The effect of large wood on river physical habitat and nutritional dynamics

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Abstract

There is a need for the exploration and validation of the mechanisms regulating the relationship between ecosystem structure and function. This thesis investigates how large wood (LW), wood pieces over 1 m long and 10 cm in diameter, causes cascading changes in physical habitat, availability and nutritional quality of food resources, and consumer communities. The thesis reports on four related research projects:

Chapter 2 surveys the National River Restoration Inventory (NRRI) database and demonstrates that wood is predominantly used as deflectors in lowland rural restorations. Chapter 3 examines habitat diversity in the field, around wood of different complexity in four rivers, and suggests that while all wood introduces habitat heterogeneity to the river, deflectors have a limited effect on heterogeneity compared to naturally-occurring wood and semi-natural large wood used in some restorations. Combined, this suggests deflectors may be limiting the potential of wood restoration projects.

Chapter 4 examines the potential for wood to mitigate flood disturbance by hydropower plants (“hydropeaking”) on periphyton. This study demonstrates how hydropeaking can scour both periphyton biomass and nutritional quality, while wood mitigates this loss. This is the first study to suggest a nutritional limitation on consumer communities downstream of hydropower plants, and that wood may provide a structural compensation to mitigate these effects on the trophic base.

Chapter 5 demonstrates how the presence of large wood increases the availability of various food resources, resulting in an altered, more diverse and productive macroinvertebrate community. Primarily, wood affects the trophic base by providing high-nutritional quality periphyton/bryophytes growing on wood, and by providing a superior position for filter-feeding taxa such as for net-spinning caddisflies.

This thesis demonstrates how ecological structure, particularly large wood, can alter ecological function through bottom-up biochemical pathways, and stresses the importance for a nutritional perspective to food webs.

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Chapter 1

Introduction: Physical habitat heterogeneity, large wood, and nutritional quality

1.1 Overview

The connection between ecosystem structure (*i.e.* physical shape and form) and ecosystem function (*i.e.* process and health) is frequently presented as a causal relationship: increased ecosystem structure is expected to increase the diversity of abiotic habitat conditions (*e.g.* flow and substrate) and result in increased niche space for enhanced biodiversity. While conceptually useful, this is a fundamental abstraction of the processes which underlie and support diverse biological communities. Restoration ecology is fundamentally underpinned by this conceptual relationship, as restoring “habitat heterogeneity,” the diversity of structural and abiotic conditions, is expected to result in a self-assembling biological community. Yet a number of recent studies have suggested that most restoration projects that enhance in-stream habitat heterogeneity have not resulted in an expected increase in ecological condition (Palmer et al. 2010). The ecosystem attributes and mechanisms that are linked to habitat heterogeneity are poorly understood (Kovalenko et al. 2012), and new theoretical and methodological developments are needed to help clarify these relationship (Vaughan et al. 2009).

There has been little serious consideration about how physical habitat may interact with “bottom-up” mechanisms such as the importance of basal food resources on ecological function. In particular, recent advances in lipid ecology emphasise the fundamental importance of the nutritional quality of food resources controlling consumer productivity, ecosystem efficiency, and food webs. However, there has been relatively little exploration of these dynamics in river systems, despite a previous study suggesting some physical habitat conditions can affect nutritional quality in periphyton (Cashman et al. 2013). This suggests a previously overlooked area of research into how habitat heterogeneity may affect ecosystem function.

Large wood, defined as pieces of wood greater than 10 cm in diameter and 1 m long, is an ideal focus for exploring these dynamics, due to its well-studied and notable effects on both physical habitat and ecology, interaction with flood disturbances, and particularly because of its potential to alter the availability of both autochthonous and allochthonous basal food resources. While large wood has been historically removed from rivers, today it is increasingly used to restore habitat heterogeneity in river restorations, and warrants further exploration into how it results in ecological change.

This thesis will specifically explore the “bottom-up” mechanism by which large wood causes cascading changes to physical habitat conditions, mitigates the disturbance regime, alters nutritional quality for consumers, and changes trophic relationships.

1.2 Ecosystem structure and function

The habitat heterogeneity (HH) hypothesis is a conceptual cornerstone in ecology (*e.g.* MacArthur and Wilson 1967, Lack 1969), whereby ecosystem structure, the physical shape and form of an ecosystem, is associated with a wide range of ecological functions. In river systems, the habitat heterogeneity hypothesis was first introduced by Townsend (1989) as the patch dynamics concept. In summation, structural complexity is expected to increase the "patch" diversity of habitat conditions and increase functional niche space (Bazzaz 1975), resulting in a more diverse biological community able to exploit these various niches (Ricklefs and Schluter 1993, Palmer and Poff 1997, Cardinale et al. 2002). Subsequently, increased biodiversity is assumed to result in greater ecosystem function, increased ecosystem stability, and assorted other ecosystem processes such as nutrient processing (Cardinale 2011).

This conceptual progression suggests a distinct causal relationship between ecosystem structure and function (Figure 1-1), and the importance of ecosystem structure to "good ecological status" has even been incorporated in the Water Framework Directive (WFD; 2000/60/EC). However, this relationship is a fundamental abstraction of the mechanisms which underpin diverse biological communities and ecosystem function. Rather than structural diversity directly resulting in habitat diversity, structure primarily influences a number of proximal abiotic factors (*e.g.* flow, substrate, light, temperature, cover) that characterise specific physical conditions. In addition, temporal variability is a fundamental component of habitat conditions, as flow variability, *i.e.* the Natural Flow Regime (Poff et al. 1997), and disturbance rate are essential controls in ecological communities (Townsend et al. 1997). These abiotic factors and their variability then interact with species-specific life-history traits and fundamental “bottom-up” (*i.e.* food/energy limitation), “top-down” (*i.e.* predation/grazing), and “lateral” (*i.e.* competition) ecological mechanisms. However, while habitat heterogeneity has been linked with biodiversity in previous studies, little is known about the relationship between habitat heterogeneity with other ecosystem attributes and these underlying mechanisms (Figure 2-2).

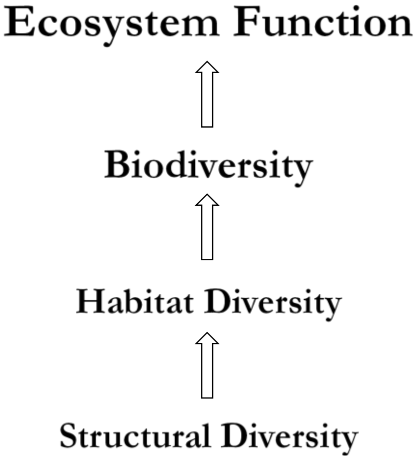


Figure 1-1: The conceptual progression underlying the habitat heterogeneity hypothesis. The physical structure of a river (*i.e.* shape and form) is assumed to cause cascading changes in other abiotic habitat conditions (*e.g.* flow, substrate, light), increase biodiversity due to increased niche space, and ultimately affect overall ecosystem function.

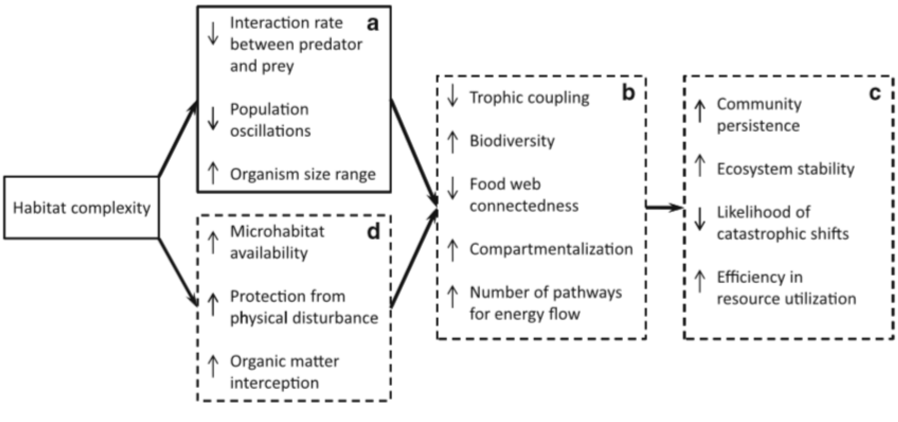


Figure 1-2: The effects of habitat complexity on population-level attributes (a) are well-documented, but with exception of biodiversity, little is known about the hypothesized effects on community and ecosystem attributes (b), their emergent properties (c), and potential underlying mechanisms (d). This thesis provides additional support for the effect of wood altering the “bottom-up” mechanism of the underlying nutritional dynamics of food resources creating changes to ecosystem attributes. Figure modified from Kovalenko et al 2012.

1.2.1 Habitat heterogeneity in river restoration

The field of restoration ecology is grounded in the habitat heterogeneity hypothesis and the principle that restoring ecosystem structure will rehabilitate ecosystem function (Feld et al. 2011). It is unquestioned that urbanization, river channelization, and impoundments have profoundly degraded water quality, physical habitat, and ecosystem health in rivers across the world (Petts 1984a, Brookes and Gregory 1988, Walsh et al. 2005b). Yet as recent interventions in the past decades have increased water quality throughout Europe and North America, there has been an increasing focus on the possible limitation of habitat heterogeneity on ecological quality (Vaughan et al. 2009). As a result, the restoration of habitat structure has been promoted not only within the EU Water Framework Directive (Wharton and Gilvear 2007) but also within the USA with the Natural Channel Design Approach (Rosgen 1994, Rosgen and Silvey 1996, Hey 2006). Databases on river restoration from the US demonstrate that increasing habitat structure is one of the most common goals cited in US restoration projects (Figure 1-3), even if overall project objectives are for the reestablishment of higher-level biodiversity or ecological function (Harper et al. 1999, Bernhardt et al. 2005, Palmer et al. 2010), and although no published database is yet known for Europe, the literature supports this trend (Harrison et al. 2004, Wharton and Gilvear 2007, Palmer et al. 2010, Nilsson et al. 2014). Typical structural restorations include channel reconfiguration such as remeandering and in-stream habitat improvements such as the creation of riffles or pools and the addition of large wood or boulders.

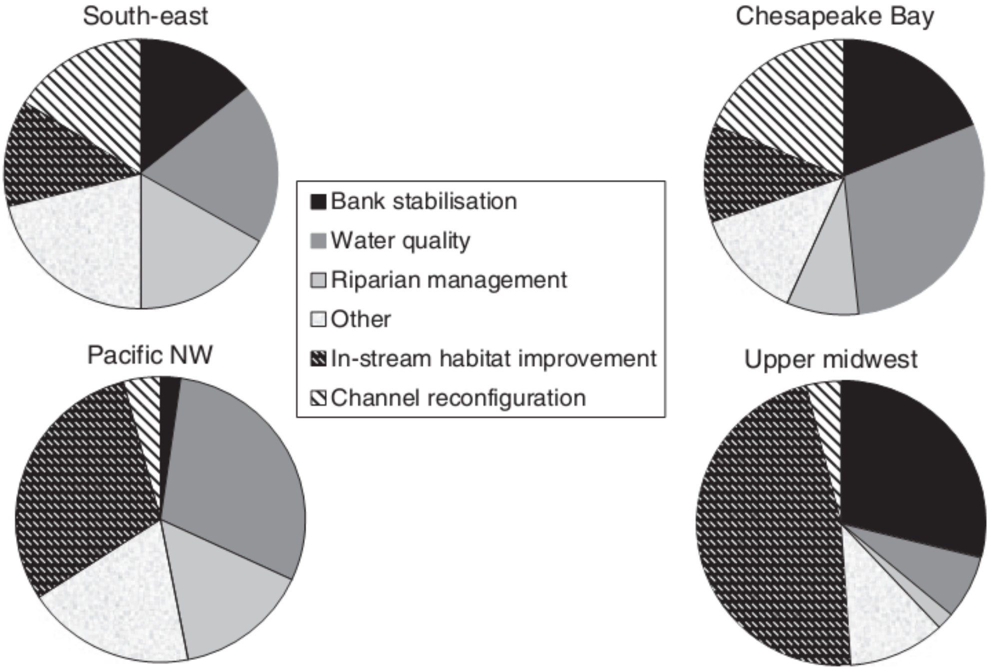


Figure 1-3: Regional breakdown of common restoration aims in the USA, illustrating the high frequency of intervention on river structure (channel reconfiguration and in-stream habitat enhancements) . Figure from Palmer et al. 2010.

1.2.2 A failure in theory or practice?

Even though restoration based on the principle of habitat heterogeneity is conceptually intuitive, there is little robust scientific evidence directly linking the restoration of habitat structure with improvements in biodiversity and ecosystem function. In fact, a growing body of literature, ranging from individual case-studies to synthetic meta-analyses, summarizing hundreds of restoration schemes, have demonstrated that the vast majority of successful restorations of habitat structure have resulted in inconclusive or minimal effects on biodiversity, even after prolonged monitoring (Lepori et al. 2005, Jähnig and Lorenz 2008, Jähnig et al. 2008, Jähnig et al. 2009, Jähnig et al. 2010, Palmer et al. 2010, Bernhardt and Palmer 2011, Louhi et al. 2011, Haase et al. 2013, Friberg et al. 2014, Nilsson et al. 2014). Some of the key findings are summarised in Table 1-1. Many projects have therefore succumbed to the myth in restoration ecology called the “Field of Dreams” by Hilderbrand et al. (2005), summarized in the iconic lines: “if you build it, they will come.” These results have suggested that the recreation of physical structure alone will not necessarily result in a self-assembling biotic community and healthy ecological function. Instead, the generalized relationship between structure and function appears to be largely one-directional, *i.e.* function may be limited by the availability of structural diversity, but the existence of structural diversity does not create function. A narrow focus on re-establishing habitat structure alone therefore may have obscured the complex factors and mechanisms limiting the rehabilitation of these rivers.

Table 1-1: An overview of recent literature in the restoration ecology field that have suggested that increased structural heterogeneity has not resulted in substantial evidence of restoration of ecology.

Reference	Study Type and Number	Location	Evaluated Metric	Conclusion
(Lepori et al. 2005)	Single Study: 7 pair	Sweden	Macroinvertebrates, Fish	Local heterogeneity did not structure biotic assemblages, and restoration may be affecting structural heterogeneity at scale not relevant to target organisms
(Jähnig and Lorenz 2008)	Single Study: 7 pair	Germany	Habitat heterogeneity, Macroinvertebrate	Increased macroinvertebrate diversity only associated with presence of specific substrates (e.g. wood), not overall other measurements of structural diversity
(Jähnig et al. 2009)	Single Study: 7 pairs	Germany	Habitat heterogeneity, Macroinvertebrates	Increased macroinvertebrate diversity only associated with presence of specific organic substrates (e.g. wood, macrophytes, CPOM), not overall other hydromorphological metrics
(Lorenz et al. 2009)	Single Study: 2	Germany	Habitat heterogeneity, Macroinvertebrate	Increased macroinvertebrate diversity only associated with presence of wood and macrophytes, not other hydromorphological metrics. 10 year recovery in macroinvertebrate assemblages
(Jähnig et al. 2010)	Survey: 26 pair	Central/Southern European	Habitat heterogeneity, Macroinvertebrates	Increased habitat diversity differently depending on river type and location. Negligible changes to macroinvertebrates. Larger scale rehabilitations predicted as necessary for biota recovery.
(Palmer et al. 2010)	Meta-analysis: 18 studies, 78 projects	USA, Canada, Australia, Japan, Venezuela	Habitat heterogeneity, Macroinvertebrate	< 50% studies show positive relationship with macroinvertebrates. 1/3 showed relationship with habitat heterogeneity and macroinvertebrates. Other factors despite physical habitat are likely limiting ecological recovery.
(Miller et al. 2010)	Meta analysis: 24 studies	USA, Canada, UK, Continental Europe, Japan,	Macroinvertebrates	Restoration success affected by land-use type: forested most effective. Channel realignments negligible effect on biota. Boulders small richness increases. LWD most predictable increase.
(Jähnig et al. 2011)	Survey: 26 pair	Germany	Habitat heterogeneity, Macroinvertebrates, Fish, River manager evaluations	Lack of improved biota with habitat heterogeneity. But objective measurements of success do not match subjective measures provided by river managers, due to self-evaluations of study: "Condemned to success"

(Violin et al. 2011)	Single Study: 4 triplicate	Urban streams, southeast USA	Habitat heterogeneity and macroinvertebrate	Restored streams indistinguishable from un-restored urban streams for habitat and macroinvertebrates. Biota correlated with environmental variables. Reach-scale restoration not large enough scale for mitigation of urban factors.
(Sundermann et al. 2011)	Single Study: 25 river, paired reaches	Germany	Habitat heterogeneity Macroinvertebrates, Distance from colonisation sources	Some change in macroinvertebrate community metrics between restored and unrestored, but water quality limiting recolonisation. Beyond 5km, recolonisation not detected
(Louhi et al. 2011)	Single Study: 22 river	Finland	Macroinvertebrates fish	BACI designed experiments showed reductions in macroinvertebrate density. Long term studied sites did not enhance biodiversity and were not dispersal limited
(Haase et al. 2013)	Single Study: 24 river, Paired reaches	Germany	Habitat heterogeneity, Macroinvertebrates, Fish, Macrophytes	Change in hydromorphology, small differences in biological parameters. Positive effects observed for fish only (11 of 24). Only 1 of 24 reach good Ecological Quality Class in Water Framework Directive. Emphasise need for catchment analysis of pollution and source populations and dispersal of macroinvertebrates.
(Friberg et al. 2014)	Single Study: 1 river	Denmark	Macroinvertebrates	Over 20 years. Habitat type somewhat affected community composition, but no effect on diversity. Little change over 11 years. Local species pool likely close to saturation.
(Nilsson et al. 2014)	Review: 18 studies	Finland, Sweden	Habitat heterogeneity, Macroinvertebrates, Fish, Riparian plants	Increased channel complexity, but weak or absent biotic responses. Damage to mosses after restoration. 20 years not sufficient time for recovery,
(Tonkin et al. 2014)	Single Study: 21 sites	Germany	Macroinvertebrates, Distance from colonisation sources	Taxon pool occupancy rate important driver of colonisation likelihood, followed by distance to nearest source. Techniques use in restoration and physical characteristics minor, outweighed by taxon pool and dispersal-related factors. Spatial planning needed for restoration projects.

Many of these studies suggest that expected gains in biodiversity may be masked by other factors such as water quality, yet even in situations where water quality does not seem to be a limiting factor, the ecological relationship with physical habitat is often weak. One potential explanation is that a restoration approach that focuses on extensive channel engineering or the use heavy machinery may actually cause damage to streams, compact soils, and even reduce diversity compared to pre-restoration conditions (Palmer et al. 2010, Laub et al. 2013). In addition, as restorations frequently intervene on habitat structure at a reach-scale, these restorations are unlikely to affect a degraded disturbance regime driven by catchment-scale issues of urbanized impervious surfaces and runoff (Walsh et al. 2005a, Walsh et al. 2005b). There may also be an important time-lag after intervention for ecological restoration, as the macroinvertebrate assemblage may take more than 10 years to recover as seen in one study (Lorenz et al. 2009), but others even fail to show substantial change even after 11 (Friberg et al. 2014) or 20 years (Louhi et al. 2011, Nilsson et al. 2014). These recovery rates post-restoration are likely controlled by the dispersal distance from local colonisation sources (Tonkin et al. 2014), and suggest that restoration more than 5km away from a healthy colonisation sources may be ineffective (Sundermann et al. 2011). As a result, restorations in forested, relatively-low impacted catchments have the best restoration potential (Miller et al. 2010).

In addition, while true habitat heterogeneity encompasses a suite of factors (including physical, chemical, and substrate properties) across all spatial scales, from entire catchments ($\geq 10^6$ m), to catchment segments ($10^4 – 10^5$ m), reach ($10^2 – 10^3$ m), mesohabitats (10^1 m), and micro-habitats (10^{-1} m), the restoration of physical habitat structure, particularly of structural elements (*e.g.* installing cobbles, boulders, or large wood) are typically limited to the reach or mesohabitat scale and do not typically affect habitat heterogeneity at other relevant scales (Palmer et al., 2010).

A major issue in understanding the successes and failure of river restoration projects is that many restoration schemes are not monitored. In one study, 40% of river managers admitted that project post-appraisal was based entirely on gut-feeling (Jähnig et al. 2011), and more than 90% of stream restorations in the USA, Australia, and Europe are not monitored except by visual means (Bernhardt et al. 2005, Brooks and Lake 2007). In addition, physical habitat assessments (*e.g.* River Habitat Survey (Raven et al. 1996)) are routinely used as a surrogate for evaluations of biodiversity and ecosystem response. Yet studies directly examining the link between macroinvertebrates and the River Habitat Survey have also proven tenuous. Multiple studies have shown only a weak relationship between the River Habitat Survey and macroinvertebrates, with a maximum r^2 of 0.25 (Friberg et al. 2009, Vaughan et al. 2009), and suggest that macroinvertebrates reflect catchment-wide degradation and the presence of specific habitats, such as wood, rather than overall morphological modification of the targeted river-reach (Balestrini et al. 2004). As a result, evaluating restorations based on physical habitat specific assessment may ignore ecologically important features and processes that may account for a large variability in macroinvertebrate response.

The restoration of structural diversity and assessment by visual means provides compelling visual differences to stakeholders (*e.g.* pre/post project photographs), compared to the detailed collection and analysis of data on ecosystem structure and function (Palmer et al. 2010). However, overall there is much work to be done in establishing the ecological relevance of assessed features in physical habitat surveys (Erba et al. 2006). Various structural features, such as remeanders, riffles, boulders, or large wood would each be expected to alter a unique combination of abiotic components, and have different effects on the specific factors limiting ecological function. For example, remeandering might re-establish morphological processes, but is unlikely to substantially mitigate an urbanized disturbance regime or alter the light and temperature regime due to a preexisting lack of canopy cover. Boulders may affect flow at ecologically relevant scales for fish, but alter abiotic conditions at scales less-relevant for macroinvertebrates (Lepori et al. 2005, Roni et al. 2006). Yet a meta-analysis of 24 studies suggests that large wood (LW) when used in restoration provides a reliable and predictable improvement to macroinvertebrate richness, and ocassionally density, when compared to other restoration techniques (Miller et al. 2010). This may be due to wood causing complex changes in both habitat structure and abiotic conditions (See Section 1.2.1) causing many notable changes on ecological communities (See Section 1.2.2), particularly mediated through the effect of large wood on affecting basal food resources (See Section 1.2.3). As a result, large wood may function as a keystone ecosystem structure (Tews et al. 2004) of special importance in river systems.

1.3 Large wood in rivers: a keystone ecosystem structure

Large wood, also known as large woody debris (LWD), coarse woody debris (CWD), or large woody vegetation (LWV), is defined as woody vegetation in the river channel ≥ 10 cm in diameter and ≥ 1 m in length (Thompson et al. 2007). In most rivers, wood is naturally accumulated in the channel from fallen and downed riparian trees, and depending on stream power, can freely orient with the flow, be transported downstream, or buried into the stream bed and banks (Keller and Swanson 1979). Historically, LW was common in most rivers, but was removed to improve navigation, flood control (Petts 1990), timber transport (Lepori et al. 2005), fish migration (Bilby 1984), and aesthetics (Piegay et al. 2005). However, particularly within the past 35 years, the scientific community has recognized the vital role of LW for both the hydromorphological and ecological processes in river systems and the maintenance of ecosystem health (Gurnell et al. 2002, Wondzell and Bisson 2003).

1.3.1 The effects of large wood on physical habitat

The effect of large wood on physical habitat have been well studied in the past several decades. LW is an important component of sediment storage within the channel (Megahan 1982, Nakamura and Swanson 1993, Smith et al. 1993a, Keller and MacDonald 1995), but also in the floodplain through overbank deposition (Gregory et al. 1985, Jeffries et al. 2003). LW has an important role in channel stability directly through bank reinforcement and through the stabilization of accumulated sediments (Bilby 1984, Montgomery et al. 2003a). Altered flows around LW create local patches of scour and deposition (Abbe and Montgomery 1996), resulting in sorted sediments (Bilby 1981, 1984). This structurally complex habitat traps transported organic matter and drifting pieces of small wood (Millington and Sear 2007), and increases nutrient retention (Smock et al. 1989). LW accumulations also have an important role in retaining and establishing the seed bank (Osei et al. 2015) and increasing the survival of propagules (Pettit and Naiman 2006). These stored and stabilized sediments, seeds, and propagules within the channel and floodplain can promote tree recruitment, ensure future supply sources for in-channel wood and drive the formation of physically diverse floodplains (Gurnell and Petts 2006, Gurnell 2012).

Rivers that contain LW have been shown to be more sinuous, narrower, deeper, and have an increasing number, area, and volumes of pools than rivers with wood removed (Bilby 1984, Fausch and Northcote 1992, Montgomery et al. 1995, Gurnell and Linstead 1998, Gurnell and Sweet 1998, Buffington et al. 2002, Montgomery et al. 2003b, Montgomery and Piegay 2003). LW is important in maintaining flow diversity, creating areas of concentrated and increased flows, along with more sheltered areas of slower flow velocity (Kreutzweiser et al. 2005). LW functions as an important physical obstruction in the river, blocking and redirecting water, dissipating energy from river flows (Gippel 1995, Curran and Wohl 2003) and attenuating flood peaks (Gregory et al. 1985). LW jams (LWJ) that block the entire channel, also known as active or complete jams, dramatically increase pool frequency by specifically creating both scour and step-pool sequences (Montgomery et al. 1995) and increase hyporheic exchange and thermal heterogeneity (Wondzell et al. 2009). During low flow periods, debris dams retain water and increases moisture in river sediments (Chadwick and Huryn 2007), where the hyporheic zone may function as an important low flow refuge for biota (Delucchi 1989, Jacobi and Cary 1996).

1.3.2 The ecological importance of wood

A large body of literature explored the effects of large wood on aquatic biodiversity (Wondzell and Bisson 2003). In particular, much of this work has focused on fishes and macroinvertebrates.

1.3.2.1 Effects of large wood on fishes

Early relationships between large wood and fishes were first seen in declining fish populations after the clearing of large wood from stream systems (Lestelle and Cederholm 1984, Benke et al. 1985). LW was subsequently identified as a fundamental habitat for fishes throughout various stages in their lifecycle (Harmon et al. 1986, Gibbons 1990). Larger and more complex wood structures, especially wood jams, result in the most beneficial effect for fishes, especially in lowland rivers (Nagayama et al. 2012). Plunge pools associated with LW are preferentially used as low-energy refugia (Lisle 1981, Lisle 1986, 1995, Thompson et al. 2007), and in restoration projects, LW placements that created pools and cover were the most successful for enhancing salmonid populations (Nagayama and Nakamura 2010). The structural complexity of LW habitat provides shade and cover from predators (Bisson et al. 1987, McMahon and Hartman 1989, Fausch and Northcote 1992, Everett and Ruiz 1993, Nagayama and Nakamura 2010). LW and its thermally regulated plunge pool habitat increases the survival and numbers of overwintering fishes (Schlosser and Angermeier 1995, Cederholm et al. 1997, Giannico and Hinch 2003). Sediment sorting induced by LW increases the availability and quality of gravels that fishes use as breeding habitat and to establish redds for eggs, increasing the number of smolts produced in each river channel (Fausch and Northcote 1992). LW allows for different salmonid life-stages to more efficiently partition habitat space (Rabeni and Jacobson 1993, Nagayama et al. 2009), and increases survivability and evenness across life-stages and life-strategies in salmonid populations (Reimers 1971, Wondzell and Bisson 2003).

1.3.2.2 *Effects of large wood on macroinvertebrates*

Macroinvertebrate richness, and occasionally density, has been shown to increase with LW in a number of studies (Wondzell and Bisson 2003, Milner and Gloyne-Phillips 2005, Schneider and Winemiller 2008). In contrast to other physical habitat enhancements such as boulders, large wood has a texturally complex surface, resulting in substantial variations in microhabitat conditions (Mathooko and Otieno 2002). Increased jam complexity also results in enhanced macroinvertebrate diversity (O'Connor 1991), abundance, and biomass, and can partly be attributed to various mechanisms such as providing stable substrate for oviposition (Anderson et al. 1978, Hoffman and Hering 2000) and increased cover from predators (Czarnecka et al. 2014). Large wood can also function as flood refugia, mitigating against disturbance, as reaches without large wood during floods lose substantially more macroinvertebrate taxa compared to reaches with LW (Palmer et al. 1996, Hax and Golladay 1998, Robinson et al. 2004), since the structure complexity of large wood itself may passively “catch” drifting invertebrates dislodged from upriver (Palmer et al. 1996), and the jam and associated accumulations of organic matter can provide a mosaic of nearby low-flow refugia for less mobile macroinvertebrates (Lancaster and Hildrew 1993). The ability for LW to function as flood refugia may be particularly important in sandy, lowland rivers or in other modified channels that lack alternative refugia (Borchardt 1993).

In addition, macroinvertebrate community structure and functioning feeding groups have been shown to change in the presence of large wood (Dudley and Anderson 1982, Benke et al. 1985, Drury and Kelso 2000, Johnson et al. 2003, Wondzell and Bisson 2003). This suggests that wood may cause a significant change in the availability of different basal food resources.

1.3.3 The effect of wood on basal food resources

One mechanistic explanation for the effect of LW on biota may be through its role in determining the availability, composition, and nutritional quality of food resources for aquatic consumers. In addition, wood may alter the relative availability of both allochthonous (“terrestrial”) and autochthonous (“aquatic”) production for consumers.

Large wood can function directly as a food source for xylophilic macroinvertebrate species, but these taxa are relatively rare compared to other macroinvertebrate species (Anderson et al. 1978, Anderson et al. 1984, Anderson 1989, Hoffman and Hering 2000). Drift feeders such as Simuliidae and Hydropychidae can potentially use the structural location of wood to feed on transported matter higher up in the water column; however, most research has focused on the ability of LW to increase organic matter retention by trapping fine sediment, leaves, twigs, and other transported matter (Bilby and Likens 1980, Bilby 1981). The erosion and decay of the wood surface can also contribute to increased organic matter in the reach (Ward and Aumen 1986), and possibly increase the quality of organic matter through microbial processing (Gessner et al. 1999).

The structural complexity of large wood can vastly increase the total surface area available for biofilm colonisation and result in increases in primary productivity, increasing food availability for consumers (Hax and Golladay 1993, Wondzell and

Bisson 2003). However, a previous review of habitat heterogeneity (Kovalenko et al. 2012) has dismissed the effect of food limitation on ecological response, principally because macroinvertebrates respond to not just substrate surface area alone, but also other aspects of substrate complexity: *e.g.* even if two habitats have similar surfaces areas, the one with greater surface complexity will have greater macroinvertebrate richness and production (Douglas and Lake 1994, Taniguchi and Tokeshi 2004). This has been interpreted to suggest that food limitation is a minimal component of habitat heterogeneity controlling macroinvertebrate response (Kovalenko et al. 2012), yet this assumes that surface area alone affects basal resources, and not also surface texture or complexity. This assumption betrays a basic understanding of primary productivity, and instead a more nuanced understanding of algal ecology and benthic biofilms would show that substrate surface complexity is of fundamental importance for the composition and nutritional quality of biofilm food resources.

Specifically for wood, the rough and complex surface texture has been shown to increase epixylic algal diversity and contain unique species assemblages, particularly of taxa sensitive to shear stress (Sabater et al. 1998). Algal community composition can vary with taxa-specific preferences for abiotic conditions and even small changes in surface texture, such as among different species of submerged macrophytes (Pip and Robinson 1984). In addition, the complex mosaic of abiotic factors created around large wood (*e.g.* light, flow, substrate) can also increase the diversity of microhabitat conditions and biodiversity in epilithic communities immediately surrounding wood. Changes in algal diversity is important for consumers, as algal community composition has important consequences for the nutritional quality (Taipale et al. 2013). Most importantly, changes in the nutritional quality of periphyton can readily change without discernible alterations in periphyton biomass (Cashman et al. 2013), indicating how simple surface-area or biomass measurements are insufficient to accurately characterize primary producer/grazer relationships. Instead, it is increasingly important to directly examine nutritional quality in primary production.

1.4 Nutritional quality, fatty acids, and physical habitat conditions: a "bottom-up" mechanism for ecosystem response?

Recent advances in limnology suggest that ecosystem processes may be regulated by "bottom-up" forces affected by not only the quantity, but nutritional quality of food resources. Until recently, the variable efficiency of energy flow across the plant-animal interface in aquatic systems has not been not well understood (Brett and Müller-Navarra 1997). Despite some early studies into the importance of the nutritional quality of food resources in lakes (Sterner and Hessen 1994, Brett and Müller-Navarra 1997, Brett et al. 2000, Müller-Navarra et al. 2000), only more recently has there been a greater and more robust exploration between nutritional quality and the relationship with the efficient transfer of energy across the plant-animal interface (Torres-Ruiz et al. 2010, Taipale et al. 2011, Perhar et al. 2013, Galloway et al. 2014b, Taipale et al. 2014). When food resources lack key nutritional components, ecosystems can experience trophic decoupling, where increases in primary production are not transferred to increases in consumer biomass, exemplified in hypereutrophic lakes undergoing algal blooms (Brett and Müller-Navarra 1997, Perhar et al. 2013). In contrast, ecosystems with high efficiency and a high-quality food base may even result in inverted Eltonian pyramids, as high assimilation efficiencies drive large herbivore productivity for the same amount of primary productivity (Figure 1-4).

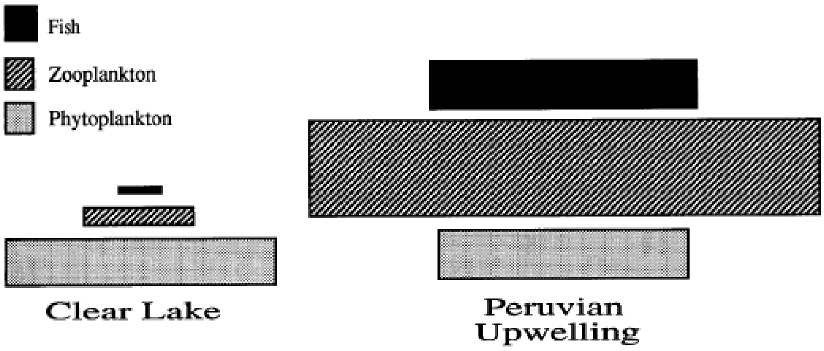


Figure 1-4: Eltonian biomass pyramids representing low efficiency ecosystems (Clear Lake) and high efficiency ecosystems (Peruvian Upwelling). Size of the boxes is proportional to relative biomass. For an equivalent amount of phytoplankton biomass, the efficient ecosystem can support up to 25-fold greater zooplankton and 50-fold greater fish production than inefficient systems. Changes in ecosystem efficiency can account for these different relationships between primary and secondary production, without increased turnover in primary productivity to account for these changes. Figure reproduced from Brett and Müller-Navarra (1997).

The assessment of ecological stoichiometry, which considers the elemental mineral ratios of C, N, and P in consumers, food, and ecosystems, has been widely used for the evaluating nutritional quality in primary production, nutrient cycling, and food web dynamics (Sterner and Hessen 1994, Brett et al. 2000, Sterner and Elser 2002, Cross et al. 2005). However, recent work has identified the more fundamental importance of a biochemical view of nutritional quality and food webs (Müller-Navarra 2008), as the studied patterns of N and P content with consumer growth has actually been due to the co-occurrence of these elemental nutrients with an underlying and much stronger relationship to fatty acid content (Figure 1-5). In subsequent studies, the assimilation efficiency and quality of basal food resources has continued to be linked to fatty acid content, as consumer growth has been shown to be fundamentally limited by fatty acid content in food resources (Muller-Navarra et al. 2004, Taipale et al. 2014). As a result, fatty acid availability, specifically of long-chain and unsaturated forms, has been suggested to be limiting secondary production in many aquatic systems (Müller-Navarra et al. 2000, Perhar et al. 2013).

However the majority of the exploration of nutritional dynamics with fatty acids have been primarily explored in marine and lake ecosystems (Muller-Navarra et al. 2004, Taipale et al. 2014), with these dynamics relatively unexplored in river systems (Lau et al. 2008, Lau et al. 2009a, Torres-Ruiz et al. 2010).

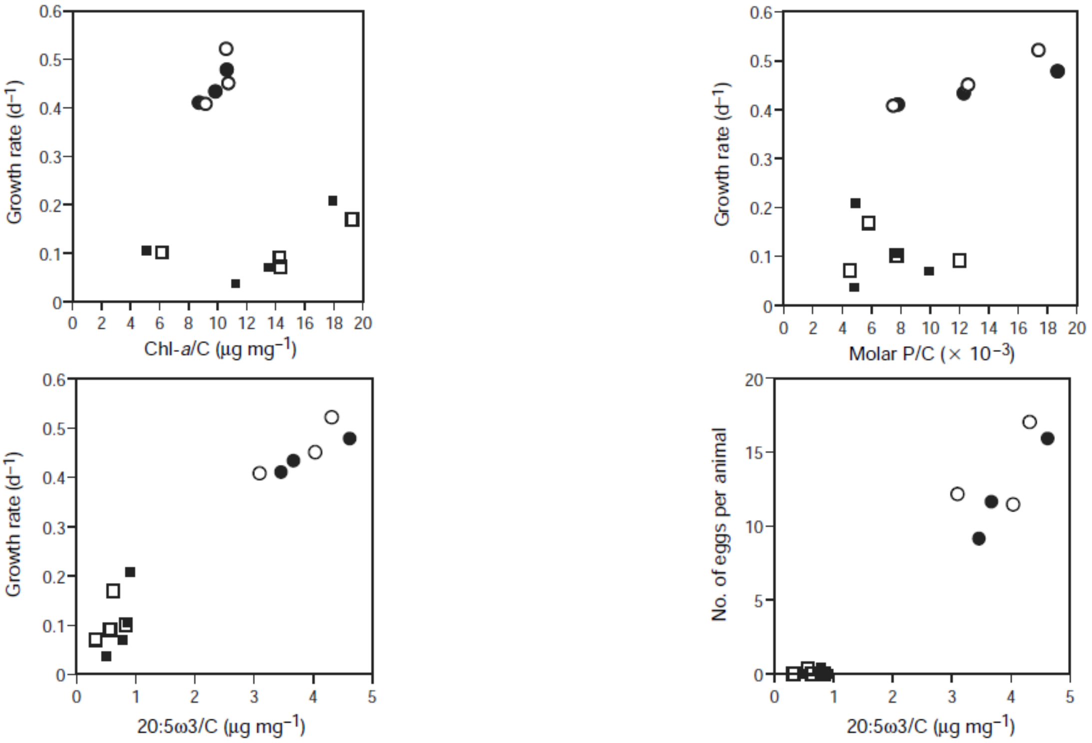


Figure 1-5: *Daphnia pulex* instantaneous somatic growth rate and clutch size when related to chlorophyll, P-content, and fatty acid content of their food resources. Growth rate and fecundity are strongly related ($r^2 = 0.95$) with the concentration of the highly unsaturated fatty acid eicosapentaenoic acid (EPA; 20:5ω3) contained in food resources. Squares represent cyanobacteria-dominated summer assemblages and circles represent diatom and cryptophyte-dominated winter assemblages. Open symbols represent seston < 30 µm and closed symbols the total seston. Figure reproduced from Müller-Navarra et al. (2000).

1.4.1 Fatty acids: an essential nutritional component

Fatty acids are the fundamental building blocks of lipids and the largest constituent of neutral lipids and phospholipids. Consisting of carbon atom chains, fatty acids typically have an even number of carbons, typically between 14-24, and 0-6 double bonds, with a methyl head and carboxyl group tail. In contrast to other essential dietary components like proteins and carbohydrates, which are typically completely broken down in digestion, fatty acids are released from ingested lipids without degradation and taken up by consumer tissues in their basic form and stored in lipid reservoirs, such as adipose tissue or insect fat bodies (Iverson 2009). Fatty acids may be synthesized or converted into various other forms through modifying carbon chain length or by adding or removing double bonds, but the enzymatic reactions necessary for these functions are often highly limited by phylogenetic group or species. In particular, while most organisms synthesize short chain fatty acids relatively easily, only primary producers can typically synthesize or elongate long fatty acids with multiple double bonds (Bell and Tocher 2009). In addition, basal food resources usually have specific indicator fatty acids that are highly retained throughout the food web, and can thus function as “biomarkers” that can thus be traced back to specific food source origins.

Fatty acids are described by the number of carbon atoms in the chain length, the degree of unsaturation (number of ethylenic or “double” bonds), and the position of their first double bond, counted from the terminal carbon (Bell and Tocher 2009). In such terminology, 16:0 represents a fatty acid chain of 16-carbons and no double bonds, and 20:5ω3 indicates a fatty acid of 20-carbons with 5 unsaturated double-bonds, with the first double bond on the 3rd-carbon from the methyl end. Fatty acids are generally grouped into four overall fatty acid classes based on their degree of saturation and length. Saturated fatty acids (SAFAs), contain no C-C double-bonds, and monounsaturated fatty acids (MUFAs) contain one C-C double-bond. Polyunsaturated fatty acids contain ≥ 2 double bonds, with more recent changes to nomenclature covering fatty acids with 16 – 18 C chains (PUFAs), while 20+ C fatty acids with ≥ 2 double bonds are called highly unsaturated fatty acids (HUFAs) (Bell and Tocher 2009).

Saturated fatty acids (SAFAs) and monounsaturated fatty acids (MUFAs) are readily synthesized by most organisms and primarily function as energy storage molecules (Napolitano et al. 1994). Generally, animals are limited to synthesising lower length saturated and mono-unsaturated common fatty acids such as 14:0, 16:0 and 18:0, and lack the necessary enzymes to elongate past 18 C or the desaturase enzymes to introduce double bonds. Algae are one of few organisms known to produce highly-unsaturated fatty acids (HUFAs) such as eicosapentaenoic acid (EPA; 20:5ω3) and docosahexaenoic acid (DHA; 22:6ω3).

HUFAs in particular have been increasingly shown to be essential dietary components for many animals (Sargent et al. 1995), and are integral to a variety of physiological processes, including macroinvertebrate somatic and population growth and reproduction (Ederington et al. 1995, Demott and Müller-Navarra 1997, Brett et al. 2009b). HUFA play an important role in the process of successful metamorphosis (Stanley-Samuelson and Dadd 1984), and are also needed in maintaining the growth, disease resistance, and health of juvenile fish (Sargent et al. 1999). HUFA are also preferentially accumulated and retained in cell tissues, even after diet-switching and starvation, due to their important physiological role (Taipale et al. 2011). In particular, DHA is a primary component of neural tissue and is found in high concentrations in fish eggs (Sargent et al. 1995). EPA, DHA, and ARA (arachidonic acid; 20:4ω6) are included in all phospholipid cell membranes, and regulate cell fluidity, especially in facilitating overwintering survival (Farkas 1979, Bennett et al. 1997). EPA and ARA are important precursors in the creation of hormone-like eicosanoids, prostaglandins, and cortisol (Sargent et al. 1995, Sargent et al. 1999, Bell and Sargent 2003).

While all of these functions depend upon the availability of specific fatty acid components, few animals are currently known, and none among benthic invertebrates, that can directly synthesize HUFAs *de novo* or efficiently elongate specific PUFA precursors, such as α-linoleic acid (ALA: 18:3ω3) and linoleic acid (LIN: 18:3ω6), into biologically important HUFAs (Stanley-Samuelson 1994, Brett and Müller-Navarra 1997, Torres-Ruiz et al. 2010). Hence, these fatty acids are considered "essential" and consumers must obtain these physiologically necessary HUFAs from their diet.

1.4.2 Physical habitat controls on fatty acid composition

The nutritional quality of primary consumers, especially fatty acid content, may be strongly influenced by localized physical habitat conditions, such as those altered by large wood (Figure 1-6). This may occur primarily through two pathways. First, specific algal taxa may alter fatty acid composition to regulate cellular membrane fluidity and homeostasis with changing environmental conditions. In lake studies, elevated light conditions resulted in decreased PUFA and HUFA content due to oxidation and UV damage (Arts and Rai 1997, Fábregas et al. 2004), and laboratory trials showed decreased ω3 fatty acids under increased light in the unicellular alga *Nannochloropsis* sp. (Fábregas et al. 2004). The second pathway is due to compositional shifts in the algal assemblage: recent studies have also demonstrated that freshwater microalgae may be clearly distinguished into four distinct classes by fatty acid profiles, suggesting that shifts in species composition can result in changes to fatty acid content (Taipale et al. 2013). While physical habitat conditions may induce variation to the fatty acid profiles of specific taxa, overall taxonomic shifts in community composition should still be identifiable (Galloway et al. 2012), and a recent study has effectively used fatty acid profiles to accurately infer phytoplankton community composition data (Strandberg et al. 2015). Broad field-based studies examining the effect of physical habitat conditions and environmental stressors may combine these two inter- and intra-taxonomic shifts in fatty acid profiles. In an *in-situ* field experiment conducted in three temperate streams, decreases in canopy cover led to reductions in long-chain essential HUFA but increased amounts of PUFA precursors (Cashman et al. 2013), which recently has been replicated in subtropical streams (Guo et al. 2015). Chlorine-pollution has also been shown to alter periphyton fatty acid composition (Napolitano et al. 1994), as well as nitrogen and phosphorus enrichment decreasing the overall proportion of HUFA in stream periphyton (Guo et al. 2015), even without inducing changes in periphyton biomass (Cashman et al. 2013). Other environmental variables, including temperature, various aspects of flow (*e.g.* velocity and turbulence), substrate, and the variability of these abiotic conditions in the disturbance regime are also hypothesized to have a strong impact on fatty acid composition, but have not yet been explicitly examined.

