods used to biomonitor their recovery following restoration.

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Appendices

Appendix 3

Appendix 3.1

Variable		Comparison	*F*	*R2*	*P*	*P adjusted*
Abundance BACI	1	Control.Before vs Restored.Before	0.591	0.040	0.697	1
	2	Control.Before vs Control.After	0.846	0.057	0.537	1
	3	Control.Before vs Restored.After	1.613	0.103	0.133	0.798
	4	Restored.Before vs Control.After	0.633	0.043	0.705	1
	5	Restored.Before vs Restored.After	1.420	0.092	0.209	1
	6	Control.After vs Restored.After	0.668	0.046	0.672	1
Spring abundance	1	Control.1 vs Restored.1	2.291	0.088	0.747	1
	2	Control.1 vs Control.3	0.734	0.109	0.661	1
	3	Control.1 vs Restored.3	2.291	0.276	0.126	1
	4	Control.1 vs Control.5	1.879	0.238	0.158	1
	5	Control.1 vs Restored.5	2.907	0.326	0.026	0.39
	6	Restored.1 vs Control.3	0.433	0.067	0.912	1
	7	Restored.1 vs Restored.3	1.083	0.153	0.427	1
	8	Restored.1 vs Control.5	0.745	0.110	0.583	1
	9	Restored.1 vs Restored.5	1.971	0.247	0.079	1
	10	Control.3 vs Restored.3	1.388	0.188	0.243	1
	11	Control.3 vs Control.5	0.146	0.024	1.000	1
	12	Control.3 vs Restored.5	1.399	0.189	0.287	1
	13	Restored.3 vs Control.5	1.680	0.219	0.156	1
	14	Restored.3 vs Restored.5	1.317	0.180	0.212	1
	15	Control.5 vs Restored.5	1.328	0.181	0.366	1
Autumn abundance	1	Control.2 vs Restored.2	0.757	0.112	0.656	1
	2	Control.2 vs Control.4	0.581	0.088	0.685	1
	3	Control.2 vs Restored.4	1.427	0.192	0.203	1
	4	Restored.2 vs Control.4	0.419	0.065	0.866	1
	5	Restored.2 vs Restored.4	0.904	0.131	0.505	1
	6	Control.4 vs Restored.4	0.480	0.074	0.755	1

Appendix 3.2

Variable		Comparison	*F*	*R2*	*P*	*P adjusted*
Biomass BACI	1	Control.Before vs Restored.Before	1.013	0.067	0.371	0.371

	2	Control.Before vs Control.After	2.220	0.137	0.059	0.177	
	3	Control.Before vs Restored.After	3.030	0.178	0.013	0.052	.
	4	Restored.Before vs Control.After	1.819	0.115	0.118	0.236	.
	5	Restored.Before vs Restored.After	3.536	0.202	0.003	**0.018**	*
	6	Control.After vs Restored.After	2.675	0.160	0.007	**0.035**	*
Spring biomass	1	Control.1 vs Restored.1	3.981	0.399	0.062	0.930	
	2	Control.1 vs Control.3	6.387	0.516	0.025	0.375	
	3	Control.1 vs Restored.3	3.816	0.389	0.032	0.480	
	4	Control.1 vs Control.5	6.583	0.523	0.026	0.390	
	5	Control.1 vs Restored.5	4.202	0.412	0.028	0.420	
	6	Restored.1 vs Control.3	3.111	0.341	0.027	0.405	
	7	Restored.1 vs Restored.3	1.631	0.214	0.267	1.000	
	8	Restored.1 vs Control.5	2.913	0.327	0.029	0.435	
	9	Restored.1 vs Restored.5	2.184	0.267	0.154	1.000	
	10	Control.3 vs Restored.3	0.974	0.140	0.359	1.000	
	11	Control.3 vs Control.5	0.709	0.106	0.714	1.000	
	12	Control.3 vs Restored.5	2.929	0.328	0.030	0.450	
	13	Restored.3 vs Control.5	1.120	0.157	0.405	1.000	
	14	Restored.3 vs Restored.5	1.108	0.156	0.469	1.000	
	15	Control.5 vs Restored.5	1.703	0.221	0.245	1.000	
Autumn biomass	1	Control.2 vs Restored.2	1.394	0.189	0.264	0.312	
	2	Control.2 vs Control.4	1.662	0.217	0.150	0.312	
	3	Control.2 vs Restored.4	3.645	0.378	0.031	0.186	
	4	Restored.2 vs Control.4	3.003	0.334	0.104	0.312	
	5	Restored.2 vs Restored.4	6.300	0.512	0.025	0.150	
	6	Control.4 vs Restored.4	1.731	0.224	0.056	0.224	

