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The ecological effects of physical habitat restoration in English chalk streams

by

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Abstract

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Chalk streams are globally rare and unique systems that have been extensively subjected to physical modification. This has contributed to the widespread degradation of ecological communities in chalk streams and failures to adhere to legislation (e.g. Water Framework Directive). Physical restoration has emerged as a key strategy to improve the condition of chalk streams, but a current lack of evidence for its effectiveness constrains the development of sound practice.

This thesis aimed to develop understanding of the effects of restoration on physical habitat and ecology in English chalk streams. A series of case study appraisals were undertaken to understand: (1) the physical and ecological effects of different techniques (i.e. weir removal and gravel augmentation); (2) the influence of time since restoration; (3) the effects of restoration on different ecological groups. Additionally, (4) a methodological approach for non-invasively evaluating fish populations was developed to help improve monitoring capabilities in chalk streams.

Weir removal rapidly altered habitat and ecological communities, especially directly upstream which became more lotic. Little evidence of sediment-pulse related impacts downstream of the weir was found, possibly due to additional silt-management methods which facilitated recovery. Gravel augmentation desirably altered habitat and ecology over the timescale studied (e.g. enhanced macroinvertebrate diversity). However, variability between sites, time periods and ecological groups signifies widespread uncertainties in restoration outcomes and the need to develop a better understanding of the drivers behind these.

Time was a key factor influencing the observed effects of restoration (e.g. due to lag-effects). Furthermore, responses varied considerably between ecological groups, where changes in macroinvertebrates (e.g. increased diversity) and fish (e.g. increased brown trout sightings) were not reciprocated in macrophytes. These findings highlight the need for appraisals to take place at commensurate temporal scales and ideally using a multi-taxa approach to understand responses more accurately.

Remote underwater video proved a useful tool for assessing fish communities and population size. Given the adaptability and utility of the technique, as well as its potential application as a citizen science methodology, it may prove useful for monitoring at chalk stream restoration projects and requires further investigation.

Overall, this thesis contributes valuable evidence suggesting restoration can be an effective tool for desirably altering habitat and ecological communities in chalk streams. However, the need to conduct more robust appraisals to consolidate knowledge is highlighted and emphasises the need to fund the development of flagship case studies to guide and inspire future restoration efforts.

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List of Accompanying Materials

Dolman, Lewis A. (2024). Dataset supporting the University of Southampton Doctoral Thesis: 'The ecological effects of physical habitat restoration in English chalk streams' by Lewis Adam Dolman. University of Southampton. doi: 10.5258/SOTON/D2945 [Dataset].

Research Thesis: Declaration of Authorship

Lewis Dolman

Title: Understanding of the effectiveness of physical habitat restoration in English chalk streams

I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. None of this work has been published before submission

Signature: .... Date: ....

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Definitions and Abbreviations

A1 Order

Common name	Latin name
Mayflies	Ephemeroptera
Stoneflies	Plecoptera
Caddisflies	Trichoptera

A2 Genus

Water starwort	Callitriche
Pacific salmon	Oncorhynchus

A3 Families

N/A	Aphelocheiridae
Small minnow mayfly	Baetidae
N/A	Bithyniidae
Non-biting midges	Chironomidae
Riffle beetle	Elmidae
Spiny crawler mayflies	Ephemerellidae
Common Burrower Mayflies	Ephemeridae
‘Scud' or gammarid	Gammaridae
N/A	Goeridae
Mud snail	Hydrobiidae
Net-spinning caddisflies	Hydropsychidae
Water scorpion	Nepidae
Nerite snail	Neritidae
Fingernet caddisflies	Philopotamidae
Ramshorn snail	Planorbidae
Black fly	Simuliidae
Valve snails	Valvatidae

A4 Species

Common name	Latin name
American mink	*Neovison vison*
Armoured catfish	*Rineloricaria aequalicuspis*
Atlantic salmon	*Salmo salar*
Blue-winged olive mayfly	*Serratella ignita*
Blunt-fruited water-starwort	*Callitriche obtusangula*
Brook lamprey	*Lampetra planeri*
Brook water crowfoot	*Ranunculus penicillatus ssp. pseudofluitans*
Brown bear	*Ursus arctos*
Brown trout	*Salmo trutta*
Canadian waterweed	*Elodea canadensis*
Common carp	*Cyprinus carpio*
Common club-rush	*Schoenoplectus lacustris*
Common dace	*Leuciscus leuciscus*
Common kingfisher	*Alcedo atthis*
Crayfish plague	*Aphanomyces astaci*
Eurasian beaver	*Castor fiber*
Eurasian minnow	*Phoxinus phoxinus*
Eurasian otter	*Lutra lutra*
European bullhead	*Cottus gobio*
European chub	*Leuciscus cephalus*
European eel	*Anguilla anguilla*
European grayling	*Thymallus thymallus*
European perch	*Perca fluviatilis*
European water vole	*Arvicola amphibius*
Filamentous green algae	*Cladophora glomerata*
Fine lined pea mussel	*Pisidium tenuilineatum*

Common name	**Latin name**
Floating water penny	*Hydrocotyle ranunculoides*
Fools water cress	*Apium nodiflorum*
Grannom fly	*Brachycentrus subnubilus*
Green drake mayfly	*Ephemera danica*
Himalayan balsam	*Impatiens glandulifera*
Japanese knotweed	*Fallopia japonica*
Lesser water-parsnip	*Berula erecta*
New Zealand mud snail	*Potamopyrgus jenkinsi*
Northern pike	*Esox lucius*
Prussian carp	*Carassius gibelio*
Rainbow trout	*Oncorhynchus mykiss*
River lamprey	*Lampetra fluviatilis*
River water crowfoot	*Ranunculus fluitans*
Sea lamprey	*Petromyzon marinus*
Signal crayfish	*Pacifastacus leniusculus*
Sockeye salmon	*Oncorhynchus nerka*
Southern damselfly	*Coenagrion mercuriale*
Stone loach	*Barbatula barbatula*
Sumatran Barbs	*Puntigrus tetrazona*
Three-spined stickleback	*Gasterosteus aculeatu*s
Topmouth gudgeon	*Pseudorasbora parva*
Unbranched bur-reed	*Sparganium emers*um
Various-leaved water starwart	*Callitriche platycarpa*
Watercress	*Nasturtium officinale*
White-clawed crayfish	*Austropotamobius pallipe*
Zebrafish	*Danio rerio*

B1 Abbreviations

Abbreviation	Meaning
ANOVA	Analysis of variance
ATS	ANOVA-type statistic
BA	Before-after
BACI	Before-after-control-impact
BL	Broad leaved
BP	Before present
CI	Control-impact
D	Downstream of weir
DCSV	Depth cross sectional variability
DFW	Distance from weir
EL	East Lodge
EPT	Ephemeroptera, Plecoptera and Trichoptera
EPT abundance	The abundance of Ephemeroptera, Plecoptera and Trichoptera
EPT richness	The taxon richness of Ephemeroptera, Plecoptera and Trichoptera
EPTA	The percentage of the total abundance comprised of Ephemeroptera, Plecoptera, Trichoptera
EPTN	The percentage of the total taxon richness comprised of Ephemeroptera, Plecoptera, Trichoptera
FGA	Filamentous green algae
GLMM	Generalised linear mixed model
HS	Home Stream
ICER	International Centre for Ecohydraulics Research
LIFE	Lotic Index for Flow Evaluation
LMM	Linear mixed model
NMax	Maximum number of individuals in a frame
NMDS	Non-metric multidimensional scaling

Abbreviation	Meaning
NMean	Mean of the maximum number of individuals viewed in a frame per minute across a video sample
NPM	Non-parametric repeated measure models
NRRI	National River Restoration Inventory
OSTN	Old Station Beat
OSTW	Old Stews Beat
PERMANOVA	Permutational multivariate analysis of variance
PSI	Proportion of Sediment sensitive Invertebrates
Q	Flow discharge
REFORM	Restoring rivers for effective catchment management
RUV	Remote underwater video
SAC	Special area of conservation
SD	Standard deviation
SSSI	Site of special scientific interest
TMC	Total macrophyte cover
U	Upstream of weir
UIF	Unique identifiable features
UP	Unique permutations
VCSV	Velocity cross sectional variability

C1 Terminology

Active restoration: Restoration that involves human-induced modifications to the habitat (e.g. flow deflectors, weir removal).

Aleatory uncertainty: Uncertainty in restoration outcomes that are caused by unpredictable variation (e.g. environment stochasticity).

Chalk stream: A river that derives over 75% of its base flow from chalk aquifers.

Classic slope-faced stream: Chalk streams that rise directly from and flow largely over chalk (CaBA, 2021).

Coarse sediments: Sediments > 2 mm in diameter.

Creation: Converting one ecosystem into another, usually to facilitate ecosystem services.

Ecological resilience: “The capacity of ecosystems to collectively adjust and adapt to shifting and potentially novel environmental conditions while preserving desired functions, species, and services” (Grantham *et al.*, 2019).

Ecosystem engineers: Taxa that can influence others and ecological processes by modifying physical habitat.

Enhancement: Projects that aim to achieve "any improvement of a structural or functional attribute" (Natural Research Council, 1992 as referenced in RPR, 1993)

Epistemic uncertainty: Uncertainty in restoration outcomes that are caused by a lack of knowledge (e.g. poor understanding of restoration theory).