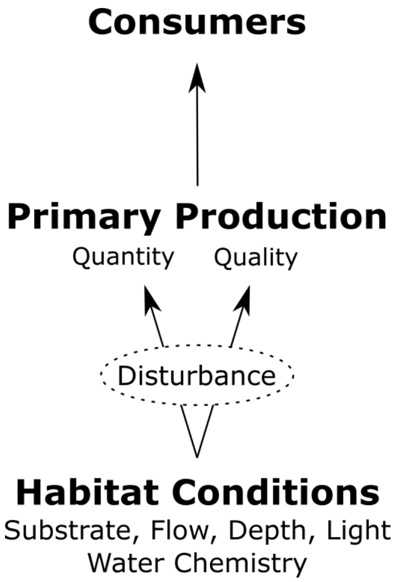


Figure 1-6: A “bottom-up” conceptual model for how abiotic factors cascade up the trophic system through effects on primary productivity. The quality and quantity of primary production may respond independently (positively and/or negatively) to physical and chemical abiotic factors due to species-specific homeostatic mechanisms and changes in community composition. These responses would then be regulated through the disturbance regime. While the quantity of primary productivity determines the potential maximum of energy transferred, food quality regulates the efficiency of these connections.

As a result, almost any stressor that might alter the community composition of algae will likely have a strong effect on fatty acid content and thus nutritional quality for stream consumers. As algae communities can vary on different substrate types (silt, stone, wood) and vary according to taxa-specific habitat preferences in light, flow, and temperature, all of these abiotic factors affected by LW may ultimately affect nutritional quality and food webs.

1.5 Thesis structure and research chapters

Overall, there has been surprisingly little evaluation of the effect of habitat complexity on the mechanisms that incorporate food webs and energy flows in aquatic systems (Woodward et al. 2010, Kovalenko et al. 2012). As a result, this thesis takes a unifying perspective of how large wood can affect “bottom-up” mechanisms driven by changes in food availability, nutritional quality, and energy flows.

This thesis presents four distinct but related research projects in the following chapters (2 – 5) exploring the mechanism by which the physical structure of large wood can alter physical habitat conditions, mitigate against flow disturbance, change the availability and nutritional quality of basal resources, and alter the trophic base of consumer assemblage (Figure 1-7). Each of the four projects have been written as separate chapters, each with an introduction and review of relevant literature, methodology, results, and discussion sections.

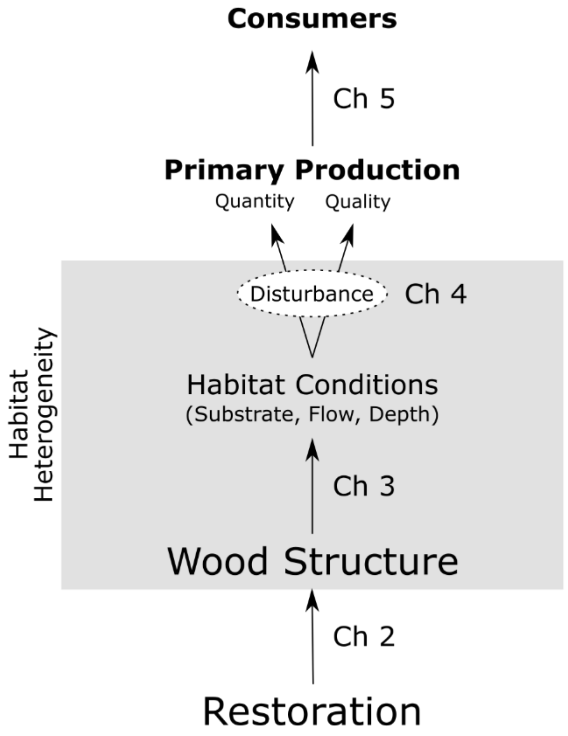


Figure 1-7: Thesis diagram showing the conceptual link between the four research chapters contained within the thesis. Each chapter explores the relationship between the two nearest components of the diagram. Habitat disturbance, a temporal variability of habitat heterogeneity, will be examined in this thesis as the intermittent releases of water from hydroelectric dams, also known as hydropeaking.

Chapter 2 is a survey of the overall context of large wood restorations in the UK and focuses on wood restoration projects contained in the National River Restoration Inventory, a database of restoration projects from throughout the United Kingdom. This chapter tests the following series of hypotheses: (1) restoration involving wood tend to use wood primarily as a deflector; (2) motivations will be focused around flow diversification and physical habitat enhancement; (3) restorations involving wood will be focused on lowland rivers; and (4) the majority of projects will not involve comprehensive monitoring. Understanding the motivations and the common trends in wood restoration projects is an important first step in understanding the potential effectiveness of these restorations in creating habitat heterogeneity.

Chapter 3 uses field data collected from four rivers in lowland England to examine the variability in large wood structural characteristics and their associated mesohabitat conditions (depth, velocity, and sediments) across a gradient of wood management conditions (near-natural to restored wood). In particular, this chapter tests two primary hypotheses: (1) that structural complexity of wood jams will decrease along a management gradient from near-natural/reference reaches, to heavily impacted sites with restored wood; and (2) there is a positive relationship between wood jam complexity and mesohabitat heterogeneity along this gradient. This chapter serves to connect the lessons learned from Chapter 2 into how the structural attributes of wood used in restoration may be related to functional attributes studied in Chapters 4 and 5.

Chapter 4 examines if large wood may mitigate the scouring influence of flood disturbance (here as the intermittent release of water from hydroelectric dams, also known as hydropeaking) on periphyton biofilms, an important basal resource for stream consumers. Specifically, this chapter reports findings from a simulated hydropeaking flood experiment conducted in a semi-natural flume system in the Italian Alps. This chapter tests the following hypotheses: (1) hydropeaking has a large effect on periphyton resources, as scour from increased discharge is expected to result in reduced periphyton quantity (Chl-*a* and AFDM) and nutritional quality (elemental nutrient and fatty acid content); (2) the magnitude of this effect is greater with increasing hydropeaking intensity; and (3) wood substrate mitigates the effects of hydropeaking on both periphyton quantity and quality. This would then have implications to the availability of basal resources for consumers and the resiliency of the consumer assemblages in hydropeaking rivers.

Chapter 5 examines how large wood affects the trophic base of the macroinvertebrate assemblage in a lowland, sand bed river through an approach combining stable isotope analysis (SIA) and fatty acid (FA) biomarkers. Two adjacent river reaches, one with large wood accumulations and another as a control without large wood, are compared to examine the different availabilities of food resources and its impact on the macroinvertebrate community assemblage. A secondary goal is for a methodological comparison of using both stable isotopes and fatty acids to examine food webs. This chapter tests the following hypotheses: (1) large wood increases biomass of the community assemblage and results in an altered consumer composition on and around LW logs compared to more distal channel areas; (2) specific diets are different between wood and non-wood habitats, with more consumption of high quality autochthonous resources around wood habitats; and (3) the overall trophic base of the system is supported by autochthonous, rather than allochthonous, production.

The concluding chapter of the thesis (6) summarizes the key findings from each chapter of this thesis, draws together the conclusions from each research project, identifies wider implications of the research, and suggests future research directions.

Chapter 2

Large wood in United Kingdom restoration schemes – conclusions from the National River Restoration Inventory

2.1 Background

An estimated 80-90% of European rivers are in a degraded state from pristine conditions (Laub and Palmer 2009), and under the European Union Water Framework Directive (EU WFD), European Member States have legislative obligations to rehabilitate these waters to good ecological status. However, restoration projects must balance multiple demands, including the needs of various national and local stakeholders, restoring healthy ecosystems, and creating data for scientific understanding (Palmer et al. 2005). In particular, these varying demands and goals may be in conflict with the direct restoration of ecosystem functions, as the need to facilitate recreational use, protect infrastructure, or mitigate flood risk may sacrifice opportunities to deliver improvements in environmental health (Palmer et al. 2005). As a result, balancing the conflicting goals of various stakeholders may limit the potential impact of overall river restoration. Regarding wood, conflicting stakeholder demands may result in trade-offs and cause important differences between the effects of wood studied in natural or near-reference conditions (natural wood) and those wood placements used in restoration schemes (restored wood). In particular, these trade-offs may revolve around issues regarding public perception of the aesthetics of large wood and concerns over flooding.

2.1.1 Public perceptions of large wood

The historical clearance of LW from river systems has been so extensive it has altered general perspectives of the place of wood in natural aquatic landscapes (Wohl and Merritts 2007). As current management practices re-introduce wood into rivers, differing perceptions over the form of an ideal river, and the failure to communicate the positive effects of LW with the public, may cause conflict and uncertainty (Chin et al. 2014) and have profound implications for restoration success (Ribe 2006). Despite recent scientific advances demonstrating the numerous benefits of large wood (See Sections 1.2.3 and 1.2.4), many negative perceptions of wood remain.

In forests of the US Pacific Northwest, woody debris was identified to decrease the aesthetic value of the forest by the public (Ribe 2009). Even among undergraduate geography and environmental studies students, national and international surveys found strong negative perceptions of wood in rivers (Piegay et al. 2005, Chin et al. 2008, Le Lay et al. 2008, Chin et al. 2014). Rivers with wood were rated as less aesthetically valuable, more dangerous, and more in need of human intervention than rivers without wood (Le Lay et al. 2008). These responses varied among countries, with students in China and India having the least favourable opinions of wood, and students in Germany, Sweden, and Oregon (USA) having overall high favourability of LW (Le Lay et al. 2008). However, surveys in Poland and the United States have identified that favourable views of wood were positively correlated with the length of university education, professional training, and years working in river management (Wyzga et al. 2009, Chin et al. 2014). Overall, a top rationale for negative perceptions of these rivers was a need to be cleaned for flood risk management (Chin et al. 2014).

2.1.2 The perceptions of flood risk

2.1.2.1 Effects of large wood on resistance and flow attenuation

The removal of large wood for flood control is based on the principle of minimizing flow resistance, as minimal channel roughness allows water to flow at higher velocities, increasing total conveyance. Since discharge is a function of stage and flow velocity, for an equivalent discharge, increased velocity should reduce river stage, thereby reducing the chance the river may overtop its banks. Indeed, LW is associated with increased water levels upstream of jams, which may increase local overbank flows (Dudley et al. 1998, Jeffries et al. 2003), and some studies have suggested that LW blockages can lead to local erosion upstream as the channel migrates to account for this obstruction (Brown et al. 1997). In fact, the clearing of LW does reduce water depth, increases average velocity, and exhibits more uniform flows at baseflow (Shields and Smith 1990). However, management decisions informed by this simple conveyance relationship alone may be overlooking the complex interaction of river processes at various spatial scales that may affect flooding.

Channel roughness, while greatest at low discharge in sites with LW, converges to similar values at high discharges as wood obstructs an increasingly smaller fraction of the channel cross-section (Lisle 1986, Shields and Smith 1992, Gippel 1995). As a result, during large flood peaks, the presence of LW may have little difference on mean local-flow velocities (Gippel 1995), and there is little evidence for increased flood risk outside of the immediate zone upstream of LW (Lester and Wright 2008). Across a landscape scale, LW may actually mitigate flood risk by retaining water in certain land-use types, such as rural or forested headwater reaches, and thus attenuating flows in more flood-sensitive land-use types. In particular, this can protect lowland areas from flooding, where there is generally a higher population density and greater floodplain development (Woltemade and Potter 1994).

Even if wood is not removed, river management can often fix wood logs to the riverbed, so that wood cannot be transported and cause damage to downstream infrastructure. However, fixing wood can result in wood orientations that may not occur naturally, and fail to consider other key properties of the LW itself, especially wood complexity and size in relation to the channel. Simple wood placements lacking branches or structural complexity (*e.g.* stripped single logs) may not trap autumn leaf fall, which would increase LW resistance and flood attenuation during winter high-flows, when seasonal flood occurrence are greatest (Sear et al. 2010). The initial orientation of LW, and its ability to reorient with the line of flow, may also influence the total effect on channel roughness and conveyance (Gippel et al. 1996b). In rivers with wood pieces with a small size relative to channel width, LW is more likely to be mobilized and transported downstream unless anchored by sediment or other large roughness objects. But where wood is large in relation to channel width, wood pieces are most likely to become trapped in the channel, and are unlikely to be dislodged with high flows (Gurnell et al. 2002). Increases in flood risk associated with LW are particularly related to anthropogenic restrictions on wood re-orientation – through channel fixing, channel constrictions, or infrastructure – resulting in the sustained accumulation of drifting matter and growth of debris dams across the entire channel (Young 1991, Gippel et al. 1996a).

2.1.2.2 *Effects of large wood on channel geometry, erosion, and sediment storage*

LW can create jams that trap substantial organic and inorganic matter, increasing residence time and sediment storage in the reach (Nakamura and Swanson 1993, Smith et al. 1993a, Smith et al. 1993b, Millington and Sear 2007), as sediment volumes behind log steps can exceed mean annual load by tenfold (Ryan et al. 2014). However, when LW is removed from the channel, previously stabilized sediments can suddenly become mobilized, causing massive local erosion and alter channel geometries (Smith et al. 1993a, Smith et al. 1993b). Mobilized sediment can be transported and deposit in low-gradient channels downstream, elevating the bed, reducing cross sectional area, and increasing flood risk (Stover and Montgomery 2001). Since floodplain developments tend to be concentrated in lower gradient reaches where sediment deposition and bed aggradation is most likely to occur, wood removal can be extremely hazardous by actually increasing flood risk for downstream urban areas (Wheater 2006).

In contrast, sediment accumulations around wood jams can block flows and increase the frequency and extent of upstream channel migration (Brummer et al. 2006, Sear et al. 2010), increasing cross sectional area and flood storage in the headwaters (Nakamura and Swanson 1993). However, most channel adjustment and erosion after wood introduction occurs at the first bankfull flow, after which LW actually increases long-term channel stability and decreases erosion of the banks (Bilby 1984, Smith et al. 1993a, Abbe and Montgomery 2003, Lester and Wright 2008, Collins et al. 2012).

In high-energy river channels, LW helps the formation of step-pool patterns, which dissipate stream energy and further maximize flow resistance (Keller and

Swanson 1979, Wilcox and Wohl 2006). Due to the sediment retentive properties of LW, wood actually reduces the effective slope the river reach, decreasing stream power, and possibly mitigating damage to downstream infrastructure (Lancaster and Grant 2006). In addition, when river flows are high enough to mobilize debris, pre-existing stabilized LW jams function as obstructions and can reduce the energy and total distance travelled of other mobilized debris. As rivers with LW are more likely to be sinuous, more energy is needed for the initial dislodgement of LW, and transported wood is more likely to snag against channel margins, further absorbing destructive energy from being transmitted downstream (Lancaster et al. 2003).

2.2 Research Aims

The overall aim of this chapter is to improve understanding the structural complexity of wood being used in restorations as an important first step in evaluating the potential effectiveness of these restorations in creating habitat heterogeneity. The chapter provides an overview of the nature of large wood restorations in the UK, focusing on data on wood restoration projects contained in the National River Restoration Inventory, a database of restoration projects from throughout the United Kingdom. This chapter aims to identify key trends in wood restoration in the UK: the techniques and structural form of wood used in restoration, the location of projects, project motivations and monitoring schemes applied to assess project outcomes. A series of hypotheses are tested in the chapter: (1) restoration involving wood tend to use wood primarily as a deflector; (2) motivations will be focused around flow diversification and physical habitat enhancement; (3) restorations involving wood will be focused on lowland rivers; and (4) the majority of projects will not involve comprehensive monitoring.

2.3 Methods

The UK National River Restoration Inventory (NRRI), maintained by the UK River Restoration Centre, is a comprehensive database that details river restoration information from throughout the UK, with project entries dating back to the 1980s. While project entries are voluntary submissions and as such may contain some data gaps of all restorations occurring in the UK, the River Restoration Centre takes an active role in requesting submission and following-up on recent restoration works. The database contains information on catchment characteristics, objectives and techniques, background motivation and project objectives, techniques used, project partners, cost, monitoring information, and evaluation of success/failure of the projects. Project entries consisted of a combination of multiple-selection check boxes, and custom text-entry input fields, which were completed and submitted by each restoration project manager. For this study, the database was queried using the following terms to obtain projects using wood in a variety of forms: “wood” OR “deflector” OR “groyne” in the ‘Objectives’ (text box field) or indicating the Project Aim 1.12 – “Current deflectors/concentrators to create habitat and flow diversity” (tick box field). These search terms were representative of various ways wood might be referenced within the database, and examination of the results indicated a wide variety of project types and wood installations.

Data was cleaned to remove entries that were located outside the British Isles (United Kingdom and Ireland) since only a very small number of projects were located elsewhere. The custom text-entry input fields (*e.g.* Project Background and Techniques) were queried for the use of key terms (*e.g.* “overwide”, “weir”, “deflector”, “berm”), with similar terms combined for a unified topic response (*e.g.* “silt” and “fine sediment” were combined, as well as “LWD”, “woody debris”, “large wood”, and “jam”). Projects were then analysed according to the percentage of projects that identified common background issues, project objectives, restoration techniques, monitoring, and key funding partners.

2.4 Results

The National River Restoration Inventory database was accessed on 29 August 2013, and after data cleaning, the final search produced 416 unique wood restoration schemes across all areas of the UK (Figure 2-4), and covered 27% of the total 1,566 restoration schemes in the NRRI database. There was an increasing trend in wood restoration schemes over time, particularly after 1990 and again after 2008, although this generally tracked with the increasing number of all restoration schemes and did not indicate an increasing proportional use of wood (Figure 2-2). Projects durations were generally short, with over 72% of projects running for less than one year, although some projects ran over two years and a small minority of projects up to 8 years (Figure 2-3). The listings included projects at all stages of the restoration process, from initial vision and through all design stages, although more than 70% of all entries reported on fully completed river restorations (Figure 2-4). Projects at all progress stages were examined where data were available.

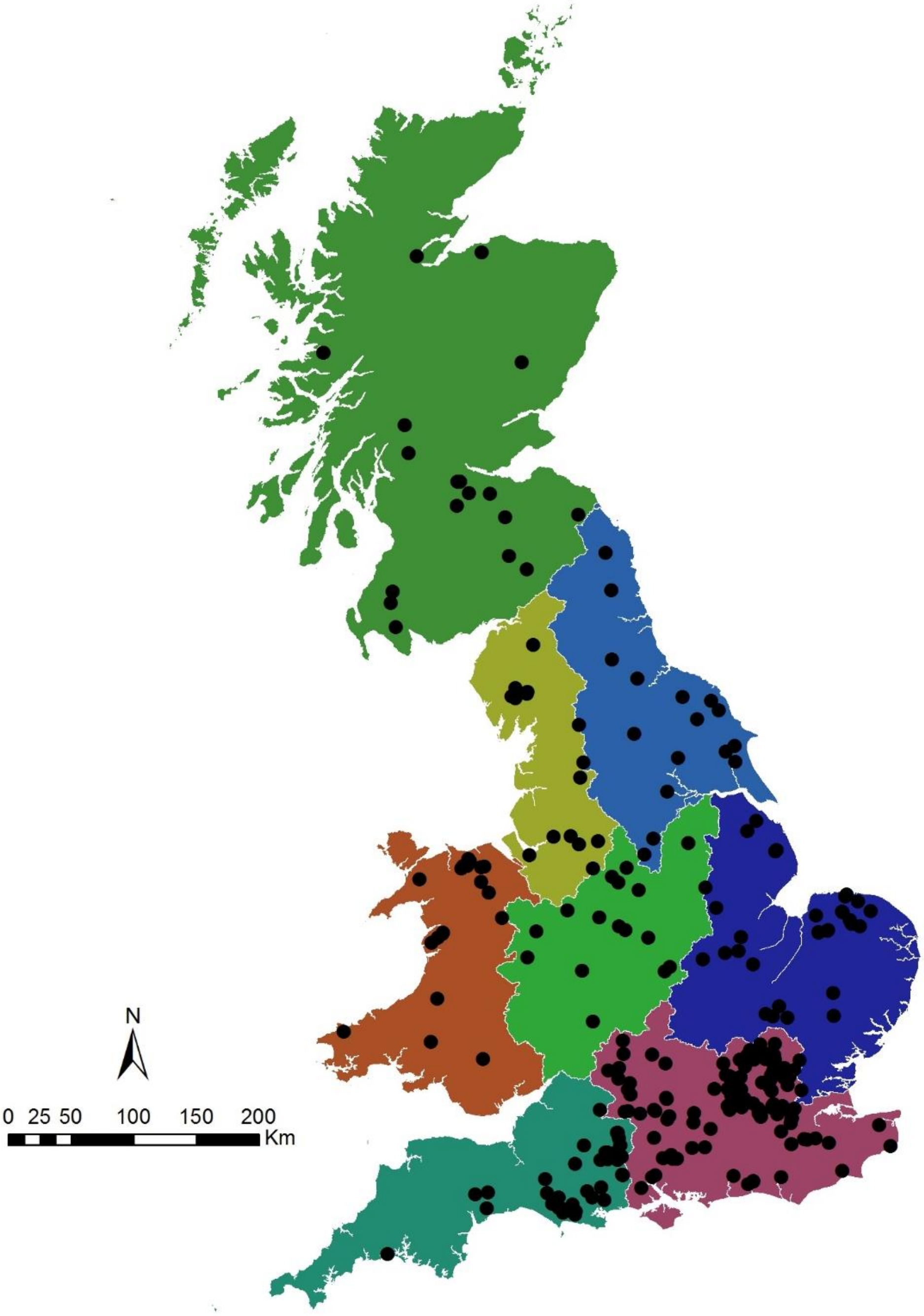


Figure 2-1: Location of all restoration schemes in Great Britain geotagged in the NRRI. Less than 4% of projects examined were located in either Northern Ireland or the Republic of Ireland. Each point is one restoration scheme. Underlying geographic blocks are regional water agency jurisdictions. Note the large cluster of restoration schemes ringing London.

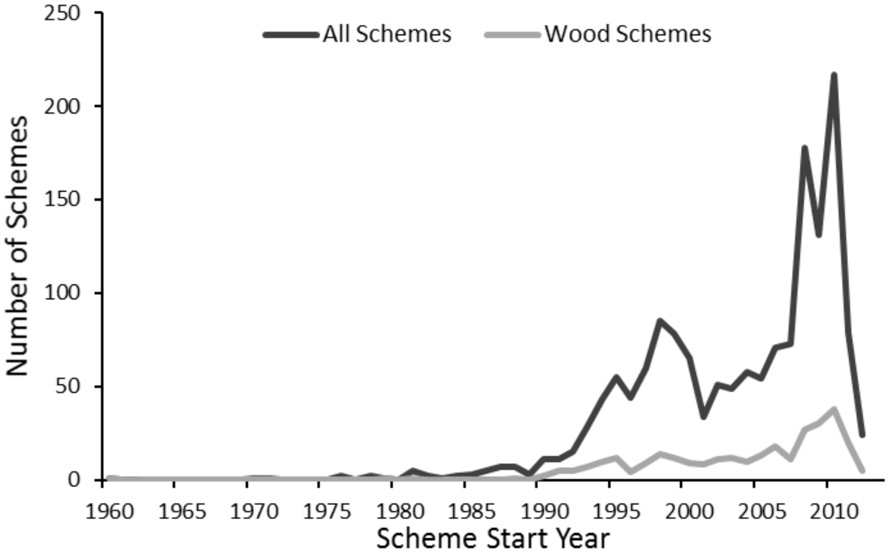


Figure 2-2: Total number of all restoration schemes and subset of wood restorations contained in the NRRI database by start year.While the first entry in the database was in 1960, the number of restoration did substantially begin to increase until 1990, with a substantial uptick in projects after 2008. The proportions of schemes using large wood broadly tracked with overall patterns of increasing restoration. The decreased number of schemes in 2011 are likely due to database incompleteness, as projects in the database were on average submitted 2-3 years after the listed start date.

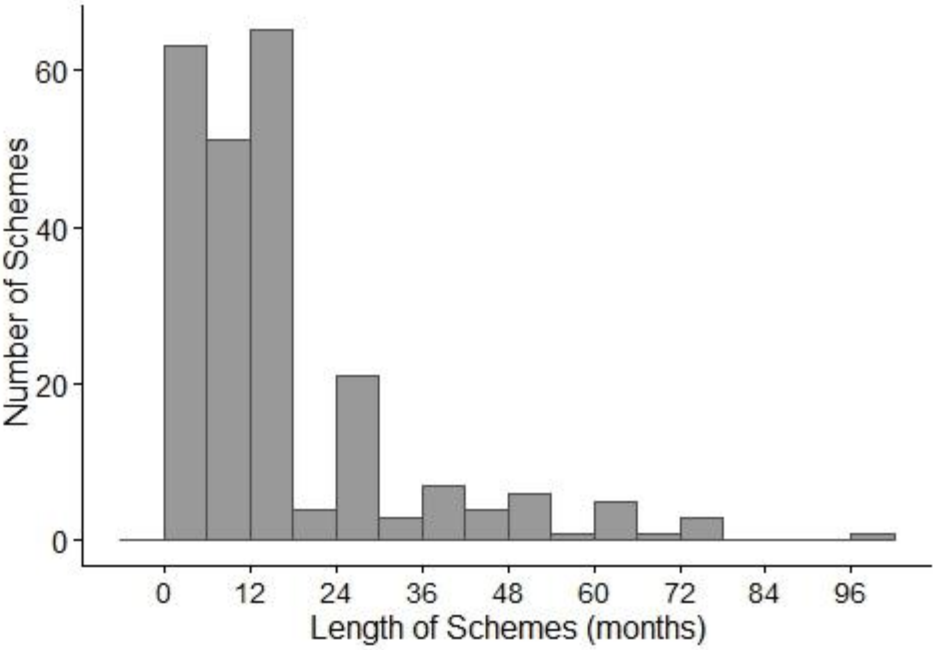


Figure 2-3: Histogram of the length of wood restoration schemes until completion in the NRRI Database. Most projects lasted less than 18 months, but there was a long tail on the distribution, with some projects taking upwards of 5 to 8 years.

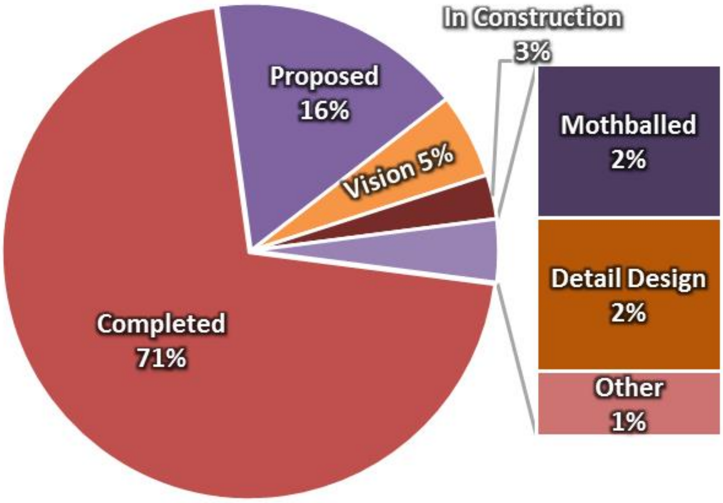


Figure 2-4: Breakdown of restoration progress status for the data on wood restorations obtained from the National River Restoration Inventory. Over 70% of projects were entered after completion, while other projects were in various phases of implementation. All project types were included in analysis.

A strong majority of all wood restorations were located in lowland rivers (84%) with only a small proportion in mid-altitude rivers (14%) and only 1% in upland areas (Figure 2-5). Over half of all restorations were in chalk streams (52%) and a minority in lowland clays (28%), and only a small fraction in gravel bed rivers (16%, Figure 2-6). Catchment land-use was quite mixed, with two-thirds of projects located in rural areas, with nearly half of those schemes on arable land (37%), and a small percentage (4%) in catchments with minimal human use, such as forestry (Figure 2-7). One-third of restoration schemes occurred in more densely populated mixed (10%) and urban (23%) catchments, accounting for primarily mixed urban and residential land-use.

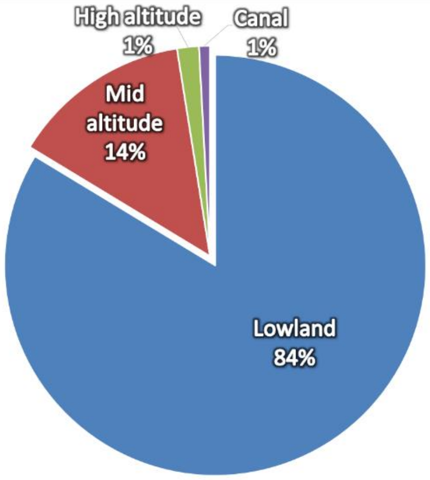


Figure 2-5: River altitude of restoration schemes using large wood in the NRRI database.

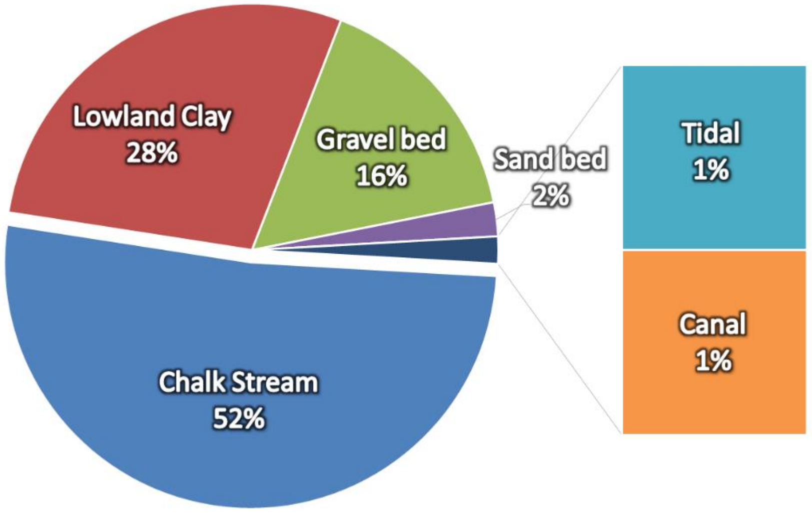


Figure 2-6: Catchment geology for restoration schemes using large wood in the NRRI database.

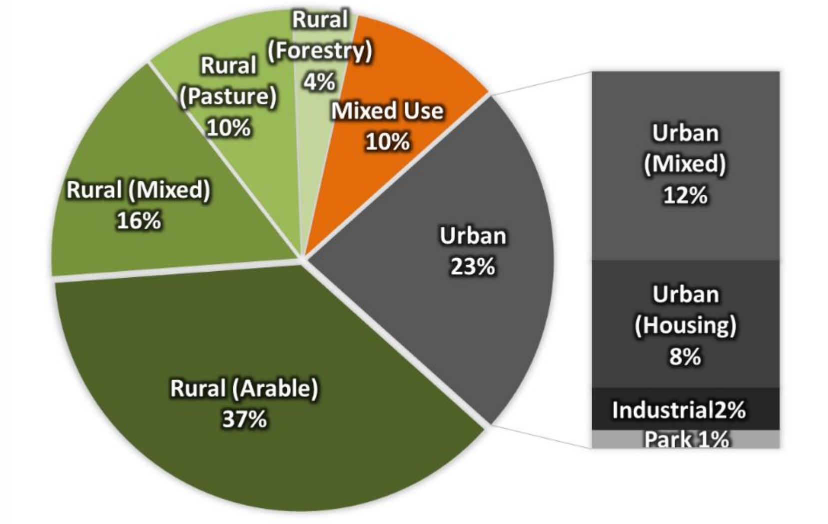


Figure 2-7: Catchment land-use for rivers undergoing wood restorations in the NRRI database. Rural conditions of various types accounted for nearly two-thirds of all restoration land-use.

The River Background input-field was queried for commonly used terms to identify the key environmental issues affecting these river reaches before project implementation. The most commonly cited issues were several closely related problems: channel over-enlargement, flood engineering and dredging, and fine sediment problems, often associated with agriculture/livestock (Figure 2-8).

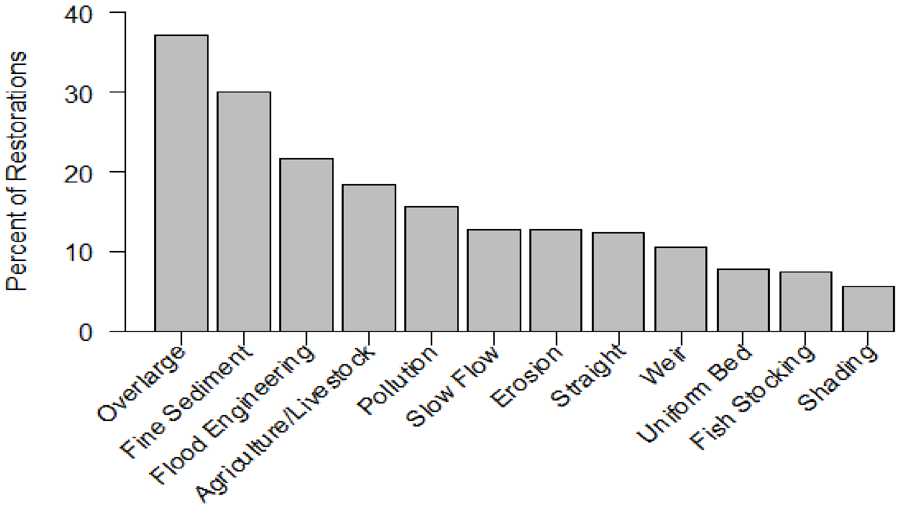


Figure 2-8: The main background conditions and environmental issues identified by the wood restoration schemes in the NRRI. Results are from a textual query of the River Background custom text input-field, with relevant and overlapping terms pooled (see text for more details).

The main project motivations were to create habitat and improve fisheries (Figure 2-9), with over half of all wood schemes concurrently listing both habitat creation and fisheries. To accomplish these project aims, 70% of projects indicated using a "current deflector or concentrator to create habitat and flow diversity" as the primary or secondary restoration technique of the scheme (Figure 2-10). The detailed textual query of text-entry input fields (*e.g.* Project Background and Techniques) was used to obtain information on project specifics. This search revealed that nearly twice as many projects made explicit reference to using deflectors and groynes (44%) than using more complex large wood (22.5%) in the project scheme.

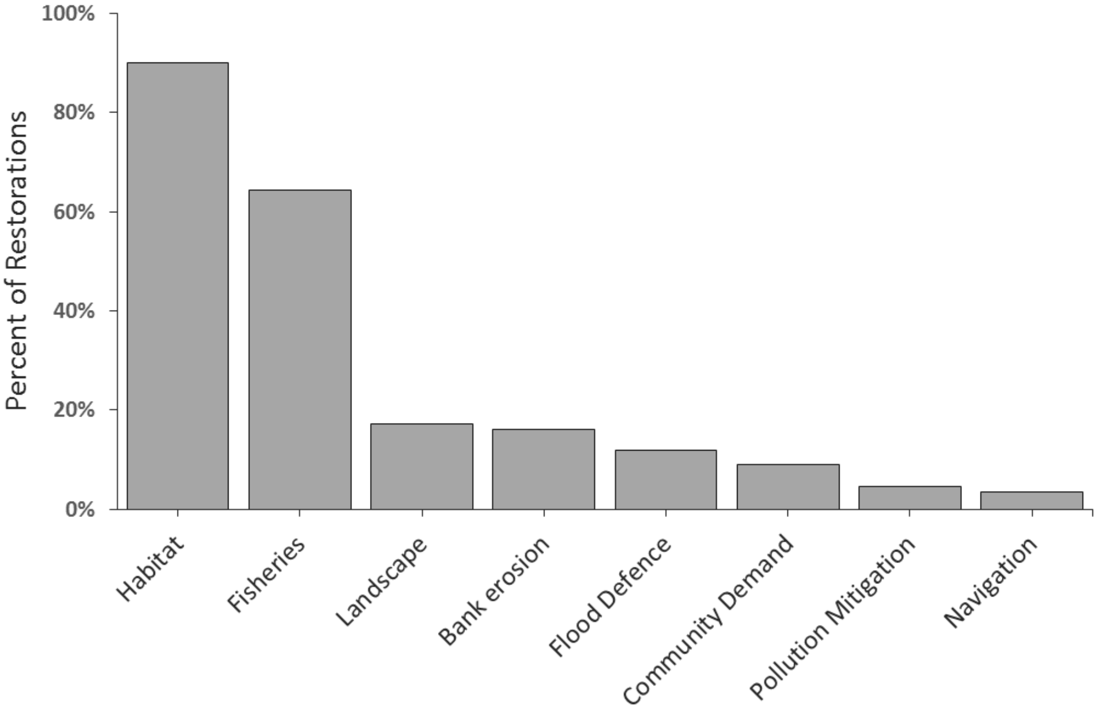


Figure 2-9: The percent of wood restoration projects citing the 8 most commonly listed restoration objectives

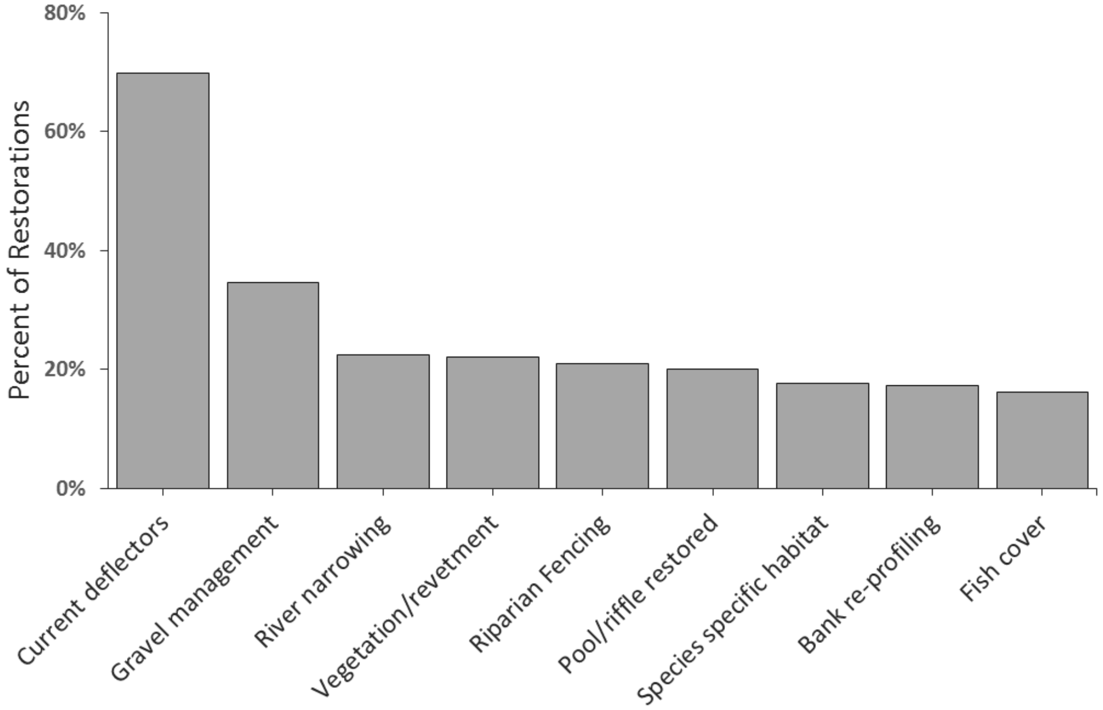


Figure 2-10: Ten most common restoration techniques used in wood restoration projects from the NRRI database. As these selections were not mutually exclusive, multiple techniques could be indicated in the same restoration scheme.

Besides creating current deflectors, wood restoration schemes focused on the rehabilitation of other watercourse features (Figure 2-10), including gravel creation/management (35%), river narrowing (22%), establishment of vegetation for structure/revetment (22%), riparian fencing (20%), and restoration of pool/riffle sequences (21%). In 15% of projects, water table levels were raised by vegetation management to increase flooding, and structures were removed to allow fish passage in 11% of all projects (data not shown).

A wide range of funding and non-funding partners, totalling more than 30 organizations across both private and public sectors, were involved in these restoration schemes. However, nearly 70% of projects obtained funding through the Environment Agency, and almost 30% through local fishing organizations, while landowners, local councils, Heritage Lottery, and the Wildlife, Wild Trout, and National Trusts also provided more limited support (Figure 2-11). Several Universities were involved as non-funding partners in some restoration schemes, but in less than 1% of all projects.

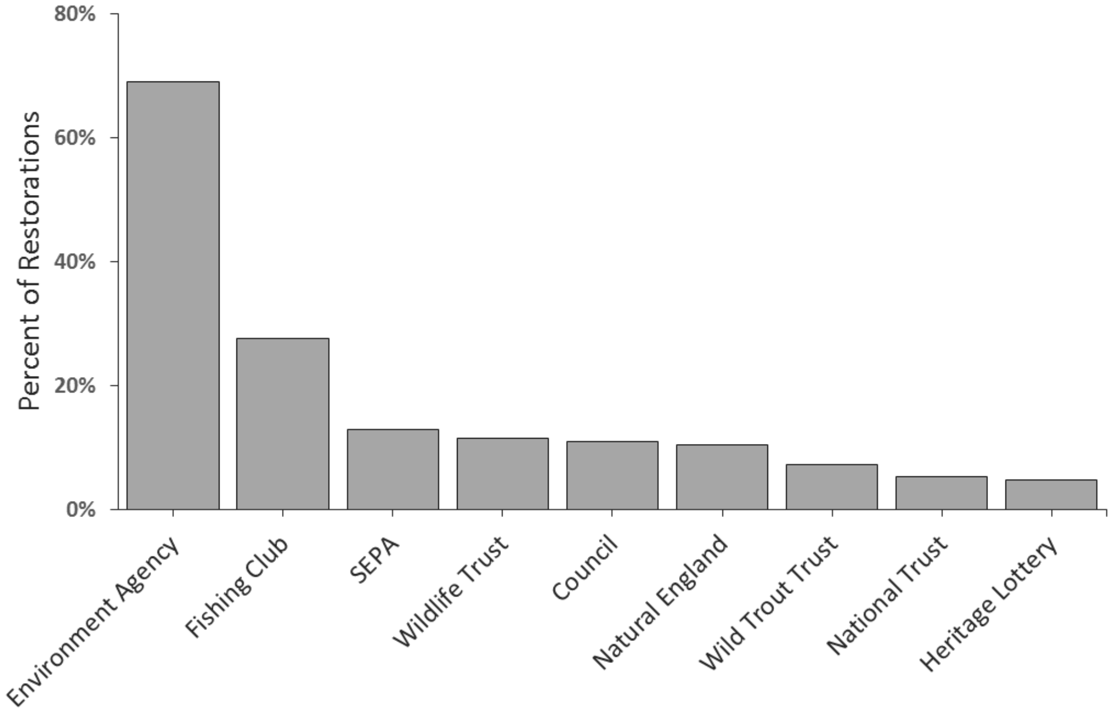


Figure 2-11: The most commonly involved external project partners in river restorations using large wood reported in the National River Restoration Inventory

67% of projects declared project expenditures, with total project costs across all schemes amounting to over £52 million. However, project expenditures were highly variable: the minimum cost was £79 for the restoration of stone ledge and deflector habitat for crayfish, and the maximum was £9 million for a proposed 3,000 hectare restoration of fenland habitat connecting the Woodwalkton Fen and the Holme Fen National Nature Reserves in Cambridgeshire. While the median project cost was £15,000, mean project cost was substantially higher, at £230,000, due to several multi-million pound large-scale projects. A breakdown of expenditures by stage (pre-project design and consultation, contract and supervision of works, and post-project monitoring and appraisal) of all reporting projects indicated that 75% of restoration budgets were spent on implementation of contract works and projects, 17%, on pre-project design, planning, and consultation, and 8% on post-project monitoring and appraisal (Figure 2-12).