Chapter 4 Appendix

Appendix 4.1 Equations used to calculate invertebrate individual dry mass. HW = head-capsule width (mm); BL = total body length (mm); SH = shell height; SL = shell length (mm). Morphologically similar taxa or higher taxonomic levels, shown in parantheses, were used where equations were unavailable for a given taxon. The source of each equation is denoted by a number indicating the reference used: 1) Benke *et al.* (1999), 2) Meyer (1989), 3) Towers *et al.* (1994), 4) Baumgärtner & Rothhaupt (2003), 5) Calow (1975), 6) Johnston & Cunjak (1999), 7) Smock (1980), 8) Hildrew & Townsend (1982), 9) Burgherr & Meyer (1997), 10) Woodward (1999), 11) Edwards *et al.* (2009), 12) Steingrímsson & Gíslason (2002), 13) Sabo *et al.* (2002), 14) Edwards (2005), 15) Ramsay *et al.* (1997), 16) www.fishbase.org, 17) Edwards unpublished.

Taxa	y	x	Regression equation	R^2	Reference
Abramis brama	DM(g)	WM(g)	y=0.267x		16
Anguilla anguilla	LnDM(g)	LnWM(g)	y =-1.6514+1.0687x	0.99	17
Barbatula barbatula	DM(g)	WM(g)	y=0.241x		16
Barbus barbus	DM(g)	WM(g)	y=0.267x		16
Cottus gobio	DM(g)	WM(g)	y=0.247x		16
Esox lucius	DM(g)	WM(g)	y=0.267x		16
Gasterosteus aculeatus	LnDM(g)	LnWM(g)	y =1.6613+0.6699x	0.87	17
Gobio gobio	DM(g)	WM(g)	y=0.247x		16
Lampetra planeri	LnDM(g)	LnWM(g)	y=-1.4633+1.3504x	0.89	17
Leuciscinae	DM(g)	WM(g)	y=0.267x		16
Perca fluviatilis	DM(g)	WM(g)	y=0.267x		16
Phoxinus phoxinus	LnDM(g)	LnWM(g)	y = -1.1318+1.0475x	0.96	17
Squalius cephalus	DM(g)	WM(g)	y=0.267x		16
Salmo trutta (W)	LnDM(g)	LnWM(g)	y= -1.4148+1.0878x	0.97	17
Apsectrotanypus sp. (Tanypodinae)	mg	HW	$y=2.1694*x^{2.623}$	0.85	1
Asellus aquaticus	Ln(mg)	Ln(BL)	y=-6.2+3.75x	0.69	4
Athripsodes spp. (*Oecetis spp.*)	Ln(mg)	Ln(HW)	y=1.913+3.3x	0.67	1
Baetis atrebatinus (*Baetis spp.*)	mg	HW	$y=1.2688*x^{3.326}$	0.96	1
Baetis buceratus (*Baetis spp.*)	mg	HW	$y=1.2688*x^{3.326}$	0.96	1
Baetis muticus (*Baetis spp.*)	mg	HW	$y=1.2688*x^{3.326}$	0.96	1
Baetis rhodani (*Baetis spp.*)	mg	HW	$y=1.2688*x^{3.326}$	0.96	1
Baetis scambus (*Baetis spp.*)	mg	HW	$y=1.2688*x^{3.326}$	0.96	1
Bithynia sp	Ln(mg)	Ln(SL)	y=-4.54+3.66x	0.95	4
Brillia longifurca (Chironomidae)	mg	HW	$y=2.7842*x^{2.835}$	0.9	1
Brillia modesta (Chironomidae)	mg	HW	$y=2.7842*x^{2.835}$	0.9	1
Caenis luctuosa (*Caenis spp.*)	Ln(mg)	Ln(HW)	y=0.73+3.11x	0.64	1
Caenis rivulorum (*Caenis spp.*)	Ln(mg)	Ln(HW)	y=-0.91+3.35x	0.63	4
Calopteryx splendens (*Calopteryx sp.*)	mg	HW	$y=0.383*x^{2.488}$	0.87	1
Centroptilum luteolum (*Baetis spp.*)	mg	HW	$y=1.2688*x^{3.326}$	0.96	1
Chirotanypus nervosus (Tanypodinae)	mg	HW	$y=2.1694*x^{2.623}$	0.85	1
Crangonyx pseudogracilis (*Gammarus fossarum*)	Ln(mg)	Ln(BL)	y = –4·95 + 2·83x	0.9	9