Field of Dream hypothesis: A hypothesis which posits that the restoration of habitat structure is sufficient to recover ecological integrity, or 'if you build it, they will come'

Fine sediments: Sediments < 2 mm in diameter.

Flow discharge: The amount of water travelling through a specific area over a certain period.

Fluvial geomorphology: aims to understand “interactions between river channel forms and processes at a range of space and time scales” (Charlton, 2007)

Form-based restoration: Restoration focussed on the recovery of habitat structure and features.

Functional redundancy: A concept where species within a system share similar functional roles. Hence, if a species becomes locally extinct, system functioning is theoretically maintained.

Habitat: The range of physical, chemical and biological factors that impact a species over space and time.

Habitat patch concept: Landscape ecology derived framework that conceptualises habitat as a mosaic of patches, or distinct homogenous areas differing from the surroundings.

Intermediate Disturbance Hypothesis: A theory positing that diversity is maximised at intermediate disturbance due to differences in species colonisation and competitive abilities.

Low-head river infrastructure: River infrastructure with a height less than five metres.

Mass effects: A metacommunity framework concept describing the circumstance when regional propagule pressure is high which allows taxa to persist in sub-optimal habitat, offsetting local sorting processes.

Metacommunity theory: A framework attempting to explain how species from multiple dispersal-linked populations interact with the local environment to shape ecological communities.

Mitigation: "Actions taken to avoid, reduce or compensate for the effects of environmental damage" (Natural Research Council, 1992 as referenced in RPR, 1993).

Mixed-geology stream: Chalk streams that do not rise from but subsequently flow over chalk (CaBA, 2021).

Passive restoration: Restoration that does not directly alter habitat, but allows natural processes to restore the ecosystem (e.g. cessation of river maintenance).

Patch dynamics: A metacommunity framework concept describing the circumstance when local scale processes (e.g. species interactions) are more important in structuring ecological communities due to a low regional propagule pressure.

Pleistocene ice-impacted stream: Chalk streams that are derived from chalk altered by Pleistocene glacial action. These can be included in any other group (CaBA, 2021).

Portfolio effect: Theory positing that a system with greater biocomplexity will be more resilient to perturbation.

Process-based restoration: Restoration focussed on the recovery of naturalised rates of processes.

Propagule pressure: The number of individuals dispersing into an area.

Regime shift: A large, long-term change in system functioning once a threshold is crossed.

Rehabilitation: "Partial structural and functional return to a pre-disturbance state" (Cairns, 1982 as referenced in RPR, 1993).

Rescue effects: A process in which migration can help stabilise the wider population by facilitating the recolonisation of extinct patches.

Restoration: "complete structural and functional return to a pre-disturbance state" (Cairns, 1982; 1991 as referenced in RPR, 1993).

River Continuum Concept: A concept relating the processing of nutrients and stream community composition to longitudinal changes in stream form.

Scarp-face stream: Scarp-slope chalk streams that rise from chalk and flow over clay rich chalk, gault clay and greensand beds (CaBA, 2021).

Shifting habitat mosaic: A concept describing the dynamic nature of the spatial arrangement of habitat patches in response to disturbance.

Species sorting: A metacommunity framework concept describing the circumstance in which communities are structured by and closely match the local habitat.

Water Framework Directive: European Union legislation created in 2000 that obligates member states to achieving 'good ecological status' on all surface waterbodies by 2027.

Weir: Structures without active water regulation and heights that do not exceed the natural bank which typically create small reservoirs with short water retention times.

γ-diversity: The total species diversity across a landscape.

Thesis structure

This body of research was carried out with the aim of developing understanding of the effects of restoration on physical habitat and ecology in English chalk streams.

The chapters within this thesis are linked and collectively form a coherent body of research towards the thesis aim. **Chapter 1** provides a brief introduction, highlighting the issues faced in freshwater ecosystems, the need for physical habitat restoration and the current problems in the field. **Chapter 2** provides an in-depth literature review on fluvial and ecological theory, river restoration, chalk streams and their restoration to identify key issues, knowledge gaps and bias in research and restoration. This was used to help guide the thesis objectives and research chapters, which are described in **Chapter 3**.

Chapters 5 - 8 presents the results of the research carried out as part of this thesis. In **Chapter 5**, the physical and ecological impacts caused by low-head weirs and effectiveness of their removal as a restoration strategy was assessed using a mixture of coarse and fine scale approaches. In **Chapter 6**, the effects of gravel augmentation on physical habitat and multiple ecological groups was assessed in two chalk streams. In **Chapter 7**, the effects of two restoration projects on habitat and macroinvertebrates were assessed over an 8-9 year period, representing a relatively long-term study when considering the wider chalk stream restoration literature. In **Chapter 8**, a passive methodological approach for monitoring fish populations in chalk streams was developed. This project feeds directly from Chapter 6, where issues with traditional fish sampling methods were faced, and indirectly contributes to the aim of this thesis by improving monitoring capabilities at chalk stream restoration sites. **Chapter 9** discusses the findings of this body of research in relation to the thesis aim and objectives, and provides advice for management and future research needs.

CHAPTER 1 **Introduction**

Freshwater ecosystems including rivers, lakes and wetlands only cover around 9.6% of the world's land surface and account for 0.01% of global water supply (Lehner and Döll, 2004; Reid *et al.*, 2019). Despite this, they represent epicentres for biodiversity, human civilisation and are fundamental for global functioning. Per unit volume, freshwater ecosystems are one of the most biodiverse habitats, containing approximately 12% of all described species (Reid *et al.*, 2019; Albert *et al.*, 2021). This includes over 18,000 fish representing approximately 50% of global fish diversity (Fricke *et al.*, 2023), roughly 3,000 macrophyte species, 12,000 crustaceans and over 100,000 insects (Grosberg *et al.*, 2012). Freshwater ecosystems also shape and support terrestrial and marine environments and ecology, for instance by providing water resources and habitat (Hauer *et al.*, 2016), facilitating nutrient cycling (Schindler and Smits, 2017; Kamjunke *et al.*, 2023), acting as a corridor for movement (Derugin *et al.*, 2016) and regulating local climate (Murakawa *et al.*, 1991). For example, the predation of migratory Pacific salmon (*Oncorhynchus sp.*) by brown bear (*Ursus arctos*) in Alaska mediates the transfer of marine-derived nutrients to terrestrial habitats, which can contribute up to 24% of riparian nitrogen budgets (Helfield and Naiman, 2006) and significantly enhance tree growth (Quinn *et al.*, 2018).

Freshwater habitats are also essential for human well-being, livelihoods and survival (Chung *et al.*, 2021; Lynch *et al.*, 2023). They provide a plethora of ecosystem services, including food and water resources, a means of energy production, waste disposal and transportation, and cultural and recreational value (Albert *et al.*, 2021) estimated to be worth US$ 29 trillion annually (Costanza *et al.*, 2014). For example, approximately 12 million tonnes of fish are captured from freshwater ecosystems every year (FAO, 2020), which provides revenue to at least 60 million people and the primary source of protein and other essential nutrients to 200 million (WWF, 2021). Hydropower has grown in capacity by over 70% in the past 20 years, becoming the most exploited form of renewable energy (55% of renewable energy) and contributing to 17% of global electricity budgets (IEA, 2020). The water derived from rivers, lakes, reservoirs and aquifers are central to human existence, not just as a domestic water supply (e.g. Southern Water, 2014), but also for agriculture (DEFRA, 2023) and to support industrial activities (Ritchie and Roser, 2018). Finally, freshwater ecosystems hold significant recreational and cultural value (Venohr *et al.*, 2018; UNESCO, 2021). For example, the River Test and Itchen (United Kingdom) are globally renowned recreational dry fly fisheries that attract tourists, provides revenue to the local economy and contributes to the 37,000 fisheries-related jobs across England and Wales (Mawle and Peirson, 2009; Skinner, 2013).

Conflicting needs between humans and freshwater ecosystems have led to the widespread degradation of habitat, biological communities and the services that they provide (Albert *et al.*, 2021). Indeed, the rates of biodiversity loss in freshwater ecosystems (81%) are more than double that of marine (36%) and terrestrial (38%) environments (according to the living planet index), with most losses arising from habitat degradation (e.g. damming, channelisation, 48%), followed by overexploitation (24%), invasive species and disease (12%), pollution (12%) and climate change (4%; WWF, 2016). For instance, a third of freshwater fish are currently threatened with extinction (WWF, 2021), many of which represent declines in migratory species (76% declines between 1970 and 2016; Deinet *et al.*, 2020) associated with the development of hydropower (Couto *et al.*, 2021) and spawning ground degradation (Louhi *et al.*, 2008). Healthy freshwater ecosystems are integral for the survival of millions of individuals, and a predicted increase in pressures caused by a growing population and climate change increases the risks of widespread humanitarian crisis (Hoeinghaus *et al.*, 2009; WWF, 2021; Albert *et al.*, 2021; Chung *et al.*, 2021). This has added impetus to understand the risks facing freshwater ecosystems and develop effective mitigation strategies (Lynch *et al.*, 2023).