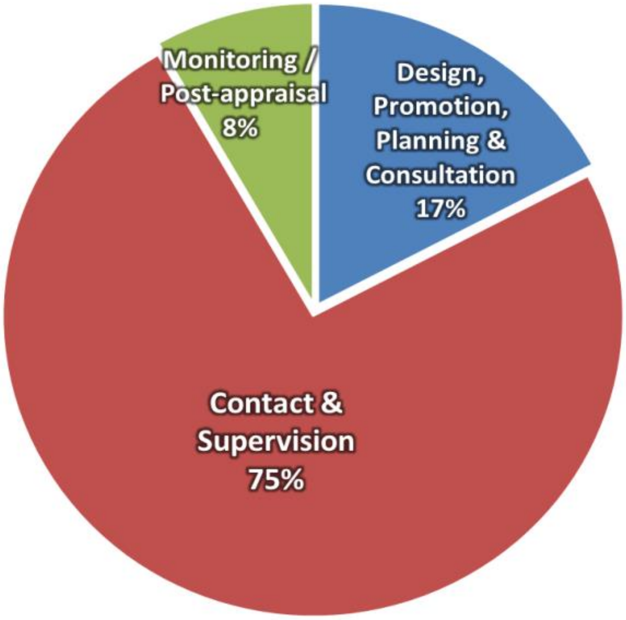


Figure 2-12: Project expenditures through each stage of restoration scheme implementation

Projects that carried out monitoring were significantly more likely to have larger budgets (median: £22,105) compared to projects without monitoring (£10,000; KW: $X^2 = 8.590$, df = 1, P = 0.0034). However, projects that reported any monitoring were a fraction of all completed projects (37%), and varied across geographic regions. Over 65% of all projects under the jurisdiction of the Northern Ireland Environment Agency and 60% of projects under the Scottish Environmental Protection Agency implemented monitoring schemes; meanwhile in England, 50% of projects under EA North West had monitoring, followed by 45% in Anglia and the South West, but in the

South East less than 30% of projects and in the Midlands only 10% were monitored in any form. Monitoring format was also variable, with the most common project assessment using photography (35%), while 18.5% of projects conducted fisheries surveys, 12% completed the visual River Habitat Survey, and only 8% had pre-project data (Figure 2-13). However, only 19% of all projects could provide explicit stated objectives for restoration evaluation.

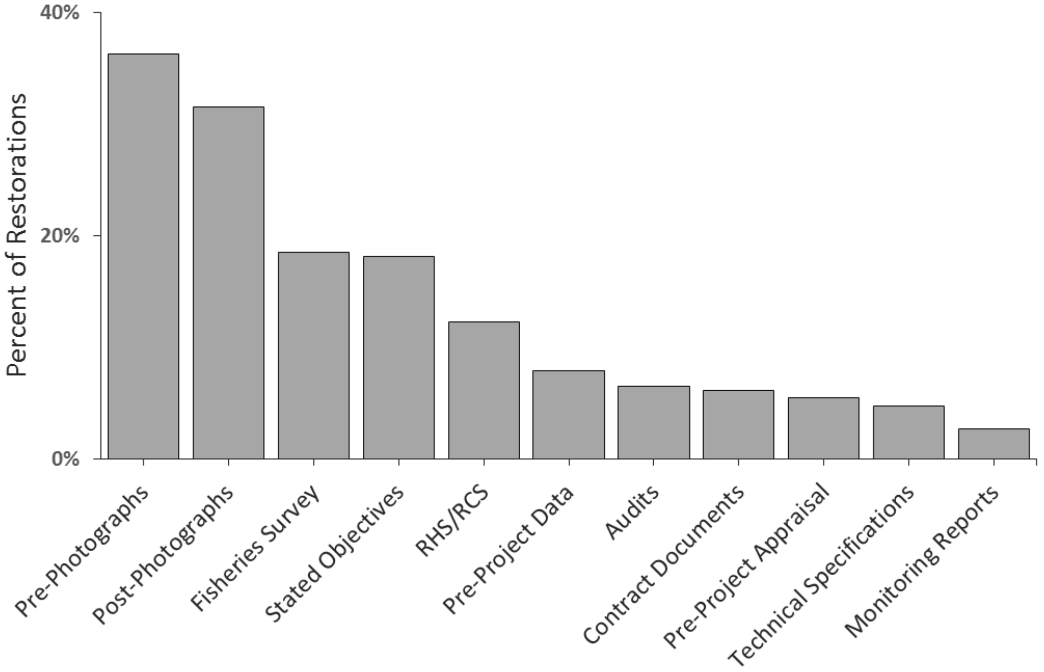


Figure 2-13: The proportion of restoration projects that used individual methods of project assessment and monitoring. RHS/RCS = River Habitat Survey or River Channel Survey.

2.5 Discussion

The survey of the National River Restoration Inventory highlighted the main trends in UK river restorations using large wood. Projects were concentrated in some of the most densely populated areas of the UK, often in the South and East. However, while these rivers were primarily in lowland areas, frequently in chalk rivers, the catchments were predominantly rural, with only a minority of schemes located in urban areas. These reaches had a history of engineering alterations, with over-wide and over-deep channels that had uniform flows and accumulations of fine sediment. Increased fine sediment is known to negatively impact river habitat, particularly within chalk rivers (Walling et al. 2006), resulting in numerous deleterious effects on primary producers, macroinvertebrates, and fisheries (Wood and Armitage 1997, Wood and Armitage 1999). As a result, general project aims were focused on improving degraded habitat and local fisheries. Large wood is known to diversity flows and hence would be expected to flush fine sediments. Wood emplacements were generally combined with other instream techniques, such as gravel enhancement, to directly increase the grain size of gravels on the bed.

Unfortunately, the majority (81%) of restorations schemes lacked testable objectives and a minority (37%) were monitored either before or after project completion, suggesting that the effectiveness of many of these projects has not been legitimately evaluated. The most common assessment method was photography, while quantitative assessment methods (*i.e.* fisheries, macroinvertebrate, or river habitat surveys) were used in less than 20% of projects, and less than 10% of projects collected pre-project data for comparison. Exploration of the qualitative comments revealed that a number of projects claimed restoration success due to anecdotal evidence of more biota when visiting at a later date. This echoes findings from Jähnig et al. (2011) where 40% of river managers admitted that project post-project appraisal was based entirely on gut-feeling, and this aligns UK estimates, at least for wood restoration projects, with findings that suggest 90% of restoration schemes in the USA, Australia, and Europe are only monitored through visual means (Bernhardt et al. 2005, Brooks and Lake 2007). In addition, a recent study comparing all NRRI river restoration projects with RHS scores before and after restoration found no predictable increase in physical habitat heterogeneity with restoration (Smith et al. 2013). As a result, there is limited potential to learn from these project outcomes without effective project assessment, and a stronger feedback between project design and monitoring is needed to learn from previous restoration schemes and inform future best practice (Palmer et al. 2005).

Specifically, restorations aimed at target species or communities should be supported by a robust knowledge of the limiting factors on these ecosystems, and use specific project techniques to address these underlying factors. For example, fine sediment may be limiting trout populations through a population bottleneck on the availability of high-quality redd habitat, but a lack of structural complexity in the channel that limits the amount of cover and niche partitioning may limit populations due to density-dependent factors such increased competition or vulnerability to overfishing or predation. Without knowing these factors, restoration schemes may manipulate habitat that is already in excess or increase population numbers that are already restricted by other constraining factors (Armstrong et al. 2003).

In general, wood restorations in the UK were more likely to use deflector/groynes than structurally complex LW jams. The choice of deflectors may be due to flooding concerns, as wood with limited structural complexity is expected to be less likely to snag drifting matter and contribute to local flooding. However, as many of these restorations occurred in rural catchments, more complex wood, even if it did have an effect on local overbank flooding, could help reduce overall flood risk downstream, especially vulnerable urban areas, within the UK "Making Space for Water" policy (Samuels et al. 2006). While this would require coordination with larger national agencies on a catchment perspective of flood risk, the Environment Agency and the Scottish Environmental Protection Agency were already involved with over 80% of wood restoration schemes, and as a result, the logistical network to connect wood restorations with this flood policy initiative is already established, but only needs to be implemented.

In conclusion, the focus on flow deflectors and simpler structures instead of more complex large wood accumulations may have profound effects on the physical habitat and ecological outcomes created by these river restorations. The differences between deflectors, large wood used in restorations, and natural wood jams were explored in Chapter 3.

Chapter 3

The variability of wood structural diversity and its effect on physical habitat conditions

3.1 Background

The management decision to preferentially use wood deflectors, rather than natural large wood pieces, as discovered in Chapter 2, may have implications for the outcome of wood restorations. While wood has been associated with a range of physical habitat attributes in natural environments (Gurnell et al. 2002), there may be differences in the way in which wood is re-introduced to rivers in restorations, with important consequences for habitat heterogeneity.

Flooding concerns may dissuade river managers from using large and complex wood structures which may be more likely to snag drifting debris and further increase jam volume, particularly since jam volume and complexity are the predominant factor in the hydraulic effect of wood (Manners et al. 2007, Manners and Doyle 2008). Restorations may fix wood into the riverbed at set positions, limiting the potential for wood mobilization and for wood to snag on downstream infrastructure and cause flooding (Kail and Hering 2005). These fixed positions may differ from patterns observed in naturally occuring wood, but orientation, buoyancy, and burial of wood in the stream channel are known to have an important influence on hydraulics, sediment dynamics, and the presence and frequency of channel mesohabitats (Gurnell et al. 1995, Gurnell and Sweet 1998, Gurnell et al. 2002). Therefore, any unaccounted difference between the studied effects of wood in a reference conditions and when implemented in a river restoration may lead to the overestimation of the predicted effect of wood in restorations on habitat heterogeneity. In addition, the levels of variability associated with restored wood jams are relatively little studied, especially for those lowland rivers highlighted by the survey of the National River Restoration Inventory (Chapter 2), and may differ from the variability in characteristics of natural wood. Thus, it is important to characterize the actual habitat heterogeneity associated with wood variability in its different forms across both natural and restored rivers.

3.2 Research Aims

Using field data collected from four rivers in lowland England, this research chapter examines the range and variability in large wood features and their associated mesohabitat conditions (depth, velocity, and sediment characteristic) across a gradient of wood management (near-natural/‘reference’ to restored wood). In particular, this chapter aims to explore the variability in physical habitat conditions to test two primary hypotheses: (1) that structural complexity of wood jams will decrease along a management gradient from near-natural/reference reaches, to heavily impacted sites with restored wood; and (2) there is a positive relationship between wood jam complexity and mesohabitat heterogeneity along this gradient.

3.3 Methods

3.3.1 Field Sites

Four field sites were chosen in regions of the United Kingdom that had a high number of restorations as identified in the NRRI survey of Chapter 2: Norfolk, Midlands, and Southern England (Figure 3-1, Table 3-1). These rivers provide a gradient of increasing levels of wood management and human intervention: unmanaged channel and riparian zone with naturally occurring large wood jams (River Dene); low levels of management in the channel and riparian zone with naturally occurring large wood jams (Highland Water); a wooded river corridor with restored large wood in an agricultural catchment (River Bure); and an urban river with a heavily modified river corridor restored using simple deflector-style wood placements (River Blackwater). All sampling was conducted in July and August 2012.

The River Dene flows through predominantly agricultural lands in Warwickshire, with the study reach located on private land that has lacked riparian management for over 60 years. Natural England has designated part of the site, a butterfly meadow set back 20 m from the river, as a site of special scientific interest (SSSI). There is some grazing land-use by sheep, but the livestock are restricted from the riverbank by fencing and a wooded riparian buffer 2 – 5 m wide. Bankside LW inputs are high throughout the reach and the channel contains notably large and complex jam accumulations. This unmanaged site, in an agricultural catchment with high fine sediment accumulations, provides a rare and ideal baseline comparison for sites with high levels of management/disturbance to the riparian corridor and river channel.

Figure 3-1: The location of the four study sites chosen for the fieldwork component of this project. The rivers were across a gradient of management intensity from the Dene to the Blackwater (see text for more details).

Table 3-1: Field location study sites, UK Grid Reference, and other site information of the four rivers selected for examination of LW jams. The Blackwater contained two studied reaches (restoration/natural) and data the paired reaches were listed in respective order. Channel width measurements are means ± 1 standard error. Geology data obtained from UK Geological Survey online viewer (1:50,000; www.bgs.ac.uk/discoveringGeology/geologyOfBritain/viewer.html).Q50 was based on annual flow data from the previous 10 years, obtained from the National Flow Archive, and flow exceedance was determined based on flow data from the sampling date (averaged over entire sampling week). Catchment and wood management characteristics were determined by visual surveys and personal communication with land managers. GQA data was the most recent data available from the Environment Agency (2009). Biology and chemistry grades are ranked from A through E. Nitrate and phosphate grades are ranked 1 through 6. Data was unavailable for Highland Water.

	Location	Channel Width (m)	Geology	Q50 ($m^3 s^{-1}$)	Flow Exceedance at Sampling	Catchment Land-Use	Wood Management	Gradient	Bio. GQA Grade	Chem. GQA Grade	NO_3^- GQA Grade	PO_4^+ GQA Grade
Dene	Warwickshire, UK GR: SP 3068 5059	5.9 ± 0.2	Mudstone/ Limestone	0.264	31.67%	Rural (arable/ pasture)	Naturally wood. Unmanaged, minimal grazing	2.07‰	A	B	4	5
Highland Water	New Forest NP, UK GR: SU 2706 0731	3.0 ± 0.4	Bracklesham and Barton: sand, silt, and clay	0.425	32.44%	Rural (forest)	Natural wood. Min. management, heavy grazing	2.72‰	n/a	n/a	n/a	n/a
Bure	Norfolk, UK GR: TG 1613 2995	9.2 ± 0.7	Wroxham Crag: sand and gravel	1.01	81.71%	Rural (arable)	Restored wood. Felled riparian trees, little fixing	1.17‰	A	A	5	2
Blackwater	Surrey, UK GR: SU 8629 5861	8.6 ± 0.4/ 7.7 ± 0.2	Bracklesham and Barton: sand, silt, and clay	0.407	89.09%	Urban (mixed-use)	Restored wood. Heavy management. Clean trunks, fixed to river bed	0.93‰	D/C	B/C	6/4	5/5

The Highland Water, part of the New Forest National Park in Hampshire, has experienced minimal management of in-channel large wood over the past 60 years, although until recently, large wood accumulations were removed for flood prevention. The catchment landcover is a combination of mixed-deciduous forest and heathland, and while the majority of the riparian zone is forested, there is heavy understory grazing by free-roaming and privately owned pigs, deer, and horses. Bedrock geology is Barton clay and Chiama sand formation with overlying alluvium and river terrace deposits (British Geological Survey 1:50,000) with acidic soils. This river has been the subject of a number of studies of large wood in lowland river systems (Gregory et al. 1994, Gurnell et al. 2002, Gurnell et al. 2005, Millington and Sear 2007, Osei et al. 2015).

The River Bure is one of three main rivers that drain the agricultural Norfolk Broadlands and flows through a 600 m wooded section of the National Trust Blickling Estate in Aylsham, Norfolk. According to the NRRI database, the river has a history of over-widening and dredging, with persistent fine-sediment problems. Large wood was previously removed from the channel, but in 2008 and 2010, the Site Manager undertook a minimal-impact, inexpensive restoration (£500) to address the issue of uniform flows and high sediment accumulation. Since machinery could not access the site, a chainsaw was used to fell riparian trees into the river, and a limited number of wood pieces were fixed to the bed to prevent downstream mobility.

The River Blackwater is a small eutrophic river running through the town of Farnborough in Surrey. The main study location was “Hawley Meadows,” a public park with a riparian area grazed by cattle that have unrestricted bankside access. The reach has a history of alterations, outlined within the NRRI database, which consists primarily of gravel extraction works and a diverted channel from construction of the A31 in the 1980s. As a result, much of this section has been straightened and deepened with little flow or bed diversity. An issue with fine sediment has been identified by local interest groups (Environment Agency, local anglers associations), and in the growing season, the river is predominantly covered by submerged and emergent macrophytes. In this reach, the Environment Agency has implemented a large wood restoration project by introducing deflectors (tree trunks) and fixing them to the riverbed with metal stakes. Approximately 3.5 km downriver, the river meanders along Moor Green Lakes and is shaded by riparian woodland. In this reach, there is reduced wood management and the reach contains a limited amount of naturally accumulated wood. In the Blackwater, wood was identified according to means of introduction into the river channel (restored and natural) which generally corresponded to the restored Hawley Meadows and "natural" Moor Green Lakes site respectively, with the exception of one restored jam in the "natural" Moor Green Lakes site and one natural jam in the restored Hawley Meadows site.

3.3.2 Wood Jam Structural Survey

The number of wood jams present in the channel was variable in each river, and therefore the number of jams surveyed at each location varied according to the number of jams present: 10 jams were surveyed for wood jam characteristics in the Blackwater and the Dene, 12 in the Highland Water, and 13 in the Bure. The wood survey method (Table 3-1) was adapted from Gurnell (*personal communication*) and included additional survey metrics outlined in Wohl et al. (2010). The method considers touching wood pieces to be part of the same functional jam unit. The survey considers many factors that may affect the morphological, hydraulic, and ecological impacts of the wood jam, including species, anchorage, and associated jam mesohabitats (Table 3-1). The primary wood jam grouping was into jam class (Gregory et al. 1985): "partial jams" which only partially span the channel, "complete jams" which span the channel but do not cause a step in water level, and "active jams" which completely span the channel and are sufficiently impermeable that it induces an active step in water level under base-flow conditions (Figure 3-2). Overall complexity was also considered in the median size and size distribution of wood pieces in the jam, as well as overall porosity of jam structure, which included both wood and associated vegetation growing in and on the jam within bankfull height. Jam volumes were calculated by a method adapted from Gurnell et al. (2000), whereby the smallest rectangular box (m^3) into which the entire wood jam (contained within the bankfull width) would fit was multiplied by the jam density (inverse of total jam porosity).

Figure 3-2: Examples of partial jams (a), complete jams (b), and active jams (c) from the River Dene, Warwickshire, England. Partial jams are single pieces of large wood that do not obstruct the whole channel. Complete jams span the channel width, but do not obstruct the flow of water enough to cause damming and a step in water level. Active jams span the entire channel width and have a damming effect on flow, causing a noticeable step in the water level. Pictures are looking downriver from centre of the channel (a,c) and from the bank (b).

Table 3-1: Jam survey variables adapted from Gurnell (*personal communication*) and Wohl et al. (2010).

Variable	Ranking	Definition	Morphological Importance	Ecological Importance
Jam Class	Categorical	Partial/ complete/ active	Hydraulic effects	Habitat creation, hyporheic exchange
Jam Orientation	Degrees	Central axis compared to river flow	Flow deflection	Habitat creation, flow refugia
Stability/ Anchorage	Categorical	Bracing or burial of jam	Stability and function	Erosion, disturbance regime
Flow Deflection	Degrees	Direction of flow from central line of channel	Sediment sorting, silt cleaning	Habitat creation
Wood 'Type'	Categorical	Living/dead Whole tree/pieces	Stability	Palatability, surface texture
Root Wad	Yes/No	Presence of root wad	Stability	Habitat creation, recruitment process
Tree Species	Categorical	Genus	LW Recruitment, retention	Decay rates, palatability, surface texture
Decay Status	Ordinal (1-5)	Schuett–Hames et al 1999	Relative age and stability	Palatability, refugia, surface texture
No of Key Pieces	Integer	# of pieces integral to entire jam stability	Stability, morphological effects, hydraulic effects	Flow refugia, flow mosaic
Median/Max Piece Size	Continuous	Diameter, length	Flow effects, recruitment process	Habitat creation, scale of mosaic
Size/distribution of wood pieces	Percentage	% of jam within certain diameter size classes	Recruitment, micro-scale habitat conditions	Flow mosaic, refugia, habitat creation
Porosity	Percentage	% of space occupied by jam below bankfull	Drag coefficient, hydraulic resistance	Flow refugia, micro-scale habitat creation
Submergence	Percentage	% of jam submerged of total jam volume	Drag coefficient, hydraulic resistance	Availability of habitat
Jam-associated mesohabitats	Yes/No presence of mesohabitat/ biotope types	# of substrate, flow-type, and channel features and vegetation surrounding jam, adapted from RHS (Raven et al. 1996)	Sediment storage, biotopes, transport	Habitat creation

3.3.3 Jam-Associated Flows

In each river, a minimum of five jams (5 in the Dene, 8 in the Highland Water, 8 in the Bure, and 7 in the Blackwater) from the total surveyed jams were sub-sampled for jam-associated flows. In and around each jam, distinct flow biotopes were visually classified by the River Habitat Survey (*i.e.* no perceptible flow, smooth boundary turbulent, rippled flow, chute flow, concentrated flows, pools, riffles) and sampled for 30 s with a FlowTracker Handheld-ADV (Sontek, San Diego, California, USA), for near turbulent flow velocity (1 s^{-1}) in 3-dimensions at 20% (near-surface), 60% (mid-column), and 80 % of total depth (near-bed). This averaged to approximately 8 (range: 4 – 12 positions) sampled flow positions per jam in each of the studied rivers, at 3 depths, totalling on average 24 (range: 12 – 36) velocity vectors per jam ("jam flow"). Flow measurements were also taken at 10 equal points at cross-sections ~5 – 10 m upstream and downstream of each measured jam to examine the normal range of river flows outside of the direct impact of the jams ("river flow"). Water depth was also measured at all jam and river flow sampling locations and evaluated for the minimum, median, and max (pool) depths.

As flow concentration was a key project aim identified in the NRRI for using large wood and deflectors, the degree of flow concentration alongside each jam was calculated as the percent increase from average river velocity to the maximum flow velocity detected alongside each jam. This flow concentration was examined for both the total velocity vectors (X, Y, and Z components), as well as the near-bed (80% of total depth) flow concentration into the bed (Z component). The standard deviation of 1 Hz (1 s^{-1}) measurements over 30 s was used a proxy for near-turbulent fluctuations, referred to as flow variability.

3.3.4 Jam Sediment Characterization

At each surveyed LW jam, surficial sediment cores were taken using a 47-mm diameter Perspex core from 4 mesohabitats around the jam (Figure 3-3; upstream, jam-created concentrated flow, within-jam, and downstream sediment plume). In the Highland Water, a fifth mesohabitat was collected – accumulated piles of organic matter and small woody debris, which were not present in the other rivers. These debris piles were partially submerged along the bank and were likely deposited during high flows or were remnants of previous dislodged jams. Due to the low angle of jam orientation in the River Bure, concentrated flows coincided with the upstream location and only three locations were sampled (downstream, within-jam, and concentrated flow). In the Bure, a series of distinct mesohabitats apart from the influence of wood jams were present (bare channel gravels, submerged macrophytes, emergent macrophytes) that were not distinctly separate mesohabitats in the other three rivers, and were sampled for comparison with jam-associated habitats. Sediment samples were kept cold and transported back to the laboratory within 24 hours, stored at -20°C, and analysed within 30 days. After thawing, all samples were dried at 100°C overnight. Effective particle size distribution smaller than gravel (< 2 mm) was determined by examining a subsample with a LS100 Beckman Coulter Counter (Beckman Coulter, Inc., High Wycombe, United Kingdom). Particle size distribution $\geq$ 2 mm was sieved by weight, and total sediment size categories were combined and analysed using Gradistat v. 8.0 to determine D50 and proportion of gravel (32 – 2 mm), sand (2 mm – 63 µm), and silt (< 32 µm), as well as clay (<2 µm), a subcategory of silt (Blott and Pye 2001).

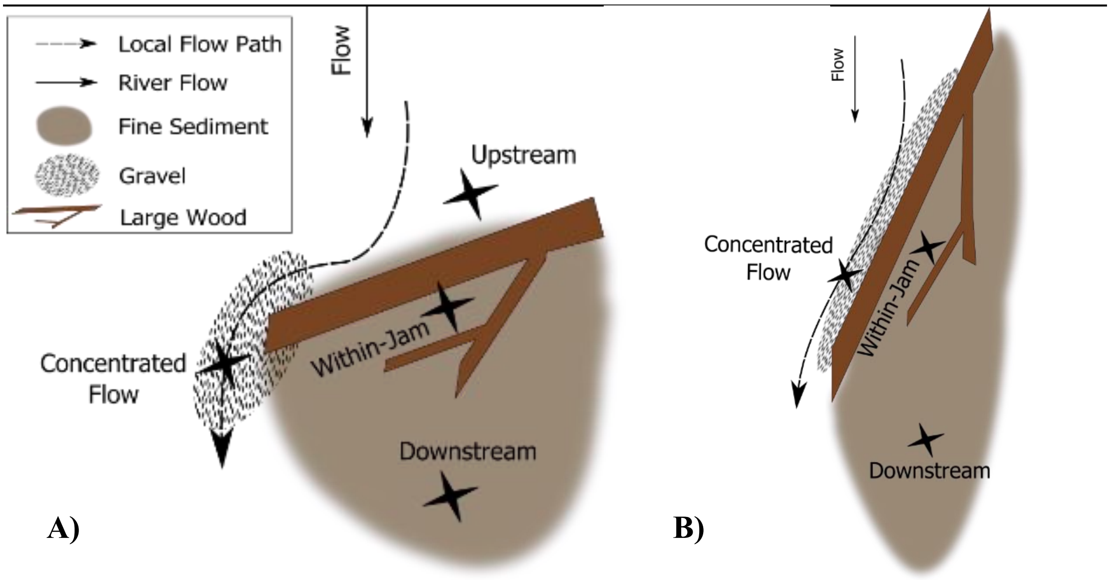


Figure 3-3: Sediment mesohabitat sampling design at the study locations. A) indicates the four locations sampled in the Dene, Blackwater, and Highland Water corresponding to upstream, within-jam, downstream, and concentrated flow locations. B) indicates how in the high-angle jams of the Bure, the upstream sampling location was subsumed within the concentrated flow location.

Data on ingressed sediments (fine sediments in gravel interstitial spaces) were determined by using a modified method of Lambert and Walling (1988). A 50-cm diameter metal core was used to isolate the gravel bed at each jam, water depth was measured, and a metal rod was used to disturb the bed at a depth of ~5 cm for 10 s to suspend ingressed sediments. The disturbed water column was then immediately subsampled using a 500 mL bottle, which was kept cold and filtered in the lab onto a Whatman 47mm GF/F filter (GE Healthcare Life Sciences, Buckinghamshire, UK). Filters containing ingressed sediments were dried overnight at 100°C overnight, which was used to back-calculate ingressed bed sediment storage, and used for analysis of organic content. Organic matter content for both surficial and ingressed sediments was calculated via ignition in a muffle furnace at 550°C for 4 h.

A 1m-long, 5-mm wide metal pin was used to survey fine sediment depths at all identified jam mesohabitats and flow biotopes sampled for flow data (ranging between 4 – 12 points, average 8 per jam per river). These depths were used to quantify the depth of surficial sediment and fine sediment accumulations around the LW and in the channel (Lisle and Hilton 1992).

3.3.5 Jam Statistical Analysis

Wood survey, water depth and velocity, and sediment measurements were analysed using a Kruskal-Wallis test in R due to heteroscedasticity in variances across rivers (R Core Team 2014, Vienna, Austria). Post-hoc tests were performed using pairwise Mann-Whitney U tests with Holm adjusted P values for multiple tests. A Principal Components Analysis (PCA) was conducted on all jam structural attributes using the base function princomp. Convex hulls calculated using the function ordihull in R Package vegan, were used as a multidimensional measure for effective structural habitat heterogeneity created by wood, as they have been previously used as a multidimensional measure of effective niche-usage for ecological communities (Cornwell et al. 2006). Lastly, a linear regression in R was used to examine if ingressed sediment properties responded to the maximum near-bed velocity vector and river identity.

3.4 Results

3.4.1 Wood Jam Structural Characteristics

Wood decay prevented the identification of tree species in most jams (~60%), but when identifiable jams predominantly comprised *Alnus glutinosa*. The proportion of different jam classes (partial, complete, active) varied by river: all three jam types were present in both the Dene and Highland Water, complete and partial jams in the Bure, and only partial jams in the Blackwater (Figure 3-4). Active jams accounted for a disproportionate amount of the total jam volume present in the channel compared to their frequency; active jams in the Dene, which were 30% of all jams, accounted for >80% of total jam volume, and in the Highland Water, active jams were 17% of all jams but accounted for 48% of total jam volume (Figure 3-4). Average jam volumes were highest in the least-managed River Dene and lowest in the Blackwater, which had the greatest amount of wood management and human intervention (Table 3-2).

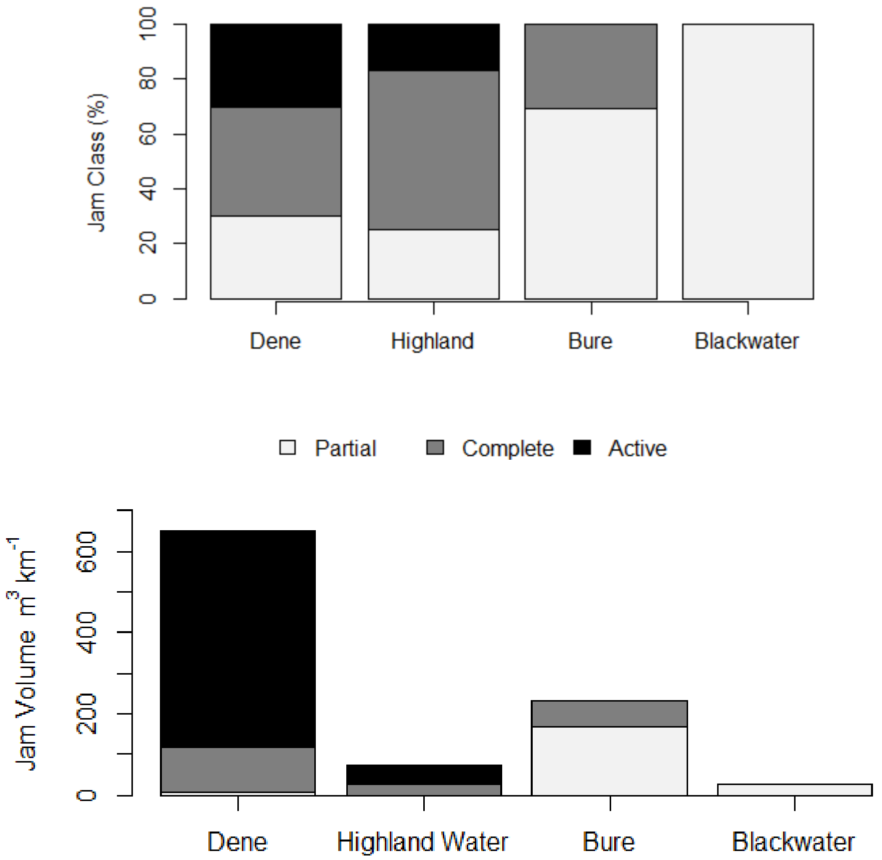


Figure 3-4: The variation in jam classes within the four study rivers and volume of wood accumulation in the bankfull width per km of river, separated by jam class type. Despite being active jams being a relatively small percentage of total jams in the Dene and Highland Water, they contained a disproportionate degree of jam volume found in the river. Active, complete, and partial jams were found in the Dene and Highland Water, while the restored large wood in the Bure contained only partial and complete jams, and the Blackwater contained only partial jams. Partial = jams which only partially span the channel width. Complete = jams which span the complete channel width, but cause no step in water level Active = active jams which span the entire channel width and cause a step in water level.

Table 3-2: Table of selected jam structural variables. Values are mean ± 1 standard error. A key piece is defined as a structurally integral piece for the stability of the jam. Mean decay status is based on an ordinal decay ranking between 1-5 from Schuett-Hames et al. (1999). Orientation and deflection the degree of wood orientation or flow deflection off the centre line of channel flow.

	# of Jams Surveyed (N)	Avg. # of Key Pieces	Length of Key Pieces (m)	Max Key Piece Diameter (cm)	Median Key Piece Diameter (cm)	Mean Key Piece Diameter (cm)	Mean Decay Status	Presence of Root Wad (%)	Orientation °	Deflection°	Mean Jam Volume (m^3)	Jam Density (m^3 km^{-1})
Dene	10	2.2 ± 0.4	6.3 ± 0.5	129 ± 25	52 ± 17	55 ± 17	2.9 ± 0.3	10	69 ± 12	28 ± 10	16.20 ± 6.50	648.0
Highland Water	12	1.8 ± 0.3	8.8 ± 1.6	113 ± 22	45 ± 8	41 ± 8	2.8 ± 0.2	16	68 ± 8	33 ± 8	2.76 ± 1.71	73.7
Bure	13	2.3 ± 0.3	11.9 ± 1.1	64 ± 10	43 ± 8	42 ± 8	2.1 ± 0.3	0	29 ± 8	21 ± 4	3.93 ± 0.63	208.7
Blackwater												
Natural	5	1.8 ± 0.4	6.4 ± 1.5	64 ± 12	53 ± 10	45 ± 11	1.6 ± 0.4	20	68 ± 11	23 ± 13	0.96 ± 0.48	17.3
Restored	5	1.2 ± 0.2	5.9 ± 0.8	73 ± 12	70 ± 14	56 ± 16	1.4 ± 0.3	0	65 ± 8	9 ± 9	1.65 ± 0.78	33.1

Jams on average had 2 structurally-important pieces, with the exception of restored jams in the Blackwater which were primarily formed of a single log (Table 3-2). The mean length of key pieces was smallest in the restored deflectors of the Blackwater (Mean ± 1 SE: 5.9 ± 0.8), and longest in the Bure (11.9 ± 1.1), where mature trees were felled directly into the river for the restoration. While the mean diameter of jam wood pieces were relatively similar across rivers (Range: 41 – 56), the maximum wood diameter in each jam was greatest in the natural jams found in the Dene and Highland Water (129 ± 25, 113 ± 22 respectively; Table 3-2). Average wood decay class was greatest in the rivers with natural wood, the Dene and Highland Water (~3; significant bark loss and possible wood loss, starting to decompose), decreased with large wood restoration in the Bure (~2; discoloration and some bark loss), and showed little noticeable decay in the deflectors in the Blackwater (~1, all bark intact, little to no discoloration or decay evident; Table 3-2).

Jam porosity, a measure of space within the jam structure accessible to water and macroinvertebrates, was highly variable by jam in most rivers, but was significantly lower in the highly-managed Blackwater reflecting the solid, single tree-trunk deflectors (KW: $X^2 = 12.5$, df = 4, $P = 0.014$; Figure 3-5). The variability in porosity in the Dene and Highland Water was directly related to the jam classes present, as active jams were significantly more porous than both complete and partial jams (KW: $X^2 = 17.03$, df = 2, $P < 0.001$). In addition, jams in the restored reach of the Blackwater were most likely to be submerged (KW: $X^2 = 10.48$, df = 4, $P = 0.033$), with restored jams in the Blackwater almost completely submerged, while no natural jams in the Dene or Highland Water were more than 50% submerged (Figure 3-6). Visible water deflection, or the change in the lateral main flow pattern around each jam compared to the central line of the river, was extremely variable across jam, with the natural jams in the Dene and Highland Water showed the greatest variability, with some jams causing nearly a 90° deflection, while the restored jams in the Blackwater had little to no detectable effect on laterally deflecting flow. However these changes in flow deflection were non-significant (KW: $X^2 = 3.56$, df = 4, $P = 0.469$; Figure 3-7).

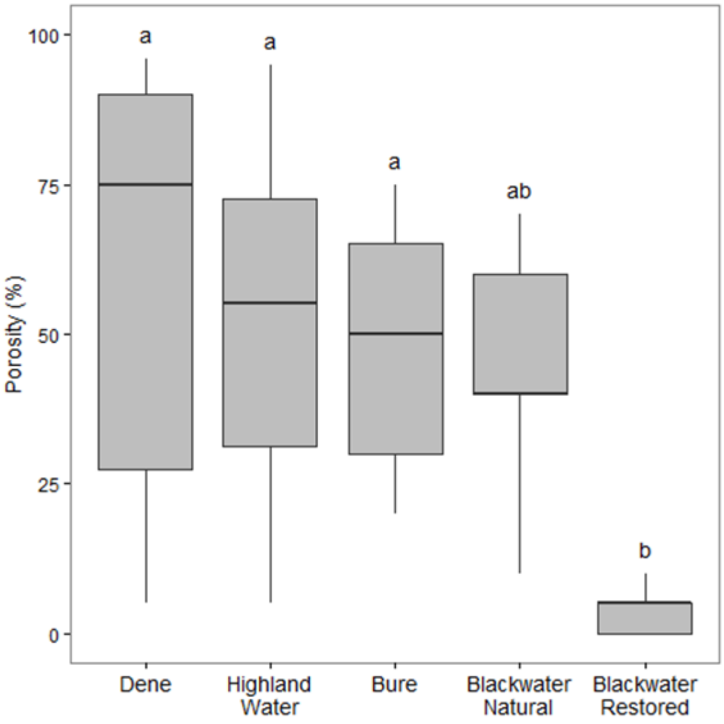


Figure 3-5: The percent of jam porosity in each of the study locations. Porosity and its variability has a general trend of decreasing with increasing management. Centre line indicates median, while box limits indicate 25 and 75% quartile ranges, with whiskers indicating 0-100% quartile range. Letters indicate significant differences at $P < 0.05$ according to post-hoc Mann-Whitney U tests with holm correction.

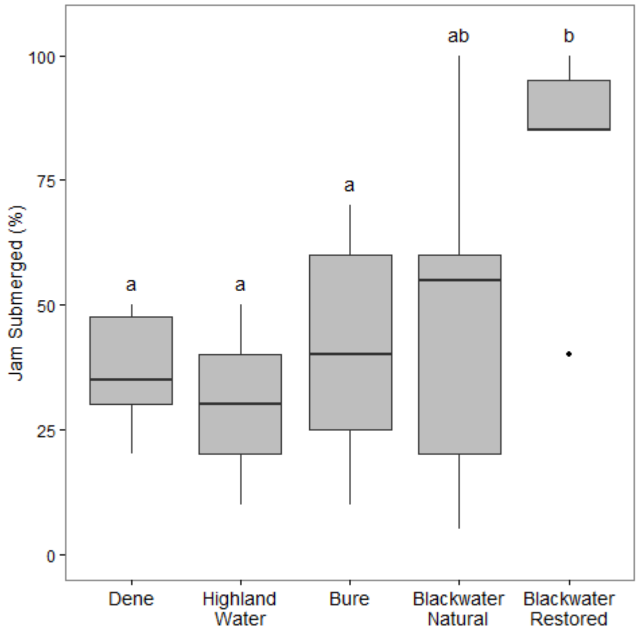


Figure 3-6: The percent of jam submerged in each of the study locations. Submergence has the general trend of increasing with increasing management. Centre line indicates median, while box limits indicate 25 and 75% quartile ranges, with whiskers indicating 0-100% quartile range. Letters indicate significant differences at P < 0.05 according to post-hoc Mann-Whitney U tests with holm correction.

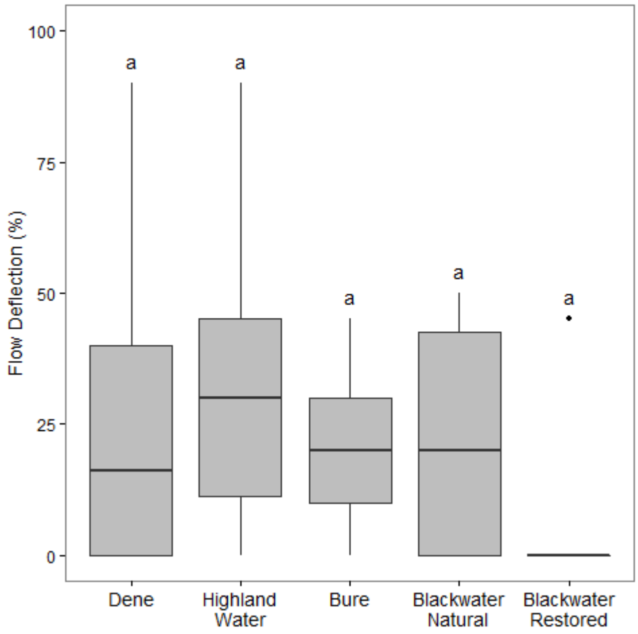


Figure 3-7: Visible deflection by the jam of water flow off the river centre-line in each study reach. Centre line indicates median, while box limits indicate 25 and 75% quartile ranges, with whiskers indicating 0-100% quartile range. Letters indicate significant differences at P < 0.05 according to post-hoc Mann-Whitney U tests with holm correction.

The presence of specific mesohabitats was recorded at each jam in each river, ranging from 3.4 ± 0.8 mesohabitats per jam in the natural jams of the Blackwater through 5.1 ± 0.9 in the Dene (Table 3-3). Backwater mesohabitats, where water was able to pool and recirculate out of the main line of flow, were common in both the Dene and Bure, but less common in the Highland Water, likely do to the narrower river width. Macrophytes were abundant in both the Bure and natural reach of the Blackwater, but not in more natural sites of the Dene and Highland Water, which had denser canopy cover. Gravel was present at a majority of jams in all rivers, but accumulations of debris and coarse particulate organic matter was only present alongside natural wood in the Dene and Highland Water. However, the total number of these mesohabitats and channel features were not significantly different across rivers (KW: $X^2 = 3.99$, df = 4, P = 0.407)

Table 3-3: Total number of jam-associated mesohabitats and percentage of jams in each reach that had the most common nearby associated mesohabitat.

	# of Associated Mesohabitats	Visible Water Deflection	Backwater	Submerged Macrophytes	Emergent Macrophytes	Gravel	Fine Debris
Dene	5.1 ± 0.9	90%	40%	0%	10%	50%	20%
Highland Water	4.8 ± 0.4	75%	16%	0%	0%	83%	42%
Bure	3.5 ± 0.6	46%	46%	53%	62%	62%	0%
Blackwater							
Restored	3.4 ± 0.8	60%	0	40%	80%	80%	0%
Natural	3.8 ± 0.7	80%	0	0%	20%	60%	0%

A PCA of all jam structural variables across the four studied rivers was conducted, indicating the effective structural heterogeneity covered by present large wood. Principal Components 1 and 2 had eigenvalues greater than 1.5 and together explained 67.5% of the variability, and were therefore explored, highlighting key differences between the restored deflectors of the Blackwater and wood in the other three rivers (Figure 3-8A). Foremost, the restored deflectors in the Blackwater were located away from the jams found in the Dene, Highland Water, Bure, and even natural jams of the Blackwater, which overlapped in functional space. These other natural and semi-natural jams had a high degree of structural variability, indicated by the area of their convex-hulls within the PCA, while the partial deflector jams in the restored Blackwater lacked this heterogeneity. Generally, active jams were grouped near the bottom of the PCA, with a high amount of porosity, low submergence, and perpendicular to flow, complete jams were located within a range of characteristics in the middle of the PCA, and partial jams were found in a band near the top of the PCA (*i.e.* higher submergence, porosity, and volume) and contained a range of orientations (*i.e.* perpendicular/parallel) and effect on water deflection (Figure 3-8B).

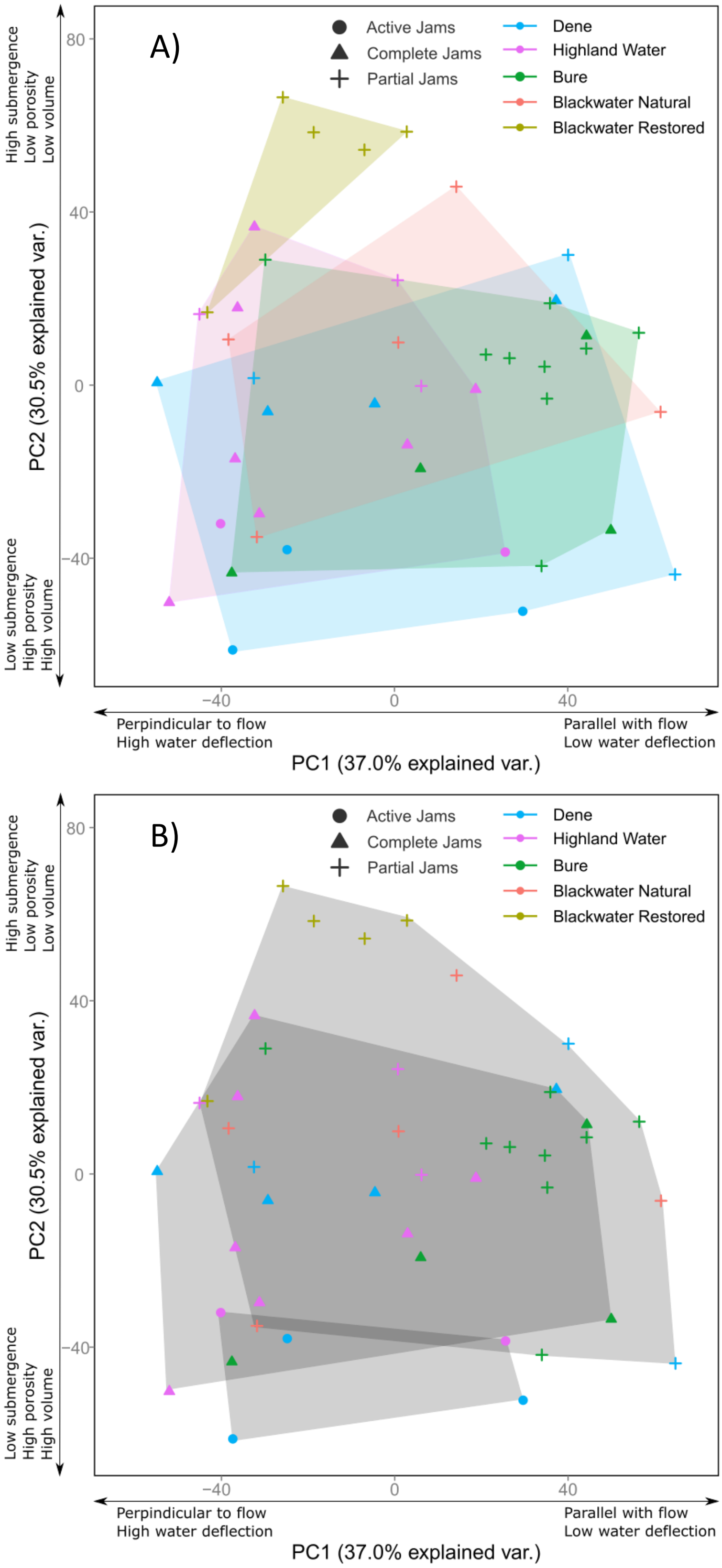


Figure 3-8: A PCA of all jam structural variables in the study, with symbols representing both river and jam classification type. The variability in jam structural properties in multidimensional space is demonstrated by convex hulls corresponding to each river (A) and to each jam type (B). Circles = active jams, triangles = complete jams, and crosses = partial jams.