Orthocladinae	mg	HW	$y=1.7899*x^{2.311}$	0.64	1
Cricotopus sp. (Orthocladinae)	mg	HW	$y=1.7899*x^{2.311}$	0.64	1
Cricotopus trifasciatus (Orthocladinae)	mg	HW	$y=1.7899*x^{2.311}$	0.64	1
Cryptochironomus (Chironomidae)	mg	HW	$y=2.7842*x^{2.835}$	0.9	1
Dendrocoelum lacteum (*Dugesia tigrina*)	mg	BL	$y=0.0089*x^{2.145}$	0.81	1
Dixa sp. (Diptera)	Ln(mg)	Ln(BL)	y=-6.21+2.52x	0.83	9
*Drusus annulatus (*Limnephilidae*)*	Ln(mg)	Ln(HW)	y=0.4109+3.1678x	0.83	2
Elmis aenea (Elmidae, larvae)	Ln(mg)	Ln(BL)	y=-6.078+3.092x	0.83	3
Ephemera danica (Ephemeroptera)	Ln(mg)	Ln(HW)	y=-0.5+1.79x	0.64	4
Epoicocladius flavens (Chironomidae)	mg	HW	$y=2.7842*x^{2.835}$	0.9	1
Eukiefferiella claripennis (Orthocladinae)	mg	HW	$y=1.7899*x^{2.311}$	0.64	1
Eukiefferiella devonica (Orthocladinae)	mg	HW	$y=1.7899*x^{2.311}$	0.64	1
Gammarus pulex (*Gammarus fossarum*)	Ln(mg)	Ln(BL)	y = –4·95 + 2·83x	0.9	9
Glossiphonia complanata	Ln(mg)	Ln(BL)	y=-2.12+2x	0.64	11
Helobdella stagnalis	Ln(mg)	Ln(BL)	y=-2.74+2.12x	0.62	11
Heterotrissocladius marcidus (Orthocladinae)	mg	HW	$y=1.7899*x^{2.311}$	0.64	1
Hydracarina spp.	Ln(mg)	Ln(BL)	y = -2.202+1.66	0.48	4
Hydropsyche spp.	mg	HW	$y=1.265*x^{2.747}$	0.87	1
Hydroptila sp. (Trichoptera, cased)	Ln(mg)	Ln(HW)	y=1.30+3.62x	0.82	4
Lepidostoma hirtum (Trichoptera, cased)	Ln(mg)	Ln(HW)	y=1.30+3.62x	0.82	4
Limnephilus flavicornis (Limnephilidae)	Ln(mg)	Ln(HW)	y=0.4109+3.1678x	0.83	2
Psychmyiidae spp.	mg	HW	$y=1.732*x^{3.384}$	0.96	1
Orthocladinae	mg	HW	$y=1.7899*x^{2.311}$	0.64	1
Microptendipes spp	mg	HW	$y=1.9574*x^{2.589}$	0.81	1
Mystacides azurea (*Oecetis spp.*)	Ln(mg)	Ln(HW)	y=1.913+3.3x	0.67	1
Nanocladius rectinervis (Orthocladinae)	mg	HW	$y=1.7899*x^{2.311}$	0.64	1
Oligochaeta spp.	g	BL & BW	$y = (\pi r^2*1.05x)/4$		15
Orthocladinae spp.	mg	HW	$y=1.7899*x^{2.311}$	0.64	1
Orthocladinae	mg	HW	$y=1.7899*x^{2.311}$	0.64	1
Elmidae larvae	Ln(mg)	Ln(BL)	y=-6.078+3.092x	0.83	3
Tanytarsini	mg	HW	$y=1.666*x^{2.484}$	0.71	1
Paratendipes albimanus (Chironominae)	mg	HW	$y=1.9574*x^{2.589}$	0.81	1
Pericoma sp. (Diptera)	Ln(mg)	Ln(BL)	y=-6.21+2.52x	0.83	9
Physa fontinalis (Gastropoda)	Ln(mg)	Ln(SH)	y=-4.76+3.21x	0.95	4
Piscicola geometra (Leech)	Ln(mg)	Ln(BL)	y=-2.69+2.11x	0.62	11
Pisidium spp.	mg	SL	$y=0.0163*x^{2.477}$	0.87	1
Planorbis	Log_{10}(mg)	Log_{10}(SL)	y=-2.331+2x	0.69	5
Plectrocnemia conspersa	Log_{10}(µg)	Log_{10}(HW)	y=2.58+2.80x		10
Polycelis tenuis (*Dugesia tigrina*)	mg	BL	$y=0.0089*x^{2.145}$	0.81	1
Polycentropus flavomaculatus	Ln(mg)	Ln(HW)	y=-0.51+3.03x	0.87	4
Polycentropus spp.	Ln(mg)	Ln(HW)	y=-0.51+3.03x	0.87	4
Polypedilum sp. (Chironominae)	mg	HW	$y=1.9574*x^{2.589}$	0.81	1
Potamopyrgus jenkinsi (Potamopyrgus	Ln(mg)	Ln(SL)	y=-2.0961+2.4506x	0.93	3