Humans have intensively modified river systems both directly (e.g. river infrastructure) and indirectly (e.g. increased sediment inputs due to deforestation) across the globe (Brown *et al.*, 2018; Mulligan *et al.*, 2020). Indeed, throughout history and to this day, rivers have been dammed, channelised, dredged, simplified and cut-off from their floodplains to facilitate energy production, agriculture, flood water conveyance, erosion protection and navigation (e.g. Lenders *et al.*, 2016; Gibling, 2018; Foster *et al.*, 2021). Whilst these may be considered advantageous from an anthropogenic viewpoint (e.g. Cook *et al.*, 2003), the ecological damage caused by river modification has been considerable (Dudgeon *et al.*, 2006). For example, physical modification accounted for approximately 20% of failures to achieve good ecological status across England under the Water Framework Directive (2000/60/EC; Environment Agency, 2021a). Moreover, an estimated one million individual structures fragment and degrade habitat and ecological communities across Europe (Belletti *et al.*, 2020), which has widely contributed to declines in biodiversity (e.g. Mueller *et al.*, 2011). Historic land drainage schemes have channelised large sections of river, disconnecting them from the floodplain and homogenising habitat and ecological communities (Brookes, 1988; Brookes *et al.*, 1983).

Physically restoring rivers back to a more favourable condition has become important in efforts to mitigate the impacts associated with modification (Friberg *et al.*, 2016; Roni, 2018). Indeed, restoration activities are currently taking place across the globe (Kaiser *et al.*, 2020), often backed by substantial funding (Feld *et al.*, 2011; Szałkiewicz *et al.*, 2018). For example, according to the River Restoration Centre's National River Restoration

Inventory (NRRI), > 5,300 projects have been implemented across the United Kingdom over the past 25 years, amounting to at least one billion pounds spent (River Restoration Centre, 2023b). Despite these frequent attempts to restore habitat, the effectiveness of these projects often deviate from expectations. For example, whilst in some projects restoration has proved an effective approach for achieving conservation goals (e.g. Merz and Ochikubo Chan, 2005), others have led to limited (e.g. McManamay *et al.*, 2013) or even negative outcomes (e.g. Albertson *et al.*, 2011). Many factors may contribute to these mixed effects (Angelopoulos *et al.*, 2017), but a lack of project appraisals, particularly in rivers with more unique characteristics that remain underrepresented within the literature, is fundamental (Pander and Geist, 2013; Kaiser *et al.*, 2020). As the use of restoration to attempt to achieve conservation goals grows (United Nations, 2023), there is an need to understand its effectiveness across a range of systems to enable the development of sound practice.

Chalk streams, those that derive over 75% of their base flow from chalk aquifers, are unique and globally rare ecosystems (O'Neill and Hughes, 2014). Confined to southern and eastern England and parts of northern Europe, they are typically characterised as having dampened hydrological regimes, cool alkaline water and rich and productive biological communities (Berrie, 1992; CaBA, 2021). Chalk streams have been intrinsically linked with humans over millennia, and as a result, have been extensively modified from their natural state widely degrading habitat and biological communities (CaBA, 2021; Environment Agency, 2021a). Restoration has become a crucial strategy to mitigate the impacts of historic modification in chalk streams (CaBA, 2021), but its value remains poorly understood due to a lack of monitoring and evidence (River Restoration Centre, 2023b). There is a need to develop research into chalk stream restoration, which will provide an evidence base to advance practice whilst contributing to a global push to better understand restoration effectiveness in a wider range of systems (Kaiser *et al.*, 2020; CaBA, 2021).

1.1 Initial research aim and objective

The aim of this thesis is:

- To develop understanding of the effects of restoration on physical habitat and ecology in English chalk streams.

To achieve this aim, an initial objective was formed:

1) Review current literature on fluvial and ecological theory, river restoration, chalk streams and their restoration to identify issues, knowledge gaps and bias in research and restoration practice.

CHAPTER 2 **Literature review**

2.1 Fluvial geomorphology and ecological theory

Fundamentally, biota are controlled by habitat. Here, habitat will be defined as the range of physical, chemical and biological factors that impact a species over space and time (Armstrong *et al.*, 2003). Looking at habitat in such a way is important as it recognises that: (1) habitat encompasses a range of conditions, for example due to variation in life stage requirements (e.g. European eel, *Anguilla anguilla*; van Ginneken and Maes, 2005) or intra-taxa preference (e.g. local adaptation; Currey *et al.*, 2019); (2) the spatial and temporal extent of habitat varies across species (e.g. the range of habitat for migratory versus a resident species); (3) biological factors are an important component of habitat (e.g. Michelot *et al.*, 2017). To sustain a population of a particular taxa an ecosystem must therefore provide a diverse set of interconnected habitats of a sufficient quality capable of fulfilling a species requirements, otherwise, a population will cease to exist.

Geomorphology, hydrology and hydrogeology represent the primary driving forces behind the formation of a lotic system, providing a physical template for the development of habitat and biological communities (Charlton, 2007). Such a view has been held by ecologists for many decades. For example, the River Continuum Concept relates the processing of nutrients and stream community composition (i.e. functional feeding groups) to longitudinal changes in stream form (e.g. depth and velocity; Vannote *et al.*, 1980). Lotic waterbodies are complex. Indeed, they are multi-dimensional, with longitudinal (upstream-downstream), lateral (river-floodplain), vertical (surface water-hyporheic zone) and temporal (dynamic systems) connections (Ward, 1989). They are also hierarchically nested. Higher levels, such as stream systems (10^3 m), operate over longer temporal scales (i.e. are more persistent), are more resilient to perturbation and set the context for lower levels such as segments (10^2 m), reaches (10^1 m), mesohabitats (10^0 m) and microhabitats (10^{-1} m; Frissell *et al.*, 1986). It is also important to recognise the directional nature of rivers due to the greater influence of upstream on downstream (e.g. most water from upstream passes downstream, but not vice versa; Melles *et al.*, 2012). Habitats and ecological communities are distributed across lotic systems in intricate ways, and first acknowledging the development of river form is key in understanding these.

2.1.1 Fluvial geomorphology

The field of fluvial geomorphology aims to understand “interactions between river channel forms and processes at a range of space and time scales” (Charlton, 2007). Fluvial systems are complex and display a high degree of variability in channel form (Hohensinner *et al.*, 2018). The processes occurring in a river, and therefore their structural form, are influenced by an array internal and external controlling factors. Internal controls are those which can be directly altered by the system, e.g. hill-slope angle, flow discharge, vegetation, sediment yield and channel pattern (Charlton, 2007). Internal controls are adjustable in response to other internal factors (e.g. the angle of a hill slope can affect the amount of sediment entering the river) as well as external controls, those which are not directly influenced by the system such as human activity, tectonics and weather (Charlton, 2007). When one of these controls are altered through natural variation or anthropogenic modification, it can impact the internal factors which drives system change. These changes are influenced by the hierarchical nature of river systems, with alterations at higher levels tending to effect lower levels greatly, although cumulative change in lower levels can effect larger ones (Frissell *et al.*, 1986). These alterations in the system can in turn be reversed (e.g. an increase in slope through tectonic shifts may eventually be eroded away by an increased stream power) or promoted (e.g. a debris dam which reduces velocity in turn increasing the amount of debris deposited) through negative and positive feedback loops, respectively (Charlton, 2007).

In fluvial systems, physical habitat features and channel form are primarily dictated by river flow and sediment (Charlton, 2007; Zeiringer *et al.*, 2018). Flow discharge (Q), the amount of water travelling through a specific area over a certain period (e.g. $m^3 s^{-1}$), is often considered the ‘master variable’ and plays a pivotal role in determining river shape, size, structure and dynamics (e.g. river-floodplain interactions; Junk *et al.*, 1989; Zeiringer *et al.*, 2018). Flow discharge is determined by an array meteorological (e.g. rainfall and temperature) and biogeophysical (e.g. drainage area, topography and vegetation) factors. For example, less and more permeable catchments will tend to display flashier (i.e. sudden peaks and troughs) and dampened responses to rainfall, respectively. Temporal variations in rainfall and other factors (e.g. vegetation) gives rise to heterogeneity in flow over a range of temporal scales (Charlton, 2007). Sediment supply is also highly variable across space and time and is often linked with stochastic events (e.g. earthquake induced landslides; Hu *et al.*, 2021). The amount of sediment entering a river system is controlled by climate (rainfall intensity and duration), catchment characteristics (Buter *et al.*, 2022), vegetation (e.g. roots protecting from bank erosion; Purvis and Fox, 2016), land-use (e.g. agricultural practices; Walling, 2006) and sediment grain size (Charlton, 2007).

The ability of a river to transport sediment downstream largely depends on stream power and sediment size (also surrounding particles, bed roughness; Charlton, 2007). Stream power determines the capacity of the river to transport sediment, and is controlled by the water discharge and river slope, e.g. steep gradients and higher discharges provide a greater transport potential (Hohensinner *et al.*, 2018). Sediments can be transported as bed, suspended or dissolved load. The entrainment and transport of sediments depends on the resistance (e.g. particle submerged weight and influence of surrounding particles) and driving forces (e.g. drag and lift force) acting on the particle (Charlton, 2007). Generally, smaller particles are entrained with lower power than larger particles (Hjulström, 1935), with the exception of those < 0.2 mm, which may require a greater power to entrain due to protection from drag forces within the interstitial spaces of larger substrates and cohesive forces between particles. The deposition of entrained particles occurs when stream power is reduced below the deposition threshold (Hjulström, 1935). Spatial variation in stream power across a lotic waterbody gives rise to thresholds for sediment transfer (Sear, 2010). In the case of mountain streams, highland reaches are typically 'supply limited' due to their high power and capacity to transport all but the largest particles, whilst downstream reaches are usually 'transport limited' due to a reduced stream power, leading to deposition (Montgomery and Buffington, 1997).