3.4.2 Jam Water Depth and Flows

Water depths surrounding each jam (jam water depth) were analysed in comparison to water depth outside the influence of the jam (river water depth). Median water depth around jams increased with increasing river management, although the relationship between jam depth and river depth varied among rivers (Figure 3-9). Overall, median water depths around jams were not significantly different than median water depths in the channel in any of the rivers (KW: $X^2 = 0.861$, df =1, P = 0.354). Around natural jams, however, the median jam depth appeared to vary according to jam class but the nature of this variation differed between rivers. In the Dene, active jams were the most shallow (median: 32.3 ± 2.33 cm), followed by complete jams (59.5 cm), and water depths were deepest around partial jams (79 cm). In the Highland Water, in contrast, river depth was relatively shallow but the shallowest depths were associated with partial jams (25.3 ± 4.5 cm), intermediate depths around active jams (36.8 ± 0.25 cm) and deepest water around complete jams (58.6 ± 15.9 cm), indicating a significant difference in depth across jam class (KW: $X^2 = 6.588$, df = 2, P = 0.037), although post-hoc pairwise comparisons did not indicate significant pairwise differences (all $P > 0.05$). However, while the maximum depths found in pools were not significantly different between the jam and elsewhere in the river in the Dene, pools (max depths) around jams were significantly deeper than elsewhere in the channel for all other rivers (Figure 3-9).

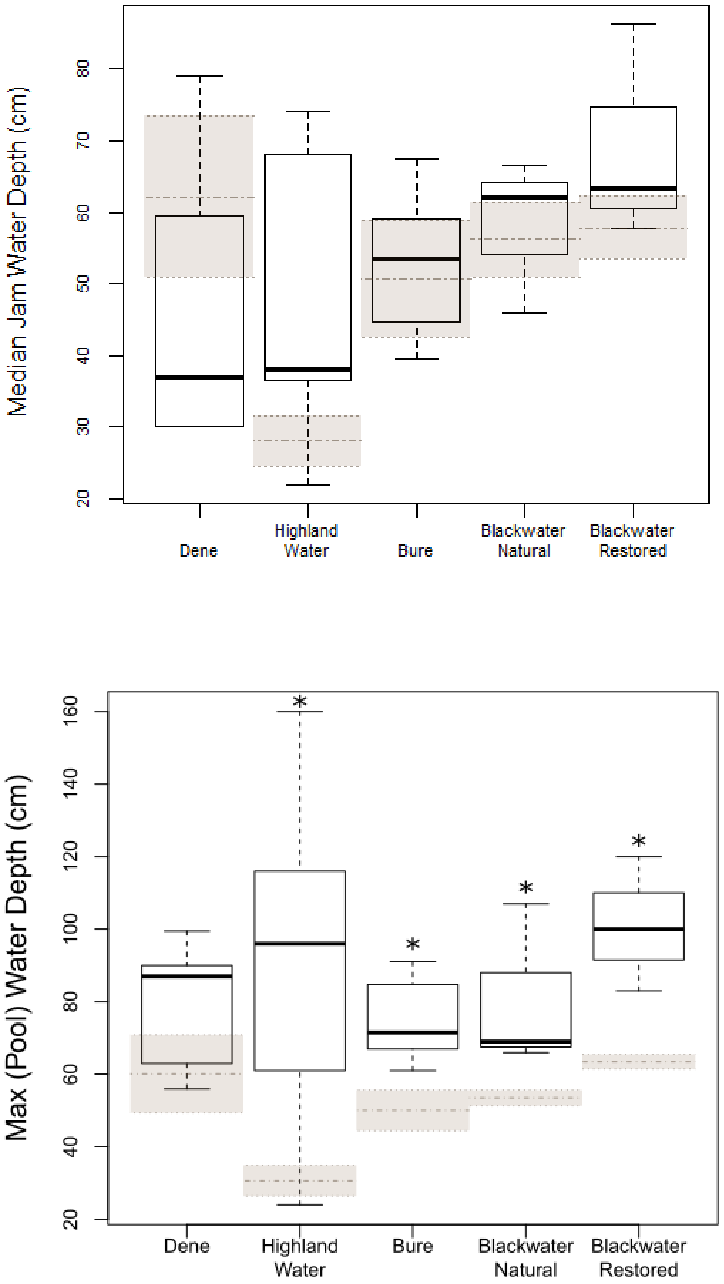


Figure 3-9: Median jam water depth in each of the study rivers. Centre line indicates median jam values, while box limits indicate 25 and 75% quartile ranges, with whiskers indicating 0-100% quartile range. Shaded backgrounds represent the corresponding river water depth outside of the influence of the jam, ± 1 SE. * indicates significant differences between jam and river depths at $P < 0.05$ according to KW test.

In addition, jams across all rivers created “flow concentration”, an increase in the current velocity over average river velocity, by deflecting water alongside the jam (Figure 3-10). However, the greatest flow concentration (>400 %) occurred around natural jams, with smaller concentrations detected in the restored jams in the Bure, and least flow concentration in the restored deflectors of the Blackwater. The near-bed (80% of depth) flow directed into the bed (negative Z component), which may have an effect on scouring sediment from the bed, decreased with increasing wood management (Figure 3-11). Within the River Dene, active jams had the greatest increase of flows into the river bed, but this could not be statistically tested since all jam classifications did not have sufficient replication. Near turbulent fluctuations were notable in some jams, particularly in the Highland Water (Figure 3-12) and the Bure, but the restored deflectors of the Blackwater had the lowest median and range of flow variability across rivers. This difference, however, was non-significant (all $P > 0.05$).

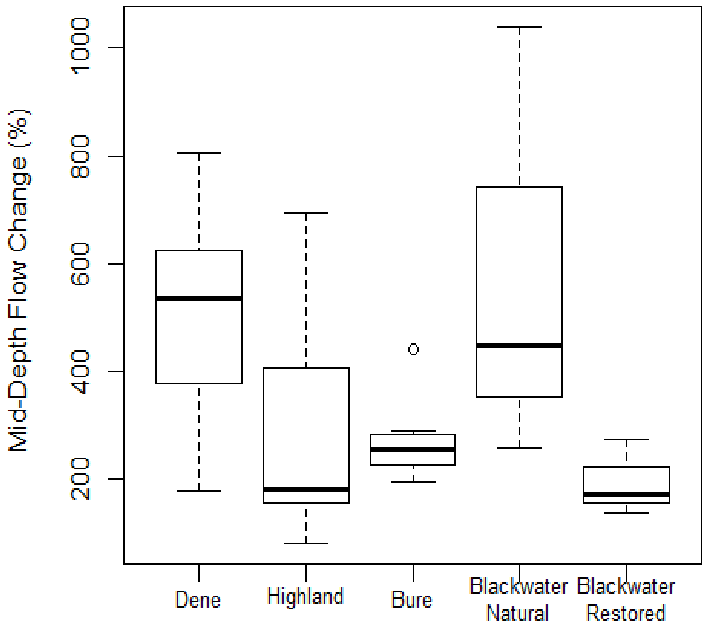


Figure 3-10: Percent increase in the total flow velocity vector alongside each jam in each of the study reaches. Centre line indicates median jam values, while box limits indicate 25 and 75% quartile ranges, with whiskers indicating 0-100% quartile range.

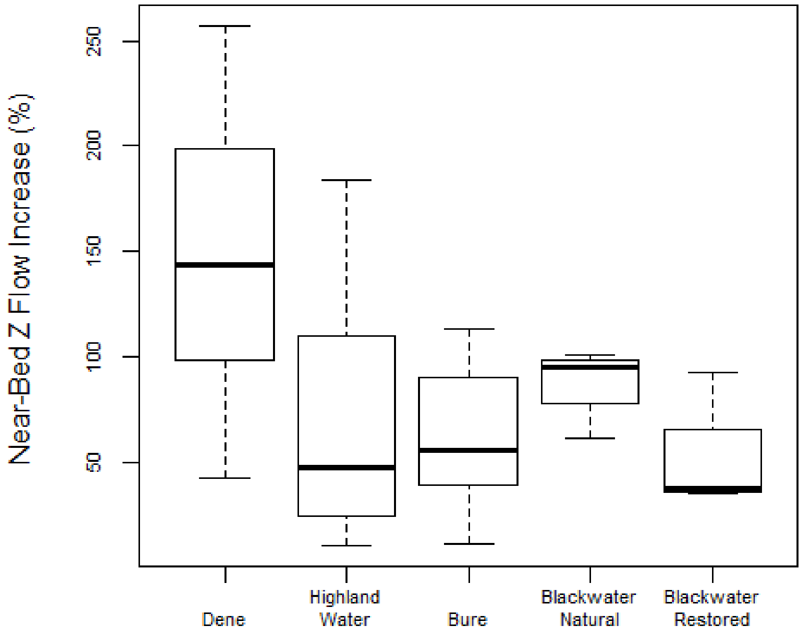


Figure 3-11: Percent increase in the near-bed (80% depth) flow values directed into the river bed (-Z component). This is standardized as percent increase over average river flows, measured at each jam for the different study reaches. Centre line indicates median, while box limits indicate 25 and 75% quartile ranges, with whiskers indicating 0-100% quartile range.

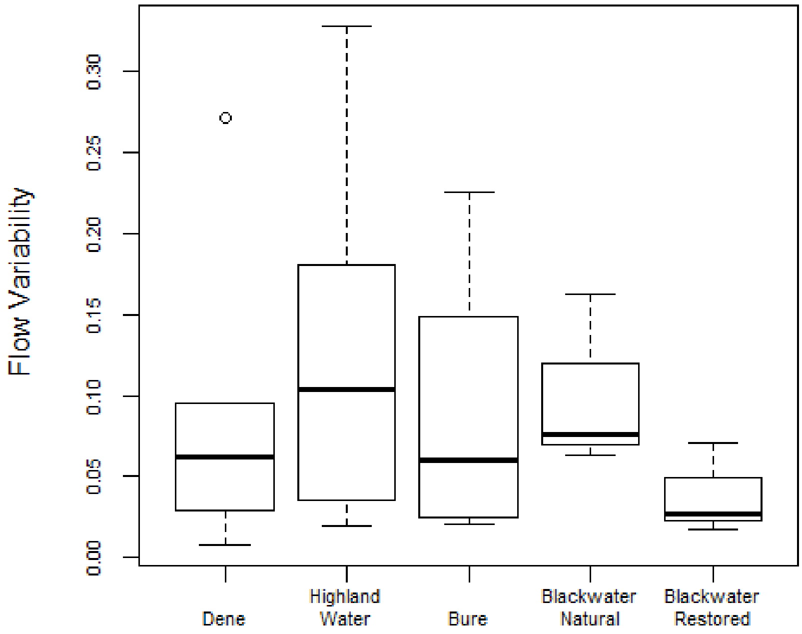


Figure 3-12: Near turbulent flow variability measured by the standard deviation of 1 s^{-1} measurements over 30 s for total velocity vector. Centre line indicates median jam values, while box limits indicate 25 and 75% quartile ranges, with whiskers indicating 0-100% quartile range.

3.4.3 Jam Sediment Characterization

The depth of fine sediment surrounding jams was highly variable across all rivers, with accumulations of fine sediment greater than 1 meter occurring in the Dene, Highland Water, and Bure. While the River Dene contained large accumulations of fine sediment elsewhere in the channel even at its points of lowest accumulation (minimum fine sediment), and the 0-75% quartiles for minimum jam sediment were below the average river minimum fine sediment accumulations (mean ± 1 SE), this difference was not significant, nor for any other jam/river comparisons (KW: all $P > 0.05$; Figure 3-13A). There was a slightly decreasing trend in sediment depth variability with increasing management and intervention, although this effect was also insignificant ($P > 0.05$; Figure 3-13D).

Detailed sediment characteristics were examined upstream, downstream, within the jam, and in the concentrated flows of each jam. In the River Dene, organic matter content significantly differed by location (KW: $X^2 = 15.9$, $df = 3$, $P = 0.001$), and organic matter content was least within concentrated flow habitats (4.7 ± 0.6%) but a Mann-Whitney U post-hoc analysis indicated significant differences only between sediments within the jam and in the concentrated flows (Figure 3-14A). Sediment D_{50} and the proportion of sediment classes were insignificant across locations and very variable due to interactions with the range of jam classes (active/complete/partial). However, several broad trends emerged: D_{50} and proportion of gravels tended to be smallest upstream and within the jam, while concentrated flows and the downstream mesohabitats had the greatest D_{50} and gravel fractions, and with lower silt and clay fractions (Figure 3-14B,C).

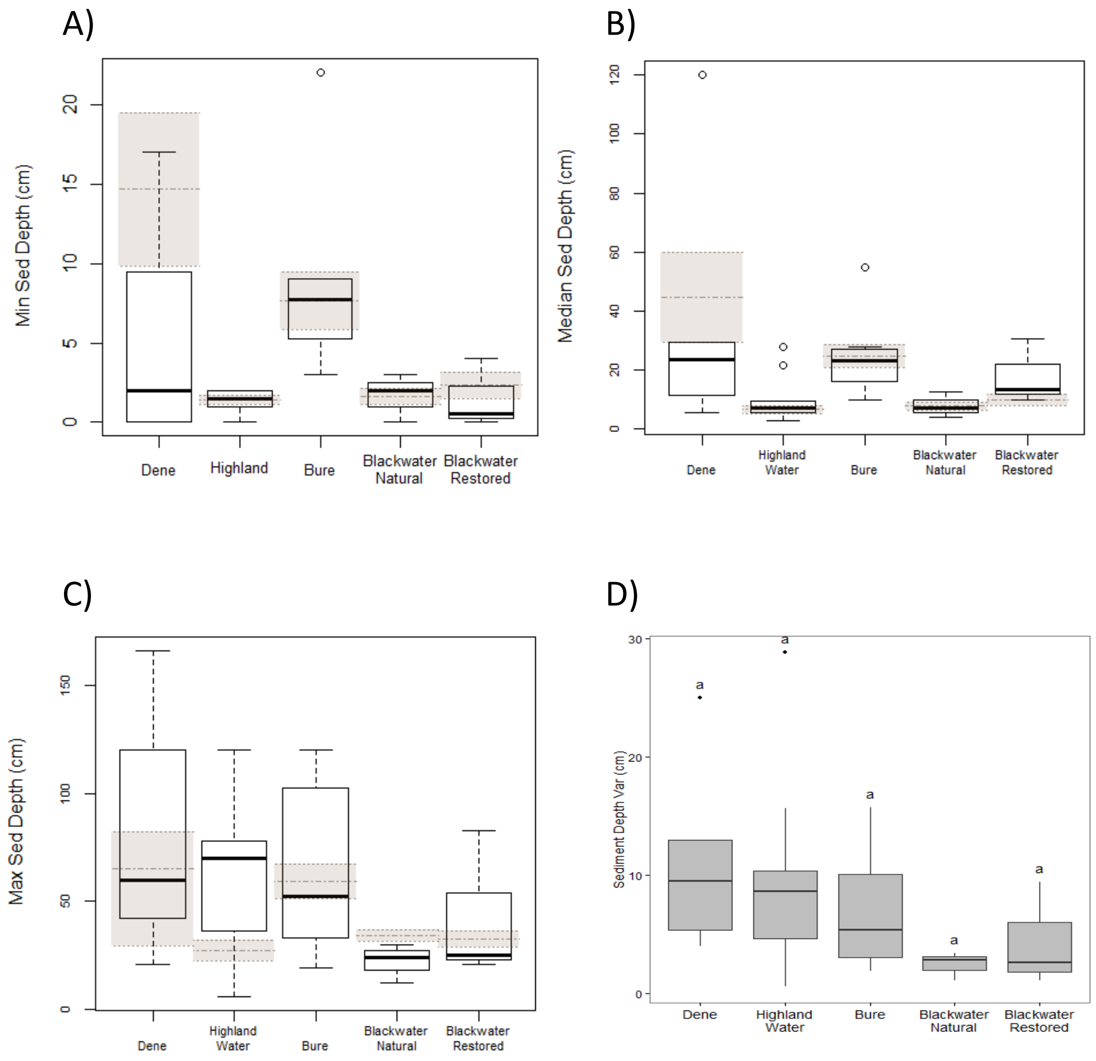


Figure 3-13: Minimum (A), median (B), and maxiumum (C) fine sediment depths and variability (D) surrounding the jams in each river. Centre line indicates median jam values, while box limits indicate 25 and 75% quartile ranges, with whiskers indicating 0-100% quartile range. Shaded backgrounds represent the corresponding river water depth outside of the influence of the jam, mean ± 1 SE. Letters indicate significant differences at $P < 0.05$ according to post-hoc Mann-Whitney U tests with holm correction.

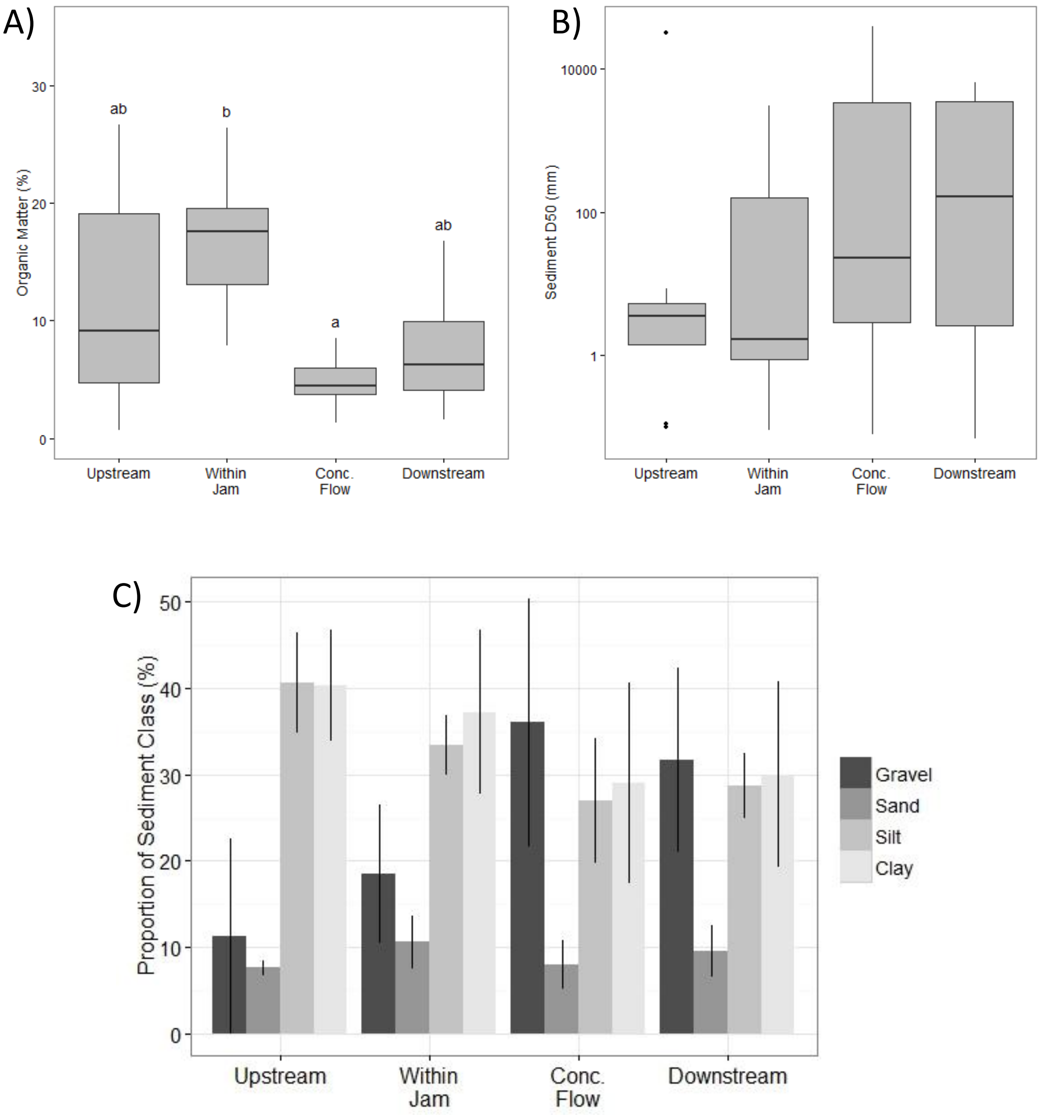


Figure 3-14: Sediment characteristics (percent organic matter (A), sediment D50 (B), and proportion sediment classes (C) in the River Dene. Centre line indicates median jam values, while box limits indicate 25 and 75% quartile ranges, with whiskers indicating 0-100% quartile range. Values in the proportion of sediment classes indicates mean ± 1 SE. Letters indicate significant differences at $P < 0.05$ according to post-hoc Mann-Whitney U tests with holm correction. No significant differences were seen in Sediment D_{50}

In the Highland Water, sediment organic matter was relatively low (<6%) at all locations, with the exception of significantly greater organic matter content within-jam and debris mesohabitats (Figure 3-15A). D_{50} was variable among jams within each mesohabitat type, and although insignificant, there was a trend for greater D_{50} and gravel fractions, along with decreased silt and clays in upstream and concentrated flow mesohabitats (Figure 3-15B,C).

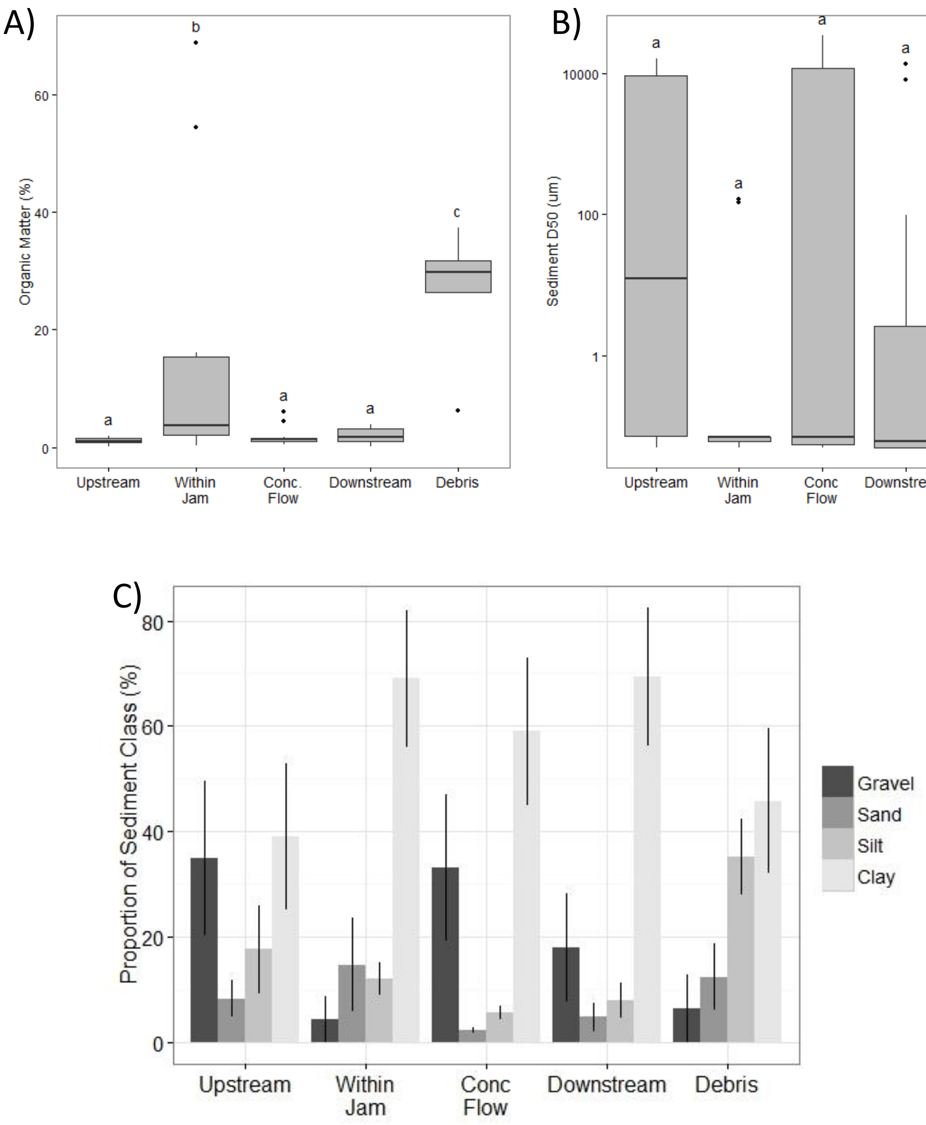


Figure 3-15: Sediment characteristics (percent organic matter (A), sediment D50 (B), and proportion sediment classes (C) in the Highland Water Centre line indicates median jam values, while box limits indicate 25 and 75% quartile ranges, with whiskers indicating 0-100% quartile range. Values in the proportion of sediment classes indicates mean ± 1 SE. Letters indicate significant differences at $P < 0.05$ according to post-hoc Mann-Whitney U tests with holm correction.

In the Bure, sediments beneath jam-created concentrated flows had significantly lower organic matter content than sediments within the jam or downstream, but this was not significantly lower than other non-jam mesohabitats elsewhere in the river (Figure 3-16A). In addition, there was a trend for concentrated flows to have increased D_{50} and gravel fraction, but these changes were not significantly different (Figure 3-16B,C). Emergent macrophytes were similar to within-jam and downstream mesohabitats, with trend towards a higher percentage of clay, although this change was also not statistically significant.

In the Blackwater, organic matter content was significantly greater within the jams than in all surrounding mesohabitats, although there were no other significant differences by mesohabitat location (Figure 3-17A). There was a large variability in D_{50} in upstream sediments, while generally sediment conditions within-jam, under concentrated flows, and in downstream habitats had relatively small variability. While the differences were not significantly different, within-jam habitat had smaller D_{50}, gravel, and increased sand fraction, while concentrated flows and downstream had greater D_{50}, gravel, and decreased sand (Figure 3-17B,C).

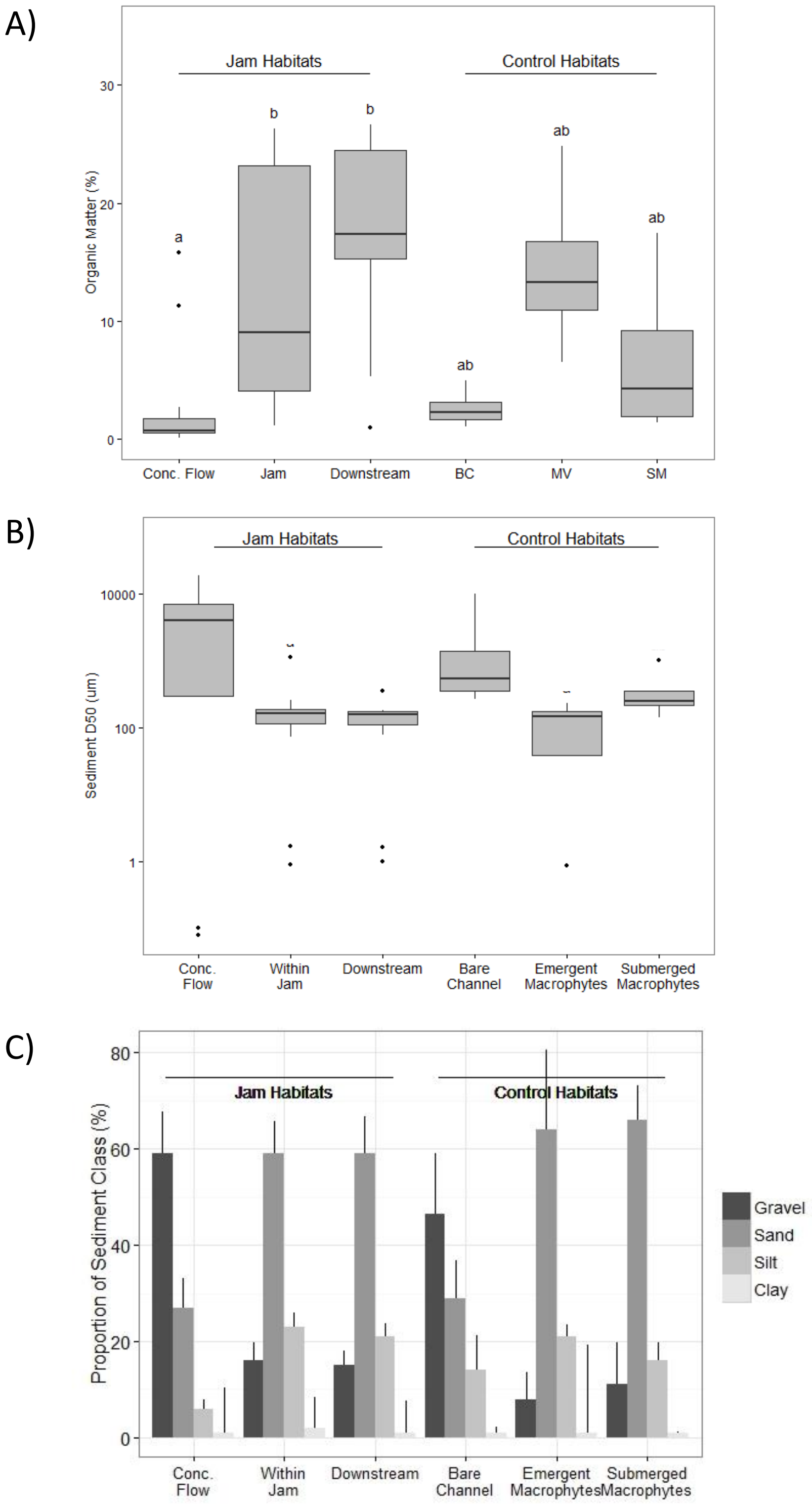


Figure 3-16: Sediment characteristics (percent organic matter (A), sediment D50 (B), and proportion sediment classes (C) in the River Bure Centre line indicates median jam values, while box limits indicate 25 and 75% quartile ranges, with whiskers indicating 0-100% quartile range. Values in the proportion of sediment classes indicates mean ± 1 SE. Letters indicate significant differences at $P < 0.05$ according to post-hoc Mann-Whitney U tests with holm correction.

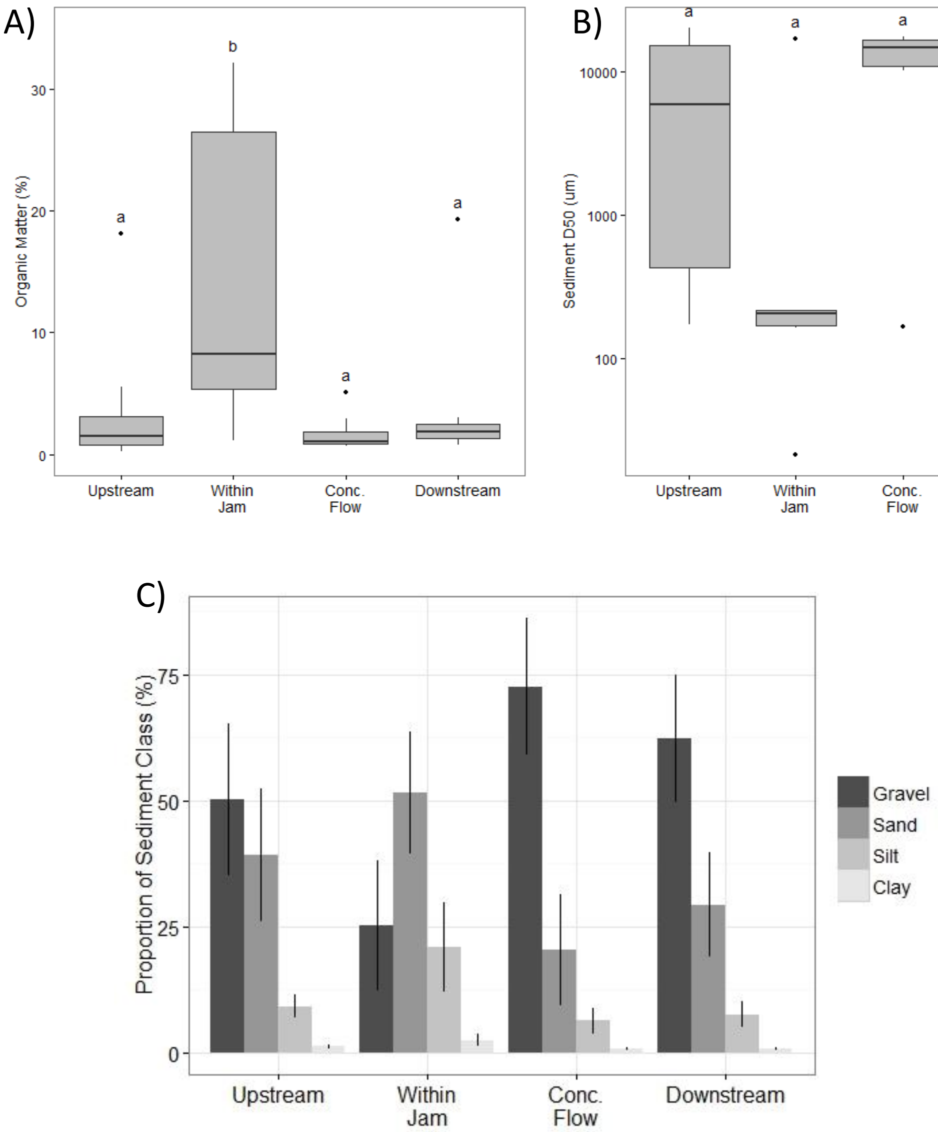


Figure 3-17: Sediment characteristics (percent organic matter (A), sediment D50 (B), and proportion sediment classes (C) in the Blackwater Centre line indicates median jam values, while box limits indicate 25 and 75% quartile ranges, with whiskers indicating 0-100% quartile range. Values in the proportion of sediment classes indicates mean ± 1 SE. Letters indicate significant differences at $P < 0.05$ according to post-hoc Mann-Whitney U tests with holm correction.

Ingressed sediment in the concentrated flow gravels at each jam was examined for both bed sediment storage and organic content. Bed sediment storage was variable by river reach (KW: $X^2 = 14.4$, df = 5, P = 0.013) but pairwise comparisons did not indicate any significant differences between individual rivers (Figure 3-18). However, a multiple regression accounting for the near-bed velocity vector and river identity was able to predict decreased ingressed sediment storage in river gravels ($F = 11.19$, df = 4,26, $P < 0.0001$, $R_{2adj} = 0.576$). The organic matter content of these sediments varied significantly across river reach (KW: $X^2 = 25.2$, df = 2, $P < 0.001$), but post-hoc comparisons did not indicate significant differences (Figure 3-18). Ingressed bed sediment organic matter content did not significantly vary with near bed flows.

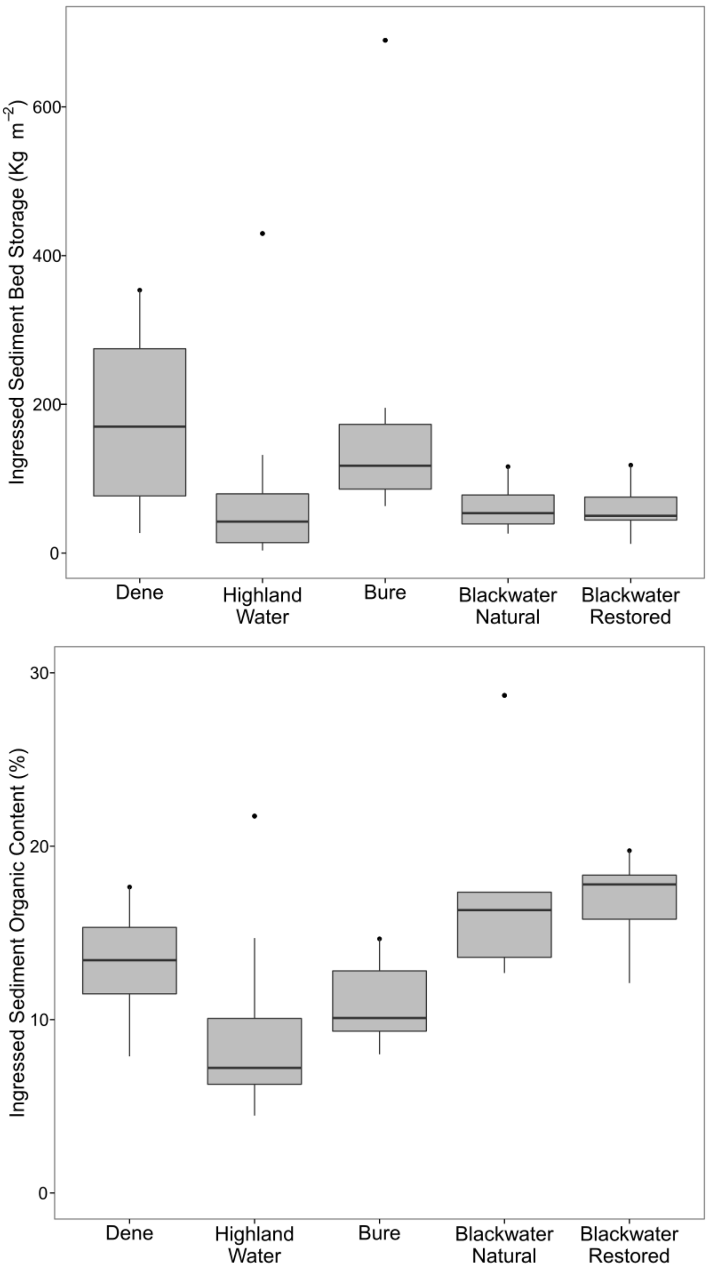


Figure 3-18: Ingressed sediment bed storage (kg m^{-2}) and organic content across all concentrated flow gravels found in the river. Significant differences across river reaches were detected with a Kruskal-Wallace test, but post-hoc Mann Whitney U tests with holm correction did not detect any significant pairwise differences between rivers.

Discussion

This field study was designed to examine the variability in physical habitat characteristics of wood and its surrounding habitat across a gradient of river management. Jam structural characteristics and mesohabitat characteristics (substrate, flow sediment) are highly variable but the results reveal some broad trends. The complexity of LW decreased with increasing management, revealed by a change in dominance of jam classes from active and complete jams to partial jams, in addition to reductions in wood volume, jam porosity, and other structural attributes such as submergence and orientation. Overall, the deflector-style restored wood in the Blackwater were the most dissimilar from the other wood types. Jam volume and complexity are key factors in the hydraulic effect of wood (Manners et al. 2007, Manners and Doyle 2008), and additional attributes such as orientation, submergence, and wood burial have been shown to have important roles in governing fluid hydraulics, sediment dynamics, and presence and frequency of channel microhabitats (Gurnell et al. 1995, Gurnell and Sweet 1998, Gurnell et al. 2002). As a result, variation in the structural complexity of these jams can have large impacts on specific aspects of habitat heterogeneity. In addition, rivers with restored wood entirely lacked active jams, which are a crucial component in creating plunge pool fish habitat and increasing hyporheic exchange (Lisle 1986, Sawyer et al. 2011, Sawyer et al. 2012). Not only does a larger and more complex structure provide more surface area for periphyton to grow (Hax and Golladay 1993), it can also more effectively trap transported organic matter and drifting macroinvertebrates (Palmer et al. 1996), and provide a mosaic of low-flow refugia (Lancaster and Hildrew 1993) and cover from predators for macroinvertebrates (Czarnecka et al. 2014). The extent of wood decay also decreased with increasing management, this may affect its availability as a food resource for xylophilic invertebrates (Wondzell and Bisson 2003) and decrease its contribution by erosion to organic matter in the channel, and may also reduce the strength of periphyton attachment (Sabater et al. 1998). However, as the restored wood emplacements age, decay may become more similar to those natural wood pieces found in the channels of the Dene and the Highland Water.

The length of key wood pieces, which is related to the stability of wood jams within the channel (Gurnell et al. 2002), was lowest in the restored jams of the Blackwater and highest in the restored jams of the Bure. This may suggest that the wood pieces in the Bure may be stable and unlikely to move, since they were generally larger than channel width (Gurnell et al. 2002). While the shorter deflectors in the Blackwater might have the potential for displacement, they were all fixed to the bed with stakes and unlikely to mobilize. However, in the Dene average key piece length was quite small, suggesting a high rate of wood transport from upriver, rather than large wood being primarily recruited from the immediate riparian zone, and the potential for mobilization. However, the width of the Dene was also relatively small compared to the Bure and Blackwater, and most jams were supported by bracing and burial into the banks and bed.

Large wood was frequently associated with pool and backwater habitats, increasing water depths in the channel, and with jam complexity appearing to regulate the magnitude of pool depth. Increasing the depth and size of pools not only has the increase the availability of this low-flow refugia used by fish species, but also provides an increasingly regulated thermal refugia in the subsurface, especially for rivers that may undergo a high-temperature stress in summers (Ebersole et al. 2003). While there was no significant difference seen in the Dene between jam pool depths and river pool depths, this is likely due to the very high wood volumes in the Dene, which appeared to create large ponding effects throughout the entire studied reach, as the water behind an active jam was frequently impounded (up to 10 m) to the previous jam. The greatest degree of flow concentration was found in the near-natural reaches, and deflector-style jams had the least effect on concentrating flow for both the total flow vector, but especially for flows directed into the river bed. Concentrated flows, especially into the river bed, were also demonstrated to alter the bed storage of ingressed sediments in gravels, which has strong implications for the successful creation and hatching of eggs in salmonid redds (Sear et al. 2014), and for the general amelioration of fine sediment degradation in many lowland rivers identified in the NRRI and around the world (Wood and Armitage 1999).

Most other sediment characteristics (*i.e.* D_{50}, sediment classes, organic matter content) were highly variable in each river, reflecting both overall catchment conditions and individual differences in jam structural properties and effects on flow. Throughout the Dene, there were large accumulations of fine sediment (finer than gravel), likely due to intensive agriculture in the catchment. Fine sediment depths as determined by pin surveys decreased in locations upstream of the jam, yet particle size analysis of these upstream sediments indicated these areas consisted primarily of sand and silt, suggesting fine sediments trapped by the jam were ingressed into the bed. However, while there was the indication of some variability in fine sediment depths overall in the channel, there was no significant differences seen in these accumulations, which may emphasize the high magnitude of fine sediment inputs which may exceed levels at which wood may be expected to mitigate impacts.

However, the structural importance of wood in trapping fine sediment may facilitate a channel narrowing process: the organic rich accumulations of fine sediments in and around jams can provide a rich growth substrate for macrophytes and other vegetation which may further stabilize the sediment, induce additional deposition (Cotton et al. 2006, Wharton et al. 2006), and possibly result in channel narrowing, increasing flow velocity in central channel areas. Organic matter was lowest in the gravel locations, important for the survival of spawning fish (Sear et al. 2014). However, even though there was a relatively high amount of gravels in the concentrated flow areas compared to other mesohabitats around wood, there were abundant silt and clay fractions in the sediment which may be beyond the threshold for successful salmonid spawning (Greig et al. 2005).

Overall, however, there was a high degree of variability in sediment properties within each river reach, and the effects of wood on flow and sediment properties appeared to be highly variable based on individual jam characteristics. While the Dene and the Highland Water did in fact contain highly complex active jams, they also contained simple partial wood pieces that had lower morphologic and hydraulic effects. As a result, naturally occurring wood results in a variety of jams of all types of structural complexity and effect. However, in restored deflectors of the Blackwater, not only was a trend for decreasing complexity with jam structural attributes, but also in flow and sediment attributes.