antipodarum)					
Procladius sp. (Tanypodinae)	mg	HW	$y=2.1694*x^{2.623}$	0.85	1
Prodiamesa olivacea	$Log_{10}(\mu g)$	$Log_{10}(HW)$	$y = 3{\cdot}50 + 2{\cdot}97x$	0.69	8
Pseudorthocladius sp. (Orthocladinae)	mg	HW	$y=1.7899*x^{2.311}$	0.64	1
Rheocricotopus spp. (Orthocladinae)	mg	HW	$y=1.7899*x^{2.311}$	0.64	1
Rhyacophila dorsalis	$Log_{10}(\mu g)$	$Log_{10}(HW)$	y=1.55+3.21x	0.72	14
Sericostoma personatum (Sericostomatidae)	Ln(mg)	Ln(HW)	y=0.1692+2.9153x	0.89	2
Sialis lutaria (*S. fuliginosa*)	$Log_{10}(\mu g)$	$Log_{10}(HW)$	y=2.68+2.90x	0.88	10
Silo nigricornis (Goeridae)	Ln(mg)	Ln(HW)	y=0.8613+3.576x	0.75	2
Silo pallipes (Goeridae)	Ln(mg)	Ln(HW)	y=0.8613+3.576x	0.75	2
Simulium spp.	Ln(mg)	Ln(HW)	$y = 0{\cdot}20 + 3{\cdot}32x$	0.93	9
Stempellina bausei (Tanytarsini)	mg	HW	$y=1.666*x^{2.484}$	0.71	1
Theromyzon tessulatum (Leech)	Ln(mg)	Ln(BL)	y=-2.69+2.11x	0.62	11
Thienemanniella (Chironomidae)	mg	HW	$y=2.7842*x^{2.835}$	0.9	1
Tinodes waeneri (Lype diversa)	mg	HW	$y=1.732*x^{3.384}$	0.96	1
Ablabesmyia monolis (Tanypodinae)	mg	HW	$y=2.1694*x^{2.623}$	0.85	1
Agabus sp. (Coleoptera, larvae)	Ln(mg)	Ln(BL)	y=-4.4518+2.4724	0.57	2
Agapetus fuscipes (Glossosoma)	Ln(mg)	Ln(HW)	y=0.96+2.98x	0.71	2

Appendix 4.2 Count and summed mass of all prey items identified from fish GCA

	Order	Family	Taxonomic level	Count	Dry Mass (mg)
1	Coleoptera	Eucnemidae	Eucnemidae	1	32.14
2	Coleoptera	Elmidae	Elmidae	5	5.93
3	Coleoptera	Curculionidae	Curculionidae	1	1.97
4	Coleoptera	Bruchidae	Bruchidae	1	1.55
5	Coleoptera	Dryopidae	Dryopidae	1	1.03
6	Coleoptera	Endomychidae	Endomychidae	1	0.90
7	Collembola	NA	Collembola	3	0.30
8	Crustacea	Gammaridae	Gammaridae	4	0.30
9	Crustacea	Gammaridae	Gammarus pulex	1	0.06
10	Cypriniformes	Botiidae	Barbatula barbatula	35	23818.58
11	Cypriniformes	Cyprinidae	Gobio gobio	3	17459.13
12	Cypriniformes	Cyprinidae	Leuciscus leuciscus	2	11276.49
13	Cypriniformes	Cyprinidae	Phoxinus phoxinus	1	91.36
14	Diptera	Bibionidae	Bibionidae	36	125.84
15	Diptera	Chironomidae	Chironomidae	179	65.94
16	Diptera	Simuliidae	Simuliidae	191	24.20
17	Diptera	Syrphidae	Syrphidae	4	5.39
18	Diptera	Calliphoridae	Lucilia sericata	1	3.77
19	Diptera	Empididae	Empididae	6	2.29
20	Diptera	Anthomyiidae	Anthomyiidae	1	1.89
21	Diptera	Ceratopogonidae	Ceratopogonidae	17	1.21