Naturally, river systems are rarely in a morphologically stable state due to the constant need to adjust to changes in internal and external controls (Harvey, 2002). The geomorphology of a lotic system reflects the equilibrium between erosional and depositional processes at any one time (Hohensinner *et al.*, 2018). Indeed, as described by Lane (1955), a balance exists between bedload supply and particle size on one side, and river slope and discharge (power) on the other. If river power is sufficient to transport the sediment supplied to the system, overall no net change in erosion (degradation) or deposition (aggradation) occurs and the channel remains stable around a "regime status". When one of these factors is altered, this can lead to system imbalance and a change in form towards a new equilibrium (Charlton, 2007). For example, an increase in discharge may enhance river power and sediment transportation ability, thereby increasing the rate of erosion. Alteration to the channel can occur across four degrees of freedom; channel cross-sectional shape, slope, planform and bed roughness, although these can be constrained by boundary conditions such as the bank materials (e.g. channels made from sand are more easily erodible than clay; Osterkamp and Hedman, 1982), vegetation (e.g. erosion protection; Purvis and Fox, 2016) and valley settings (narrow valley prevents lateral migration; Charlton, 2007). Once thresholds are exceeded, it is possible for a river to change morphology considerably and rapidly in response to disturbances (Hohensinner *et al.*, 2018). For example, morphology can shift from single channel to braided in response to pulses of sediments from hillslopes induced by flooding (Harvey, 2002).

2.1.2 Ecological theory

2.1.2.1 Habitat patch concept

Drawing from theory developed in landscape ecology, a useful way to conceptualise habitat in lotic systems is as a spatial pattern, or mosaic, of dynamic, interconnected patches, i.e. the habitat patch concept (although these sometimes patches represent a gradient of change, Pringle *et al.*, 1988; Townsend, 1989; Poole *et al.*, 2006). Central to the idea of habitat as a mosaic of patches is the following (Wiens, 2002):

(1) **Patch quality.** The quality of patches, the costs and benefits for an organism being in a particular habitat, varies across patches (Wiens, 1997; 2002). For example, at the microhabitat level, chironomids and copepods have been shown to be more abundant in leaf patches than sand substrates (Palmer *et al.*, 2000), illustrating the advantages of certain habitats over others at this life stage (i.e. likely for food resources). The quality of patches can also vary across time. For example, some fish have been shown to prefer main channel habitats during baseflow (e.g. pools, riffles), but switch to floodplain and low velocity habitats (e.g. vegetated points bars, deflection eddies) during high flow events (Schwartz and Herricks, 2011).

(2) **Patch boundary permeability**. Patches have boundaries, or ecotones, with varying levels of permeability that regulates the flow of materials, organisms, nutrients and disturbances (Ward and Wiens, 2001; Wiens, 2002). Ultimately, this variability in permeability can help shape the distribution of habitat and ecological communities (Wiens *et al.*, 1985). For example, at the micro-habitat scale, instream vegetation can retain fine sediments through a localised reduction in stream velocity (Gurnell *et al.*, 2006). Boundary permeability can also change across time (Wiens, 2002), e.g. hydrological conditions can dictate how passable beaver dams are to fish (Cutting *et al.*, 2018).

(3) **Patch context**. The arrangement and composition of patches are just as important as patch quality or boundary characteristics for controlling physical and ecological processes (Wiens, 2002). For example, the materials that enter a river will depend on terrestrial characteristics (e.g. riparian vegetation enhances bank stability consequently reducing sediment inputs; Purvis and Fox, 2016). At the micro/mesohabitat scale, riparian vegetation structure can influence the diversity of macrophytes through shading (Carmo *et al.*, 2023).

(4) **Patch connectivity.** The movement of materials, nutrients, biota and disturbances between patches is crucial for structuring ecosystems and is mediated by patch arrangement (Wiens, 2002; e.g. Isaak *et al.*, 2007). There are two types of connectivity between patches; (a) structural connectivity, the physical relationship between habitat patches (e.g. distance, quantity; e.g. Segurado *et al.*, 2013), and (b) functional connectivity, the biotic response to landscape structure (e.g. organism mobility, habitat requirements; Bowne *et al.*, 2006; Seliger and Zeiringer, 2018). Connectivity between patches depends on their context, arrangement, quality (e.g. persistence) and boundary permeability (Wiens, 2002). For example, whilst two pairs of patches may have similar structural connectivity, the presence of a weir between one pair may act as a barrier, reducing functional connectivity. Patch connectivity is especially important in the context of habitat management. For example, the restoration of a mesohabitat within a degraded river segment may lead to patch isolation, which can ultimately restrict recolonisation (Sear, 2010; e.g. Harrison *et al.*, 2004; Sundermann *et al.*, 2011).

(5) **Organism characteristics.** The responses to the habitat mosaic will naturally vary between taxa and individuals due to differences in characteristics (Wiens, 2002); for example, behaviour (e.g. drift rates; Arevalo *et al.*, 2019), habitat preference (e.g. Carmo *et al.*, 2023), life stage requirements (Mitchell, 2016) or local adaptation (Primmer, 2011). Consequently, landscapes should be looked at from an organismal perspective rather than solely a human viewpoint (Wiens, 2002).

(6) **Scale.** The previous five points can all change with changes in scale (Wiens, 2002). For instance, species mobility or size can alter the extent to which they interact with the landscape, resulting in scale-dependent differences at which they respond to patches (e.g. riffles [meso-habitat] versus cobbles [micro-habitat]; Wellnitz *et al.*, 2001).

Under this conceptual model, abiotic and ecological patterns and processes are shaped by the composition, structure, context and connectivity between habitat patches. As the habitat patch concept can be applied across hierarchical scales, it provides a useful framework for the management of lotic systems (Poole, 2002; Sear, 2010).

Disturbance plays a key role in determining patch composition and mosaic development (Ward, 1998; Hohensinner *et al.*, 2018). In a natural state, lotic systems are regularly subjected to stochastic disturbances such as changes to flow (e.g. flooding or drought; Poff *et al.*, 1997), fluxes of large wood (Tonon *et al.*, 2017) and sediment inputs (Hu *et al.*, 2021). In response, the river habitat mosaic adjusts with the destruction of some patches and rejuvenation of others, creating a ‘shifting habitat mosaic’ (Stanford *et al.*, 2005). For example, the creation of structurally complex logjams have been found to promote sediment deposition within the jam, ultimately leading to the formation of vegetated marginal benches (Harvey *et al.*, 2018). This dynamic nature of lotic systems creates a diverse mosaic (e.g. in quantity, quality, connectivity, contexts) of ever changing habitat patches of differing ages, which theoretically facilitates the persistence of populations (e.g. by providing habitat for different life stages; Sear, 2010) and diverse communities (e.g. by maintaining niche heterogeneity; Hohensinner *et al.*, 2005). For example, moderate levels of disturbance theoretically allows taxa with colonising and competing focussed life strategies to coexist in a dynamic equilibrium within a system, enhancing γ-diversity (i.e. the Intermediate Disturbance Hypothesis; Connell, 1978). In the context of river restoration, this highlights the need for interventions to focus on the recovery of natural processes to facilitate the self-maintenance of spatially and temporally diverse habitats (Beechie *et al.*, 2010).

2.1.2.2 Metacommunity theory

The metacommunity theory attempts to explain how species from multiple dispersal-linked populations interact with the local environment to shape ecological communities (Leibold *et al.*, 2004). The key idea to the theory is that local sorting processes may be constrained by wider-scale dispersal (Patrick *et al.*, 2021). Indeed, when propagule pressure (the number of individuals dispersing into an area) is high, the influx of individuals may allow taxa to persist in sub-optimal habitat, offsetting local sorting processes (i.e. 'mass effects'). When regional propagule pressure is low, the importance of local-scale processes (e.g. competition, demographic fluctuations) in structuring ecological communities becomes greater, and so taxa may be absent from optimal habitat ('patch dynamics'). Theoretically, it is under an intermediate propagule pressure in which ecological communities are expected to closely reflect the local environment, otherwise known as 'species sorting' (Leibold *et al.*, 2004; e.g. Stoll *et al.*, 2016). This theory has been used in a range of theoretical and empirical applications, and has proven to be especially useful for guiding river management (Patrick *et al.*, 2021). For example, isolated headwaters have been shown to respond more strongly to restoration than well-connected mainstem sites, presumably due to the overarching influence of mass effects in the latter (Swan and Brown, 2017). Furthermore, this theory can help guide restoration strategies. For example, an insufficient propagule pressure may signify the need to restore connectivity between patches (e.g. infrastructure removal; Birnie-Gauvin *et al.*, 2018) or potentially translocate species (Jourdan *et al.*, 2019) to improve the likelihood of recovery (Patrick *et al.*, 2021). This theory provides a useful framework to understand ecological community assembly processes following restoration, and highlights the need to fully understand biological distributions and potential barriers inhibiting recovery prior to project implementation.