A limitation of the study is the lack of replication of sites for each level style of management intervention. However, this reflects the lack of suitable locations due to the rarity of wood and particularly natural jams in UK rivers. Sites with a long history of minimal wood management (*e.g.* the Dene) are extremely rare, and few restorations have used large wood in such complex forms as the Bure. While the trends from these data may be indicative of rivers of similar restoration type (*i.e.* deflectors, complex large wood), these results may be only representative of these sampled rivers, and the trends seen in the variability of wood and habitat types should continue to be explored in new and alternative sites using large wood in the UK particularly as further wood-based restorations take place.

Overall, this study highlights how the management decisions made during restoration, and whether semi-natural large wood or deflectors are used can strongly influence the complexity of wood in the channel. While wood may be generally used in river restorations to create habitat heterogeneity, this study indicates how the complexity of wood that enters the channel can alter the degree and type of habitat heterogeneity created. The effect of wood on habitat heterogeneity in river systems is highly variable, and this must be considered in the design and implementation of river restorations. Management decisions to limit the quantity and complexity of wood in each project, whether for fear of flooding or other concerns, may be limiting the habitat heterogeneity that the restoration may be initially trying to achieve. This echoes recent findings from a more general survey of river restoration projects contained in the National River Restoration Inventory that failed to find a significant increase in physical habitat heterogeneity, let alone ecological improvements, between before and after restoration data (Smith et al. 2013).

Given that money for restoration projects is limited, the semi-natural large wood restorations as exemplified in the Bure offer a cheap (~£500) and minimal-disturbance alternative to more labour and cost-intensive fixed-deflector emplacements, yet result in enhanced wood and habitat complexity. This sort of project would be replicable in regions where there is already a pre-existing forested riparian buffer to supply the wood. Along these lines, it is also recommended for restorations to generally re-establish wooded riparian zones, not only to provide heterogeneity in light and shading, but to allow for the natural accumulation of wood in more varied and complex forms in a manner dependent on continuous restoration, management, and maintenance.

Chapter 4

The potential for large wood to mitigate scour of periphyton nutritional quality caused by hydropower hydraulic extremes

4.1 Background

4.1.1 Hydroelectric power and renewable energy

The European Union Renewable Energy Directive (2009/28/EC) has set national targets for renewable production by 2020 to reduce overall greenhouse gas emissions derived from energy production. Hydroelectric power’s pumped storage reservoirs can easily regulate energy production to the constantly fluctuating demands of the market; during periods of low-demand, excess energy can be used to pump water for storage in higher reservoirs, and during peak hours, stored water is released from these reservoirs to drive electricity production. Dams also serve a functional purpose in limiting the destructive potential of water by retaining flood peaks in the storage reservoir (Magilligan and Nislow 2005), thereby reducing flood risk as required by the Flood Directive (2007/60/EC). Hydroelectric power generation, while seen as key to achieve targets in the Renewable Energy Directive and the Floods Directive, may conflict with other European Union Directives, such as the Habitat (92/43/EEC) and Water Framework Directives (2000/60/EC). In the European Alps, the construction and operation of high-head storage hydroelectric plants with large dams is recognized as one of the most substantial factors impacting river ecosystems (Fette et al. 2007, Zolezzi et al. 2009, Meile et al. 2011).

Worldwide at the turn of the millennium, there were more than 45,000 large dams (> 15 m high) in operation, with extensive plans for development in the coming decades (WCD 2000). Currently, worldwide hydroelectric development plans include Turkey (Akpınar et al. 2011), Amazonia (Lima and Lall 2010, Fearnside 2014), Sub-Saharan Africa (Cole et al. 2014), China (Huang and Yan 2009), the Himalayas (Grumbine and Pandit 2013), and southeast Asia (Keong 2005, Hasan et al. 2012). As of 2005, 40 of 46 planned dams on large river systems were in non-OECD (Organization for Economic Cooperation and Development) member states (Nilsson et al. 2005). In contrast, large dam construction in developed countries has decreased as the most economically viable locations have already been completed (Beck et al. 2012). In the United States, dam removal has actually overtaken the rate of construction since 1988 (WCD 2000), with dam removal becoming a restoration tool to restore river habitat, especially for anadromous salmonids, e.g. the Elwha River in Washington State (Bednarek 2001, Gowan et al. 2006, Brenkman et al. 2012). Therefore, hydroelectric power should not be considered a no-impact “green” energy source, but rather one that, like other energy sources, provides a series of trade-offs: greenhouse gases, energy market integration, socioeconomic costs, and environmental health. To properly make informed decision-making, it is vital to understand the processes by which hydroelectric power impacts river ecosystems, and the potential for mitigation of these impacts.

4.1.2 Disruption of river connectivity

Dams affect over half of the world’s large river systems (Nilsson et al. 2005) and cause a serial discontinuity of the longitudinal, lateral, and vertical components of the river system (Ward and Stanford 1983). Longitudinally, impoundments can dramatically create sediment transport discontinuities and alter channel morphology through many mechanisms. Impoundments function as a sediment trap and disrupt suspended and bedload sediment transport (Anselmetti et al. 2007), reducing catchment sediment yield (Vörösmarty et al. 2003). The removal of sediment loads can result in rapid erosion below the dams, in some cases for over 150 km (Stanford and Ward 1979). Impoundments reduces particle-size longitudinally and laterally, influencing change in channel morphology (Petts 1984b). Along with inorganic sediment, impoundments trap transported organic matter, disrupt patterns of seston transport, and alter the natural longitudinal cycling of nutrients (Wanner et al. 2002, Humborg et al. 2006). Dams and impoundments result in the mass conversion of lotic to lentic habitats and interrupt the migration and dispersal of macroinvertebrates and fish, isolating local populations and communities (Jansson et al. 2000, Lundqvist et al. 2008). Some estimates suggest that, worldwide, over 20% of all freshwater fish species are considered threatened or endangered as a result of the environmental impact of dams (Truffer et al. 2001).

Impoundments also result in a lateral discontinuities, reducing overbank flooding and aquatic-terrestrial connectivity, and resulting in lower productivity in both riparian and aquatic ecosystems (Ward and Stanford 1995). Due to the reduction in overbank flows and sedimentation, dispersal of sediment and flow-mediated propagules into the riparian zone is reduced, decreasing colonization and recruitment of riparian organisms, and hence riparian diversity (Galat and Lipkin 2000, Kingsford 2000). Proposed dam locations are often associated with riparian biodiversity hotspots, especially for angiosperms, birds, and butterflies, and the completion of these proposals is predicted to lead to extinctions in these riparian communities (Pandit and Grumbine 2012).

Vertical connectivity, although often overlooked, is also affected by river regulation and hydroelectric power generation. The release of fine sediment from intermittent releases of power plants can cause clogging in interstitial spaces in the benthos, result in bed armouring, reduce interstitial habitat, and diminish hyporheic exchange which regulates oxygen levels and temperature variation (Poole and Berman 2001, Calles et al. 2007). This has been shown to result in losses of hyporheic taxa (Brunke and Gonser 1997, Bruno et al. 2009) and reduce egg survival in salmonid redds (Curry et al. 1994, Calles et al. 2007).

4.1.3 The ecohydrology of rivers with hydroelectric dams

Hydroelectric dams fundamentally alter river hydrology, particularly by altering the temporal pattern of variation in river flows, commonly known as the natural flow regime. The natural flow regime is characterized by the seasonality, variability, duration, magnitude, and frequency of flow events (Poff et al. 1997), and is a fundamental driver in structuring physical processes, biological communities, and the maintenance of ecological function (Poff and Ward 1989, Poff et al. 1997, Bunn and Arthington 2002).

Impoundments change the hydrology of the river system, altering the timing, magnitude, and frequency of both high and low flows (Ligon et al. 1995, Magilligan and Nislow 2005). Dams can retain high-flood peaks typical in the wet season or during spring-snow-melt – diminishing annual maximum flows – and release these flows during summer low-flows – increasing annual minimum flows (O'Reilly and Silberblatt 2009) This results in a reduction inannual flow variability. The loss of seasonal flow patterns may decrease the availability of temporally limited habitat required by some life-stages for development, reduce growth rates, and fail to provide the necessary signals for some important biological processes, such as fish migrations with spring floods (Gehrke et al. 2002). In addition, discharge magnitude is an important driver of geomorphology, as it can regulate channel form, habitat complexity, and patch stability (van der Nat et al. 2003), and as a result, the alteration to the flow regime has reduced habitat creation and homogenized flows across regions and river systems, causing a shift to widespread and non-indigenous generalist species at the expense of locally adapted biota (Poff et al. 2007).

According to the Intermediate Disturbance Hypothesis, intermediate levels of flood disturbance are optimum for river health and expected to result in the greatest biodiversity and ecosystem function (Townsend et al. 1997). Aquatic flora and fauna communities are well adapted to the periodic spates of the natural flow regime, which regulate the abundance and structure of these communities. While non-hydroelectric dams (*i.e.* storage or supply reservoirs) reduce both the frequency and magnitude of flood disturbance, hydroelectric dams create a high-disturbance regime associated with the intermittent release of water used in the electric generation process. This process can vary by the design of the hydroelectric dam: storage dams which have an outlet at the dam base release a constant minimum vital discharge, marked by periods of high discharge when the turbines are operational. In contrast in many high-head pumped storage reservoirs, water is released downstream of the impoundment by several km. As a result, the several km reach between the dam and release point experiences little to no fluctuation in discharge, as this stabilized reach is buffered from natural flow events by the dam and is upstream of the discharge disturbance due to turbine operations. These areas, without the disturbance necessary to regulate community dynamics, may result in the loss of poor competitors (Townsend et al. 1997) and become more susceptible to invasions.

4.1.4 The impacts of hydropeaking

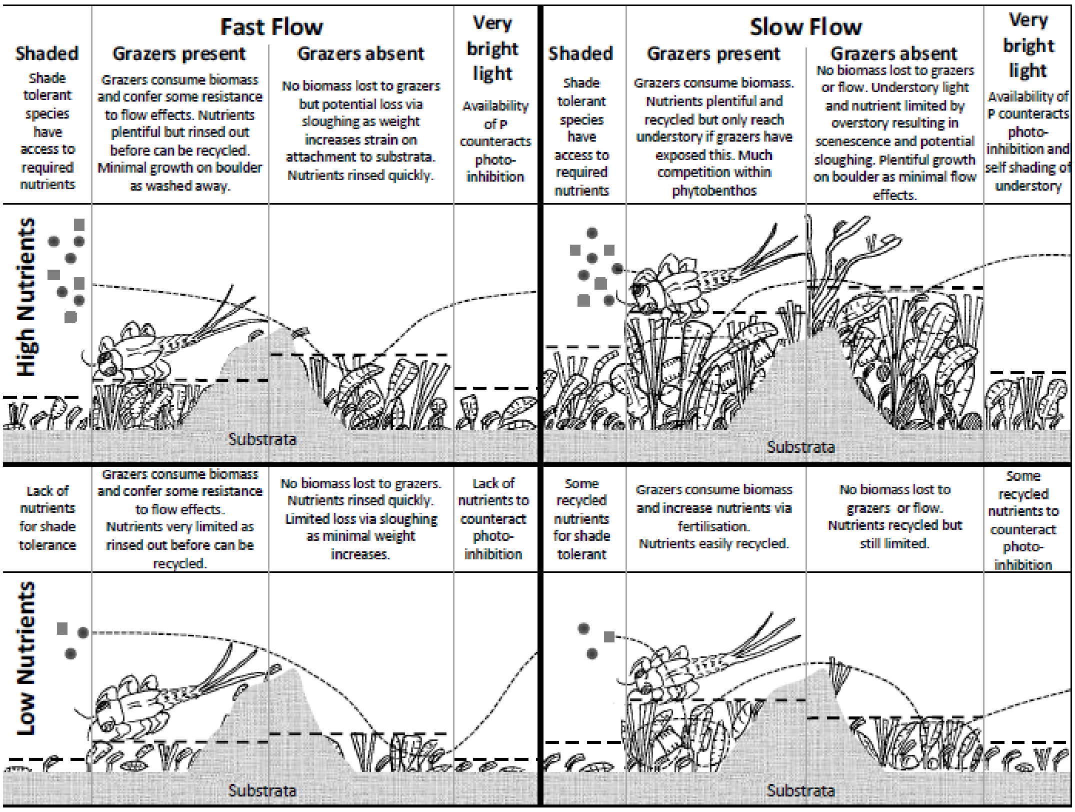
The characteristic intermittent water releases by hydroelectric power plants, known as "hydropeaking", is typically a high-frequency (daily – sub-daily), high-intensity disturbance (2 – 10-fold or greater increases in discharge) of hypolimnetic water released during scheduled hydroelectric operations (Zolezzi et al. 2011), which causes a wide range of effects on downstream aquatic communities. Hydropeaking increases scour and shear stress and can undermine the banks (Grelsson 1985), and the rapid discharge fluctuations cause changes to channel width and the dry/wet cycling of the riparian margins, leading to vegetation loss and failed establishment of riparian organisms (Northcott et al. 2007). This rapid change in river width can dramatically increase density-independent fish mortality due to stranding along channel margins (Saltveit et al. 2001, Harnish et al. 2014).

Hydroelectric river regulation is known to decrease the density and biomass of benthic invertebrates along a longitudinal gradient below power plant outlets (Céréghino and Lavandier 1998, Céréghino et al. 2002, Céréghino et al. 2004, Bruno et al. 2009, Ellis and Jones 2013). While, natural floods provide warning signals, such as a slow rise in ground water level which may allow a behavioural response to find flow refugia (Lytle and Poff 2004), the sudden and sporadic rise in discharge with hydropeaking may not provide any opportunity for an adapted response by the biota (Bretschko and Moog 1990). Hydropeaking is expected to affect these benthic communities not only through increased shear stress resulting in catastrophic drift (Gore et al. 1989, Gore et al. 1994, Zolezzi et al. 2011, Bruno et al. 2013, Bruno et al. 2015) and reductions in the availability of benthic habitat (Blaschke et al. 2003, Anselmetti et al. 2007, Bruno et al. 2009), but also due to increased behavioural drift due to sudden shifts of up to 6°C in water temperature occurring with hypolimnetic releases, known as thermopeaking (Carolli et al. 2012, Bruno et al. 2013). However, several studies have indicated that catastrophic drift rates seen during hydropeaking were insufficient to account for the depletion in the benthic population alone (Miller et al. 2014). This may reflect the fact that these changes may only take place over timeframes much longer than those studied, and/or that incoming drift from upstream may compensate for these losses (Bruno et al. 2015), raising the possibility that other factors may be limiting the size of the benthic consumer population.

4.1.5 Periphyton and the altered flow regime

Periphyton, the mixture of algae, cyanobacteria, detritus, and heterotrophic microbes contained in biofilms and attached benthic macro-algae, have a fundamental role in nutrient dynamics and represent an important food source for aquatic ecosystems (Wetzel 2001, Torres-Ruiz et al. 2007). In regulated river reaches where impoundments trap detrital inputs from upriver (Blinn et al. 1998), periphyton are likely to assume even greater importance as the trophic base for the food web and facilitating energy exchange across the plant-animal interface. While periphyton growth and composition are affected by a wide variety of environmental factors such as light, temperature, substrate, nutrients, and the presence of grazers (Figure 4-1), flow velocity is considered one of the most important factors regulating primary productivity in river systems (Suren and Riis 2010, Law 2011).

Periphyton accrual is typically biphasic: Phase 1, which happens in all streams, occurs over daily to weekly timescales and is dominated by r-strategist taxa with high rates of immigration and reproduction and/or taxa with high resistance to disturbance (*e.g.* low-growing diatoms such as *Achnanthes minutissima*, *Cocconeis placentuala*, and *Fragilaria vaucheriae*). Phase 2 leads to greater species richness and requires considerable more time, from one to many months, and is dominated by competitively superior taxa sensitive to disturbance, such as high biomass cyanobacteria and filamentous green taxa (Smolar-Žvanut and Klemenčič 2013). Since flood disturbance can regulate large biomass accumulations, the frequency of disturbance regulates the time available for benthic algal accrual (Figure 4-2), while during the inter-flood period, the availability of light and nutrients, loss by grazing, spatial differences in water velocity and turbulence, and taxa-specific growth strategies and sensitivity to shear stress are important in determining community development (Biggs and Thomsen 1995, Biggs 1996, Biggs et al. 2005).



	Fast Flow				Slow Flow			
	Shaded	Grazers present	Grazers absent	Very bright light	Shaded	Grazers present	Grazers absent	Very bright light
High Nutrients	Shade tolerant species have access to required nutrients	Grazers consume biomass and confer some resistance to flow effects. Nutrients plentiful but rinsed out before can be recycled. Minimal growth on boulder as washed away.	No biomass lost to grazers but potential loss via sloughing as weight increases strain on attachment to substrata. Nutrients rinsed quickly.	Availability of P counteracts photo-inhibition	Shade tolerant species have access to required nutrients	Grazers consume biomass. Nutrients plentiful and recycled but only reach understory if grazers have exposed this. Much competition within phytobenthos	No biomass lost to grazers or flow. Understory light and nutrient limited by overstory resulting in scenescence and potential sloughing. Plentiful growth on boulder as minimal flow effects.	Availability of P counteracts photo-inhibition and self shading of understory
Low Nutrients	Lack of nutrients for shade tolerance	Grazers consume biomass and confer some resistance to flow effects. Nutrients very limited as rinsed out before can be recycled.	No biomass lost to grazers. Nutrients rinsed quickly. Limited loss via sloughing as minimal weight increases.	Lack of nutrients to counteract photo-inhibition	Some recycled nutrients for shade tolerant	Grazers consume biomass and increase nutrients via fertilisation. Nutrients easily recycled.	No biomass lost to grazers or flow. Nutrients recycled but still limited.	Some recycled nutrients to counteract photo-inhibition

Figure 4-1: The impact of flow, light, nutrients, and grazing on periphyton communities. Thick dashed lines indicate biomass in each scenario. Thin dashed lines indicate nutrient transport and cycling. Figure from Law et al. (2011).

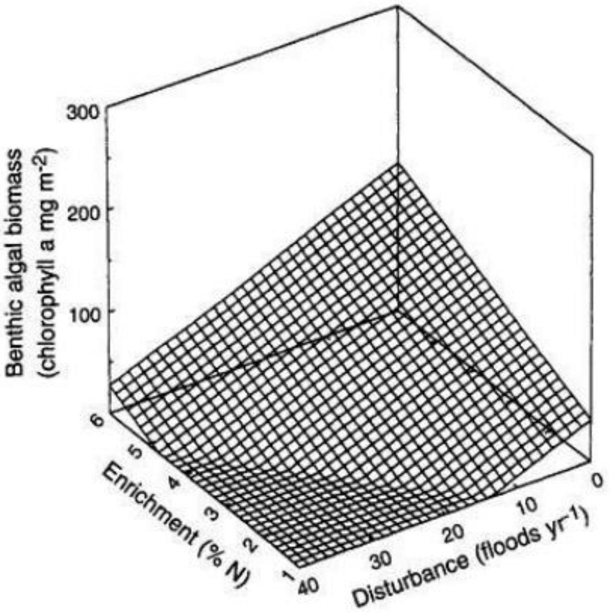


Figure 4-2: Mean monthly benthic chlorophyll-*a* in relation to both flood frequency and nitrogen enrichment. Response surface created from data taken from across 15 sites.Figure from Biggs and Thomsen (1995).

Several studies have examined the effect of river regulation and hydroelectric disturbances on algal communities (Smolar-Žvanut and Mikoš 2013, Smolar-Žvanut and Klemenčič 2013, Tang et al. 2013). Stable environmental low flows have strong effects on algal communities by altering habitat quality (Suren and Riis 2010), decreasing bed stability, and resulting in high algal biomass (Smolar-Žvanut and Mikoš 2013, Smolar-Žvanut and Klemenčič 2013). During hydropeaking, the dry-wet cycling of the lateral margins of the river results in little marginal area contributing to aquatic productivity, since algae are generally unable to tolerate drying conditions (Bergey et al. 2010). In one example on the Colorado river, these dry-wet marginal areas generated ten-fold lower productivity than permanently wet areas (Blinn et al. 1998).

Studies looking at the impacts of regulated rivers on periphyton have primarily focused on diatom communities (Growns and Growns 2001, Wu et al. 2010, Tang et al. 2013), and not on the whole periphyton community (diatoms and soft bodied taxa) which may more representative of overall ecosystem function. While frequent flow disturbance is known to limit periphyton algal diversity (Clausen and Biggs 1997), this has not been explicitly studied in hydropeaking conditions. Floods released from dams may scour periphyton biomass up to 2 km downriver due to the scour (Jakob et al. 2003), but there has been little attention paid to the effect of daily hydropeaking disturbance, and the change of the functional characteristics of the periphyton community under hydropeaking pressures.

In particular, little is known about how hydrologic disturbance may affect the biochemical composition and nutritional quality of the periphyton community.

Periphyton nutritional quality, especially essential fatty acids content, has been shown to vary with light and nutrients (Cashman et al. 2013), and while it is hypothesized to change with other physical habitat conditions, this has not yet been extensively explored in the literature. A recent study has indicated that different algal taxonomic groupings maintain distinctive fatty acid profiles (Taipale et al. 2013), and thus changes to algal diversity by disturbance should be reflected within the fatty acid profile. Wood has previously been shown to increase algal diversity, particularly by increasing shear-stress sensitive taxa, due to the complex texture of the wood surface (Sabater et al. 1998). In addition, sheltered areas around wood pieces, may have a mitigating effect on the scouring high-flows associated with hydropeaking. Therefore, wood may have the potential not only as a refugia for animal species (Hax and Golladay 1998), but to mitigate the effect of scouring high flows on periphyton biofilms.

Any change in the composition of fatty acids, particularly of long-chain highly unsaturated fatty acids which are hypothesized to be limiting resources in aquatic systems (Müller-Navarra 2008), may cause changes in the nutritional base of the ecosystem and have cascading effects on the persistence of consumer communities in these locations. Understanding how the nutritional base of this ecosystem is incredibly important to understanding the dynamics by which hydropeaking affects these disturbed ecosystems.

4.1.6 The benefits of an experimental flume system

The impacts of flow regulation and altered flows are difficult to study because their effects are often confounded by other covarying factors (*i.e.* temperature, sediment deposition, regional land-use), and coordination with local managers and hydroelectric power operators to schedule flows for experimental designs is often difficult or impractical. As a result, experimental flume channels have been suggested as suitable systems to isolate the effect of flow without altering other variables (James and Suren 2009). Flume systems enable varying conditions to be altered in a controlled way and experiments to be replicated.

Few studies have examined the response of downstream biota to repeated hydropeaking events over short-time periods, which may lead to an additive effect on the benthic community (Troelstrup and Hergenrader 1990, Zimmerman et al. 2010, Smokorowski et al. 2011, Miller et al. 2014). Furthermore, the majority of flume experiments have been single-repetitions (Carolli et al. 2012, Bruno et al. 2013), which may be unrepresentative of the actual effect of repeated hydropeaking waves. Repeating flow disturbances in a flume therefore not only allows for the effect of flow to be isolated, but also to look at the change in this disturbance over time with multiple sequential disturbances during a realistic timeframe.

4.2 Research Aims

This chapter examines the influence of the repetition of long-lasting hydropeaking events on periphyton biofilms and whether the structural complexity represented by wood) may mitigate these effects. This study tested the following hypotheses: (1) hydropeaking has a large effect on periphyton resources, as scour from increased discharge is expected to result in reduced periphyton quantity (Chl-*a* and AFDM), and nutritional quality (elemental nutrient and fatty acid content); (2) the magnitude of this effect is greater with increasing hydropeaking intensity; and (3) wood substrate mitigates the effects of hydropeaking on both periphyton quantity and quality.

This hydropeaking study was set up in a series of ongoing experiments at the Fondazione Edmund Mach under the direction of Dr Cristina Bruno and Bruno Maiolini. These experiments have combined both flume and in-situ work to examine the effect of hydropeaking in the Trentino Province of Italy, in collaboration with Faculty of Engineering at the University of Trento.

4.3 Methods

4.3.1 Research area and experimental design

The experiment was conducted in an experimental, open-air, metal flume system located in the riparian zone of the River Fersina at 577 m a.s.l. (46° 04’ 32” N, 11° 16’ 24” E). The Fersina is a 14 km long, snowmelt-fed 2nd order gravel-bed river that originates at 2005 m a.s.l., drains a 171 km^2 catchment, and joins the Adige River at 181 m a.s.l. in Trento, Trentino Province, Northeast Italy. The flume system (Figure 4-3), previously described in Carolli et al. (2012) and Bruno et al. (2013), diverts water directly from the river via a weir (Figure 4-3.a.i) into a collecting tank (Figure 4-3.a.ii), which feeds five, 30 cm wide x 20 m long U-frame metal flumes (bottom surface area: 6.0 m^2; Figure 4-3.a.iii) that contain a sluice gate at the upstream end to control discharge. The flumes had previously been filled to an equal depth of 2 layers of cobbles of approximately 20 cm diameter, and a fine layer of silt/sand/gravel has naturally collected around the stones through deposition from river flows. Water exits the bottom of the flumes through a spout (Figure 4-3.a.iv) where it re-enters the channel.

A baseflow of 0.05 $m^3 s^{-1}$ (velocity: 0.4 $m s^{-1}$) was established in each flume on the 10th of March 2013, and was left unaltered for 33 days until the beginning of the experiment on the 12th of April 2013. Flume treatments were based on a factorial design of substrate type and hydropeaking intensity (Figure 4-4a). Substrates were installed in the flumes 23 days before the experiment, on the 20th of March 2013. Twelve unglazed terracotta tiles (Figure 4-4b; surface area: 240 cm^2) were placed in each flume A and D, and 12 wood substrates (attached to tiles at 45 degrees from the main line of the flow: Figure 4-4b) were placed in flumes B and E (wood surface area: 284 cm^2). Both substrates (6 of each) were placed in flume C. All substrates were equally spaced throughout the 20 m length of all flumes. Periphyton were allowed to colonize the substrates naturally for the remaining 23 days until the start of the experiment, a timeframe sufficient for periphyton accrual to plateau in a previous study (Cashman et al. 2013).

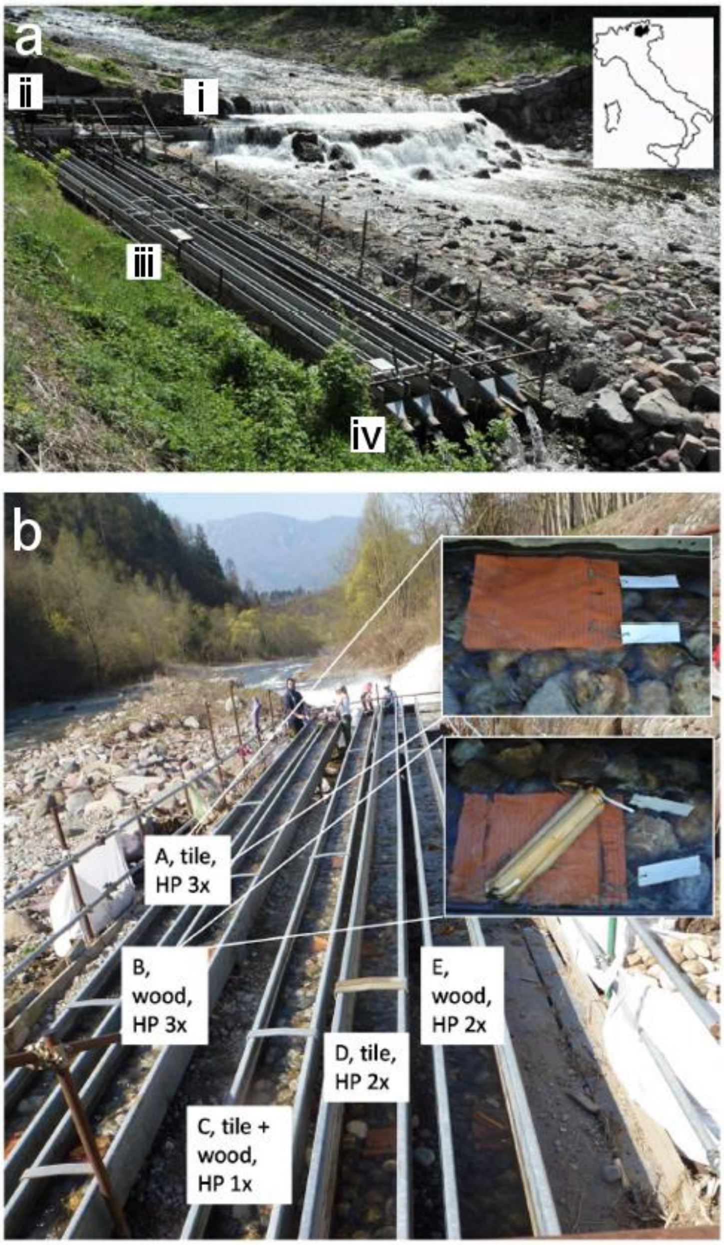


Figure 4-3: Photographs of the experimental flume system alongside the River Fersina a) Water is diverted from the main river channel by the weir (i) into a collecting tank (ii) located just above the flumes. Discharge from the collecting tank into each of the five flumes (iii) is controlled by an adjustable sluice gate. Water exits the bottom of the flumes through a spout (iv) where it re-enters the channel. b) View looking down the flume system from the loading tank, indicating flume name, substrate and hydropeaking treatment in each of the five flumes, along with pictures of both the tile substrate (top) and wood substrate (bottom). White strips at the downflume end of the tiles were used for Simuliidae colonization for a separate experiment. Figure from Bruno et al. (2015).

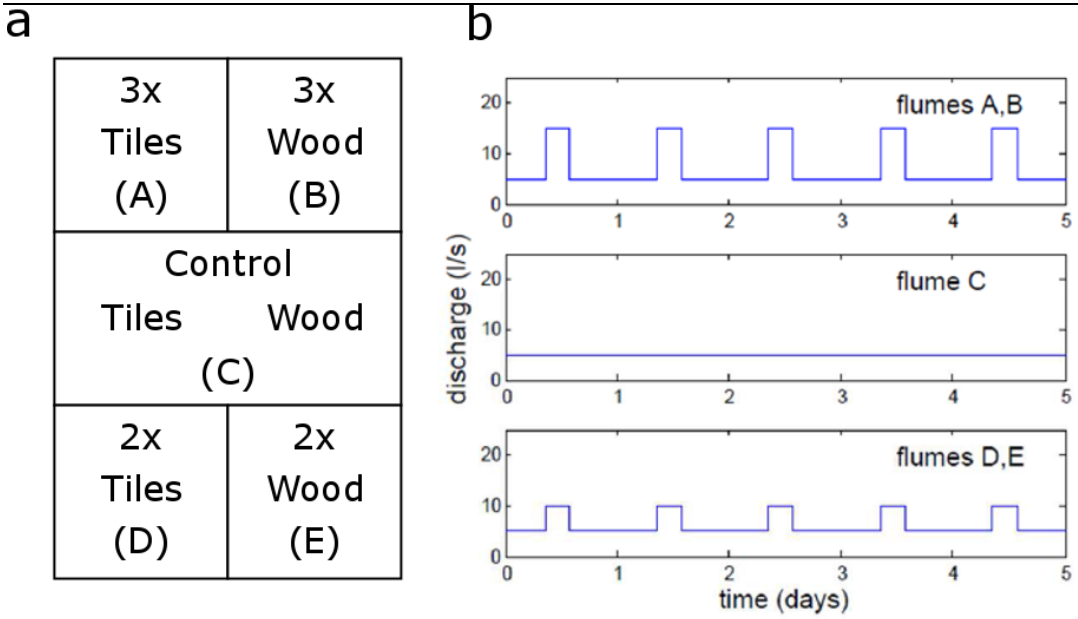


Figure 4-4: a) Factorial design for the 5 flumes within the experiment, showing hydropeaking intensity (3x discharge, 2x discharge, Control), substrate (Tiles, Wood), and flume name (A-E). Flume C had both tiles and wood substrate, which were analysed separately in the analysis. b) Change in discharge due to the hydropeaking treatment in each of the five flumes over the course of the 5-day experiment.Increased discharge lasted for 5 hours per day, followed by a 19 hour baseflow period until repetition the following day. Part b) adapted from Bruno et al. (2015).

Starting on the 12th of April 2013, daily hydropeaking events were simulated in the flumes over the course of 5 consecutive days (Figure 4-4b). In flumes A and B, discharge was increased 3x (to 0.15 m^3 s^{-1}), which resulted in a 2.25x increase in baseflow velocity (to 0.9 m s^{-1}). In flumes D and E, discharge was increased 2x (to 0.10 m^3 s^{-1}), which resulted in a 1.75x increase in baseflow velocity (to 0.7 m s^{-1}). The 5th flume, C, functioned as the control, as it was not subject to hydropeaking and contained both tile and wood substrates. Hydropeaking was conducted by rapidly raising the sluice gate (< 10 s) at the top of each flume until 2x or 3x discharge was reached. Flumes were kept at this increased discharge for five hours and then quickly (< 10 s) returned to baseflow conditions for 19 hours until repetition the following day. The duration of hydropeaking was chosen to fall within the range of hydropeaking operations that occur on regulated rivers within the study region of Trentino (Zolezzi et al. 2011). This hydropeaking simulation was repeated from 9:00 – 14:00 daily for 5 consecutive days (Figure 4-4).

The hydropeaking experiment was repeated for additional replication. The first experiment took place in the spring from 12-18 April 2013, during peak spring snowmelt. The second experiment was originally to take place immediately following the first experiment (following a new colonization period), but during recolonization, a large flood destroyed the established flume setting. The second experiment was then re-established on August 1st, left to colonize over the same timeframe as the first repetition of the experiment, and hydropeaking occurred from 2-6 September 2013. While no longer direct replicates, this staggered timeframe allows for a comparison between responses in both spring and summer seasons.

4.3.2 Periphyton processing and laboratory analysis

Before and after each 5-day experiment, 3 periphyton samples were collected from each flume for its respective substrate type (3 wood in B/E; 3 tiles in A/D; 3 wood and 3 tiles in C) according to Stevenson and Balls (1999). The collected suspensions were mixed, kept on ice, and brought back to the lab where they were frozen at -20°C for less than one week and until all samples could be analysed simultaneously. After thawing, all periphyton samples were homogenized with a hand blender for 5 s and processed within 24 h for biomass (chlorophyll-*a*, ash-free dry mass [AFDM]), elemental nutrient content (carbon, nitrogen, phosphorus content, and C:N:P ratios) and fatty acids. Samples for chlorophyll-*a* were filtered onto a Whatman® 47mm GF/F filter (Sigma Aldritch S.r.l., Milan, Italy)., extracted in 90% acetone and stored at -20°C in the dark until analysis on a Schimadzu spectrophotometer for phaeophytincorrected chlorophyll concentrations (Lorenzen 1967). Periphyton carbon and nitrogen were determined from subsamples dried in 9 x 10 mm tin cups using a Thermo Scientific 2000 CHN analyser. Periphyton phosphorus was determined following a digestion (Solórzano and Sharp 1980) and analysed as SRP (Kopp and McKee 1979). All stoichiometric ratios were determined on a molar basis. Aliquots for AFDM and fatty-acid analysis were dispensed onto pre-weighed, pre-ashed Whatman® 47mm GF/F filters (Sigma Aldritch S.r.l., Milan, Italy). AFDM samples were dried overnight at 80°C, weighed for dry weight, and ashed at 450°C for 2 hours and re-weighed for final ash-weight. Fatty acids samples were stored at -20°C until extraction.

4.3.3 Fatty acid analysis

Fatty acids were extracted in the organic lab at the IGB-Berlin following a method adapted from Torres-Ruiz et al. (2007), and originally modified from Parrish (1999). Samples were extracted in 2 washes of chloroform:methanol (2:1 v/v), sonicated on ice, and the chloroform phase was separated for methylation into fatty acid methyl esters with BF_3 (10–14%) at 80°C. Fatty acid methyl esters were suspended in hexane and measured on an Agilent 6890 gas chromatograph with Agilent 5973-N mass selective detector that was fitted with a CP Sil 88 for FAME fused-silica capillary column (100m x 250 µm x 39 µm) set in splitless mode. Carrier gas (He) flow rate was constant at 0.2 mL min^{-1}. Inlet temperature was 300°C, with initial temperature 70°C with an increase of 720°C min^{-1}. The temperature program was started and held at 80°C for 1 min, increased at a rate of 4°C min^{-1} until a temperature of 220°C, maintained for 4 min, then heated at 4°C min^{-1} until 240°C, where it was maintained for a final 15 min. Detector temperature was set at 280°C. Fatty acid methyl esters were identified by retention times and mass spectra in full scan mode previously calibrated with standards: 37-Component FAME Mix (47885-4), PUFA No1; Marine Source (47033) and PUFA No3; Menhaden Oil (47085-4; all Supelco, Germany). Fatty acid data were examined by fatty acid concentration (standardized per unit periphyton dry mass), as a relevant measure for consumers, and as percent of total fatty acids for determining the total fatty acid profile.

4.3.4 Statistical analysis

A three-way repeated measures factorial design examined the effect of hydropeaking intensity and substrate type over time on periphyton biomass, nutrient content, and fatty acid content and composition. Data were analysed in R statistical software (R Core Group, Vienna, Austria), using a linear model with “season” (April/September), “time” (Before/After), “hydropeaking intensity” (Control, 2x-hydropeaking, 3x-hydropeaking) and “substrate” (Wood/Tiles) as factor variables, which was examined with the function Anova in the package car (Fox et al. 2012). Repeated measures post-hoc pairwise comparisons were completed using an F test with Holm adjusted P values using the testInteractions function in the R package phia (Rosario-Martinez 2013). Fatty acid profiles were ordinated using principal coordinates ordination (PCO), also known as metric dimensional scaling (Gower 1966), based on a Bray-Curtis dissimilarity index. Changes in the fatty acid profile with experimental conditions were examined using a PERmutational Multivariate ANalysis Of VAriance (PERMANOVA) (Anderson 2001), both in R package vegan (Oksanen et al. 2013). Data were log-transformed to best fit statistical assumptions and α was set at 0.05 for all tests.

4.4 Results

4.4.1 Periphyton biomass

Periphyton chlorophyll accumulations at the beginning of the experiment were different between both seasons, with nearly double the chlorophyll accumulation in April (Figure 4-5; April: 2.79 ± 0.56 µg cm^{-2}, September: 1.82 ± 0.13 µg cm^{-2}). While the differences between the two seasons were significant (Month: F = 7.04, df = 1, P = 0.011), this was attributable to less accumulation in April on tiles (Month*Tiles: F = 13.2, df = 1, P = 0.001), as there was no significant difference on wood (Month*Wood: F = 0.003, df = 1, P = 0.950). Chl-*a* concentrations were particularly high in the April experiment in one-flume (D; Tiles, 2x-discharge), due to a patchy colonization of the cryophilic filamentous Chrysophyceae *Hydrurus foetidus* (Vill.), which was subsequently scoured during the hydropeaking experiment (Figure 4-5). In April, chlorophyll concentrations decreased by ~80% for both hydropeaking discharges, although the 3x-discharge treatment resulted in lower absolute Chl-*a* values. In the control, there was also a slight decrease (-25%). In September, however, the decrease was smaller, with a 51% decrease in the 3x-discharge treatment and a 31% decrease in the 2x-discharge, in contrast to the overall increase of 117% in the control. Overall, hydropeaking treatments significantly decreased periphyton chlorophyll (Time*Intensity: F = 4.36, df = 2, P = 0.018), although post-hoc analysis showed that significant decreases in periphyton chl-a were only in the 3x discharge treatment (Time*3x: F = 11.1, df = 1, P = 0.005), and despite the large decrease on the 2x treatment in April, the change in the 2x discharge treatment was not significant (Time*2x: F = 3.21, df = 1, P = 0.117). Response varied by substrate type (Time*Substrate: F = 7.71, df = 1, P = 0.008), as there was a significant loss on tiles

(Time*Tiles: F = 14.5, df =1, P < 0.001), but not on wood (Time*Wood: F = 0.016, df =1, P = 0.901). The response did not vary by month for either the experimental hydropeaking treatments (Month*Time* Intensity: F = 0.166, df = 2, P = 0.848) or by substrate (Month*Time*Substrate: F = 3.453, df = 1, P = 0.069).

Change in periphyton AFDM was highly variable in both hydropeaking treatment and substrate in both seasons (Figure 4-6). There was a significant interaction between Time and Hydropeaking treatment (Time*Intensity: F = 4.53, df = 2, P = 0.016), but post-hoc analysis did not show significant changes in the experimental response of each hydropeaking treatment (all pairwise comparisons: F < 4.50, df = 1, P > 0.117), but instead that final AFDM values were significant smaller in the 3x-hydropeaking treatment compared to both 2x and the control (all pairwise comparisons: F > 8.072, df=1, P < 0.033). There was a significant response during the experiment dependent on substrate (Time*Substrate: F = 10.807, df = 1, P = 0.002), with a significant decrease of AFDM on tile substrates (Time*Tiles: F = 4.257, df = 1, P = 0.045) and an increase on wood substrates (Time*Wood: F = 7.117, df = 1, P = 0.021). No significant differences by month were detected.

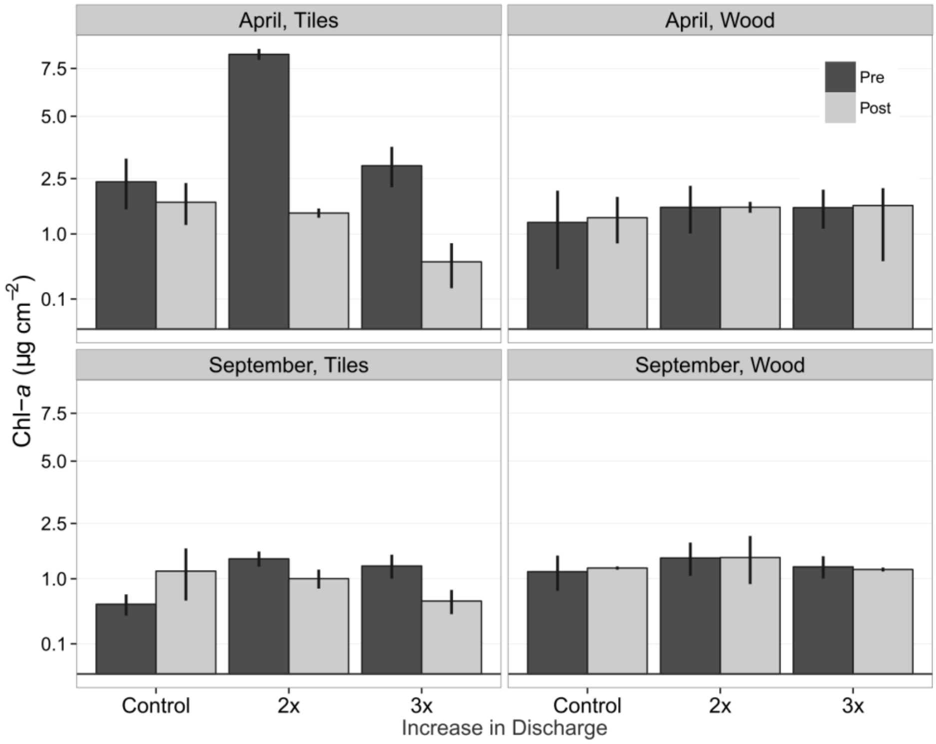


Figure 4-5: Changes in chlorophyll-a concentrations on tile and wood substrates for both hydropeaking intensity treatments in both seasons. Values are mean ± 1 standard error. Data are paired, with pre- and post-experiment samples adjacent for comparison.

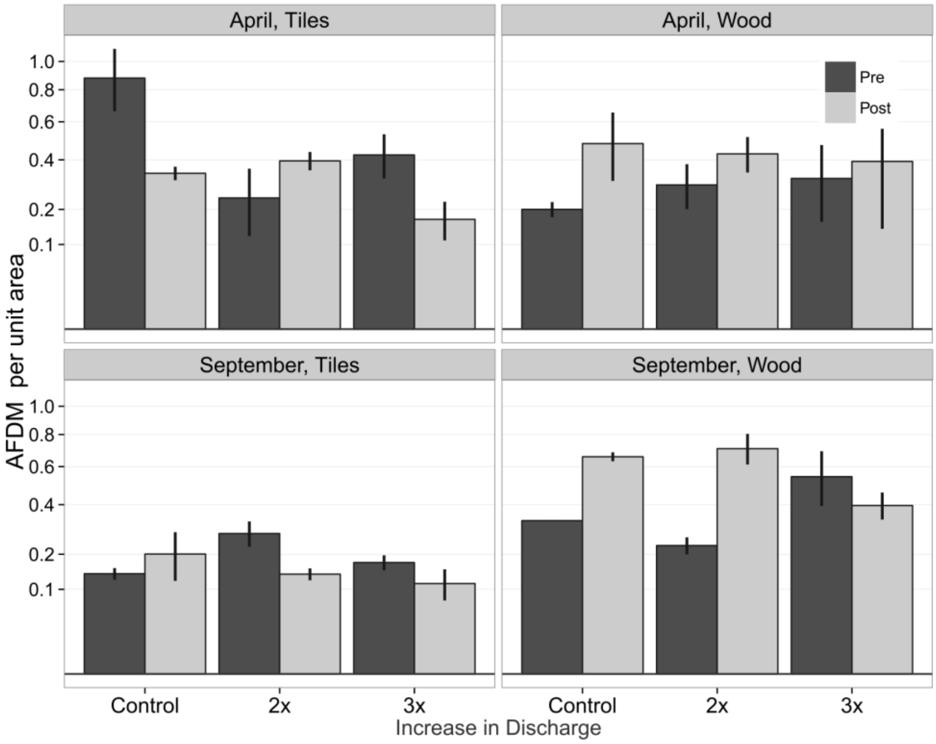


Figure 4-6: Changes in ash-free dry mass on tile and wood substrates for both hydropeaking intensity treatments in both seasons. Values are mean ± 1 standard error. Data are paired, with pre- and post-experiment samples adjacent for comparison.