22	Diptera	Sphaeroceridae	Sphaeroceridae	1	0.10
23	Ephemeroptera	Baetidae	Baetidae	88	43.11
24	Ephemeroptera	Ephemeridae	Ephemera danica	35	34.81
25	Ephemeroptera	Ephemerellidae	Serratella ignita	72	23.64
26	Hemiptera	Corixidae	Corixa punctata	1	1.04
27	Hemiptera	Aphididae	Aphididae	1	0.07
28	Hemiptera	Notonectidae	Notonecta glauca	1	0.06
29	Hymenoptera	Formicidae	Lasius mixtus	1	0.07
30	Hymenoptera	Figitidae	Figitidae	1	0.04
31	Isopoda	Asellidae	Asellidae	3	0.16
32	Mollusca	Bithyniidae	Bithyniidae	5	123.33
33	Odonata	Calopterygidae	Calopteryx splendens	3	17.17
34	Scorpaeniformes	Cottidae	Cottus gobio	41	15996.26
35	Trichoptera	Glossosomatidae	Agapetus fuscipes	479	477.18
36	Trichoptera	Sericostomatidae	Sericostomatidae	61	148.22
37	Trichoptera	Hydropsychidae	Hydropsychidae	5	9.20
38	Trichoptera	Limnephillidae	Limnephillidae	3	7.11
39	Trichoptera	Leptoceridae	Leptoceridae	6	5.91
40	Trichoptera	Lepidostomatidae	Lepidostomatidae	1	4.26
41	Trichoptera	Sericostomatidae	Sericostoma personatum	1	2.15
42	Trichoptera	Hydroptilidae	Hydroptilidae	2	0.91

Appendix 4.3 Feeding links identified by GCA of fish stomach contents

UI	Prey order	Prey family	Resource	Consumer	Cou	Dry Mass
1	Trichoptera	Glossosomati	*Agapetus fuscipes*	*Barbatula*	62	35.097
2				*Esox lucius*	1	1.646
3				*Gobio gobio*	139	78.453
4				*Leuciscus*	49	23.459
5				*Perca fluviatilis*	8	13.341
6				*Phoxinus*	1	1.205
7				*Rutilus rutilus*	21	9.396
8				*Salmo trutta*	198	314.582
9	Diptera	Anthomyiidae	Anthomyiidae	*Salmo trutta*	1	1.889
10	Hemiptera	Aphididae	Aphididae	*Salmo trutta*	1	0.069
11	Isopoda	Asellidae	Asellidae	*Perca fluviatilis*	3	0.157
12	Ephemeropte	Baetidae	Baetidae	*Barbatula*	39	7.157
13				*Gobio gobio*	4	1.177
14				*Perca fluviatilis*	19	15.839
15				*Phoxinus*	8	0.577
16				*Salmo trutta*	18	18.357
17	Cypriniforme	Botiidae	*Barbatula*	*Esox lucius*	35	23818.580
18	Diptera	Bibionidae	Bibionidae	*Salmo trutta*	36	125.843
19	Mollusca	Bithyniidae	Bithyniidae	*Leuciscus*	1	6.586