2.1.2.3 Ecological resilience

Ecological resilience is defined as "the capacity of ecosystems to collectively adjust and adapt to shifting and potentially novel environmental conditions while preserving desired functions, species, and services" (Grantham *et al.*, 2019). Central to the idea is that a system with a greater biocomplexity (e.g. species diversity, life history, age structure, behaviour, genetics) will be more resilient to change than one with a lower biocomplexity (Penaluna *et al.*, 2018). Indeed, the 'portfolio effect', akin to that in economics, posits that whilst disturbance may lead to local extirpation, diversified communities allow the regional scale persistence of populations which can limit overall temporal fluctuation and facilitate the recolonisation (i.e. rescue effects; Eriksson *et al.*, 2014) and maintenance of normative functioning (functional redundancy; Biggs *et al.*, 2020), preventing a 'regime shift' (i.e. large persistent changes in system functioning once a threshold is crossed; Dodds *et al.*, 2010; Schindler *et al.*, 2015). Theoretically, the temporal asynchrony of subpopulations in interconnected heterogeneous habitat patches should give rise to a greater ecological resilience (McCluney *et al.*, 2014). For example, Schindler *et al.* (2010) demonstrated that changes in the overall population size of sockeye salmon (*Oncorhynchus nerka*) in Bristol Bay (Alaska) was two times lower when considering distinct subpopulations (e.g. with variable life histories, ages, adaptations) than would be seen in a single homogeneous population. The anthropogenic modification of lotic systems can impact ecological resilience and enhance the threat of a regime shift (McCluney *et al.*, 2014). For example, damming can reduce connectivity preventing recolonisation following disturbance (Yujun *et al.*, 2022) and may spatially and temporally homogenise habitats (Im *et al.*, 2020) and biocomplexity (Trottier *et al.*, 2022). This emphasises the need for restoration to focus on the recovery of natural processes and disturbances to facilitate habitat heterogeneity, biocomplexity and asynchrony which ultimately enhances ecological resilience to perturbation (e.g. climate change; Penaluna *et al.*, 2018).

2.2 River restoration

Efforts to protect the biotic integrity of lotic waterbodies in the face of anthropogenic manipulation have spanned centuries (e.g. Preservation of the Thames Act; UK Parliament, 1535). However, it wasn't until the 20th century that active efforts to mitigate the impacts of historic degradation through restoration were made (Smith *et al.*, 2014). Now, significant allocation of funding and legislative backing are promoting restoration on a global scale (Szałkiewicz *et al.*, 2018; American Rivers, 2021). For example, the European Union's Water Framework Directive (2000/60/EC) places an emphasis on restoration to meet ecological targets (EU Parliament Council, 2000), encouraging substantial investment (e.g. estimated > €1 billion annual investment in Europe; Feld *et al.*, 2011). With the United Nations naming 2021 to 2030 as the "decade on ecosystem restoration" (United Nations, 2023), there is a need to thoroughly investigate the topic to provide valuable guidance to river managers.

2.2.1 Nomenclature

Before further discussing the topic of river restoration, it is important to accurately define the relevant nomenclature. This is imperative in that, whilst restoration is often used as a catch-all term (Wheaton *et al.*, 2006; Roni *et al.*, 2008), projects have differing goals and targeted endpoints which can in turn alter the way in which they will be appraised. Several key definitions are:

Restoration: the "complete structural and functional return to a pre-disturbance state" (Cairns, 1982; 1991 as referenced in RPR, 1993).

Rehabilitation: the "partial structural and functional return to a pre-disturbance state" (Cairns, 1982 as referenced in RPR, 1993). Unlike restoration, a river subjected to rehabilitation is not expected to have been returned to a 'pristine' state (Bradshaw, 2002).

Enhancement: "any improvement of a structural or functional attribute" (Natural Research Council, 1992 as referenced in RPR, 1993), which does not necessarily aim to move towards a unimpacted state.

Creation: "the conversion of an ecosystem into a different one" (Jungwirth *et al.*, 2002), usually undertaken to enhance ecosystem services (e.g. recreational fisheries).

*Mitigation: "*Actions taken to avoid, reduce or compensate for the effects of environmental damage" (Natural Research Council, 1992 as referenced in RPR, 1993).

By the above definition, true restoration requires a reference state (i.e. undisturbed by humans) to orient and guide project goal setting (i.e. a 'Leitbild'; Bradshaw, 2002).

Jungwirth *et al.* (2002) posited that there are three ways to determine this reference state; (1) select a contemporary site in a desirable condition (e.g. 'pristine site'; Laasonen *et al.*, 1998); (2) select a condition based on historical analyses (e.g. historic maps or palaeoecological sampling; Seddon *et al.*, 2019; Guzelj *et al.*, 2020); (3) use modelling to determine a reference (Schmutz *et al.*, 2000). However, reference conditions can be difficult to establish with low uncertainty (e.g. if historic data is poor; Wohl and Merritts, 2007) and achieve given the long-term, often irreversible damage caused to most catchments (Wheaton *et al.*, 2006; 2008; Friberg *et al.*, 2010). Therefore, many so-called restoration projects often fit within other categories; for example, those tackling single stressors within a deteriorated watershed (i.e. rehabilitation, e.g. Robertson *et al.*, 2021) or aiming to promote specific socio-economically important species (e.g. enhancement of salmonid spawning gravels; Merz and Ochikubo Chan, 2005). This also highlights the importance of defining the goals of the restoration, which should be clear and quantifiable so as to not overstate expected results and to facilitate the evaluation of project success (Brudvig and Catano, 2021). Fitting with most of the literature, 'restoration' will be the main term used within this thesis, although where required a more specific term will be used.

2.2.2 Legislative drivers of restoration

In the context of Europe and the United Kingdom, many forms of legislation have driven the proliferation of restoration. Perhaps the most influential is the European Union's Water Framework Directive (2000/60/EC; EU Parliament Council, 2000), which was created in 2000 and obligates member states to achieve 'good ecological status' on all surface waterbodies by 2027 (Kallis and Butler, 2001; Muhar *et al.*, 2018). This focus on the ecological condition of rivers largely changed the direction of restoration in Europe from local scale, single-species orientated projects (e.g. salmonid spawning grounds; Zeh and Donni, 1994) towards the more holistic, catchment-wide and biodiversity-driven projects seen more recently (Smith *et al.*, 2014). Other examples of legislation include the European Union's Habitats Directive (92/43/EEC; European Communities, 1992) and Flood Directive (2007/60/EC; EU Parliament Council, 2007), which drives restoration efforts to protect threatened habitat and biota and promotes the use of natural flood management methods (e.g. floodplain restoration; Serra-Llobet *et al.*, 2022), respectively. Other, more focussed legislation such as The Eel Regulations (2009; UK Government, 2009) and Wild Bird Directive (2009/147/EC; EU Parliament Council, 2009) encourage specific restoration activities that target particular organisms or groups, such as fish passage projects and the creation of wetland habitats for birds. Whilst these are examples of legislation specifically driving restoration activity within Europe, similar legislation exists globally (e.g. United States 1977 Clean Water Act [EPA, 2022], 1980 'Superfund' Act [EPA, 2023]) and has resulted in widespread adoption of restoration practices.

2.2.3 Form-based restoration

Restoration taking place in the 20th century was largely dominated by species orientated projects (e.g. salmonids; Zeh and Donni, 1994) on the reach-scale concentrating on the creation of desired habitat characteristics using a narrow suite of techniques (e.g. pool-riffle sequences, flow deflectors; Wohl *et al.*, 2005; Beechie *et al.*, 2010; Smith *et al.*, 2014). Central to these projects is the assumption that restoring river form or features, often habitat heterogeneity, will enhance biodiversity and ecosystem health, although evidence for such a relationship is limited (Palmer *et al.*, 2010). Indeed, the 'Field of Dreams hypothesis' posits that the enhancement of habitat structure towards a naturalised state is sufficient to re-establish biotic integrity, or "if you build it, they will come" (Palmer *et al.*, 1997).

Despite their prolific use (Bernhardt *et al.*, 2005; Friberg *et al.*, 2016), form-based projects often fail to elicit ecological benefits (Pretty *et al.*, 2003; Harrison *et al.*, 2004), or only do so at limited temporal scales (e.g. Pulg *et al.*, 2013). In part, this may be due to their failure to tackle the source of deterioration (e.g. altered processes; Pretty *et al.*, 2003; Smith *et al.*, 2014) and the assumption of unlimited colonisation potential (e.g. failing to consider barriers to dispersal and sufficient species pools; Sundermann *et al.*, 2011; Tonkin *et al.*, 2014). Moreover, form-based restoration often favour over-engineered projects that ignore local settings and control natural processes and dynamics (Wheaton *et al.*, 2019). Ultimately, this can lead to short-term, unsustainable solutions that are unsuitable for the system and restoration location (Kondolf *et al.*, 2001; Pretty *et al.*, 2003; Beechie *et al.*, 2010). For example, the introduction of artificial riffles and flow deflectors to rivers across England had little effect on fish (Pretty *et al.*, 2003) or macroinvertebrates (Harrison *et al.*, 2004), likely due to catchment-scale deterioration in processes (e.g. migration) and water quality. Despite this lack of success and the growing consensus that a different approach is required (Beechie *et al.*, 2010; Wheaton *et al.*, 2019), form-based restoration carried out on the reach-scale remains widely used in practice (Wheaton *et al.*, 2019; e.g. Lenar-Matyas *et al.*, 2015; Favata *et al.*, 2018). Some have argued that this may be due to the implementation of restoration by engineering companies with a lack of hydrogeomorphological and ecological expertise (e.g. Grantham *et al.*, 2019).