4.4.2 Nutrient content and stoichiometry

Periphyton nutrient ratios in the experiment often differed (mean April: 190:20:1, September: 186:14:1) from the Redfield's ratio of 119:17:1 C:N:P suggested for optimal growth by periphyton (Hillebrand and Sommer 1999), particularly in C:N. However, periphyton C:N did not significantly vary due to hydropeaking (Time*Intensity: F = 0.556, df =2, P = 0.578), but did change due to different substrates (Figure 4-7; Time*Substrates: F = 12.9, df = 1, P = 0.0008). Pairwise post-hoc analyses indicated that there was a significant decrease in the C:N ratio on tiles substrates (Time*Tiles: F = 5.158, df = 1, P = 0.028) and a significant increase on wood substrates (Time*Wood: F = 7.735, df = 1, P = 0.016). There was no significant change in the response of C:N ratios by month for hydropeaking (Month*Time*Intensity: F = 1.35, df = 2, P = 0.271) or substrate (Month*Time*Substrate: F = 0.0369, df = 1, P = 0.848559). Periphyton C:P varied throughout the experiment (Figure 4-8), but these changes were not predictable for either hydropeaking intensity treatment (Time*Intensity: F = 1.055, df = 2, P = 0.357) or for substrate (Time*Substrate: F = 2.72, df =1, P = 0.1253).

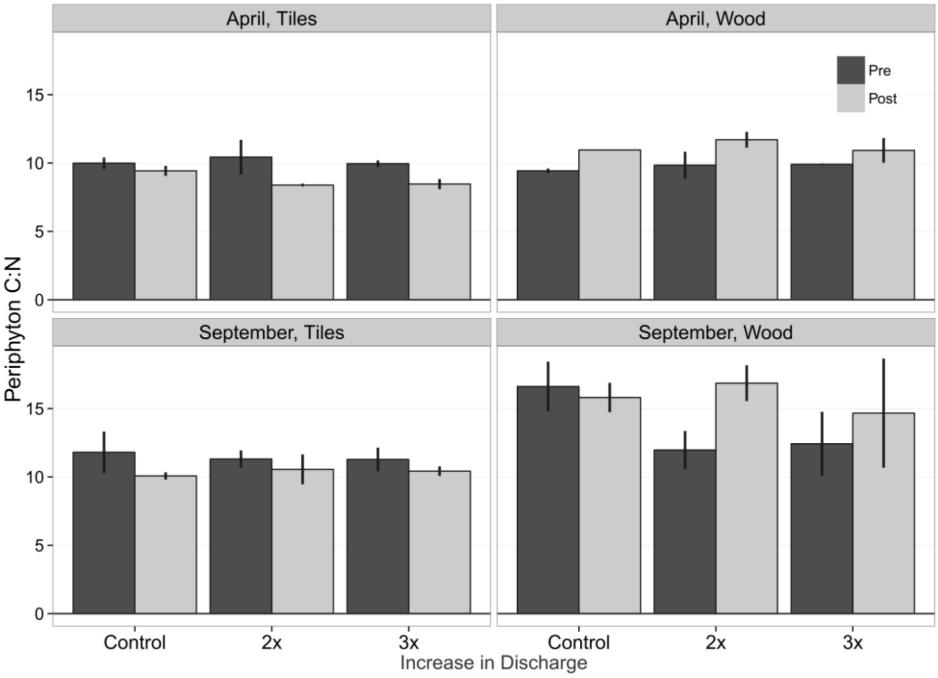


Figure 4-7: Changes in periphyton C:N ratio on tile and wood substrates for both hydropeaking intensity treatments in both season. Values are mean ± 1 standard error. Data are paired, with before and after samples adjacent for comparison. Redfield C:N ratio for periphyton is 7.

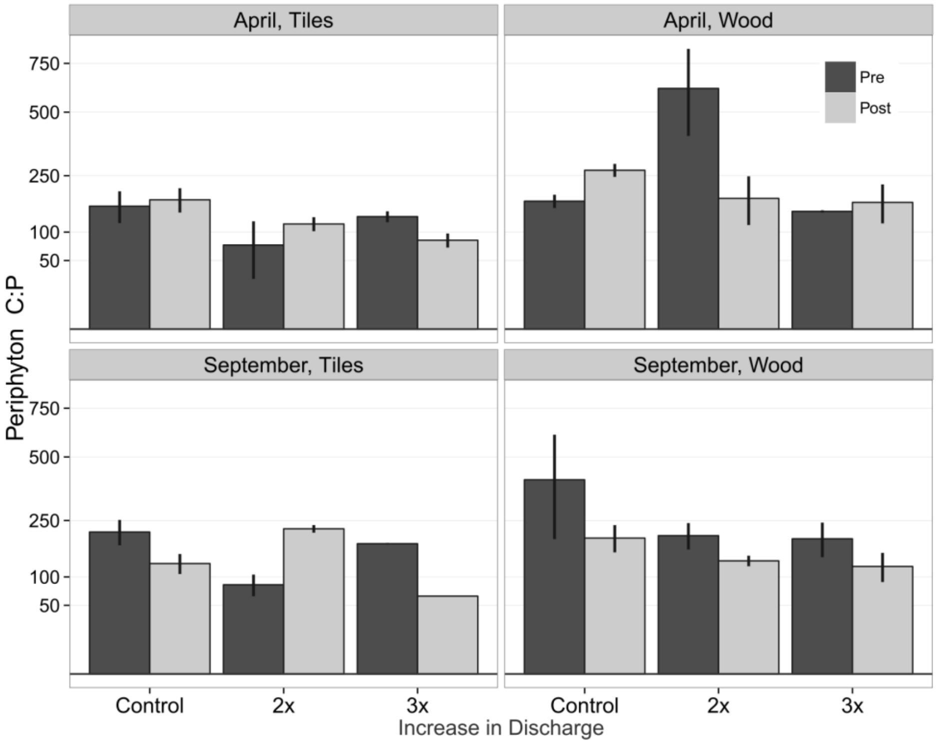


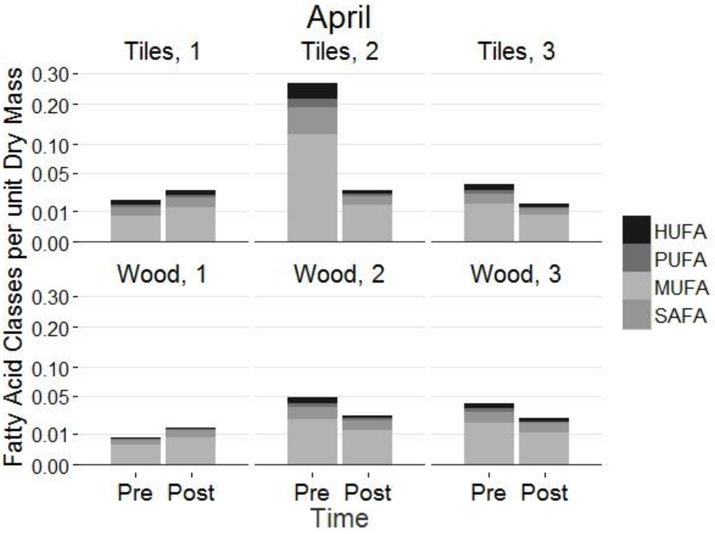
Figure 4-8: Changes in periphyton C:P ratio on tile and wood substrates for both hydropeakingintensity treatments in both season. Values are mean ± 1 standard error. Data are paired, with before and after samples adjacent for comparison. Redfield C:P ratio for periphyton is 119.

4.4.3 Periphyton fatty acids

Both spring (April) and summer (September) fatty acid values are presented here. However, September samples contained low extract volumes due to both smaller seasonal periphyton accrual and additional subsampling in the extraction procedure, which resulted in the majority of fatty acids being below established calibration curves and many fatty acids entirely below the detection-limits of the GC-MS. Thus, September fatty acid values are unreliable and unlikely to be representative of the true fatty acid content of September periphyton. Mechanical failures in GC-MS meant that the low sample concentrations could not be detected for some time and there was no opportunity to re-run samples at higher concentrations within the timeframe of the PhD thesis. Since many fatty acids were not detected at all in September, principal coordinate ordination (PCO) is only presented for April.

Total fatty acid concentration standardized per unit dry mass of periphyton changed with hydropeaking treatment in April, increasing 57% in the control, but decreasing by 90% and 55% on 2x- and 3x- discharge hydropeaking treatments respectively (Figure 4-9). The change across the experiment was significantly different by hydropeaking intensity (Time*Intensity, Pre-Post: $F = 6.781$, $P < 0.001$) but not according to substrate (Time*Substrate, Pre-Post: $F = 1.851$, $P = 0.176$). However, differences between hydropeaking treatment were only statistically significant in the 2x hydropeaking treatment (Time*2x: $F = 7.80$, $df = 1$, $P = 0.028$), not in the 3x treatment (Time*3x: $F = 4.380$, $df = 1$, $P = 0.092$).

The decrease in total fatty acid content was not equivalent across the different classes of fatty acids. Saturated fatty acids (SAFAs) were the most abundant fatty acid category in the initial sampling of periphyton from all flumes (44 – 50% of all fatty acids), followed by monounsaturated fatty acids (MUFAs; 25-29%), 20-C highly-unsaturated fatty acids (HUFAs; 13-20%), and 18-C polyunsaturated fatty acids (PUFAs; 7-9%). The greatest decrease in fatty acid categories occurred in the physiologically important HUFAs, where HUFA per unit dry mass decreased 80% in the 2x-discharge treatment, 55% in the 3x-discharge treatment, and increased approximately 70% in the control (Figure 4-10). HUFA content was significantly affected by hydropeaking treatment (Time*Intensity: $F = 5.9176$, $df = 4$, $P = 0.001$), however, this response was in hydropeaking was only significantly decreased in the 2x treatment (Time*2x: $F = 12.107$, $df = 1$, $P = 0.005$) and not in the 3x treatment (Time*3x: $F = 3.158$, $df = 1$, $P = 0.174$), and there was no difference in response by substrate (Time*Substrate: $F = 1.622$, $df = 1$, $F = 0.219$).



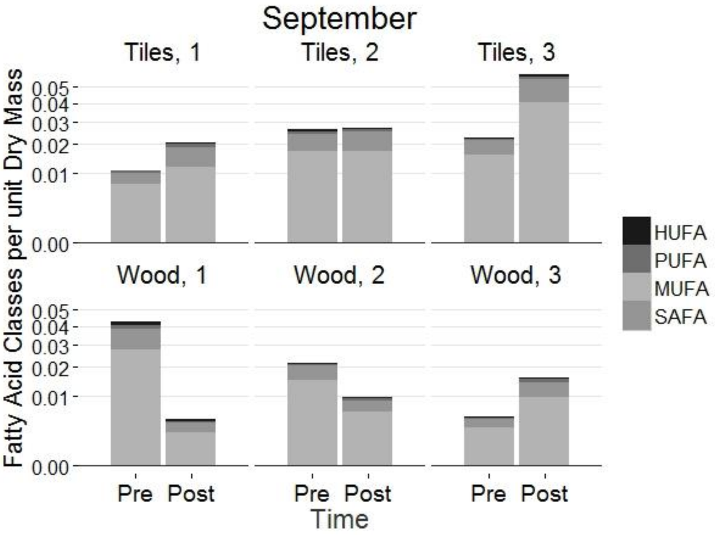


Figure 4-9: Changes in the mean fatty acid classes per unit dry mass for the three hydropeaking treatments. Note the difference in sample scale between April and September and relative lack of PUFA and HUFA detected in September.

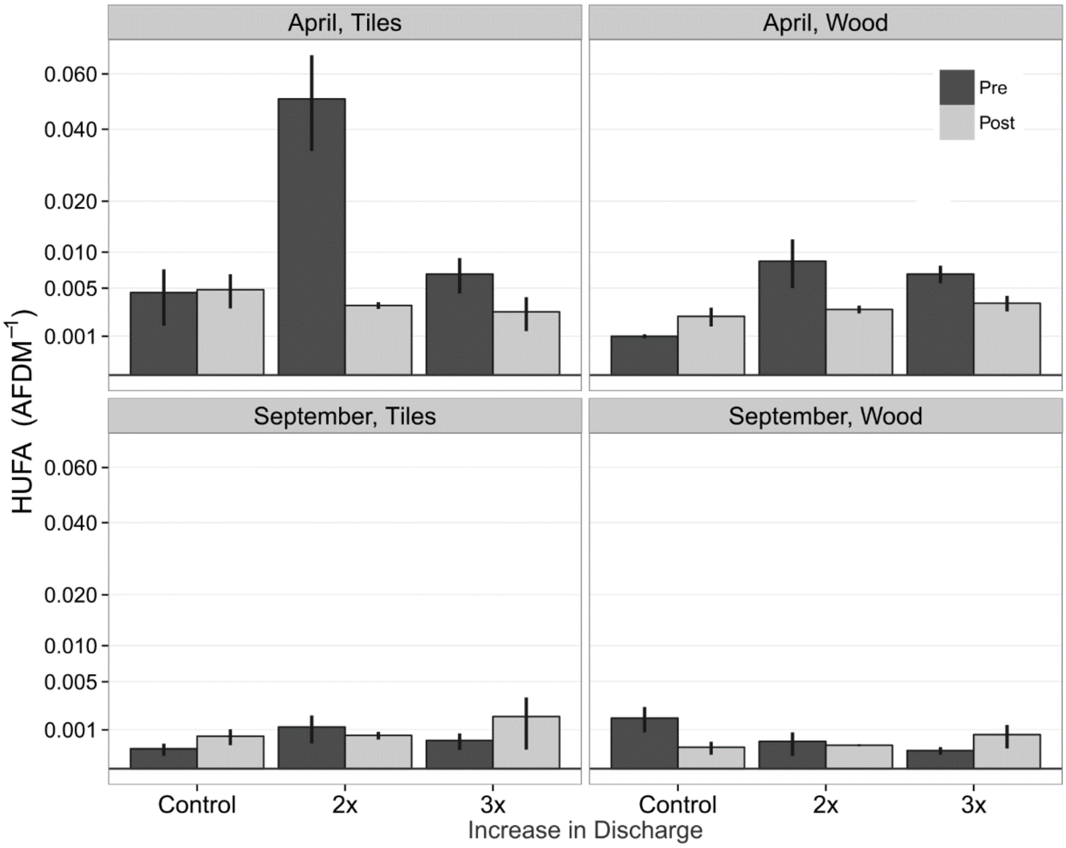


Figure 4-10: Change in 20-C highly unsaturated fatty acids (HUFA) per unit dry mass of periphyton for both seasonal experiments. Note the lower values in September.

There was also a significant loss in the physiologically important highly-unsaturated eicosapentaenoic acid (EPA: 20:5ω3) for both the 2x treatment (F = 9.743, df = 1, P = 0.014) and the 3x treatment (F = 5.165, df = 1, P = 0.047). The 2x treatment also had significant losses in both docosahexaenoic acid (DHA; 22:6ω3; F = 18.556, df = 1, P < 0.001) and arachidonic acid (ARA; 20:4ω6; F = 8.223, df = 1, P = 0.026), but losses were not significant in the 3x treatment (DHA: F = 3.448, df = 1, P = 0.149; ARA: F = 0.462, df = 1, P = 0.508). The ω3:ω6 ratio decreased with hydropeaking in both the 2x (F = 8.483, df = 1, P = 0.021) and 3x (F = 7.478, df = 1, P = 0.022) treatments, but this was not significantly different by substrate (F = 1.144, df = 1, P = 0.333).

The total fatty acid profile for April, when ordinated in a principal coordinates analysis, showed distinct fatty acid profiles according to both substrate and before/after periods of the hydropeaking experiment (Figure 4-11). The primary axis, which explained 55.8% of the variation, was negatively correlated with essential highly unsaturated fatty acids (*i.e.* EPA and DHA) and positively with many saturated fatty acids (*i.e.* 16:0, 18:0) and can generally be considered a gradient in nutritional quality. The 2nd axis, which explained 13.4% of the variation, was negatively correlated with 14:0 and both trans (18:2ω6t) and cis (18:2ω6t) forms of linoleic acid and positively correlated with 16:1 and the cis and trans forms of 18:1ω9. Fatty acid profiles were significantly different by substrate (PERMANOVA: Substrate: Pseudo-F = 4.548, P = 0.005), with tile and wood substrates largely separating along axis 2, with tiles containing more 14:0 and 18:2ω6 and wood containing more 16:1 and 18:1ω9. Before and after the hydropeaking experiment also resulted in different profiles (PERMANOVA: Time*Hydropeaking: Pseudo-F = 2.122, P = 0.037), indicting a shift in profile away from EPA and DHA towards 16:0 and other saturated fatty acids.

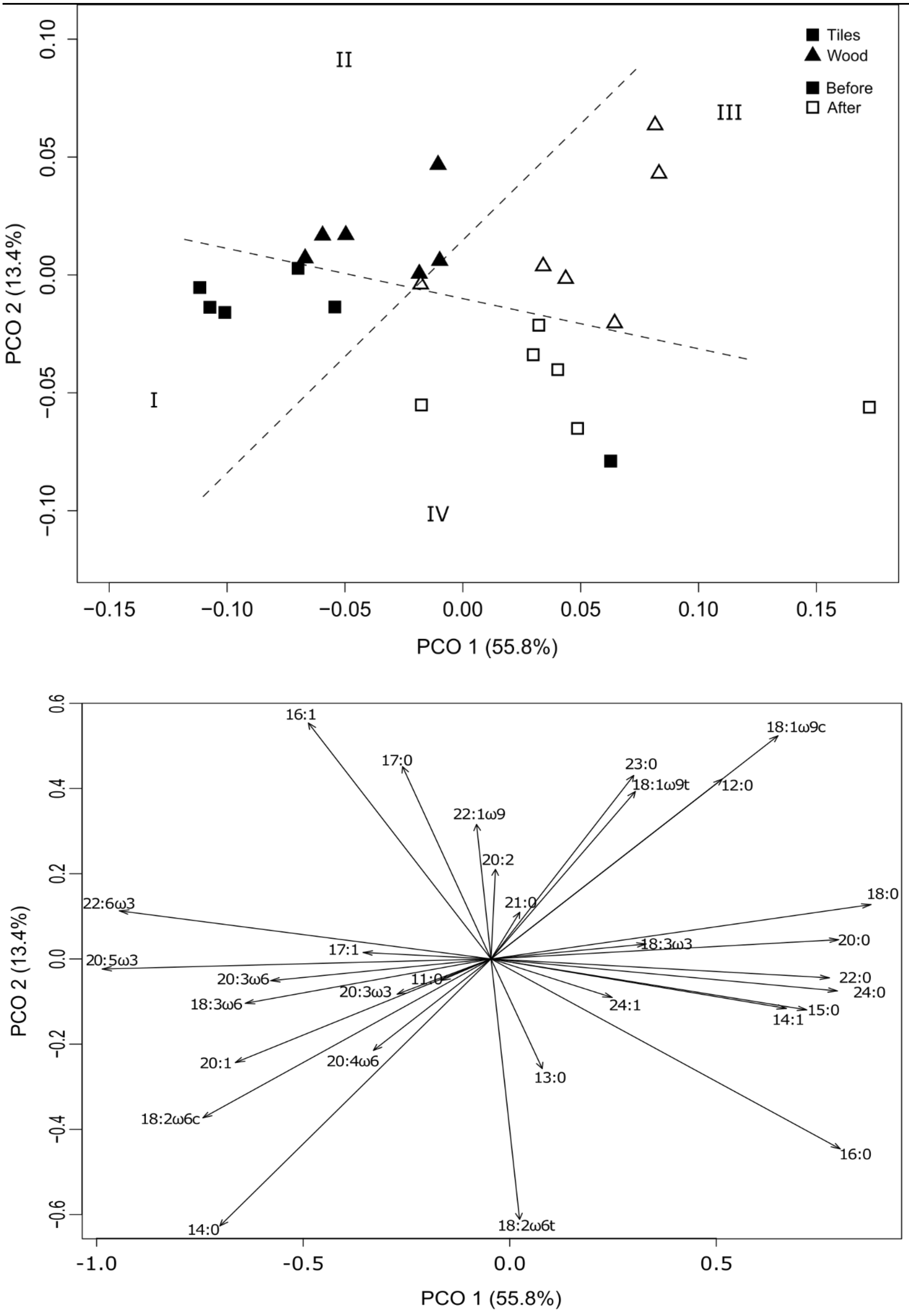


Figure 4-11: Principal coordinates ordination (metric multidimensional scaling) of periphyton fatty acid profiles both before (filled symbols) and after (hollow symbols) the hydropeaking experiment on both tiles (square) and wood (triangle) substrates of only hydropeaking treatments (control excluded for clarity). PCO axis 1 accounts for 55.8% of the total variation, while axis 2 accounts for 13.4%. Substrates and before/after experiment are separated into 4 different quadrants (I-IV). Bottom figure shows the relationship between axes and individual fatty acids.

4.5 Discussion

This study examined the potential for wood substrates to mitigate the effect of 5 days of repeated hydropeaking on periphyton communities. The experiments showed that hydropeaking had a significant effect on reducing both the biomass and the nutritional quality of the periphyton. Since periphyton are one of the most important food resources for benthic consumers in river ecosystems (Torres-Ruiz et al. 2007), further limitations on the quantity nutritionally important biochemical components (HUFA) of periphyton may have further effects on ecosystem processes and macroinvertebrate consumers in hydropeaking-impacted rivers.

Overall periphyton biomass at the start of the experiment was low compared to other studies in alpine areas (Biggs and Close 1989), and an increase in biomass in the September experimental control suggests that periphyton biomass growth had not yet plateaued at the start of the experiment. Even though low biomass biofilms are typically more strongly-attached and more flow-resistant than larger accumulations of biomass (Biggs and Close 1989, Biggs 1996), in this study hydropeaking still resulted in the scour of periphyton Chl-*a* on tile substrates. This degree of scour likely would have been even greater with larger accumulations of biomass (*e.g.* loss of *Hydrurus* in flume D) and increasing hydropeaking intensity. In contrast, wood substrates mitigated this scour, as they did not see any significant change in chlorophyll-*a* content. This could be explained by the increased roughness on wood and the greater strength of algal attachment on wood substrates (Sabater et al. 1998), as well as the presence of sheltered areas of lower shear stress created by wood.. However, there was no predictable response seen in ash-free dry mass to hydropeaking on either substrate. As Chlorophyll-*a* represents the autotrophic biomass contained within the periphyton, while AFDM is representative of the entire autotrophic and heterotrophic community (*i.e.* bacteria, fungi, protists, and the extra-cellular protein matrix), this suggest that hydropeaking preferentially scours algal biomass, while the remainder of the heterotrophic community can persist through hydropeaking flows.

This study demonstrates that the periphyton community changes with hydromorphological alteration, not only by changes to the flow regime, but also to the heterogeneity of substrates in the river channel. While this experiment occurred only over the course of 5-days, examinations over longer time-scales might reveal more changes to the periphyton community that were seen in this limited-timeframe experiment. However, while some recent studies have concluded that the periphyton community does not alter with flow regulation (Growns and Growns 2001, Wu et al. 2010, Tang et al. 2013), these have analysed only the diatom fraction and not the overall periphyton community (diatom and soft-body taxa). This study examined fatty acid content, not only for the implication of nutritional quality for consumers, but also as a proxy for changes in community composition, as fatty acid content has been shown to be directly related to taxonomic groupings within algae (Taipale et al. 2013) and can contain indicator bacteria or fungal fatty acids. Therefore, the different fatty acid profiles between tile and wood substrates, and before and after hydropeaking are expected to reflect a shift in overall periphyton composition.

Hydropeaking created a greatest scour effect in the spring replication of the experiment, likely due to the patchy colonization by *Hydrurus foetidus* (Villars), and a higher load of suspended sediments observed in the water column, which normally occurs during the spring-snowmelt in alpine rivers (Füreder et al. 2001, Lenzi et al.

2003). The spring snowmelt is typically associated with dislodged *H. foetidus* in Alpine rivers (Robinson et al. 2002), and increased suspended sediments can increase scour and abrasion of other components of the benthic biofilms, particularly of diatoms, whose silica shells are vulnerable to damage by suspended sediments (Delgado et al. 1991, Francoeur and Biggs 2006). A non-quantitative microscope examination suggests that the periphyton biofilm was primarily composed of mainly adnate diatoms (dominated by *Ceratoneis* sp, *Anchnanthes* spp., *Diatoma* sp.) and a small unidentified coccoid cyanobacteria. Other taxa present include the diatom taxa *Fragilaria* spp*., Nitzchia spp.*, *Encyonmea minutum*, and *Cocconeis placentula*, as well as the Chrysophyceae macro-algae *Hydrurus foetidus*. These examinations also exhibited a high frequency of broken diatom frustules, providing further evidence of damage by transported sediment. This suggests that the sediment load in water released from hydropower plants may also play a role in the impacts on downstream communities.

There were few changes in periphyton-C, -N, or -P content with hydropeaking, but there was a change in periphyton C:N ratio based on substrate type. Periphyton C:N decreased on tiles, suggesting further maturation and concentration of nitrogen in the biofilm, while increasing C:N on wood substrates may indicate increased utilization of C directly from the wood tissues. However, all C:N and most C:P values were greater than the Redfield Ratio of 7 and 119 for C:N and C:P values respectively. The Redfield Ratio is the theoretical nutrient ratio needed for optimal periphyton growth, and deviation from these values may suggest growth limitation by one or both nutrients (Hillebrand and Sommer 1999). These ratios suggest that nutrients may partly be limiting the growth of the periphyton in this ecosystem, although the ratio does not account other physical habitat limitations such as flow or light. However, while there were few changes in elemental nutrient content, there were substantial changes in fatty acid content standardized by dry mass of the periphyton. This suggests that the nutritional quality of food resources may be changing with alterations to physical habitat that are not detected in traditional stoichiometric ratio measurements of food quality, as seen in a previous study (Cashman et al. 2013).

Changes in fatty acid content were standardized by dry mass of the periphyton. This measure controls for the change in biomass with scour, and is expected to be the most relevant to periphyton feeding taxa as it quantifies the amount of fatty acids obtained per mg of periphyton consumed. Hydropeaking in the 2x treatment decreased all individual fatty acids and fatty acid classes in the periphyton, with the greatest decrease in the HUFAs, especially of the physiologically important EPA and DHA. The 3x hydropeaking treatment frequently resulted in the lowest fatty acid values in the study, but the difference before and after the experiment in many specific fatty acids was non-significant. However, the 3x hydropeaking treatment did result in a significant decrease in EPA content, along with an increased ω3:ω6 ratio, which must be balanced in the diet of consumers (Sargent et al. 1999). Ordination of the fatty acid profiles also resulted in a clear separation from before to after hydropeaking, accounting for a loss in HUFA and increase in saturated fatty acids, indicating a clear shift in the periphyton community. While no quantitative microscopy work was completed to assess periphyton community composition, this finding may support a recent field study in the eastern European Alps that demonstrated a decrease of periphyton biodiversity in hydropeaking rivers (Smolar-Žvanut and Mikoš 2013).

The repetition of long-lasting hydropeaking events did result in a significant loss of fatty acid content on wood substrates, including of HUFA. However, since algal biomass was not scoured on wood substrate as it was on tiles, this resulted in wood retaining a greater amount of fatty acids per unit area of substrate, an effective increase in the availability of fatty acids for consumers, even if fatty acids decreased by weight as a proportion of the biofilm. In addition, wood substrate had a significantly different fatty acid profile compared to tiles, resulting in a greater diversity of fatty acids available for consumers. Wood provided more 18:1ω9 (oleic acid, OA), while tiles contained more arachidonic acid (20:4ω6) and its precursor linoleic acid (18:2ω6).

4.5.1 Conclusions

This experimental study is the first to demonstrate that hydropeaking may preferentially remove algal biomass and reduce the nutritional quality of periphyton for aquatic consumers in hydropeaking regulated rivers, causing longitudinal discontinuities downstream of dams in both food quantity but also food biochemical quality. The effects of hydropeaking on periphyton biomass as seen in this study are in accordance with studies examining the effects of experimental floods released from reservoirs in alpine rivers . Although not studied in the context of the daily repetition of hydropeaking rivers, these experimental floods diminished periphyton biomass by up to 2 km downriver (Jakob et al. 2003). However, the experimental study contained in this chapter examined repeated high flow, totaling 25 hours over 5 days, and suggests that the daily repetition of hydropeaking does not provide sufficient timing for periphyton to recover after disturbance. Therefore, this “bottom-up” daily disturbance on basal food resources may be incredibly important in shaping the longitudinal distribution of macroinvertebrate communities below hydropeaking dams, which has previously been predominantly attributed primarily to benthic depletion by catastrophic drift (Céréghino et al. 2002, Céréghino et al. 2004, Bruno et al. 2009). As hydropeaking diminishes the quantity and quality of periphyton, alternative basal food sources, particularly seston released from the reservoir during hydropeaking, are likely to increase in importance in the trophic base and drive a shift in community structure, as suggested by high densities of collector-filterer taxa downstream of dams (Voelz and Ward 1996). Those taxa not able to feed on drifting seston may behaviourally drift out of the system due to the limited quantity and quality of accessible benthic food resources, or omnivorous taxa may also increase carnivory to obtain limited HUFA in their diets. Hydropeaking is therefore expected to substantially alter the downstream ecosystem by altering the dominant patterns of energy flow and basal food support.

Wood has the potential to mitigate some of these impacts, by retaining the availability of limiting biochemical components primarily through higher periphyton biomass. Furthermore, this study suggests that these ecosystems in the absence of sufficient habitat heterogeneity are particularly vulnerable to disturbance, and that the availability might increase the resilience of downstream ecosystems. This provides further, ecologically grounded support for restoration using wood in rivers affected by hydropeaking and other extreme flow regimes in order to mitigate the negative impacts on instream communities. Improving structural complexity and the availability of wood in hydropeaking-impacted rivers can therefore potentially mitigate serial discontinuities in downriver primary production, changes to consumer communities, and alterations to the food web.

Chapter 5

Large wood in a lowland river enhances resource availability as demonstrated by combined fatty acid and stable isotope analyses

5.1 Background

Large wood may influence the abundance and composition of local consumers due to its effect on the availability and composition of available basal food resources. While wood can be directly consumed as food for xylophagous species, these taxa are generally rare (Anderson et al. 1978, Anderson et al. 1984, Anderson 1989, Hoffman and Hering 2000), and instead wood can change availability of other allochthonous ("terrestrial") and autochthonous ("aquatic") sources. The structure of large wood can trap drifting leaves, twigs, and other coarse transported matter, and its effect on nearby flows can induce the settling of fine sediment and other organic matter, increasing organic matter retention around wood (Bilby and Likens 1980, Bilby 1981). Furthermore, the erosion and decay of the wood surface can also contribute to increased organic matter within the reach (Ward and Aumen 1986). In addition, the increased residence time and quantity of trapped organic matter may result in greater microbial processing and the quality and relative importance of allochthonous matter for the food web (Smock et al. 1989, Fry and Fuller 1991). Large wood can also increase autochthonous productivity by increasing the total surface area of hard substrate available to support greater autochthonous production of biofilms, filamentous algae, or bryophytes (Hax and Golladay 1993, Wondzell and Bisson

2003). The ability for large wood to alter the relative availability and quality of both allochthonous and autochthonous basal resources may affect the trophic base of macroinvertebrate assemblages surrounding large wood, and thus result in an altered food web. No studies are currently known that have examined how large wood can cause a shift in the trophic bases of these communities.

The trophic base of heavily-shaded stream ecosystems have traditionally been hypothesized to be supported by allochthonous (terrestrial) organic inputs of primarily autumn-shed leaves (*i.e.* River Continuum Concept: Vannote et al., 1980; Smock et al., 1989). Similarly, sand-bed rivers that have minimal in-steam production and high terrestrial inputs may also be considered to be supported primarily by terrestrial matter along the same conceptual framework. However, allochthonous resources are recalcitrant, have lower concentrations of nitrogen and phosphorus, and contain fewer other essential biochemical components such as fatty acids than more labile autochthonous sources (Brett and Müller-Navarra 1997, Thorp and Delong 2002, Torres-Ruiz et al. 2007), and recent assimilation-based food web analyses have demonstrated that even in heavily-shaded food webs, the trophic base can be dominated by less-abundant autochthonous sources of superior nutritional-quality (Torres-Ruiz et al. 2007, Lau et al. 2008, Brett et al. 2009a, Lau et al. 2009b, Torres-Ruiz et al. 2010, Lau et al. 2014, Taipale et al. 2014).

Assimilation-based food web analyses utilize chemical biomarkers to trace the relative importance of food sources in the diet and account for variable assimilation rates integrated across time (Parkyn et al. 2001). Generally, these methods are more sensitive to rare food items that contain biochemical compounds essential for consumers and are considered more reliably indicative of long-term diet than traditional ingestion-based food web methods (Iverson et al. 2004). Stable isotope analysis (SIA) is the most common assimilation-based method, and uses changes in the carbon and nitrogen isotopic values from food resources to consumers to indicate the food web's trophic base and estimate food chain length. In combination with Bayesian mixing models (i.e. MixSIR and SIAR), stable isotopes can reasonably account for mixed trophy and provide quantitative estimations of diet composition (Parnell et al. 2008). However, basal resources with overlapping signatures, high levels of mixed trophy among consumers, and statistical limitations from using a limited number of tracers (over-determination) can lead to difficulty in the interpretation of the datasets using stable isotopes alone, as has been explored in several reviews (El-Sabaawi et al. 2009, Allan et al. 2010).

Fatty acid biomarkers are an alternative method for examining trophic relationships, as certain fatty acids are only synthesized in biologically relevant amounts by particular phylogenetic lineages (*i.e.* bacteria, diatoms, green plants), and thus can be traced through the aquatic environment even in cases of mixed trophy (Gladyshev et al. 2009). In contrast to the two source signals (C/N) used in stable isotope analysis, FA avoids many of the problems of mixed source signals and statistical over-determination common to stable isotope analysis by using more than a dozen specific fatty acid biomarkers tracers. In addition, while stable isotopes can have large seasonal shifts in consumers, FA signatures maintain relatively consistent profiles reliably predictive of the taxonomic grouping of primary producers (Dethier et al. 2013). The combination of fatty acids with stable isotopes can help facilitate the interpretation of both data sets, particularly in the case of mixed trophy (Galloway et al. 2012). The advantages of combining these approaches has been increasingly used in recent studies (Alfaro et al. 2006, Budge et al. 2008, El-Sabaawi et al. 2009, Allan et al. 2010, Wang et al. 2014) although have primarily focused on marine, tidal, or estuarine systems, with the few known studies in river systems restricted to a limited number of taxa (Lau et al. 2009a, Gladyshev et al. 2012).

5.2 Research Aims

This chapter examines how large wood may affect the trophic base of the macroinvertebrate assemblage in a lowland, sand bed river through an approach combining stable isotope analysis (SIA) and fatty acid (FA) biomarkers. Particularly since ecosystem productivity in sand bed rivers is generally very low due to sediment instability (Popperl 1996, Atkinson et al. 2008), large wood is expected to have a large effect on the food web by increasing the availability of both autochthonous and allochthonous resources for consumers. As a result, this chapter tests the following hypotheses: (1) large wood increases biomass of the community assemblage and results in an altered consumer composition on and around LW logs compared to more distal channel areas; (2) specific diets are different between wood and non-wood habitats, with more consumption of high quality autochthonous resources around wood habitats; and (3) the overall trophic base of the system is supported by autochthonous, rather than allochthonous, production.

This study has been conducted in collaboration with Francesca Pilotto at the IGB Berlin (SMART EMJD PhD candidate), and has been prepared as a separate joint manuscript (Cashman et al., *in prep*). Analysis of stable isotope data was conducted by Francesca Pilotto, and fatty acid data was conducted by Matthew J. Cashman, the author of this thesis. This study is one of a set of ongoing studies on the role of wood in lowland sand-bed rivers, conducted in the Drawa National Park, Poland.

5.3 Methods

5.3.1 Field procedures

Field sampling was carried out on 25-26 April 2012 in the Płociczna River of the Drawa National Park in Western Poland (Figure 5-1). The Drawa National Park is in the southern part of the Pomeranian Lake District, with a geology of early-glacial outwash plains and land cover consisting of mixed coniferous plantation and hardwoods. The Płociczna is a 41 km long lowland, sand-bed river that flows through a series of lakes until its confluence with the Drawa River, and the riparian zone is dominated by alder (*Alnus* sp.). Sampling was conducted 1 km downstream of Lake Sitno, a 67 ha^{-1} eutrophic throughflow lake, at a reach with minimal large wood ("non-wood") and a second reach an additional 200 m downstream with higher natural LW loadings ("wood"). Large wood accumulations consisted of single logs or with some branches, and wood orientation was uniformly aligned perpendicular to channel flow. Due to the low gradient and stream power of the river, there was no evidence of large wood having been transported or re-orientated.

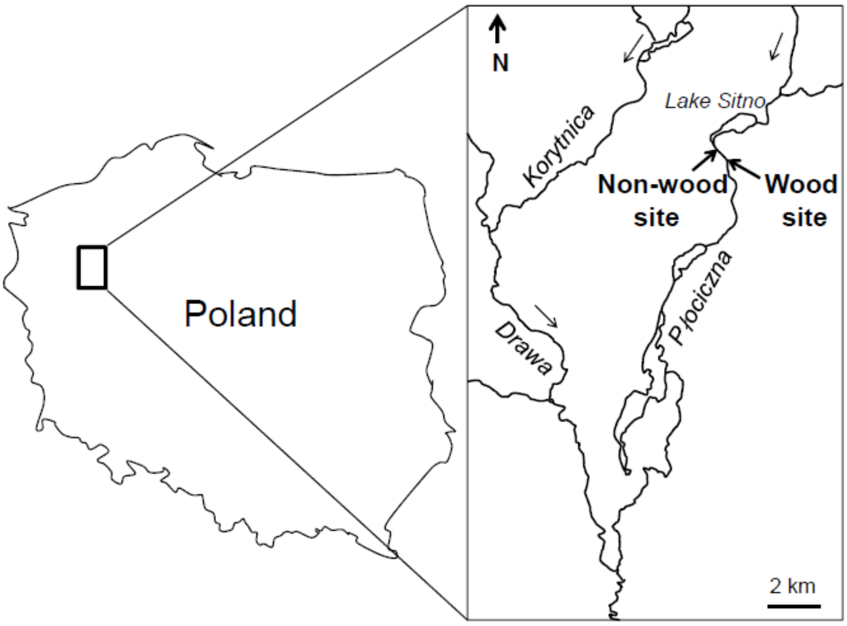


Figure 5-1: Study locations on the Płociczna River in the Drawa National Park, Poland, at the southern part of the Pomeranian Lake District. The Płociczna flows through a series of lakes before its confluence with the Drawa, and both non-wood and wood site sampling locations were located approximately 1 km downriver of the outlet to Lake Sitno. Figure from Cashman et al. (in prep).

Basal food resources were sampled from each reach and included wood, grass, leaf litter, sediments, bryophytes, filamentous algae, periphyton collected on wood ("wood periphyton"), periphyton collected on mussel shells ("mussel periphyton"), and transported organic matter ("TOM"). 3 replicate samples were collected for each resource type. Leaf litter and grass were collected from the riparian zone. The top 5-cm of sediment (sand and organic matter deposits) were collected with a Perspex sediment core. Bryophytes were collected from both wood and trailing riparian vegetation on the river banks. The filamentous green alga, *Cladophora* sp., was only found in the wood reach and collected off submerged pieces of wood, and was cleaned of organic matter and epiphytes under a 10x dissecting microscope in the lab. Wood periphyton was also collected from submerged pieces of large wood, which were sampled for periphyton on the river bank using a toothbrush. Small pieces of woody debris (*i.e.* bark, small branches) were present in the non-wood site and were sampled for the wood periphyton samples in the non-wood reach. After periphyton was removed from the wood surface, wood fragments were broken and removed with a razor blade and screwdriver for the wood sample. Mussel periphyton was collected in the non-wood reach with a toothbrush, as mussels were the only other hard substrate available in the channel. All periphyton slurries were collected in vials and put on ice until return to the laboratory. TOM was collected mid-river with a 125 µm phytoplankton net over 30 minutes at 3 equidistant points (upstream, mid-point, downstream) along 100 m of each reach. The isotopic signature of total seston was further inferred from the isotopic signature of bulk unionid mussel tissue ("unio-derived seston": *Unio tumidus* and *Unio pictorum*), as unionid signatures have been previously used as a reliable time-integrated proxy for the isotopic values of total seston (Post 2002, Atkinson et al. 2013).

Macroinvertebrates were collected from 6 replicate pieces of large wood. One sample was taken directly from the wood surface (WW), by brushing an area of 0.26 m^2 in a hand net. Macroinvertebrates samples were also collected from five Surber samples (23x23 cm, mesh size: 500 µm) upstream, laterally, and downstream of each wood piece, and pooled for the wood sediment collection (WS; total surface area: 0.26 m^2). Six replicate samples were also collected from the non-wood sediment by pooling 5 Surber samplers (NW; 0.26 m^2). In all, macroinvertebrate assemblages were sampled from two wood-associated substrates (WW and WS) and one non-wood substrate (NW). Macroinvertebrates were sorted in the field, identified under a 10x microscope in the lab, and left alive for >20 h to allow for gut clearance.

5.3.2 Sample processing & extraction

Periphyton and TOM slurries were filtered onto pre-ashed 25-mm Whatman® GF/F filters (Sigma Aldritch Chemie Gmbh, Munich, Germany). Leaves and grass were ground into a fine powder with a ball tissue grinder. Whole macroinvertebrates (singly or in pooled groups for low-mass animals) were used for the analysis, and separated into subsamples of the most common taxa for stable isotope and fatty acid analyses. For stable isotopes, animals were dried at 60°C for 48 h, weighed, and ground into a fine powder with a ball tissue grinder. 1 mg subsamples of each animal and 1 – 30 mg subsamples of each food resource were placed in 4 x 6 mm tin capsules and sent for analysis at the UC Davis Stable Isotope Facility.

All fatty acid samples were stored in a -80°C freezer until extraction. Fatty acids were extracted in the organic lab at the IGB-Berlin following a method adapted from Torres-Ruiz et al. (2007) and originally modified from Parrish (1999). Samples were extracted in 2 washes of chloroform:methanol (2:1 v/v), sonicated on ice, and the chloroform phase was separated for methylation into fatty acid methyl esters with BF_3 (10 – 14%) at 80°C. Fatty acid methyl esters were suspended in hexane and measured on an Agilent 6890 gas chromatograph with Agilent 5973-N mass selective detector that was fitted with a CP Sil 88 for a FAME fused-silica capillary column (100m x 250 µm x 39 µm) set in splitless mode. Carrier gas (He) flow rate was constant at 0.2 mL min^{-1}. Inlet temperature was 300°C, with initial temperature 70°C with an increase of 720°C min^{-1}. The temperature program was started and held at 80°C for 1 min, and then increased at a rate of 4°C min^{-1} until a temperature of 220°C was reached, and then a steady temperature was maintained for 4 min, and then heated at 4°C min^{-1} until 240°C, where it was maintained for a final 15 min. Detector temperature was set at

280°C. Fatty acid methyl esters were identified by retention times and mass spectra in full scan mode previously calibrated with standards: 37-Component FAME Mix (47885-4); PUFA No1 Marine Source (47033) and PUFA No3 Menhaden Oil (47085-4; all Supelco, Germany).

5.3.3 Macroinvertebrate community assemblages

Community composition of the macroinvertebrate assemblages on the non-wood sediments (NW), wood-associated sediment (WS), and wood surface (WW) were compared by non-metric multidimensional scaling (nMDS) and analysis of similarities (ANOSIM) in the R package vegan. Data were log (x+1) transformed using a Bray-Curtis dissimilarity index. Total species composition was calculated via a Shannon-Wiener diversity index, and the rarefied taxonomic richness was estimated in vegan. ANOVA was used to compare diversity measurements among all substrates.