20				*Salmo trutta*	4	116.748
21	Coleoptera	Bruchidae	Bruchidae	*Salmo trutta*	1	1.554
22	Odonata	Calopterygida	*Calopteryx*	*Salmo trutta*	3	17.166
23				*Perca fluviatilis*	2	12.000
24	Diptera	Ceratopogoni	Ceratopogonidae	*Barbatula*	7	0.595
25				*Gobio gobio*	9	0.588
26				*Salmo trutta*	1	0.032
27	Diptera	Chironomidae	Chironomidae	*Barbatula*	28	4.913
28				*Esox lucius*	2	0.574
29				*Gobio gobio*	6	1.527
30				*Leuciscus*	2	0.544
31				*Perca fluviatilis*	4	0.967
32				*Phoxinus*	1	0.319
33				*Salmo trutta*	136	57.095
34	Collembola	Collembola	Collembola	*Salmo trutta*	3	0.035
35	Hemiptera	Corixidae	*Corixa punctata*	*Salmo trutta*	1	1.037
36	Scorpaenifor	Cottidae	*Cottus gobio*	*Esox lucius*	35	11609.160
37				*Perca fluviatilis*	3	3245.625
38				*Salmo trutta*	3	1141.480
39	Coleoptera	Curculionidae	Curculionidae	*Salmo trutta*	1	1.974
40	Coleoptera	Dryopidae	Dryopidae	*Salmo trutta*	1	1.032
41	Coleoptera	Elmidae	Elmidae	*Gobio gobio*	3	5.727
42				*Rutilus rutilus*	1	0.189
43				*Squalius*	1	0.015
44	Diptera	Empididae	Empididae	*Salmo trutta*	6	2.292
45	Coleoptera	Endomychida	Endomychidae	*Salmo trutta*	1	0.091
46	Ephemeropte	Ephemeridae	*Ephemera danica*	*Esox lucius*	1	0.874
47				*Perca fluviatilis*	5	4.987
48				*Salmo trutta*	29	28.949
49	Coleoptera	Eucnemidae	Eucnemidae	*Salmo trutta*	1	32.139
50	Hymenoptera	Figitidae	Figitidae	*Leuciscus*	1	0.039
51	Crustacea	Gammaridae	Gammaridae	*Gobio gobio*	1	0.019
52				*Salmo trutta*	4	0.350
54	Cyprinidae	Cypriniformes	*Gobio gobio*	*Esox lucius*	3	17459.130
55	Trichoptera	Hydropsychid	Hydropsychidae	*Barbatula*	2	2.789
56				*Salmo trutta*	3	6.415
57	Trichoptera	Hydroptilidae	Hydroptilidae	*Salmo trutta*	1	0.219
58				*Squalius*	1	0.687
59	Hymenoptera	Formicidae	*Lasius mixtus*	*Salmo trutta*	1	0.067
60	Trichoptera	Lepidostomati	Lepidostomatidae	*Salmo trutta*	1	4.262
61	Trichoptera	Leptoceridae	Leptoceridae	*Gobio gobio*	3	3.353
62	Trichoptera	Leptoceridae	Leptoceridae	*Leuciscus*	2	2.104
63				*Salmo trutta*	1	0.451
64	Cypriniforme	Cyprinidae	Leuciscinae	*Esox lucius*	1	10399.650
65				*Perca fluviatilis*	1	876.843
66	Trichoptera	Limnephillida	Limnephillidae	*Salmo trutta*	3	7.111
67	Diptera	Calliphoridae	*Lucilia sericata*	*Salmo trutta*	1	3.768
68	Hemiptera	Notonectidae	*Notonecta glauca*	*Salmo trutta*	1	0.062
69	Cypriniforme	Cyprinidae	*Phoxinus phoxinus*	*Esox lucius*	1	91.355