2.2.4 Process-based restoration

Process-based restoration focusses on restoring pre-disturbance rates of physical (e.g. erosion and accumulation of sediments), chemical (e.g. nutrient dynamics) and biological (e.g. woody material recruitment and migration) processes that supports the development of river structure and function (Beechie *et al.*, 2010; Wheaton *et al.*, 2019). In doing so, process-based restoration aims to alter the trajectory of the river towards a state of recovery (Beechie *et al.*, 2010). For example, whilst form-based restoration may focus on the installation of over-engineered large woody material structures (Roni *et al.*, 2015) or flow deflectors (Pretty *et al.*, 2003), process-based restoration may take a more dynamic approach by restoring wood recruitment (e.g. restoring riparian woodland; Spray *et al.*, 2022) and promoting accumulation (e.g. Wheaton *et al.*, 2019). Restoring in such a way offers many benefits over form-based restoration. For example, process-based projects typically offer longer-term solutions, avoid unnatural/unsustainable designs, allows the system to respond to disturbance and enhances ecological resilience and biocomplexity by promoting habitat dynamics (Beechie *et al.*, 2010; Wheaton *et al.*, 2019; Tullos *et al.*, 2021). Disadvantages include a greater initial time to recovery (Beechie *et al.*, 2010), the scale of which can be dictated by system characteristics (e.g. river discharge; Carlson *et al.*, 2018). Main principles for successful process-based restoration have been set-out by Beechie *et al.* (2010), and are as followed:

(1) **Restoration should target the root cause of the habitat deterioration rather than treating a symptom.** For example, where fine sediment accumulation is high, the aim should be to reduce inputs from across the catchment rather than gravel washing.

(2) **Restorative action should be tailored to the physical and biological potential of the site.** River reaches have a limited range of natural conditions that match their environmental context (e.g. climate, position on the catchment), and restoration efforts should aim to alter the trajectory of these reaches back to this range (Beechie *et al.*, 2010). To understand this, the historic environment of the river should be sufficiently analysed to determine an appropriate target range of conditions (Beechie *et al.*, 2010; Gurnell *et al.*, 2016). Alongside historic states, it is also important to consider modern constraints when determining recovery potential given the major and often irreversible changes to the landscape (Fryirs, 2015). With this information, quantifiable and achievable aims can be created which is crucial for project appraisal, understanding monitoring requirements and managing stakeholder expectations (Wohl *et al.*, 2005; Wheaton *et al.*, 2019; Brudvig and Catano, 2021).

(3) **Restoration scale should match that of deteriorated processes** (Lake *et al.*, 2007; Polvi *et al.*, 2020). For instance, recovering normative rates of sediment inputs (Kondolf *et al.*, 2001) or depleted salmonid stocks (which typically require catchment-wide life stage dependent habitats; Thorstad *et al.*, 2010) may require efforts across the catchment (Beechie *et al.*, 2010). Conversely, other processes may be recovered with actions taken at a smaller scale, such as restoring river-floodplain interactions through embankment removal (Clilverd *et al.*, 2016). Given that most projects operate over the reach-scale (e.g. due to resource availability, willingness of landowner participation; Lake *et al.*, 2007), implementing projects within an integrated catchment management plan can be crucial for tackling landscape scale issues (Environment Agency, 2017; Spray *et al.*, 2022).

(4) **Restoration projects should clearly detail expected recovery times and the range of possible outcomes** (Beechie *et al.*, 2010; Wohl *et al.*, 2015). Process-based restoration typically operates over the long-term and can theoretically achieve a range of possible outcomes (Beechie *et al.*, 2010; Wohl *et al.*, 2015; Hiers *et al.*, 2016). For example, the regeneration of riparian woodland may take decades to take effect (Beechie *et al.*, 2000), whilst changing environmental (e.g. climate change) or societal (e.g. protective legislation, abstraction rates) factors may alter project outcomes in ways which are difficult to predict (Brudvig and Catano, 2021). Defining anticipated timelines and outcomes for recovery is therefore important for conveying realistic expectations to stakeholders and ensuring the implementation of appropriate monitoring and adaptive management plans (Beechie *et al.*, 2010; Brudvig and Catano, 2021).

2.2.5 Active versus passive approaches to restoration

There are two methodological approaches to restoration; active and passive (Jähnig *et al.*, 2010; Jones *et al.*, 2018). Active approaches include those which implement direct habitat modifications, such as the placement of flow deflectors, infrastructure decommissioning, channel reconfiguration and invasive species removal. By contrast, passive approaches do not implement direct modification but rather utilise natural recovery processes to achieve the desired change. For example, ceasing river maintenance activities (e.g. riparian management; Jähnig *et al.*, 2010; Atkinson and Bonser, 2020; Chazdon *et al.*, 2021) represents a form of passive restoration. The decision to implement an active or passive approach depends on various societal (e.g. stakeholder opinion), economic (e.g. level of funding), political (e.g. timeline for legislative goals) and environmental factors (e.g. river characteristics and level of modification; Wheaton *et al.*, 2008; Prach *et al.*, 2019; Atkinson and Bonser, 2020). For example, as active approaches are often costly they are typically carried out over small spatial scales (Jähnig *et al.*, 2010; Díaz-García *et al.*, 2020), but may be preferred over passive restoration when natural recovery timelines are exceedingly long (Montgomery and Bolton, 2003) and degradation is high (Reid *et al.*, 2018b). Conversely, passive approaches are less invasive and comparatively cheap relative to active restoration, and can be easier to implement over greater spatial scales and where degradation is lower (Jähnig *et al.*, 2010; Prach *et al.*, 2019). Whilst these approaches are dichotomous, it is often appropriate to combine methods to achieve a restoration goal; for example, when recovery is difficult without upfront intervention (e.g. using natural sediment transport to redistribute augmented substrates; Arnaud *et al.*, 2017). Philosophical and scientific debate regarding the relative benefits of active versus passive approaches to restoration are ongoing (Jähnig *et al.*, 2010; Zahawi *et al.*, 2014; Prach and del Moral, 2015) and reflect underlying uncertainties surrounding restoration research, outcomes and best practice (Wheaton *et al.*, 2008).

2.2.6 Uncertainty in restoration

Given the stochasticity of nature and the complexity of river systems and restorative action, restoration inherently holds uncertainties that can make it difficult to accurately predict outcomes (Darby and Sear, 2008; Brudvig and Catano, 2021). Uncertainty, or a lack of confidence (Wheaton *et al.*, 2008; Yoe *et al.*, 2010), can manifest within restoration in two main ways:

Aleatory uncertainty. Uncertainty attributable to unpredictable variability (Yoe *et al.*, 2010), such as changes to the weather or flood events, the societal view towards restoration, stakeholder opinion (Newson and Large, 2006) and policy (van Ginneken and Maes, 2005; Gamborg *et al.*, 2019). There are five classes of aleatoric uncertainty: *natural stochasticity* (unpredictability of nature, e.g. flood intensity; DEFRA, 2021), *value diversity* (differences in people's views, Pahl-Wostl, 2006), *behavioural variability* (differences in people's behaviour, e.g. discrepancies between what people say and do over time; Gamborg *et al.*, 2019), *societal randomness* (social, economic and cultural dynamics, e.g. changes to policy and attitudes to the environment; Smith *et al.*, 2014) and *technological surprise* (unpredicted scientific breakthroughs; van Asselt and Rotmans, 2002; Wheaton *et al.*, 2008). Given their unpredictability, theoretically, little can be done to reduce these aside from attempting to model and account for their impacts (Yoe *et al.*, 2010).

Epistemic uncertainty. Uncertainty attributable to a lack of knowledge (Yoe *et al.*, 2010), such as a poor understanding of the focal system (e.g. distributions of species pools for colonisation), gaps in hydrogeomorphological, ecological and restoration theory, and uncertainties surrounding the validity of mathematical and conceptual models (Darby and Sear, 2008; Graf, 2008; Brudvig and Catano, 2021). Seven forms of epistemic uncertainty have been proposed: *irreducible ignorance* ("we cannot know"), *indeterminacy* ("we will never know"), *reduceable ignorance* ("we do not know what we do not know"), *conflicting evidence* ("we don't know what we know"), *practically immeasurable* ("we know what we don't know"; e.g. responses to restoration over centuries), *lack of observations and measurements* ("could have, should have, would have, but didn't"; e.g. lack of restoration appraisal) and *inexactness* (low precision or 'fuzziness"; descriptions from van Asselt and Rotmans (2002) and Wheaton *et al.* (2008)).

Although not all uncertainty is inherently problematic, its ubiquity in ecological restoration can have significant consequences. Indeed, it can determine the difference between success and failure, create a need for costly adaptive management and potentially reduce the willingness to participate in and funding available for restoration (Brudvig and Catano, 2021). There are five main strategies to deal with uncertainty (Wheaton *et al.*, 2008). More often than not, the primary method is simply to **ignore uncertainty**, potentially due to the fear of admitting its presence (e.g. by policy makers; Wheaton *et al.*, 2008). However, given that uncertainty can lead to negative consequences (e.g. Orr *et al.*, 2008a), this approach is unethical and risks backlash when projects fail. On the opposite end of the scale, another approach is to **eliminate uncertainty**; although given the omnipresence of unpredictable uncertainties (e.g. weather and policy change) it is naïve to believe this is possible (Wheaton *et al.*, 2008). For those that can be measured and controlled, it may be possible to **reduce uncertainties** (e.g. through monitoring/model development; Brudvig *et al.*, 2017; Brudvig and Catano, 2021), although this will not be possible for all (Wheaton *et al.*, 2008). We can therefore **cope with uncertainty** by developing specific methods to deal with them (Osidele *et al.*, 2003; Wheaton *et al.*, 2008). A more highly advocated approach, however, is to **embrace uncertainty**, for example, by accounting for it within models and restoration design/objectives (e.g. quantifying magnitude of natural variability; Wheaton *et al.*, 2008). Such an approach allows river managers to gain an understanding of the significance of uncertainties, manage stakeholder expectations, and make informed adaptive management decisions (Wheaton *et al.*, 2008; Nagarkar and Raulund-Rasmussen, 2016; Applestein *et al.*, 2021). Given the ubiquity of uncertainties and the risks they pose, it is proposed here that there is a need to attempt to reduce uncertainties (Brudvig and Catano, 2021), and where this is not possible, it should be embraced within restoration planning and through adaptive management (Applestein *et al.*, 2021).