5.3.4 Stable isotope and mixing models

Stable isotope data are expressed as the difference between the ratios of samples and standard gases (Vienna PeeDee Belemnite and air), as

$$\delta\, R(‰) = \left(\frac{R_{sample}}{R_{standard}} - 1\right) x\ 10^3$$

and where $R = \frac{^{13}C}{^{12}C}$ or $R = \frac{^{15}N}{^{14}N}$. δ^{13}C and δ^{15}N are the per mil deviation of the sample from the corresponding isotope standard.

The contribution of basal resources to the diets of the collected macroinvertebrate taxa was estimated using Bayesian mixing models in the SIAR package in R (Parnell et al. 2008, Parnell et al. 2010). Bayesian models estimate probability distribution to the consumer diet from the δ^{13}C and δ^{15}N of each trophic resource and consumer. Since δ^{13}C and δ^{15}N are known to change as body tissues are incorporated in increasing trophic levels (trophic enrichment factor: TEF), the TEF values in Post (2002) were used: 0.4 ± 1.3 ‰ for δ^{13}C and 3.4 ± 1.0 ‰ for δ^{15}N. TEF were doubled for predator taxa. Since *Hydropsyche* are known to be omnivores, both TEF and double TEF were included in the model. Since mixing models are unable to distinguish between multiple trophic resources occupying the same isotopic space (Ward et al. 2011, Parnell et al. 2013), stable isotope models were checked for correlation and resources showing strong (>60) negative correlations in at least one model were combined *a-posteriori*. Due to negative correlations in multiple models, unio-derived seston was combined with filamentous algae, as well as wood periphyton with bryophytes. Grass and leaves were combined *a-priori* because of ecological similarity.

Trophic Base

The trophic base of the entire macroinvertebrate community assemblage was calculated by the sum of all diet contributions from single taxa in the mixing model, weighted by the respective biomass within the assemblage (Junger and Planas 1994, Choy et al. 2009). The biomass of each taxon was calculated from the average of individual dry weights used for the isotope analysis, multiplied by the mean abundance of that taxon.

5.3.5 Fatty acid analysis

All fatty acids greater than 1% of all quantified fatty acids were included in the analysis. The fatty acid profiles of both basal resources and consumers were ordinated using non-metric dimensional scaling using the percent composition of all quantified fatty acids. Differences among the overall profiles were compared using ANOSIM, and SIMPER tests were used to determine the specific fatty acids responsible for the difference between profiles. Wood and leaves, being *Alnus* sp., had highly similar and non-significantly different profiles between bulk wood trunk tissue and leaves, and were grouped *a-posteriori* grouped for the ordination. The nMDS, ANOSIM, and SIMPER were conducted in the R package vegan.

Fatty acids were subdivided into the 4 major fatty acid classifications (SAFA, MUFA, PUFA, and HUFA), in addition to bacterial fatty acids (BrFA), the sum of quantifiable bacterial fatty acids in this study (15:0 and 17:0), as has been done in previous studies (Rajendran et al. 1993, Alfaro et al. 2006). The ratio between the sum of all omega-3 and omega-6 fatty acids was also calculated as an indicator of the influence of allochthonous or autochthonous matter (Torres-Ruiz et al. 2007). For basal resources, total fatty acid content was listed per unit weight, to indicate FA content ingested by consumers per unit weight of food, and as a percentage to examine indicative biomarkers. Consumer fatty acid content was also examined as a percentage of all fatty acids to determine diet biomarkers. Differences in fatty acid classes and trophic biomarkers were compared across basal resources and across mesohabitat locations for individual consumers, using ANOVA in the R package car. Significance level was set at $\alpha < 0.05$.

5.4 Results

5.4.1 Community composition

A total of 32 taxa were collected across the three sampled mesohabitat locations (Table 5-1). Chironominae were the most abundant taxa, representing 72% of the abundance in both the NW and WS habitat locations, and 80% of the abundance on WW. The second most abundant taxa was *Caenis* sp. in NW and WS (16% and 7% of total abundance), while Oligochaeta were 14% of total abundance on WW. WW contained the highest benthic abundances, with 3326 ± 1788 ind. m^{-2}, while WS contained 1925 ± 740 ind. m^{-2}, and NW had the least abundance with 1658 ± 1054 ind. m^{-2}. These differences in abundance were not significantly different (ANOVA: df = 2, P = 0.08).

Rarefied taxa richness was significantly different between the three locations (ANOVA: F = 43.68, df = 2, P < 0.01) and greatest in WS (25.5 ± 4.0), medium in NW (16.3 ± 1.9) and lowest on WW (11.0 ± 1.7). This pattern was similar for the Shannon-Wiener diversity index (ANOVA: F = 12.36, df = 2, P < 0.01), with highest diversity (1.53 ± 0.18) on WS, medium on (1.17 ± 0.18) NW, and lowest (1.11 ± 0.06) on WW. These overall assemblages were significantly different (ANOSIM: R = 0.92, p = 0.001; Figure 5-2).

Table 5-1 Taxa collected in the 3 mesohabitat locations in the Płociczna River, along with the description, order, dominant functional feeding group, and assimilation analysis test conducted. Orders indicated by a * are separate classifications (suborder or superfamily) used to distinguish between related taxa in later figures. Mesohabitats are in order, non-wood sediments (NW), wood-sediments (WS), and on the wood surface (WW). Shr=shredders; Grz=grazers; Prd=predator; Gat=gatherers; AFF=active filterers; PFF=passive filterers; Min=miners.

Taxon	**Order**	**Functional Group**	**SIA**	**FA**	**NW**	**WS**	**WW**
Anabolia sp.	Trichoptera	Shr/Grz/Prd/Gat	X		X		
Anodonta anatina	Unionoida	AFF	X	X	X		
Aphelocherius aestivalis ad	Heteroptera	Pred	X	X		X	
Aphelocherius aestivalis lv	Heteroptera	Pred	X	X	X	X	X
Asellus aquaticus	Isopoda	Gat/Grz/Shr	X		X		
Baetis sp.	Ephemeroptera	Grz/Gat	X	X		X	X
Bithynia tetaculata	Gastropoda	AFF/Grz/Gat	X	X	X	X	
Caenis sp.	Ephemeroptera	Gat	X	X	X	X	X
Calopteryx sp.	Odonata	Prd	X		X	X	
Chironomidae	Diptera	Gat/AFF/Grz/Min/Prd	X	X	X	X	X
Dreissena polymorpha	Dreissenoidea*	AFF	X	X	X	X	
Ephemera danica	Ephemeroptera	AFF/Gat	X	X	X	X	X
Gammarus pulex	Amphipoda	Shr/Gat/Grz/Prd		X		X	
Gammarus roselii	Amphipoda	Shr/Gat/Grz/Prd		X		X	
Glossiphonia	Glossiphoniidae	Prd	X	X	X		
Gomphus sp.	Odonata	Prd	X	X	X	X	
Hydropsyche pellucidula	Trichoptera	PFF/Prd/Grz	X	X	X	X	X
Limnephilidae	Trichoptera	Shr/Grz/Prd/Gat	X			X	
Nemouridae	Plecoptera	Shr/Gat	X	X	X		
Neureclipsis bimaculata	Trichoptera	PFF/Prd	X			X	
Oligochaeta	Oligochaeta*	Gat	X		X	X	
Omphigomphus cecilia	Odonata	Prd	X	X	X		
Orectochilus villosus	Coleoptera	Prd	X	X	X	X	X
Platycnemis sp.	Odonata	Prd	X	X	X		
Polycentropodidae	Trichoptera	Prd / PFF	X	X	X	X	X
Potamopyrgus antipodium	Gastropoda	Oth/Gat/Shr/Graz	X	X	X		
Psychomia pusilla	Trichoptera	Grz/Gat/PFF/Prd	X				X
Sphaeriidae	Sphaeriacea*	AFF	X	X	X	X	X
Tabanidae	Diptera	Prd	X	X	X	X	
Theodoxus fluviatilis	Gastropoda	Grz	X		X		
Unio pictorum	Unionoida	AFF	X	X	X	X	
Unio tumidus	Unionoida	AFF	X	X	X	X	

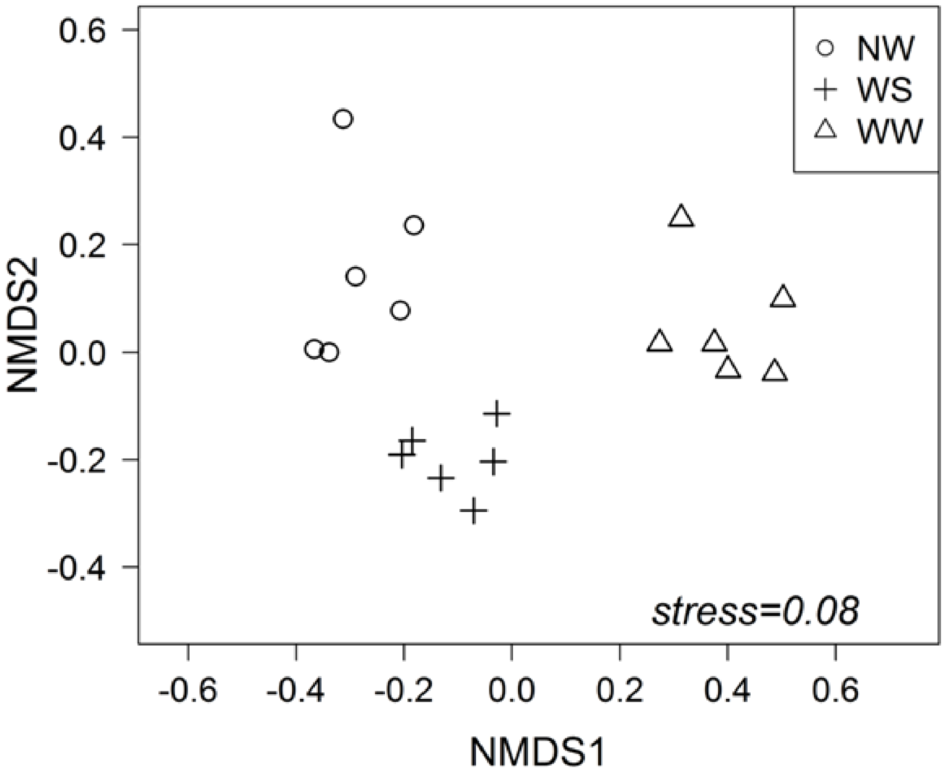


Figure 5-2: Non-metric multidimensional scaling of the total community composition collected at each mesohabitat location, performed on log(x+1)-transformed abundances and with Bray-Curtis distance. NW is sediment from the non-wood reach, WS is sediment from nearby wood, and WW is wood surface. Figure from Cashman et al. (in prep).

5.4.2 Diet estimation – Stable isotopes

All consumers were extremely C depleted, with average δ^{13}C values of -35.59 ± 0.19, while most food resources were substantially more enriched in δ^{13} and ranged from -31.45 – -13.50. Only filamentous algae and unio-derived seston had the most depleted δ^{13}C signals similar to many consumers (Figure 5-3). Periphyton on mussels had the most enriched δ^{13}C signal of all food resources, ranging from -21.7 – -27.87. Since seston and filamentous algae had similar stable isotope profiles, they were combined for the mixing model.

The stable isotope mixing model indicate that unio-derived seston/filamentous algae was the most dominant energy source in the river (Figure 5-4). This combined seston/filamentous algae signature was the greatest portion of the diet for all analysed taxa, with the exception of Oligochaeta where there was a similar contribution from wood-periphyton/bryophytes (~50%) in NW and a greater contribution from wood-periphyton/bryophytes in WS (Figure 5-4D). The estimated diets were similar for most taxa across the three mesohabitats, but there were several trends: Chironomidae, *Caenis,* and *Ephemera danica* had the greatest dependence on seston in NW, with a shift towards increased periphyton and bryophyte consumption in WS and WW locations, but this was not significant according to the 95% diet confidence intervals (Figure 5-4A,B,C).

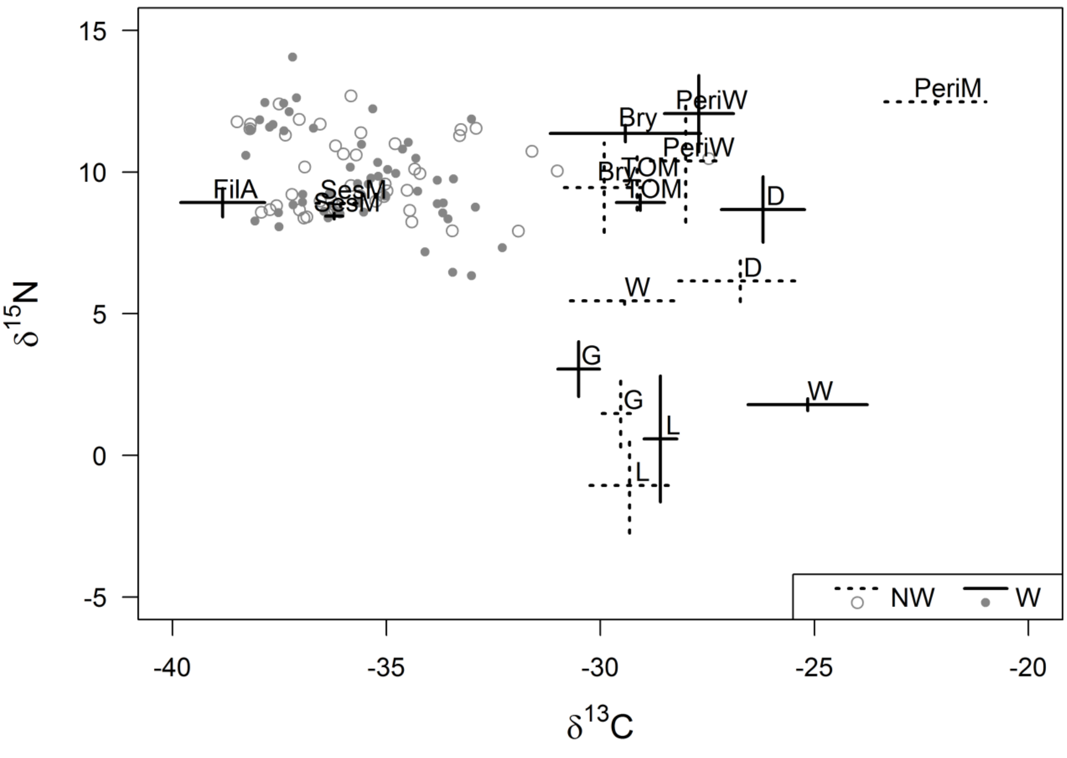


Figure 5-3: Biplot of stable isotope signatures of basal resources (lines, mean ± s.d.) and macroinvertebrates (circles) in the non-wood site (NW, dotted lines and open circles) and wood-site (W, solid lines and solid circles). The isotopic signatures of resources were corrected by the trophic enrichment factor: 0.4 ± 1.3 ‰ for δ13C and 3.4 ± 1.0 ‰ for δ15N (Post 2012). Note the depleted δ13C signatures for most macroinvertebrates. Resource abbreviations: FilA= filamentous algae; B= bryophytes; TOM= transported organic matter; SesM= seston inferred from the isotopic signature of unionid mussels (see text for explanation); PeriW= periphyton on wood; PeriM= periphyton on the shells of unionid mussels; D= detritus; W= wood; G= grass; L= leaves. Figure from Cashman et al (in prep).

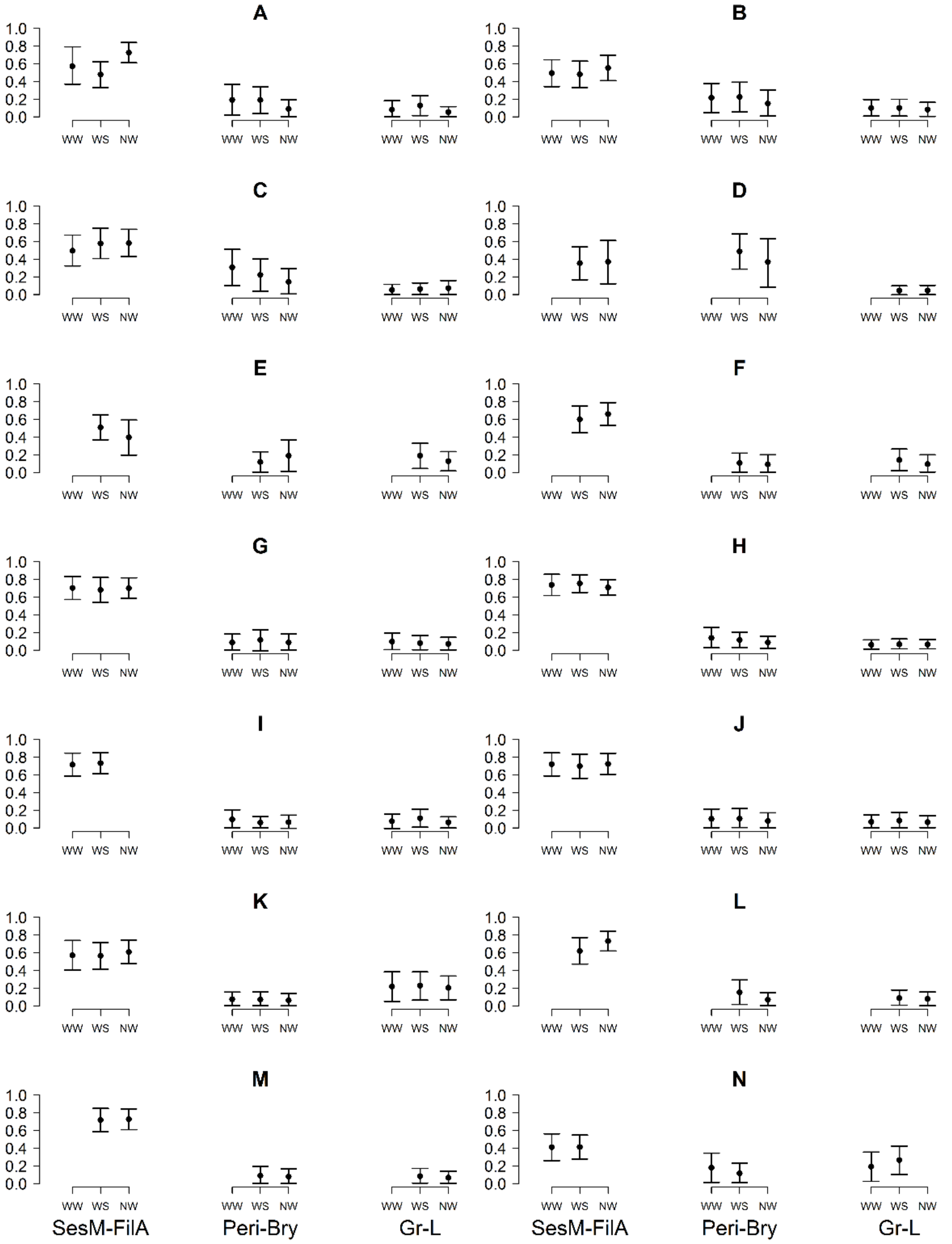


Figure 5-4: Percent contributions of the basal trophic resources to the diet of collected macroinvertebrates in the three sampling locations according to the result of the isotopic mixing model (see text for details), mean ± 95% credible interval. Figure shows results obtained for taxa collected in both wood and non-wood sites, and only displays trophic resources which contributed >10% to the diet of at least one taxon. WW is wood surface, WS is sediment from nearby wood, NW is sediment from the non-wood reach. SesM-FilA= seston inferred from Unionids (see text for explanation) and filamentous algae, PeriW-Bry= periphyton on wood and bryophytes, Gr-L= grass and leaves.A: Chironomidae, B: *Caenis* sp. C:*Ephemera danica*, D: Oligochaeta, E: *Bithynia tentaculata*, F: Gomphidae, G: Sphaeriidae, H: *Hydropsychae* sp. I: *Orectochilus villosus*, L: Policentropodidae M: *Aphelocheirus aestivalis*, N: Tabanidae, O: *Dreissena polymorpha*, P: Baetis sp. Figure from Cashman et al (in prep).

5.4.3 Diet estimation – Fatty acids

The major fatty acid constituents, 14:0, 16:0, 18:0, 18:1ω9c (oleic acid, OA), and 20:5ω3 (eicosapentaenoic acid, EPA) accounted for 60% of the total fatty acids present in the study. However, the proportion of these FAs, and other important FA biomarkers, varied considerably across the basal resources and taxa examined.

5.4.3.1 Basal resources

Fatty acid profiles of the basal resources were not significantly different between wood and non-wood reaches. Autochthonous sources, with the exception of filamentous algae, contained the greatest amount of total fatty acids by weight (Table 5-2). Mussel periphyton had the greatest amount of fatty acids available for consumers (51.93 ± 4.97 mg g^{-1}); in contrast, organic sediments had fatty acid concentrations an order of magnitude smaller (5.68±2.43 mg g^{-1}; Table 5-2). Saturated fatty acids (SAFAs) were the most abundant fatty acid class across all basal resources (48 – 68%), and highly unsaturated fatty acids (HUFAs) were the least abundant fatty acid class on average, although this highly variable by source (Grass: 4.58+0.58%, Mussel periphyton: 19.08±0.85%; Table 5-2).

Table 5-2: Fatty acid composition data for the various food resources. Values indicate mean and standard error. Total fatty acid content is given by weight (mg g-1) and indicates the sum of all quantified FA, and the subdivision into the 4 main fatty acid classes is indicated by percentage of all quantified fatty acids. No significant differences were seen between wood and non-wood locations, and data is the average across locations. SAFA = saturated fatty acids. MUFA = monunsaturated fatty acids. PUFA = polyunsaturated fatty acids. HUFA = highly unsaturated fatty acids. EPA = eicosapentaenoic acid; 20:5ω3, DHA = docosahexaenoic acid; 22:6ω3, and ARA = arachidonic acid; 20:4ω6. BrFA = the sum of quantified bacterial fatty acids (15:0, 17:0). ω3:ω6 = the ratio of the sum of all omega-3 to omega-6 fatty acids. Letters indicate post-hoc significant differences at $P < 0.05$.

Basal Resources	Total FA Content (mg g^{-1})	Proportion of Fatty Acid Classes (%)				Specific Fatty Acid Biomarkers (%)				Biomarker Ratio
		SAFA	MUFA	PUFA	HUFA	EPA	DHA	ARA	BrFA	ω3:ω6
Mussel Periphyton	51.93 ± 4.97^{a}	55.08 ± 1.46^{a}	14.33 ± 2.48^{d}	11.51 ± 0.65^{ab}	19.08 ± 0.85^{a}	12.36 ± 0.75^{a}	2.27 ± 0.03^{ab}	1.72 ± 0.09^{ab}	2.16 ± 0.26^{b}	3.46 ± 0.11^{a}
Wood Periphyton	44.32 ± 22.82^{ab}	60.69 ± 1.00^{a}	17.86 ± 0.57^{cd}	8.39 ± 0.38^{abc}	13.07 ± 0.62^{ab}	7.97 ± 0.76^{ab}	1.63 ± 0.38^{abc}	1.55 ± 0.18^{ab}	4.37 ± 0.90^{ab}	2.45 ± 0.25^{ab}
Bryophyte	40.87 ± 8.76^{ab}	56.61 ± 5.57^{a}	18.28 ± 2.93^{cd}	10.78 ± 0.75^{abc}	14.32 ± 1.51^{a}	7.56 ± 1.31^{ab}	2.53 ± 0.72^{a}	2.71 ± 0.33^{a}	3.43 ± 0.52^{ab}	1.91 ± 0.29^{ab}
Grass	16.82 ± 3.24^{bc}	58.67 ± 1.67^{a}	22.44 ± 1.85^{abc}	14.31 ± 2.34^{a}	4.58 ± 0.58^{c}	2.46 ± 0.44^{c}	0.43 ± 0.09^{cd}	0.92 ± 0.13^{b}	4.43 ± 0.65^{ab}	0.76 ± 0.09^{c}
Wood & Leaves	15.66 ± 2.35^{c}	59.29 ± 1.52^{a}	21.38 ± 0.73^{bc}	11.33 ± 1.07^{abc}	8.00 ± 1.14^{bc}	4.58 ± 0.77^{bc}	0.71 ± 0.13^{bcd}	1.39 ± 0.19^{b}	3.87 ± 0.36^{ab}	1.02 ± 0.11^{c}
TOM	10.20 ± 2.44^{c}	63.26 ± 1.61^{a}	22.05 ± 0.36^{abc}	7.22 ± 0.45^{bc}	7.47 ± 1.54^{bc}	3.79 ± 0.73^{bc}	1.20 ± 0.43^{abc}	1.29 ± 0.19^{b}	5.34 ± 0.63^{a}	1.35 ± 0.24^{bc}
Filamentous Algae	9.85 ± 4.23^{c}	52.61 ± 1.27^{a}	32.68 ± 2.67^{a}	5.65 ± 1.09^{c}	9.06 ± 0.62^{abc}	6.12 ± 0.24^{abc}	0.31 ± 0.23^{d}	1.77 ± 0.29^{ab}	4.26 ± 1.45^{ab}	1.58 ± 0.98^{abc}
Sediment	5.68 ± 2.43^{c}	59.58 ± 1.24^{a}	25.49 ± 0.70^{ab}	7.26 ± 0.72^{bc}	7.67 ± 0.89^{bc}	4.28 ± 0.62^{bc}	0.56 ± 0.11^{cd}	1.61 ± 0.19^{ab}	4.16 ± 0.27^{ab}	1.18 ± 0.16^{bc}

A non-metric multidimensional scaling (nMDS) ordination of the fatty acid profile separated the available basal resources into roughly 3 groups (Figure 5-5): 1) mussel periphyton, 2) wood periphyton and bryophytes, and 3) filamentous algae, wood/leaves, grass, and sediment. TOM had a highly variable signature, with some profiles similar to sediment and others to wood periphyton and bryophytes.

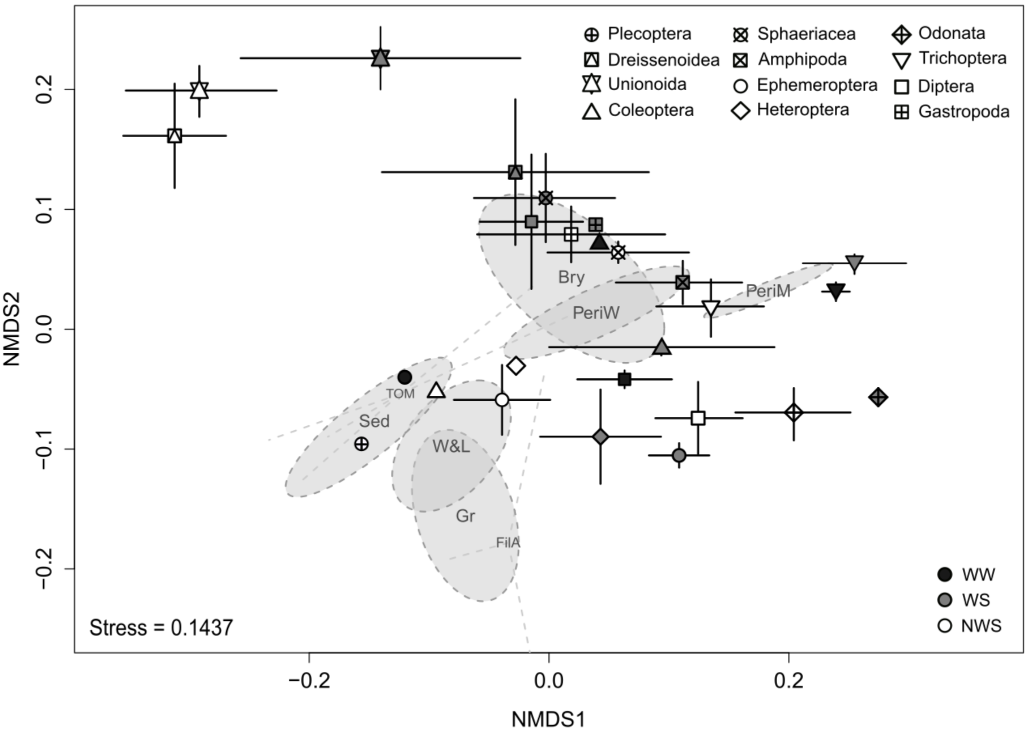


Figure 5-5: Non-metric dimensional scaling of all basal resources and collected macroinvertebrates in the study locations. Ellipses represent 95% confidence intervals around the centroid for each basal resource. Ordispider lines are used for filamentous algae (Fil A) and transported organic matter (TOM) to indicate high variability in the samples. Consumer values (symbol) represent the centroid and 1 standard error, and consumer proximity with food resources indicate feeding preferences. All consumers are grouped by order in the figure to aid interpretation of the figure, except for Sphaeriidae and D. polymorpha. Glossiphoniidae is outside of viewable chart area. WW (wood surface; black fill), WS (wood sediment; grey fill), and NWS (non-wood sediment; white fill). Bry = bryophytes. PeriM = Mussel Periphyton. PeriW = Wood Periphyton. Gr = Grass. W&L = Wood and leaves. Sed = Sediment

Mussel periphyton was located to the right side of the nMDS ordination (Figure 5-5) and was characterized by the greatest ω3:ω6 ratio (3.5) and high levels of HUFA (19.08 ± 0.85%), particularly of eicosapentaenoic acid (EPA: 20:5ω3; 12.36±0.75%), a fatty acid indicative of diatoms, and high levels of docosahexaenoic acid (DHA: 22:6ω3; 2.27 ± 0.03%; Table 5-2). In addition, it contained a low amount of bacterial fatty acids, averaging only 2.16 ± 0.26% of all quantified fatty acids, less than half the proportion found in other trophic resources (Table 5-2).

Wood periphyton and bryophytes occupied the central area of the nMDS plot ordination (Figure 5-5), and although contained lower ω3:ω6 ratios (2.45 ± 0.25 and 1.91 ± 0.29) than mussel periphyton, although still significantly greater than allochthonous sources (Table 5-2). Wood periphyton and bryophytes both contained relatively high amounts of HUFA; although lower than mussel periphyton, wood periphyton contained the second-highest levels of EPA quantified in the study (7.97 ± 0.76%) and bryophytes contained the highest levels of both arachidonic acid (ARA: 20:4ω6; 2.71 ± 0.33%) and DHA (2.53±0.72%; Table 5-2).

Terrestrial matter and sediments covered a wide area in the bottom-left area of the ordination plot, and contained significantly lower amounts of HUFA than autochthonous sources (Table 5-2). Overall, the grouping of filamentous algae, terrestrial matter, and sediment had significantly different profiles than mussel periphyton (ANOSIM: R = 0.864, P = 0.002), with mussel periphyton containing greater 12:0, EPA, and ALA (α-linoleic acid; 18:3ω3), while the terrestrial and sediment group contained greater 16:0, 16:1, and 18:0 (66% of variation, SIMPER). The ratio of omega-3:omega-6 fatty acids (ω3:ω6) was lowest in allochthonous sources, near or below 1, and sediment was slightly greater than 1 (Table 5-2). Filamentous algae, which was collected only in wood habitats, had a similar fatty acid profile to terrestrial material (grasses, wood, and leaves), although one sample contained a profile similar to wood periphyton.

Transported organic matter (TOM) was also highly variable, with several samples similar to organic sediments and two with a more autochthonous signal. TOM also exhibited the greatest levels of bacterial fatty acids seen in the study (5.34±0.63%) and the ω3:ω6 ratio was 1.35±0.24%, indicating a composition strongly composed by predominately consisting of allochthonous sources.

5.4.3.2 Consumers

Most macroinvertebrate taxa had fatty acid profiles similar to the range of available food resources, with many consumers located within or nearby the signature of bryophytes/wood periphyton and mussel periphyton (Figure 5-5). The Amphipoda, *Gammarus roselii,* was only found in WS, and while considered a shredder/gatherer, contained a HUFA enriched, high algal influence, and had a signal similar to mussel- and wood-periphyton (Table 5-3). Gastropoda found in NW were located primarily within the bryophyte profile, but were highly variable. *Bithynia tentaculata* had an autochthonous signature (ω3:ω6 = 2.162 ± 0.438), in contrast to the detritovore New Zealand Mud Snail *Potamopyrgus antipodarum*, which had a more autochthonous signature (ω3:ω6 = 1.315) and very low concentrations of HUFA, especially ARA, in comparison to other consumers (Table 5-3). Sphaeriacea in both WS and NW grouped with bryophytes despite being filter feeders, and had high concentrations of EPA and DHA

Table 5-3: Fatty acid composition data for all consumers. Values indicate percentage mean and standard error.SAFA = saturated fatty acids. MUFA = monunsaturated fatty acids. PUFA = polyunsaturated fatty acids. HUFA = highly unsaturated fatty acids. EPA = eicosapentaenoic acid; 20:5ω3, DHA = docosahexaenoic acid; 22:6ω3, and ARA = arachidonic acid; 20:4ω6. BrFA = the sum of quantified bacterial fatty acids (15:0, 17:0). ω3:ω6 = the ratio of the sum of all omega-3 to omega-6 fatty acids. Letters indicate post-hoc significant differences at $P < 0.05$.

Group		N	SAFA%	MUFA%	PUFA%	HUFA%	EPA%	DHA%	ARA%	ω3:ω6	BrFA
A. aestivalis adult		2	43.45±4.05	21.09 ±4.42	15.17 ±0.11	20.30 ±0.48	13.142 ±0.368	0.899 ±0.451	4.236 ±0.359	1.382 ±0.131	2.34+0.21
A. aestivalis larvae		3	61.31 ±6.66	18.34 ±4.57	9.33 ±1.13	11.01 ±0.99	7.268 ±0.609	0.329 ±0.154	2.026 ±0.232	1.378 ±0.129	2.94+0.66
Baetis		2	60.33 ±1.21	21.94 ±2.46	8.03 ±0.94	9.69 ±0.31	7.500 ±0.293	0.199 ±0.090	1.061 ±0.190	2.359 ±0.446	4.06+0.01
Bithynia		3	53.43 ±0.42	13.99 ±2.17	9.81 ±0.82	22.77 ±1.71	9.845 ±1.556	5.275 ±0.996	4.758 ±0.527	2.162 ±0.438	3.44+0.51
Caenis		3	50.95 ±4.72	22.81 ±0.57	9.93±1.09	16.31 ±4.10	10.322 ±2.380	0.418 ±0.042	3.919 ±1.574	1.299 ±0.050	3.78+0.08
Chironomidae	NW	3	46.43 ±2.49^{a}	23.83 ±0.24^{a}	14.75 ±1.41^{a}	14.99 ±0.95^{a}	11.358 ±0.806^{a}	0.590 ±0.179^{a}	1.659 ±0.329^{a}	1.727 ±0.166^{a}	1.43+0.48^{a}
	WS	3	54.98 ±0.11^{a}	17.98 ±2.09^{a}	10.34 ±1.33^{a}	16.71 ±3.04^{a}	6.604 ±0.662^{b}	3.908 ±2.130^{a}	4.113 ±1.272^{a}	1.495 ±0.406^{a}	5.02+0.70^{b}
	WW	3	52.67 ±2.68^{a}	18.45 ±3.10^{a}	12.96 ±0.14^{a}	15.92 ±1.74^{a}	11.758 ±1.366^{a}	0.857 ±0.226^{a}	1.689 ±0.046^{a}	1.712 ±0.203^{a}	2.83+0.26^{ab}
Dreissena		5	60.21±10.95	23.17 ±11.10	4.86 ±2.00	11.75 ±2.49	3.576 ±1.783	3.146 ±0.878	1.528 ±0.494	2.057 ±0.471	3.21+0.50
Ephemera		5	51.50 ±2.61	20.47 ±1.85	9.96 ±0.94	18.06 ±2.10	12.368 ±1.889	0.868 ±0.309	3.188 ±0.241	2.017 ±0.170	3.41+0.37
Gammarus		2	51.38 ±1.79	15.94 ±2.19	11.78 ±0.66	20.89 ±0.25	12.466 ±0.982	3.006 ±0.830	2.713 ±0.811	2.630 ±0.446	3.21+0.68
Glossiphonia		1	22.09	22.39	6.23	49.29	10.932	2.877	26.231	0.550	2.02
Gomphidae		4	51.20 ±0.87	10.24 ±2.35	16.80 ±1.51	21.76 ±0.66	16.288 ±0.924	1.321 ±0.210	2.904 ±0.048	2.614 ±0.132	1.53+0.20
Hydropsyche	NW	3	57.65 ±1.83^{a}	17.73 ±2.03^{a}	10.18 ±0.40^{a}	14.43 ±0.57^{a}	9.675 ±0.200^{a}	1.447 ±0.292^{a}	1.513 ±0.089^{a}	2.925 ±0.085^{a}	4.24+1.02a
	WS	6	50.75 ±1.69^{b}	14.58 ±1.15^{a}	12.41 ±0.66^{b}	22.25 ±1.08^{b}	13.821 ±0.638^{b}	3.180 ±0.189^{b}	1.794 ±0.093^{a}	3.809 ±0.072^{b}	3.01+0.60a
	WW	7	50.23 ±1.05^{b}	15.37 ±1.17^{a}	12.60 ±0.27^{b}	21.80 ±0.78^{b}	14.596 ±0.602^{b}	2.363 ±0.195^{c}	1.689 ±0.127a	3.834 ±0.106b	2.64+0.37a
Nemouridae		1	59.05	25.71	8.60	6.64	3.476	0.467	1.497	0.780	5.70
Orectochilus		4	50.38 ±3.94	22.43 ±2.39	12.58 ±1.22	14.61 ±2.79	9.792 ±2.074	1.000 ±0.196	1.228 ±0.240	2.761 ±0.431	2.80+0.33
Platycnemis		1	55.54	14.89	12.60	16.97	12.409	0.401	3.302	1.635	3.16
Polycentropodidae		2	48.07 ±1.06	15.22 ±7.40	13.11 ±0.25	23.60 ±6.10	14.316 ±2.376	4.191 ±3.006	1.813 ±0.157	3.711 ±1.198	1.97+0.04
Potamopyrgus		1	59.66	19.82	7.25	13.27	4.957	2.175	3.168	1.315	3.92
Sphaerium		5	52.63 ±2.88	19.39 ±1.54	10.45 ±1.30	17.54 ±2.11	6.617 ±1.429	4.491 ±0.625	3.896 ±0.644	1.773 ±0.238	3.99+0.57
Tabanidae		1	59.77	21.48	7.59	11.16	5.820	1.879	1.917	1.885	4.75
Unionidae		10	64.50 ±5.97	13.63 ±1.62	5.59 ±1.07	16.28 ±3.50	4.454 ±1.586	2.561 ±0.867	5.308 ±1.690	0.739 ±0.137	4.96+0.34

The profiles of the Coleoptera predator, *Orectochilus villosus*, were most similar to the profiles of consumers found near wood periphyton and bryophytes, and contained relatively high ω3:ω6 ratios (Table 5-3). However, in WS, Coleoptera were highly variable, stretching from a signature close to mussel periphyton across wood periphyton (Figure 5-5), suggesting that they are predating on a range of prey sustained by a variety of different basal resources in the WS location.

Among Trichoptera, all had high autochthonous signatures and were ordinated near mussel periphyton. The net-spinning caddisfly *Hydropsyche pellucidula* was present in all three locations, while the trumpet-net caddisfly Polycentropodidae found exclusively in NW. *Hydropsyche* had substantially different fatty acid compositions according to wood and non-wood locations. Both WS and WW samples grouped closely with mussel periphyton, containing high levels of HUFA and ω-3 fatty acids, and was significantly different from non-wood sediment locations which grouped with wood periphyton (Figure 5-5; ANOSIM: R = 0.682, P = 0.002). Compared to both wood *Hydropsyche* populations, *Hydropsyche* in NW had decreased 12:0, ~50% lower EPA, 16:1, ALA, and 50% lower DHA, but increased 16:0, 18:0, OA, and 14:1 (SIMPER: 80%, descending order of importance; Figure 5-5). However, the ω3:ω6 *Hydropsyche* in NWS, even though lower than in both wood habitats, was still extremely high, indicating a diet dominated by autochthonous sources (Table 5-3). Polycentropodidae had high variability in its profile, but generally contained a high algal signature with a high ω3/ω6 ratio and high amounts of HUFA, especially EPA and DHA (Table 5-3).

Diptera were primarily composed of Chironomidae, which were significantly different among all three wood and non-wood locations, although this separation was not along any clear resource gradient (Figure 5-5; ANOSIM: R = 0.589, P = 0.006). WW Chironomidae were located centrally in the plot near wood periphyton, while NW Chironomidae were located to the lower right, and WS Chironomidae to the upper left, overlapping with the bryophyte signal. In comparison to WW, NW had increased 16:1ω9, 14:0, 18:2ω6c and ALA, but decreased concentrations of 16:0, 18:0, 14:1, EPA, and 12:0 (SIMPER NWS-WW: 82%). NW Chironomidae in comparison to WS Chironomidae contained higher 16:1ω9, 40% greater EPA content, 18:2w6c, 14:0, and 18:3w3, but lower 16:0, 18:0, 85% less DHA, ARA and 17:0 (SIMPER NW-WS: 79%). Chironomidae profiles in the two wood locations (WS and WW) differed from one another, with WS having decreased EPA, 18:2ω6c and 14:0 but greater 16:1ω9, DHA, and ARA (SIMPER WS-WW: 57%). One sample of Tabanidae was analysed, which was found in NW, and had a much different profile than Chironomidae – its profile was located within the bryophyte-wood periphyton and had medium levels of HUFA, but a large amount of bacterial fatty acids (Table 5-3).

A small number of taxa were located within the range of the cluster of sediment and allochthonous resources. The Plecoptera, Nemouridae, a shredder/gatherer stonefly which was only found in NW, had a profile highly similar to sediment (Figure 5-5). While Ephemeroptera were found in all three mesohabitat locations, in WW *Baetis* diets were similar to Sediment and TOM, and in NW the shredder *Caenis* and filter feeder *Ephemera Danica* had a profile similar to wood and leaves.

The predatory Coleopetera in NW, *Orectochilus villosus*, had a similar profile with both sediment and wood and leaves, and likely fed on the nearby Plecoptera and Ephemeroptera present in NW. The Heteroptera in NW, *Aphelocheirus aestivalis* larvae, while having a slightly different profile than most terrestrial sources, was likely feeding on the Ephemeroptera present in NW. *Ephemera* found in WS was located away from other resources, in a cluster to the bottom right of the ordination. Several other taxa were located in this area, including NW Diptera (Chironominae), and the predators Heteroptera *A. aestivalis* in WS, and the Odonata in both WS and NW locations which were likely feeding on these consumers in their respective locations.

Unionoida (*Unio* and *Anodonta*) and Dreissenanoida (*Dreissena polymorpha*) contained high levels of long-chain and branched fatty acids (*e.g.* 24:0, 22:2) and ARA, and with the exception of *Dreissena* in WS, grouped separately from all measured food resources. Despite feeding on seston, Unionoida and *Dreissena* profiles may not accurately match diets, as they are known to retain and possibly elongate commonly present fatty acids into long-chain branched forms which are not present or rare in seston (Gladyshev et al., 2011) and preferentially retain ARA (Newton et al. 2013). However, these two mussel taxa had substantially different ω3:ω6 ratios, with *Dreissena* containing high ω3:ω6 (2.057±0.471) and Unio with low ω3:ω6 (0.739 ±0.137).

The leech *Glossiphonia* sp., which was collected in only one sample, had a distinct fatty acid profile with extremely high levels of ARA (~26% of total FA), likely due to its particular feeding mechanism of sucking body fluids, and was very different from all food resources (outside plot viewing area).

5.4.4 Overall contributions

Seston/filamentous algae had the greatest source contribution to nearly all organisms as estimated in the stable isotope mixing model, and sustained the most biomass out of all trophic resources to the consumer assemblage (Figure 5-6). While the total biomass supported by seston increased with increasing proximity to wood (NW→WS→WW), the total % of biomass supported by seston decreased (66% in NW, 53% in WS and 48% in WW). This was due to the increased contributions from the combined wood periphyton/bryophyte signal: in WS, periphyton/bryophytes supported 1.4-fold greater biomass compared to NWS, and nearly 4.3-fold biomass in WW. While there was some small increases in the average contribution from detritus, grass-leaves, and TOM from NW to wood locations, this was a relatively insignificant proportion of the diet (6.6-9.7%), and differences were not significantly different due to overlap in the 95% credible intervals (Figure 5-6).