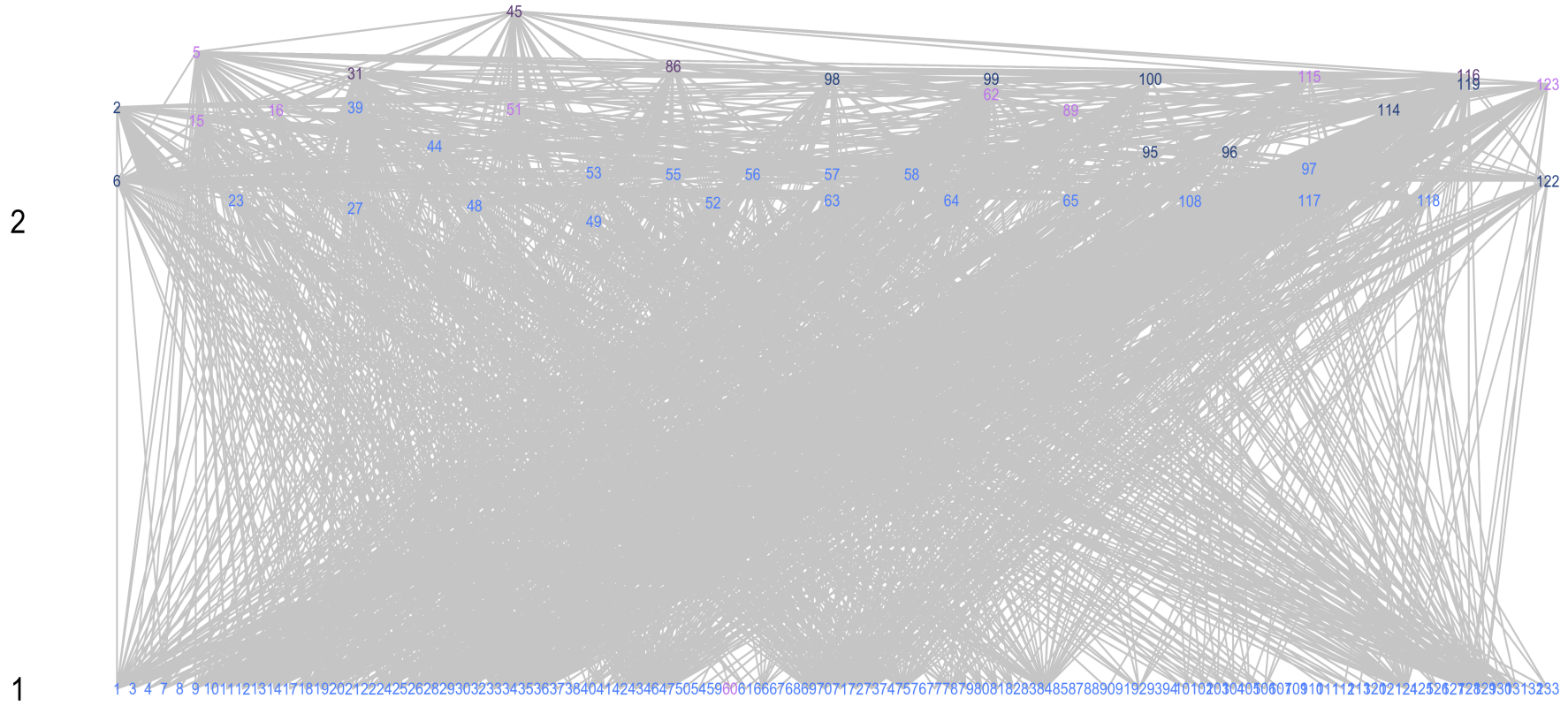
70	Trichoptera	Sericostomati	Sericostoma	*Barbatula*	1	2.147
71	Trichoptera	Sericostomati	Sericostomatidae	*Leuciscus*	2	0.742
72				*Perca fluviatilis*	5	13.186
73				*Salmo trutta*	54	134.296
74	Ephemeropte	Ephemerellida	*Serratella ignita*	*Barbatula*	54	16.265
75				*Esox lucius*	1	0.072
76				*Gobio gobio*	7	1.468
77				*Perca fluviatilis*	5	2.004
78				*Phoxinus*	1	0.612
79				*Salmo trutta*	4	3.221
80	Diptera	Simuliidae	Simuliidae	*Barbatula*	159	18.692
81				*Esox lucius*	1	0.095
82				*Gobio gobio*	5	0.696
83				*Leuciscus*	1	0.185
84				*Perca fluviatilis*	2	0.297
85				*Phoxinus*	5	0.409
86				*Salmo trutta*	16	3.198
87				*Squalius*	2	0.625
88	Diptera	Sphaerocerida	Sphaeroceridae	*Salmo trutta*	1	0.103
89	Diptera	Syrphidae	Syrphidae	*Salmo trutta*	4	5.394

Appendix 4.4 Invertebrate LMMs log transformed data

Variable		Estimate	SE	df	T	P
Ephemeroptera abundance	Treatment	0.16	0.68	11	0.228	0.824
	Year	0.81	0.57	6	1.440	0.200
	Treatment: Year	-0.07	0.80	6	0.090	0.931
Trichoptera abundance	Treatment	0.02	0.50	7	0.037	0.972
	Year	0.31	0.19	6	1.596	0.162
	Treatment: Year	0.22	0.27	6	0.806	0.451
Diptera abundance	Treatment	0.27	0.67	10	0.401	0.697
	Year	-0.72	0.52	6	1.386	0.215
	Treatment: Year	0.36	0.73	6	0.491	0.641
Ephemroptera mass log	Treatment	0.08	0.39	12	0.193	0.850
	Year	-0.14	0.38	6	0.361	0.730
	Treatment: Year	0.05	0.53	6	0.086	0.935
Trichoptera mass log	Treatment	0.52	0.49	12	1.058	0.311
	Year	1.04	0.49	12	2.111	0.056
	Treatment: Year	-0.17	0.70	12	0.251	0.806
Diptera mass log	Treatment	-0.33	0.42	12	0.790	0.445
	Year	-0.44	0.42	12	1.071	0.305
	Treatment: Year	1.38	0.59	12	2.358	0.090

Appendix 4.5 Complete binary food web for the River Great Stour, showing trophic links in grey between individually numbered species nodes of invertebrates (blue), fish (purple) and cannibalistic taxa (black). Species are positioned based on their trophic position, with primary consumers on at the base and piscivorous fish at the top. The corresponding species for each number is provided in Appendix 6.