2.2.7 A lack of restoration 'success'

In response to the increasing use of restoration, a number of studies monitoring, modelling and reviewing river restoration have been published over the past few decades; particularly across North America, Europe and Asia (Figure 2.1). Through this increasingly large body of evidence, it is clear that despite best efforts, restoration is not always successful in achieving the desired outcome (e.g. Pretty *et al.*, 2003; Orr *et al.*, 2008a; Friberg *et al.*, 2016). There are many potential explanations underpinning this lack of restoration success, including inappropriate goal setting (Suding, 2011) and restoration scales (Polvi *et al.*, 2020), a failure to consider wider catchment scale issues (Harrison *et al.*, 2004; Wolff *et al.*, 2021), limited species pools for recolonisation (Sundermann *et al.*, 2011) and inadvertent effects of the restoration (Orr *et al.*, 2008a). Two key points which are a focus of this thesis is a lack of monitoring (England *et al.*, 2020) and bias within current research (e.g. Kaiser *et al.*, 2020).

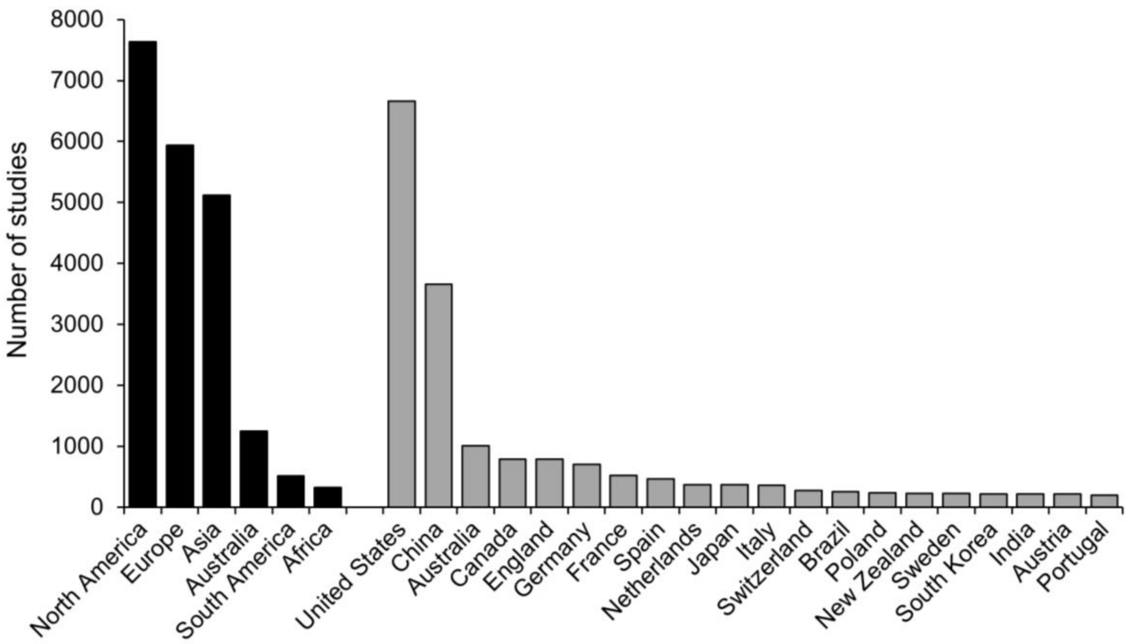


Figure 2.1 The number of publications listed of Web of Knowledge when searching the terms 'river*' OR 'stream*' OR 'lotic' AND 'restor*' filtered for 'ecology' and 'environmental sciences' topics. Total number of studies = 20,775. The number of studies by continent are shown in black and the top 20 contributing countries are shown in grey.

2.2.8 Project monitoring and appraisal

It has long been recognised that critically evaluating restoration projects is invaluable for the development of the field (e.g. Wohl *et al.*, 2005; England *et al.*, 2020). Indeed, monitoring is crucial for the evaluation of project success, to assess whether adaptive management is required, understand when and why outcomes deviate from expectations, provide learning opportunities, data for modelling and economic appraisal, and to contribute evidence towards the body of literature describing restoration effectiveness (England *et al.*, 2008; Smith *et al.*, 2014; Weber *et al.*, 2018). Despite this, few projects are comprehensively monitored (Pander and Geist, 2013). For example, analysis of 671 projects in the European REFORM (Restoring rivers for effective catchment management) database showed only 15% reported ecological outcomes (Angelopoulos *et al.*, 2017). In Bavaria (Germany), €300 million was spent restoring rivers between 1994 and 2001, but only 4% of projects collected baseline data and 10% < 1 km in length were monitored, none for more than a year (Pander and Geist, 2013). In part, the low levels of monitoring observed are due to the lack of incentives, resources and funds, especially in smaller projects (Palmer *et al.*, 2007; Smith *et al.*, 2014). Even when funding is set aside, this is typically short-term (Borgström *et al.*, 2016), low in quantity (< 10% of total budget), and often goes towards assessing project effectiveness (i.e. whether the design fitted the project) rather than physical and ecological responses (Roni *et al.*, 2018).

In projects that do encompass monitoring, efforts are often limited in scope. For example, understanding the long-term recovery of restoration projects is crucial (Lu *et al.*, 2019; England *et al.*, 2021a) but remains poorly investigated and a major source of uncertainty (England *et al.*, 2020). Indeed, studies have shown that project age can be a significant predictor of restoration outcomes (Kail *et al.*, 2015; Lu *et al.*, 2019), and that trajectories can be non-linear (e.g. initial decline in condition, lag effects, slow deterioration of restored site; Kail *et al.*, 2015) and vary with system characteristics (Gurnell *et al.*, 2016; Groll, 2017), colonisation potential (Li *et al.*, 2016; Stoll *et al.*, 2016) and restoration methodologies (Feld *et al.*, 2011). Therefore, long-term monitoring has been widely highlighted as key (e.g. England *et al.*, 2008; Lu *et al.*, 2019), especially for understanding the effectiveness of process-based restoration (e.g. Beechie *et al.*, 2000), but also for providing evidence of expected recovery times to stakeholders, assessing adaptive management requirements and quantifying responses to perturbation. Long-term monitoring may be particularly important in fully understanding the effects of restoration in systems with low power, such as chalk streams, given their naturally slow response to physical change (Sear *et al.*, 1999). Despite this, projects are rarely monitored over the long-term, e.g. due to a lack/limited duration of funding and the need for immediate results to satisfy stakeholders (Smith *et al.*, 2014; Borgström *et al.*, 2016; Al-Zankana *et al.*, 2020). For example, a review of 74 mesohabitat restoration appraisals found that monitoring was conducted for a median of 2.5 years (Feld *et al.*, 2011). To comprehensively appraise restoration projects, a minimum 10 year monitoring period has been previously quoted (e.g. Kondolf and Micheli, 1995), although in practice, the scale of monitoring efforts should align with system characteristics. For example, systems with lower power (e.g. chalk streams; Sear *et al.*, 1999) should ideally be monitored over a longer duration to fully establish outcomes.

Monitoring has typically focussed on single taxa or organism groups of interest (i.e. most often fish/salmonids; e.g. Pulg *et al.*, 2022) and assume that these responses can be extrapolated across groups. However, this thinking is problematic because different taxa and organism groups can occupy separate niches and respond to the same intervention in opposing ways (Pander and Geist, 2013; Theodoropoulos *et al.*, 2020). For instance, while gravel-spawning taxa might respond positively to gravel augmentation (e.g. Brown trout [*Salmo trutta*]; Palm *et al.*, 2007), those that depend on silt for all or part of their lifecycle (e.g. river lamprey [*Lampetra fluviatilis*]; Aronsuu and Virkkala, 2014) and benthic organism groups might be smothered, exhibit a population decline and ultimately fail to re-establish following restoration (e.g. Mueller *et al.*, 2014). Although it is rarely considered (e.g. due to the added cost of conducting several different surveys), monitoring with a ‘multi-taxa approach’ can provide a more holistic understanding of its effectiveness (Mueller *et al.*, 2014). For example, these analyses may reveal linkages between different groups, informing on the mechanistic drivers behind the response observed (Thompson *et al.*, 2018a).

2.2.9 Area and research bias

The restoration field is confounded by bias in the underlying science that informs practice (e.g. Reid *et al.*, 2018b). For example, much of the knowledge used to develop restoration practice in Europe, including unique and understudied systems such as chalk streams, was derived from research carried out in the United States (Figure 2.1). Biases such as these create issues due to the disparities in river and landscape character, restoration practice and research between regions and river-types, which ultimately leads to the development of methodologies poorly suited to non-local and unique river systems (Kail *et al.*, 2007). For example, rivers in the United States typically have fewer historical modifications and land-use pressures compared to European rivers such as chalk streams (Kail *et al.*, 2007). Additionally, whilst projects in the United States have typically aimed to enhance fish habitat, those in Europe, influenced by the Water Framework Directive, usually place a greater emphasis on the ecosystem and ecology (Kail *et al.*, 2007; Smith *et al.*, 2014). Therefore, whilst methodologies may be suitable for achieving goals in the United States, in systems such as chalk streams, they may fall short of expectations. Ultimately, biases such as these can lead to uncertainties and the failure of restoration projects to achieve their goals, and emphasises the need for research to focus on appraisal of projects in a variety of systems to allow the system-specific optimisation of restoration practices.