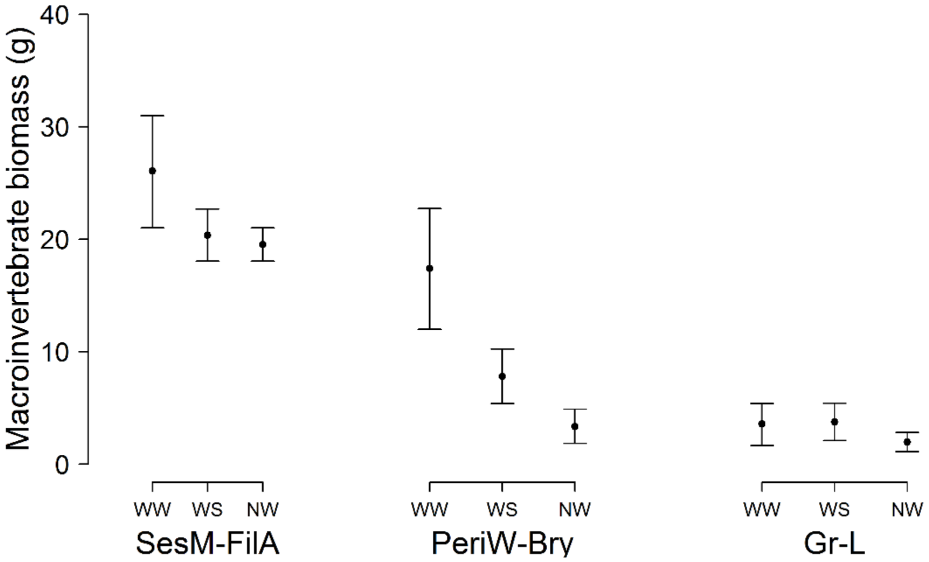


Figure 5-6: Contributions of the studied trophic resources to the biomass of the macroinvertebrate assemblage on the three substrata. Mean values ± 95% credible interval. NW is bed sediment in the non-wood site. WS is bed sediment in the wood site. WW is the wood surface. SesM-FilA= seston inferred from Unionids (see text for explanation) and filamentous Only the three groups of food resources which contributed the most to macroinvertebrate biomass are shown: SesM-FilA= seston inferred from Unionids (see text for explanation) and filamentous algae, PeriW-Bry= periphyton on wood and bryophytes, Gr-L= grass and leaves. Figure from Cashman et al. (in prep).

5.5 Discussion

The objective of this study was how determine how the presence of large wood altered the trophic base of a macroinvertebrate consumer assemblage. Combining stable isotope analysis with fatty acid biomarkers provided complementary data about the trophic base of the macroinvertebrate assemblage, particularly for addressing a mix of lacustrine and riverine resources, estimating the relative influence of autochthonous and allochthonous material, and determining the nutritional quality of the various basal trophic resources. This data demonstrates how large wood alters the availability and quality of basal trophic resources and shifts the trophic base of the macroinvertebrate assemblage from being supported predominantly by seston to epixylic autochthonous production, namely periphyton and bryophytes.

Stable isotope data suggested that the consumer community in the Płociczna River was largely supported by seston/filamentous algae across all three habitat locations. While seston was combined with filamentous algae in the mixing model, filamentous algae was uncommon in the river and present exclusively on wood substrates. Thus, the overall community was largely dependent on seston, which originated from Lake Sitno, located 1 km upstream of the sampled reaches. However, the presence of wood clearly decreased the reliance of the macroinvertebrate assemblage on seston, as the trophic base shifted to be more dependent on epixylic autochthonous production, namely periphyton and bryophytes. In the sediments around wood, however, the accumulations of grass, leaves, detritus, and fine organic matter contributed relatively little to the overall trophic base of the macroinvertebrate assemblage.

Fatty acid profiles supported this conclusion and suggested that most consumers were predominantly supported by high-quality autochthonous resources high in HUFA content and ω3:ω6 ratios, such as bryophytes and periphyton. In addition to consumer fatty acid profiles overlapping with autochthonous signatures, most consumers maintained a ω3:ω6 ratio greater than 1, an indicator of a diet dominated by autochthonous matter (Torres-Ruiz et al. 2007). Terrestrial matter, sediment detritus, and TOM contributed little to the trophic base, with a notable exception for several taxa in non-wood sediments, where wood, leaves, and detritus supported the Ephemeroptera *Caenis* and the Plecoptera *Nemouridae*, which were prey for *A. aestivalis* and *Orectochilus.* However, other taxa in the NW location, including the Gastropoda *Bithynia tentaculata*, Sphaeriacea, and the Tricoptera *Hydropscyche* had profiles similar to autochthonous sources, even though there were limited autochthonous resources available in the benthos. Instead, they all had the ability to function as filter feeders.

Fatty acid profiles suggesting an autochthonous trophic base, therefore, does not explicitly contradict the stable-isotope data that suggests seston was a dominant part of the diet of consumers. Seston is a mix of allochthonous and autochthonous sources, and includes phytoplankton, bacteria, and processed terrestrial matter, and while fatty acid profiles can discriminate between the taxonomic origin of food resources (*i.e.*

allochthonous or autochthonous), it may lack the resolution to distinguish between riverine or lacustrine origins (*e.g.* a “diatom signature” is similar whether from periphyton or phytoplankton sources (Dethier et al. 2013, Taipale et al. 2013)). As a result, a consumer that has stable isotope signature indicating a seston diet and a fatty acid profile indicating an autochthonous diet may be selectively feeding on the autochthonous fraction of the seston, a feeding behaviour noted in other studies (Thorp and Delong 2002, Delong and Thorp 2006).

The presence of large wood also interacted with how some filter feeding taxa fed on seston. In the stable isotope mixing model, the netspinning caddisfly *Hydropsyche* was estimated to have a diet uniformly dominated by seston in all three habitat locations, but fatty acid profiles indicated differences in diet across habitats. Specifically, those individuals collected in wood substrates had a greater ω3:ω6 ratio and higher tissue concentrations of HUFA and EPA, indicative of a large autochthonous, and specifically diatom, supported diet. Since the stable isotope data suggests that *Hydropsyche* feeds primarily on seston (>75%) and not on epixylic periphyton or bryophytes, this change in fatty acid content may indicate a change in the quality of accessible seston. Wood provides an elevated position in the water column for caddisfly larvae to attach their nets, possibly increasing the ability to filter the higher-quality plankton component of seston that remains close to the water surface.

Large wood also interacted with the export of seston from the lake in other ways, as slow flows around wood enhanced the deposition of fine transported organic matter from the seston, increasing its availability as a food resource for some taxa, resulting in a high seston signature in gatherer and shredder taxa. Stable isotopes suggest *Caenis* consumed seston in the diet and its fatty acid profile was similar in some locations to Chironomidae in the non-wood sediments. Stable isotopes indicate Chironomidae had a strong (>75%) seston signature in the non-wood location, yet its fatty acid profile indicates a diet on a different seston fraction than *Hydropsyche*. As Chironomidae and *Caenis* profiles were located away from all quantified food resources, this may indicate a diet on the an ultrafine seston fraction that was not otherwise captured, and was located lower in the water column and most likely to deposit on sediment. Therefore, large wood likely enhances the amount of seston that deposits in the low flow areas, resulting in more seston food resources for the gatherer *Caenis*. However, as deposited seston was likely a small layer on top of the 5 cm collected for sediments, any δ^{13}C depleted seston signature may have been masked by the overall sediment signature.

While the NW Chironomidae fatty acid profile suggests filter feeding on an ultrafine seston fraction, stable isotopes did not indicate any significant change in diet. This may suggest a change in the diet on different fractions of the seston, or indicate that fatty acid profiles, even without a quantitative mixing model, may be more sensitive to diet changes. In the fatty acid profile, however, the WS profile does not exhibit a similar signature to wood and leaves, but has a profile similar to bryophytes. WS Chironomidae have low EPA content, indicative of less contribution of diatoms in their diet, yet high values of DHA and ARA. This may indicate the preferential feeding on bryophytes compared to periphyton, increased carnivory, or even a shift in the functional feeding groups within Chironomidae away from filter feeding taxa towards gatherer/collectors.

Consumers in this study had highly depleted δ^{13}C signals, more depleted than most available food resources, and thus the seston value derived from *Unio* mussels, which has been previously used to exhibit a time-integrated seston signal (Atkinson et al. 2013), was needed to resolve the consumer signals in the study. The δ^{13}C of *Unio*-derived seston was substantially different from the >125 μm TOM fraction collected during the sampling campaign which was a minimal part of the diet in the stable isotope mixing model. As this was early in the sampling season (25-26 April), animals may have retained a time-integrated, δ^{13}C depleted winter seston signature that was no longer present in the 125 μm TOM sample. However, the most likely explanation may be that *Unio* mussels may have been selectively feeding on ultra-fine nutritive particles not collected in the 125 μm sample, such as δ^{13}C depleted bacteria (Nichols and Garling 2000) that likely contributed to NW Chironomidae. TOM samples did exhibit somewhat higher levels of bacterial fatty acids compared to other basal resources, and Unio, in addition to several other filter feeding consumers, had high levels of bacterial fatty acids (4 – 5%), further suggesting the strong influence of this ultra-fine bacteria-component of the seston.

The depleted δ^{13}C of the seston suggests that carbon is being produced via a microbial link (*i.e.* bacteria-flagellate-ciliate-daphnia) in the lacustrine environment (Kankaala et al. 2006), which then enters the river ecosystem and provides a cross-ecosystem food subsidy for benthic consumers that are limited by other available food resources. However, other studies have shown that production based on this bacterial carbon source is still highly dependent on the availability physiologically essential lipids and fatty acids derived from a phytoplankton base, without which bacteria cannot support plankton productivity (Taipale et al. 2014). Therefore, by providing an additional source physiological essential fatty acids in the autochthonous production on wood, this may also allow for further growth if these lipids were already in limited amounts.

While Unio tissues, as a filter-feeding mussel, are commonly used in the literature as a proxy of total seston, it had the lowest ω3:ω6 (0.739±0.137) of all consumers, and lower than all other basal resources except grass. The ω3:ω6 ratio for Unionid in this study is comparable to the range of 0.4-0.8 listed elsewhere in the literature (Newton et al. 2013). Dreissena ω3:ω6 was substantially higher (2.057±0.471), similar to bryophytes and wood periphyton, although slightly lower than the range of 2.8-5.8 in another study (Wacker and von Elert 2004). As low ω3:ω6 (*i.e.* < 1) not only indicates a strong influence by terrestrial food sources (Torres-Ruiz et al. 2007) but also a deposit feeding ecology (Ahlgren et al. 2009), the difference in these ratios may suggest that these taxa exhibit different feeding ecologies and preferences on different fractions of the seston, as fatty acid profiles suggest Unionids may primarily feed on bottom-deposits and terrestrial matter, and Dreissena on higher more autochthonous components of the seston. While Dreissena has not been frequently used in the literature for representing a time-integration signature for seston, it may be more representative of the autochthonous component of the seston that was preferentially fed on by certain filter feeding taxa in this study, such as *Hydropsyche*.

5.5.1 Conclusion

Large wood created accumulations of organic matter and allochthonous resources (*i.e.* leaves) which were otherwise minimal and limited to marginal areas of the channel, yet this oft-noted ability for wood to accumulate organic matter (Smock et al. 1989) had little effect on the trophic base of the macroinvertebrate assemblage. In contrast, large wood dramatically increased the amount of stable substrate for colonization by periphyton and bryophytes (Golladay and Sinsabaugh 1991, Hax and Golladay 1993, Wondzell and Bisson 2003), served as an attachment site for some filter feeding taxa to feed on a more nutritive component of the seston, and overall increased the contributions of high-quality autochthonous primary production to the trophic base of the macroinvertebrate community.

This study shows how the combination of stable isotope and fatty acid analyses can complement each other in the study of freshwater food webs, particularly where basal resources may come from a mix of lacustrine and riverine origins. Since stable isotopes are subjected to seasonal and local phenomena, SIA allows for distinguishing among the contribution of food resources based on spatial origin *(i.e.* riparian zone, lake, and river), but may give confounding results due to the seasonal changes in the signature of food resources (Woodland et al. 2012). On the other hand, fatty acids can be used to accurately estimate taxonomic groupings even with variations in season and abiotic conditions (Dethier et al. 2013, Taipale et al. 2013), and provide a more sensitive measure of diet changes not detected by stable isotope mixing models, even if it may not be able to distinguish between lacustrine or riverine origins without directly measuring these sources.

These results suggest that even in a forested, sand-bed river, which may be hypothesized to be driven by accumulations of terrestrial inputs and fine organic matter (Vannote et al. 1980), trophic relationships were predominantly supported by autochthonous material, not only by the autochthonous fraction of seston originating from a nearby lake, but also by periphyton and bryophytes growing directly on large wood in the channel. This supports previous work emphasising the importance of high quality autochthonous resources for lotic production, even in light-limited rivers that contain high terrestrial inputs (Torres-Ruiz et al. 2007, Lau et al. 2008, 2009b).

The strong influence of lake seston on the trophic base of benthic macroinvertebrates in the Płociczna river in effect results in primary productivity from the lake subsidizing increased productivity downstream, creating a strong coupling between lake and river productivity (Perry and

Sheldon 1986, Junger and Planas 1994). This lake-river coupling is expected to be typical for other rivers in the Pomeranian Lake District, as the series of small-lake and river connentions seen in the Płociczna is common throughout the region. This river-lake coupling is expected to be especially strong in low-productivity lowland sand-bed rivers, as sediment instability limits in-stream production to support overall ecosystem productivity (Atkinson et al. 2008). Similarly, this coupling is likely to be applicable to other river systems, as other rivers lacking hard substrate (*i.e.* the lowland rivers with high levels of fine sediment in Chapter 3) or otherwise deficient in in-stream productivity (*i.e.* scoured phytobenthos in Chapter 4) would be expected to have a trophic base largely dependent on basal resources supplied from upriver (*i.e.* a lake or reservoir).

The results presented in this paper show that the presence of large wood decreases the strength of river-lake coupling by providing alternative basal resources primarily through its role as a hard substrate supporting colonisation by periphyton/bryophytes and hence increasing local, high-quality autochthonous productivity. As the influence of lake seston would decrease with distance from the lake (Richardson and Mackay 1991, Hillbricht-Ilkowska 1999), the role of large wood to support the trophic base of the consumer assemblage would only be expected to increase. Therefore, river management strategies that incorporate instream LW have the potential to increase the quantity and quality of food resources and improve ecosystem productivity.

Chapter 6

Conclusions

6.1 Summary

The research presented in this thesis has examined the connection between large wood, physical habitat conditions, flood disturbance, and the “bottom-up” effect of the quantity and nutritional quality of basal resources on ecological function and trophic dynamics (Figure 6-1). This thesis is one of the first studies to examine the relationship between river physical habitat and trophic dynamics from a nutritional, fatty acid perspective, and has examined these relationships through an applied context of large wood, river restoration, and the mitigation of altered flow regimes.

After a general introduction to the main themes in Chapter 1, this thesis explored the relationship between ecosystem structure and function through four research projects contained in Chapters 2 – 5. Each chapter examined one component of the “bottom-up” cascade by which wood can influence ecosystem function through nutritional dynamics (Figure 6-1).

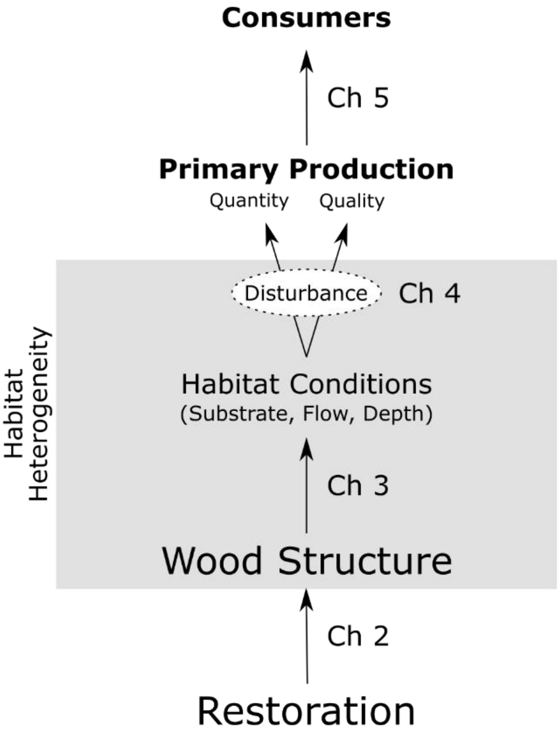


Figure 6-1: Thesis diagram showing the conceptual link between the four research chapters contained within the thesis. Chapter 2 surveyed broad trends in wood restoration, but particularly the relative use of different types of wood structural forms. Chapter 3 explored how wood structural complexity was associated with different physical habitat conditions. Chapter 4 investigated how wood could mitigate flood disturbance on the quantity and quality of algal biofilms. Chapter 5 examined how the relative availability and quality of different food resources around wood influenced the trophic base of the macroinvertebrate consumer assemblage.

6.1.1 Chapter 2: Large wood in UK restoration schemes – conclusions from the National River Restoration Inventory

The objective of Chapter 2 was to identify the broad trends in wood restoration in the United Kingdom, including where restorations occurred, project motivations, monitoring conditions, and the types of wood being used in restoration, as these are all an important first step in understanding the potential effectiveness of these restorations. The survey of the National River Restoration Inventory database highlighted several key trends in the use of large wood in river restorations throughout the UK. Wood restorations primarily occurred in lowland rivers that had a history of engineering alterations, with over-wide and over-deep channels that had uniform flows, low habitat heterogeneity, and accumulations of fine sediment. General project aims were overwhelmingly to improve this homogenous and degraded habitat, and improve local fisheries, and funding generally came from the Environment Agency. However, only a small minority of projects had clearly defined objectives, and monitoring was rare, with projects most likely to be assessed visually or with photography, and pre- and post-project comparisons were lacking.

Wood restoration was often used in conjunction with many other techniques, such as gravel installation; however, the restored wood used in these projects were often structurally simple, as it was twice as likely for projects to use simple deflectors to concentrate flow, rather than install "semi-natural" large wood forms. The implications of the potential difference between deflectors and semi-natural large wood on creating habitat heterogeneity in river restorations were then explored in Chapter 3.

6.1.2 Chapter 3: The variability of wood structural diversity and its effect on physical habitat conditions

The objective of Chapter 3 was to examine the effects of wood structural complexity on mesohabitat conditions (depth, velocity, and sediments) using field data collected from four rivers in lowland England across a gradient of wood management conditions (near-reference to restored wood). This chapter serves to connect the lessons learned from Chapter 2 into how the structural attributes of wood used in restoration may be related to restoration success and functional attributes later studied in Chapters 4 and 5. Chapter 3 indicated a decrease in the complexity and variety of habitat conditions with increasing river management, despite high variability of all habitat conditions associated with wood. In particular, there was a clear decrease in the number and size of wood jams as management and human intervention increased in the channel. Active wood jams were only present in rivers with natural wood, the river restoration with semi-natural “large wood” had complete and partial jams, and the restoration site with deflectors only contained partial jams. The complexity of the wood was also greatest in rivers with natural wood, and the smallest and least variable structural conditions in deflectors, these being the most different to all other large wood types.

Pool depth increased around jams in most rivers, with the complexity of the jams having a potential influence on the overall pool depth. In addition, wood in more managed rivers, particularly restored deflectors, had a smaller impact on flow in the channel, with lower levels of flow concentration in areas adjacent to the wood jam.

Riverbed sediment conditions were highly variable with overall catchment conditions, particularly with the overall amount of fine sediment, organic matter, and size fractions in the channel. However, large wood had a trend of altering the patterns of fine sediment around jams. Increased flow velocity associated with jams significantly reduced the degree of ingressed fine sediment storage in gravels, and sediments beneath the concentrated flows around jams also appeared to have the lowest organic matter content – an important component for fish spawning, one of the main project objectives identified in the NRRI. However, despite the effect of large wood on improving sediment conditions for fish, the high silt and clay fractions in some of these rivers appear to be beyond thresholds for redd survivability (Greig et al. 2005), and indicate overall catchment limitations. This supports the suggestion that restoring large wood may improve habitat heterogeneity overall, but degradation due to land-use and catchment conditions are still likely to be limiting the ecological response in some restored rivers (Palmer et al. 2010).

Chapter 3 indicated that the general restoration practice to preferentially install simple deflectors has important implications for restoration success, as simple deflectors has a smaller effect on habitat heterogeneity than semi-natural large wood installations or natural wood, and may be limiting the potential ecological response of restoration. The relationship between abiotic habitat conditions on primary productivity was then examined in Chapter 4.

6.1.3 Chapter 4: The potential for large wood to mitigate scour of periphyton nutritional quality caused by hydropower hydraulic extremes

The objective of Chapter 4 was to examine if wood may mitigate the scouring of periphyton biofilms by flood disturbance from hydropower dams (*i.e.* "hydropeaking"). While hydropeaking has been previously studied for its effects on inducing catastrophic drift on benthic macroinvertebrates, the effect of hydropeaking on food resources, and nutritional quality in particular, is significantly under-researched.

The hydropeaking simulations scoured algal biomass on both wood and control (tile) substrates, however wood periphyton biomass was relatively unaffected, as on wood substrates there was no scour of chlorophyll-*a* and AFDM actually increased. While hydropeaking did not cause a detectable change in periphyton nutrient stoichiometry, it did preferentially scour the physiologically-important highly-unsaturated fatty acids, especially eicosapentaenoic acid (EPA; 20:5ω3) from the periphyton. While the loss of fatty acids also occurred on wood, this was to a lesser degree than on the control substrate.

This project is the first to reveal a previously overlooked mechanism that may be affecting the ecosystem resilience of communities in hydropeaking-impacted rivers by reducing the quality, in addition to quantity, of periphyton biofilms, especially when these channels lack wood or other elements of structural complexity. Due to the daily nature of hydropeaking throughout the year, rivers undergoing this type of regulation are likely to have a persistently depressed baseline of periphyton abundance and nutritional quality compared to non-disturbed conditions.

Wood has the potential to mitigate some of these impacts, by retaining higher biofilm biomass and thereby retaining more absolute availability of fatty acid concentrations in the ecosystem. Improving the structural complexity and the availability of wood in hydropeaking-impacted rivers can therefore potentially mitigate serial discontinuities in downstream primary production. Furthermore, this study suggests that the presence of wood may increase the resilience of the downstream ecosystem to this type of disturbance, by providing more and increased quality of food resources for those macroinvertebrates able to tolerate, find refugia during, or recolonize after the hydropeaking flows. While mitigation strategies that require the alteration of hydroelectric plant operation schemes face economic challenges (Person et al. 2014), structural changes such as adding wood within the downstream channels have the potential to simultaneously work towards fulfilling several key EU Directives (*i.e.* Renewable Energies, Floods, Habitats and Species, and Water Framework Directives).

The findings emphasise the importance of considering food webs and energy pathways in river management strategies. In these hydropeaking rivers, energy resources primarily come from three main sources: terrestrial inputs, seston released in hydropeaking flows, and periphyton available on benthic substrates (Cross et al. 2013). The results in this chapter demonstrate the potential for a loss of high-quality algal periphyton from the benthos in alpine rivers, and as a remaining food resource, seston from reservoir releases may provide a proportionally larger contribution to the trophic base. Even high-flow tolerant scraper, grazer, and collector communities may later leave the system as benthic food resources may be insufficient to sustain their populations, resulting in a shift in the benthos community towards rheophilic filter feeding taxa such as *Simuliidae*. As these findings come from an experimental setup, however, the results of this study and its implication for overall ecosystem function would need to be validated in the field. This approach to considering food webs and energy flows is not restricted to hydropeaking rivers; however, but also to other ecosystems, and this was explored in Chapter 5.

6.1.4 Chapter 5: Large wood in a lowland river enhances resource availability as demonstrated by combined stable isotope and fatty acid analyses

The objective of Chapter 5 was to examine how large wood would affect the trophic base of the macroinvertebrate assemblage in a lowland, sand bed river. A secondary objective was for a methodological comparison using both stable isotope analysis (SIA) and fatty acid (FA) biomarkers to examine the food web and trophic base. Two adjacent river reaches, one with large wood accumulations and another as a control without large wood, were compared to examine the different availabilities of food resources and its impact on the macroinvertebrate community assemblage.

Chapter 5 demonstrated that the trophic base of the macroinvertebrate assemblage was highly dependent on seston that was exported from a nearby lake, indicating a high degree of coupling between lake and riverine productivity. However, the macroinvertebrate assemblage on the wood surface and sediments around wood reduced their dependence on the seston by utilizing their greater access to other food resources, including the accumulations of organic matter and terrestrial matter around wood, but most importantly the high-quality autochthonous sources growing on the wood surface. High-quality algal production on wood was largely responsible for changes in the trophic base and increasing consumer production. In addition, wood provided a high-quality attachment site for filter-feeding taxa, altering their feeding patterns to a more nutritive component of the seston, and increasing the amount of highly-unsaturated fatty acids in their diet, which has implications for growth and fitness (Müller-Navarra et al. 2000, Torres-Ruiz et al. 2010).

This is the first known study that has used stable isotopes and fatty acids to examine changes in the food web with river structural complexity. The joint use of SIA and FA in this study was complementary, particularly for addressing the mix of allochthonous and autochthonous resources from lacustrine and riverine origins. FA did not effectively detect seston but differentiated between allochthonous and autochthonous components of the trophic base, and demonstrated the higher nutritional value of autochthonous primary producers. When paired with stable isotope results, FA suggested that many seston-feeding consumers preferentially fed on the autochthonous fraction of seston. This study suggests the use of fatty acids in conjunction with stable isotopes in order to resolve a complex mix of similar trophic resources in freshwater food webs.

The presence of large wood, therefore, decreased the strength of river-lake coupling by increasing the number of pathways for energy flow by providing alternative basal resources primarily through its role as a hard substrate to increase local, high-quality autochthonous productivity. In addition, the possibility of coupling with external food resources is likely to be applicable to other river systems, as other rivers lacking hard substrate (*e.g.* the lowland rivers with high levels of fine sediment in Chapters 2 and 3) or otherwise deficient in in-stream productivity (*e.g.* scoured phytobenthos in Chapter 4) would be expected to have a trophic base largely dependent on basal resources supplied from upstream (*e.g.* a lake or reservoir). Large wood, therefore, as an element of ecosystem structure, can influence ecosystem function through altering the patterns of energy flow and basal support in these ecosystems.

6.2 Future developments needed for fatty acid analysis in riverine ecosystems

This thesis has summarized the connection between fatty acid content with ecosystem responses, and demonstrated how large wood and physical habitat conditions can alter nutritional quality and fatty acid content available for stream consumers. However, there are still important methodological developments needed to further progress this line of research on the connections between physical habitat change, fatty acid content, and ecosystem response. Particularly, there are additional experiments needed to translate findings from fatty acid studies in lakes to adapt and apply them to riverine ecosystems.

A Bayesian mixed modelling method has recently been developed for fatty acids that can produce quantitative diet estimations for food web analysis similar to stable isotope mixing models (Galloway et al. 2014a, Galloway et al. 2015). The benefit of a fatty acid mixing model is that it utilizes the strength of specific fatty acid biomarkers and a greater number of sources (20-30 individual fatty acids compared to 2 or 3 stable isotopes) to resolve overlapping trophic source signals and problems with model over-determination (more source signals than tracers) that are common in stable isotope mixing models. Adapting this model would allow for a quantitative estimation of the macroinvertebrate diet using fatty acids in Chapter 5, but with the added benefits of the increased diet resolution of fatty acid analysis, and allowing a more direct comparison between fatty acid and stable isotope methods. However, as this model was developed for planktonic and not benthic food webs, there is additional work needed for it to be applied to the benthos. Just as trophic enrichment factors are used in stable isotope modelling to account for changes in δ^{13}C and δ^{15}N signatures with increasing trophic levels, the model must account for how fatty acids are bioactive molecules and different taxa may be selectively accumulated or bio-converted from the diet (Kainz et al. 2004, Taipale et al. 2011). As a result, controlled feeding experiments with benthic taxa are needed to develop reference libraries for the fatty acid profiles of benthic consumers fed on known diets, so that these values may be referenced within a new benthic-focused Bayesian fatty acid mixing model.

In addition, a fatty acid Bayesian mixing model approach to the periphyton has the additional potential to improve current Biological Quality Elements methods in the Water Framework Directive by linking biodiversity more closely with ecosystem function. Current phytobenthos methods focus almost exclusively on the response of diatoms to specific chemical pressure gradients, and thus may be redundant with direct physiochemical monitoring (Kelly 2011). If Biological Quality Elements are intended to inform ecosystem function, rather than simply identify chemical pressures, new methods are needed that are relevant to overall ecological status and the function of higher trophic levels (Kelly 2013). Since algal classes have unique fatty acid profiles (Dethier et al. 2013, Taipale et al. 2013), this suggests that fatty acid profiles may be a useful chemotaxonomic marker to determine a quantitative taxonomic shift in periphyton community composition. The different fatty acid profiles identified on wood and tiles in Chapter 4 of this thesis, and their change with hydropeaking, suggests a shift in the taxonomic composition of periphyton, but there are no current reliable means to quantify these changes in community composition with fatty acid profiles. A recent study has shown that phytoplankton community composition can be inferred with a fatty acid mixing model (Strandberg et al. 2015), with results strongly correlating to traditional microscopic analysis. However, the exploration of the fatty acid composition of cultured benthic algal taxa and other components of periphyton would be needed to establish a reference library relevant to the benthos, and that this method, adapted for periphyton, likewise validated against direct microscopic counts. If completed, fatty acid profiles may prove an effective alternative to training- and time-intensive microscopy counts, and provide both detailed quantitative information about periphyton taxonomic shifts and relevant information about the nutritional quality of periphyton as a food resources for consumers.

6.3 A new nutritional paradigm of the ecosystem structure-function relationship

While the effects of habitat structure and complexity on population level attributes has been well-studied in the literature, there has been little examination of other functional attributes (*e.g.* trophic pathways, compartmentalization) or their underlying mechanisms (Figure 6-2; Kovalenko et al. 2012). This thesis has specifically demonstrated how wood has the potential to alter ecosystem function by increasing physical habitat complexity, driving a change the quantity and quality of basal food resources, and affecting the diversity, productivity, and basal support of the consumer assemblage. In addition, this thesis has also demonstrated how the structural complexity associated with wood can change community and ecosystem-level functional attributes, such as decreasing river-lake coupling, increasing consumer biodiversity, increasing the number of pathways for energy flows, and increasing resilience to disturbance (Figure 6-2). In addition, this thesis has demonstrated several mechanisms that regulate this response, specifically increased food quantity (organic matter interception and algal colonization), the mitigation of the scour of these food resources from physical disturbance, and increased food biochemical quality, which has been shown to affect emergent properties such as resource assimilation efficiency (Taipale et al. 2014).

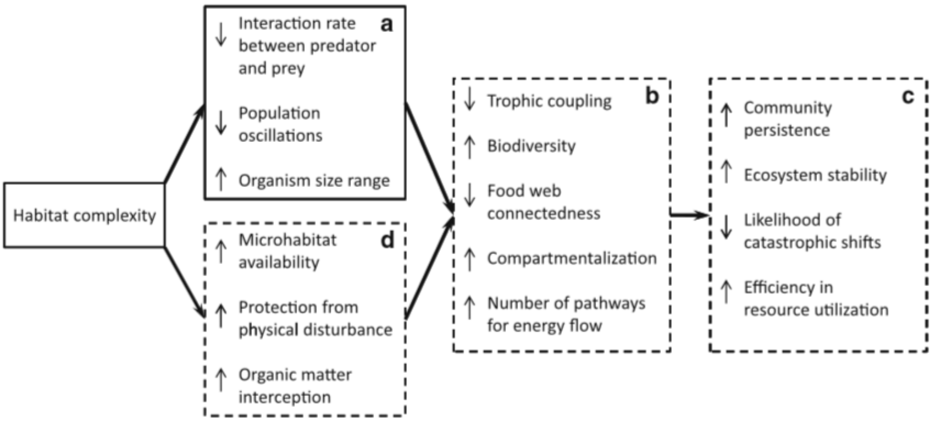


Figure 6-2: This thesis provides additional support for the effect of wood altering the underlying nutritional dynamics of food resources creating changes to ecosystem attributes, as originally outline in Kovalenko et al 2012. Generally, the effects of habitat complexity on population-level attributes (a) are well-documented, but with exception of biodiversity, little is known about the hypothesized effects on community and ecosystem attributes (b), their emergent properties (c), and potential underlying mechanisms (d). Figure from Kovalenko et al 2012

This work highlights that a new paradigm that more fundamentally incorporates nutritional dynamics and energy flows is needed for understanding the river structure-function relationship. Previous explanations of the ecosystem structure-function relationship through a diversity cascade (Figure 6-3) is missing this key component. Food availability and efficiency in the transfer of energy from primary production into consumers is one of the most basic and fundamental questions in ecology, and the examination of habitat diversity must not be limited to the consideration of physical attributes alone, but must also account for the diversity of food resources, and more importantly their biochemical and nutritional quality. Without habitat conditions supporting diverse basal resources, the response by consumers would be fundamentally limited, particularly due to biochemical controls on the assimilation efficiency across the plant-animal interface (Taipale et al. 2014).6

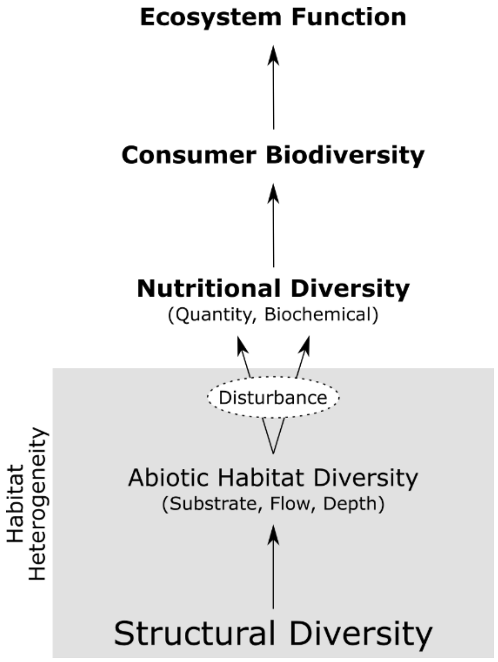


Figure 6-3: The conceptual progression underlying a new nutritional paradigm for understanding the habitat heterogeneity hypothesis. The physical structure of a river (i.e. shape and form) causes cascading changes in other abiotic habitat conditions (e.g. flow, substrate, light), which, mediated by temporal aspects and the disturbance regime, alters the quantity and biochemical nutritional diversity of food resources. This in turn regulates consumer community assemblages and ultimately affect overall ecosystem function.

This thesis has explored how wood has the potential to alter the patterns of basal trophic support and energy flows by affecting the nutritional quality and quantity of food resources across a variety of river ecosystems and types. However, the pattern of energy flows across all of the rivers in this thesis reveals many similarities in their function: the alpine rivers subject to hydropeaking and simulated in Chapter 4, and the lowland, sand-bed river in Chapter 5, although very different in hydromorphology, contain low benthic production (due to benthic scour in hydropeaking and little available hard substrate for periphyton colonization respectively) resulting in benthic consumer communities that are largely subsidized by external seston. The lowland rivers in the United Kingdom dominated by unstable fine sediments (identified in the NRRI in Chapter 2 and surveyed in Chapter 3), also contain many similar properties to the sand-bed lowland river in Chapter 5: a bed predominantly covered by unstable fine sediment (silt and clays in the lowland UK rivers, sand in the Płociczna River in Poland), which bury, damage, or otherwise limit the availability of hard substrates and epilithic biofilms (Wood and Armitage 1997). Despite the large accumulations of organic sediments, the results of Chapter 5 suggest that this is a low quality resource for benthic consumers, and while it may be used by some consumers, it does not have the quality necessary for supporting robust macroinvertebrate production as do the food resources colonizing wood.

Therefore, the results of this thesis, although occurring across different river types, are complementary and highlight the importance of the availability of high quality basal resources locally supported by wood, especially in ecosystems lacking other local high-quality autochthonous production. Therefore, the management decisions to remove, or re-introduce, large wood could be generally expected to alter the patterns of energy flows and ecosystem function by altering the availability and quality of basal food resources. However, negative perceptions about large wood persist, and the use of simple deflectors in river restorations, rather than more structurally-complex large wood similar to more natural forms, may be limiting the ecological potential of river restorations using large wood. As concerns about flood risk and aesthetics may drive these decisions, collaboration with national agencies already involved in financially supporting these restorations may help improve the decision-making of these projects to increase the complexity of wood used in river restorations without increasing flood risk to downstream infrastructure and development.

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Glossary of Terms

AFDM – Ash-free dry mass. The mass of organic matter contained in the sample (after the mass of mineral ash is removed).

ALA – α-linoleic acid, 18:3ω3, precursor of EPA and DHA

Allochthonous – Originating from outside the system. In aquatic ecology typically refers to production from terrestrial sources that has entered into aquatic systems.

ANOSIM – Analysis of Similarity, a test for statistical differences between two or more groups of sampling units, operating directly on a dissimilarity matrix.

ARA – Arachidonic acid, 20:4ω6, a generally accepted essential fatty acid

Autochthonous matter – Originating from within the system. In aquatic ecology typically refers to production from within the channel such as bryophytes, periphyton, filamentous algae, and macrophytes.

Bacillariophyceae – Diatoms. Algae consisting of silica cell walls and contains high levels of EPA and other HUFA

BQE- Biological Quality Elements

Chl-*a* – Chlorophyll-*a*. The main photosynthetic pigment used in eukaryotes, cyanobacteria, and prochlorophytes. Frequently used as a measure of autotrophic biomass.

DHA – Docosaxhanoic acid, 22:5ω3, an essential fatty acid

EPA – Eicosapentaenoic acid, 20:5ω3, an essential fatty acid

FA – Fatty acids. A carboxylic acid with an aliphatic tail and may be saturated or unsaturated.

FAME – Fatty acid methyl esters. Derived from fatty acids for detection on GC-MS and quantification of fatty acid content in samples.

GC-MS – Gas chromatography mass spectrometry

HUFA – Highly unsaturated fatty acids. A fatty acid with 2 or more double bonds and 20 carbons or greater.

LW – Large wood. Defined as wood ≥ 10 cm in diameter and ≥ 1 m in length.

LIN – Linoleic acid, 18:2ω6, precursor of ARA

MUFA – Monounsaturated fatty acids. A fatty acid with one double bond.

NMDS – Non-metric multidimensional scaling. An ordination technique that preserves true distances between samples and with no hidden axes of variation. Makes no assumptions about linearity or modal relationships.

OA – Oleic Acid, 18:1ω9, linked as a saporotrophic fungal fatty acid in soil literature, but is a common fatty acid intermediate synthesized by most aquatic consumers.

Omega-3 fatty acid: Poly- or highly-unsaturated fatty acids with the first double bond occurring on the 3rd-carbon atom from the methyl end.

Omega-6 fatty acid: Poly- or highly-unsaturated fatty acids with the first double bond occurring on the 6th-carbon atom from the methyl end.

ω3/ω6: The ratio of omega-3 to omega-6 fatty acids. Frequently used as a proxy of aquatic or terrestrial food resources. Aquatic resources have higher ω3/ω6 than terrestrial, generally with a value greater than 1 indicated aquatic dominance.

Periphyton – Mixture of algae, cyanobacteria, detritus, and heterotrophic microbes often contained in biofilms in aquatic ecosystems. In this thesis also includes attached macro-algae.

Phytobenthos – Biological Quality Element considered in Water Framework Directive for benthic plants. Broadly defined as any photosynthetic component of the benthos, but assessment methods typically consider micro- but not macro-algae.

PUFA – Polyunsaturated fatty acids. A fatty acid with 2 or more double bonds and 18 carbons or less.

SAFA – Saturated Fatty Acids. A fatty acid without any double bonds.

SDA – Stearidonic acid, 18:4ω3

SIMPER – Similarity Percentage, a test to examine the individual components of the overall Bray-Curtis dissimilarity index

TOM – Transported Organic Matter. Organic matter that is transported by river flow.

WFD – Water Framework Directive. Directive 2000/60/EC of the European Parliament committing European Union member states to achieve good ecological status for all water bodies.

Zoobenthos – The zoological component of the benthos.

Appendix I – Methods

SOP: Preparation of Stream Samples for Fatty Acid Analysis

Updated 05-11-11

Sample Location	**Processor Name**	
Collection Date	**Processing Date(s)**	

Materials	
Chloroform-washed 15 mL centrifuge tubes	HPLC-grade chloroform
Pre-ashed Whatman® GF/F 47 mm filters	HPLC-grade methanol
Glass fiber wool	Chloroform: methanol (2:1) reagent
Rubber stoppers for tube support in centrifuge	HPLC-grade hexane
Electric grinder, chloroform washed tip	(14%) BF_3/MeOH
2 mL amber crimp-seal vials (septa should be Teflon lined), chloroform washed	$NaSO_4$ anhydrous powder (ashed)
11 mL borosilicate tubes (16 x 100 mm) with Teflon caps, chloroform washed	Borosilicate Pasteur pipettes, hexane washed (cotton removed) (With shortened tip)
Vial crimping tool	

Collection and Initial Preparation

Check ☐ or **X** or add **data**

Macroalgae or Invertebrates	**Replicate #** ⟶	**1**
Rinse in several changes of freshwater water to remove silt and epiphytes		
Blot the material dry on Kimwipes©		
Measure fresh mass to nearest 0.0001 g **(≈ 0.10 g)** (If [FA] per unit dry mass is required, another set of fresh-to-dry mass samples will be needed.)	**Rep** **Data**	**1**
Place the sample in a clean 15 mL centrifuge tubes.		
Purge with N_2 and cap tightly → store @ -20°C until extraction		

Phytoplankton, mixed periphyton, FPOM	**Replicate #** ⟶	**1**

Record volume and/or surface area of collected sample **Data**	
Filter 5 to 25 mL of suspension using 47 mm pre-ashed GF/F filter **Data**	
Record the volume of sample water or periphyton extract filtered **Data**	
Measure fresh mass to nearest 0.0001 g **(≈ 0.10 g)** **Rep**	
Data	
Fold filter algae-side in, then lengthwise → clean 15 mL centrifuge tubes	
Purge the head space with N_2 and cap tightly	
Purge with N_2 and cap tightly → store @ -20°C until extraction	

Extraction

3 – 4 hours per 20 samples

Check ☐ or **X** or add **data**

All Samples **Replicate #** →	**1**
Defrost sample from freezer	
Transfer sample into a 16 x 100 mm (11 mL) borosilicate tube (chloroform washed) with a Teflon-lined cap. **Put tube on ice**	
MOVE SAMPLE INTO FUME HOOD	
Add 3 mL chloroform: methanol (2:1). **Data** *(Sometimes 6 mL necessary with filters)*	
Rinse electric grinder rod in chloroform: methanol.	
Grind sample: keep cold (tubes on ice)	
Add 1 mL of chloroform: methanol (2:1)	
Add 0.5 mL of ultra pure water (Millipore)	
Sonicate sample for 2 min, on ice (optional)	
Vortex for 5 sec	
Centrifuge at 800 rpm for 2.5 min at 0^0 C (use rubber stopper)	
Pipette chloroform phase (bottom) into new chloroform clean tube	
Concentrate to dryness under N_2 using 24-tube Visidry© rack	

Sample can be stored in freezer under N_2 in amber test tube for up to a year or overnight if no centrifuge is available to separate the phases.

Methylation

3 – 4 hours per 20 samples, 1 hour per last step Check ☐ or **X** or add **data**

All Samples **Replicate #⟶**	**1**
Add 0.5 mL hexane **to dry sample**	
Add 1mL BF$_3$	
Purge with N$_2$ and cap tightly	
Vortex for 5 seconds	
Incubate in water bath for 1 hour at 80°C	
While incubating **prepare** a NaSO$_4$ column	
- **Use** ashed NaSO$_4$ (15 min at 450°C)	
- **Place** a little glass fiber wool in the bottom of a Pasteur pipette	
- **Put** approx 1.5cm of NaSO$_4$ inside pipette	
- **Rinse** column with 3 mL hexane	
Add 0.5ml ultra pure water (Milli-Q) to sample	
Vortex for 5 seconds	
Add 2ml hexane	
Centrifuge at 1000 rpm for 2 min	
Pipette off supernatant (hexane phase) into clean NaSO$_4$ column that has been placed on top of hexane-clean 11 mL borosilicate tube *Fraction eluted from column can be stored in an amber test tube under N$_2$ for up to a year*	
Evaporate hexane extract under N$_2$ to dryness using 24-tube Visidry© rack.	
Re-suspend in desired volume (usually 1ml) of hexane	
Place extract in labeled GC auto-sampler vial (amber)	
Insert 10 µL of 19:0 Internal Standard (@ 1ppm/mL)	
Crimp-seal vial closed (store – 20° C prior to analysis)	

Sample can be stored like this for up to a year if not punctured.

References. Methods based on the following:

Parrish, C. C. 1999. Determination of total lipid, lipid classes, and fatty acids in aquatic samples. Pages 4–20 in M. T. Arts and B. C. Wainman (editors). Lipids in freshwater ecosystems. Springer, New York.

Torres-Ruiz, M., Wehr J.D. and Perrone, A.A. 2007. Trophic relations in a stream food web: importance of fatty acids for macroinvertebrate consumers. Journal of the North American Benthological Society 26:509–522.

Appendix II – Manuscripts & Articles