Stour Food Web



Appendix 4.6 All the taxonomic groups in the River Stour food web in alphabetical order and with numbers corresponding to the food web shown in Appendix 4.5 above.

1. Ablabesmyia longistyla
2. Agabus
3. Agapetus fuscipes
4. Ancylus fluviatilis
5. Anguilla anguilla
6. Apsectrotanypus trifascipennis
7. Asellus aquaticus
8. Athripsodes cinereus
9. Baetis
10. Baetis buceratus
11. Baetis fuscatus
12. Baetis rhodani
13. Baetis scambus
14. Baetis vernus
15. Barbatula barbatula
16. Barbus barbus
17. Bithynia leachii
18. Brillia longifurca
19. Brillia modesta
20. Caenis
21. Caenis luctuosa
22. Caenis rivulorum
23. Calopteryx splendens
24. Centroptilum luteolum
25. Ceratopogonidae
26. Chironomidae
27. Conchapelopia melanops
28. Copepoda
29. Corynoneura lacustris
30. Corynoneura lobata
31. Cottus gobio
32. Crangonyx pseudogracilis
33. Cricitopus
34. Cricotopus trifasciata
35. Demicryptochironomus vulneratus
36. Dicrotendipes nervosus
37. Dugesia
38. Dugesia polychroa
39. Dytiscidae
40. Elmis aenea
41. Empididae
42. Ephemera danica
43. Epiciocladius flavescens
44. Erpobdella octoculata
45. Esox lucius
46. Eukiefferiella claripennis
47. Eukiefferiella ilkleyensis
48. Gammarus pulex
49. Glossiphonia complanata
50. Glossosoma conformis
51. Gobio gobio
52. Helobdella stagnalis
53. Heterotrissolcladius marcidus Type
54. Hydracarina
55. Hydropsyche angustipennis
56. Hydropsyche instabilis
57. Hydropsyche pellucidula
58. Hydropsyche siltalai
59. Hydroptila
60. Lampetra planeri
61. Lepidostoma hirtum
62. Leuciscus leuciscus
63. Limnephilus lunatus
64. Limnephilus marmoratus
65. Limnephilus rhombicus
66. Limnius volckmari
67. Lype reducta
68. Metalype fragilis
69. Micropsectra bidentatus
70. Micropsectra contracta
71. Microspectra chinyensis
72. Microtendipes pedellus
73. Microtendipes rydalensis
74. Mystacides azurea
75. Nanocladius rectinervis
76. Nebrioporus elegans Ad
77. Niphargus aquilex
78. Oligochaeta
79. Orthocladiinae Sp A
80. Orthocladius
81. Orthocladius trianulatus
82. Orthocladius/Cricotopus Sp
83. Oulimnius tuberculatus
84. Paratanytarsus penicillatus
85. Paratendipes albimanus
86. Perca fluviatilis
87. Phaenospectra flavens
88. Phaenospectra Type A
89. Phoxinus phoxinus
90. Physa fontinalis
91. Piscicola geometra
92. Pisidium
93. Planorbis contortus
94. Planorbis planorbis
95. Plectrocnemia conspersa
96. Plectrocnemia geniculata
97. Polycelis tenuis
98. Polycentropus
99. Polycentropus flavomaculatus
100. Polycentropus kingi
101. Polypedilum convictum
102. Polypedilum nubifer
103. Polypedilum pedestre
104. Polypedilum scalaneum
105. Polypedilum sp
106. Potamopyrgus jenkinsi
107. Potthastia longimana
108. Procladius
109. Prodiamesia olivacea
110. Pseudorthocladius
111. Rheocricotopus chalybeatus
112. Rheotanytarsus curtstylus
113. Rheotanytarsus sp
114. Rhyacophila dorsalis
115. Rutilus rutilus
116. Salmo trutta
117. Sericostoma personatum
118. Serratella ignita
119. Sialis lutaria
120. Silo nigricornis
121. Silo pallipes
122. Simulium
123. Squalius cephalus
124. Stempellinella
125. Stenochyronymous
126. Synorthocladius semivirens
127. Tanypodinae
128. Tanytarsus
129. Tanytarsus mendax
130. Thienemanniella
131. Thienemanniella vittata
132. Tinodes waeneri
133. Tventinia calvescens