2.3 Chalk streams

Chalk streams, those that derive over 75% of their base flow from chalk aquifers, are among the rarest freshwater habitats on Earth (Smith *et al.*, 2007; O'Neill and Hughes, 2014). Distributed exclusively within chalk outcrops, a geology mostly confined to southern and eastern England and parts of northern Europe (e.g. France; Berrie, 1992), a total of 283 chalk streams with a combined length of 4,000 km have been identified in England (Figure 2.2; Bond, 2012; CaBA, 2021). This accounts for around 85% of chalk streams found globally (Salter and Singleton-White, 2019).

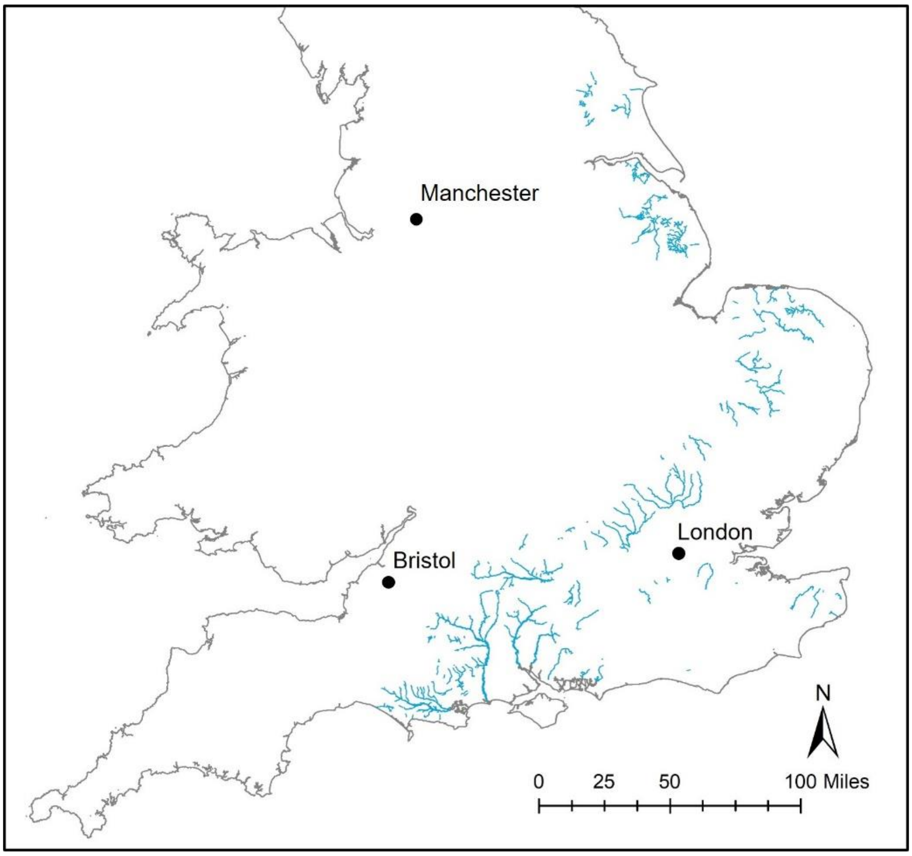


Figure 2.2 The distribution of chalk streams (blue lines) across the United Kingdom. Country and river network shapefiles were acquired from Ordnance Survey (2023) and Environment Agency (2023a), respectively.

2.3.1 Chalk aquifers

Chalk streams are formed through the percolation of rainfall through chalk aquifers which emerge as springs on the Earth's surface (Berrie, 1992). Chalk (primarily $CaCO_3$) is a soft limestone formed 65 - 100 million years ago in the Cretaceous period from the accretion of calcareous coccoliths from coccolithophore phytoplankton (Berrie, 1992; Raven *et al.*, 1998; CaBA, 2021). Deepening approximately 1 mm every 100 years, large deposits of chalk formed across Europe towards the Ural Mountains (also Americas, Australia and Arabia; CaBA, 2021). However, the upper chalk geology that form chalk streams has been influenced by tectonics, namely the coming together of Europe and Africa which uplifted and caused fracturing, and subsequence erosion by glacial formation and retreat which led to its exposure (CaBA, 2021).

One key property of chalk is its porosity, which may account for as much as 55% of its volume (Wellings and Cooper, 1983; Bloomfield *et al.*, 1995). As a result, rainfall percolates slowly through chalk beds (e.g. hydraulic conductivity 1.0-2.5 mm/day^{-1} in Wellings and Cooper, 1983) until impermeable rock is reached, after which, large volumes of water forms as an aquifer (Berrie, 1992). Here, stored water can reside for thousands of years (Downing *et al.*, 1979), although the levels of fracturing and lithology (e.g. chalk hardness) can influence aquifer properties (MacDonald and Allen, 2001). Where aquifers are exposed at the Earth's surface, typically valleys, water emerges as springs which source chalk streams and provides the unique characteristics for which they are renowned. For example, the water of chalk streams reflect the rich sources of $CaCO_3$ and insulation of groundwater, typically emerging at a stable alkaline pH (7.4-8.0) and relatively cool temperatures (5-17 °C; Mackey and Berrie, 1991; Mainstone, 1999).

2.3.2 Hydrology and morphology

As a result of their geology and predominantly groundwater derived flow, chalk streams tend to display dampened, less flashy hydrology compared with those with more impermeable geologies (Raven *et al.*, 1998; Mainstone, 1999; CaBA, 2021). However, the response may vary across streams due to chalk (e.g. degree of fracturing, hardness; MacDonald and Allen, 2001) and land (e.g. vegetation, land-use; Jackson *et al.*, 2011) characteristics and the influence of other geologies. For example, glacial deposits in the River Nar catchment make responses more flashy compared to other chalk streams (Sear *et al.*, 2005; CaBA, 2021). Considering this geological variability, CaBA (2021) identified four types of chalk stream (see appendix H in CaBA (2021) for list of rivers):

(1) *Classic slope-faced stream*: rise directly from and flow largely over chalk (e.g. River Itchen and Test).
(2) *Mixed-geology stream*: typically do not rise from but subsequently flow over chalk (e.g. Hampshire Avon and River Colne).
(3) *Scarp-face stream*: scarp-slope rivers that rise from chalk and subsequently flow over gault clay, greensand beds and clay rich chalk (e.g. River Rother and Adur).
(4) *Pleistocene ice-impacted stream*: rise from chalk altered by Pleistocene glacial action (e.g. River Wissey and Wensum). These can be included in any other group.

Seasonally, the lowest discharges occur in the summer and autumn and highest in the winter and spring (bank full flow up to 30% of year; Mainstone, 1999; CaBA, 2021). This is due to differences in rainfall between seasons, as well as variation in vegetation growth and temperature that impact the percolation of water and aquifer recharge (Berrie, 1992; Mainstone, 1999). The extent to which an aquifer is recharged during seasons of high precipitation can influence hydrological characteristics for the following year. For example, high winter rainfall may result in the formation of ephemeral 'winterbourne streams' due to the generation of springs at higher altitudes. Inadequate recharge may burden the river with low flows and an impacted hydrograph over the next year (Mainstone, 1999).

The stable flow regime of chalk streams is mirrored in their morphology. At the system scale, chalk streams tend to have limited tributary networks due to their tendency to form in valleys and ephemeral winterbourne reaches may develop periodically at higher altitudes (Mainstone, 1999; Sear *et al.*, 2005; CaBA, 2021). In a more naturalised state, planform is often meandering or comprised of multiple anastomosing channels (CaBA, 2021). Chalk streams typically feature high width to depth ratios and low magnitudes of sediment supply due to their low levels of bank erosion and weak connectivity to the catchment (i.e. supply limited; Sear *et al.*, 2005; Sear, 2010; CaBA, 2021). Moreover, their low power (i.e. due to stable low peak discharge and shallow slopes) means chalk streams are poorly equipped to mobilise their glacial deposited flint gravel substrates, which are often strengthened by calcareous tufa concretions developing at springs (Acornley and Sear, 1999; Sear *et al.*, 1999). As a result, chalk streams show a limited capacity for channel modification and the formation of coarse sediment storage bedforms (e.g. riffles), with morphological features tending to be inherited depending on previous management and vegetation growth (Sear *et al.*, 1999; 2005; Sear, 2010). Owing largely to their limited connection to the land, chalk streams tend to show relatively low levels of suspended sediment under natural conditions, providing high water clarity (Acornley and Sear, 1999; Heywood and Walling, 2003).

Given their low power, ability to mobilise bedload and gravel supplies, ecosystem engineers, taxa that can influence others and ecological processes by modifying physical habitat (Byers *et al.*, 2006), play an significant role in shaping morphology (CaBA, 2021). For example, riparian vegetation can strengthen rivers banks (Simon and Collison, 2002) and introduce large woody materials which encourages habitat diversification by enhancing or decreasing flow velocity, the rates of deposition and scour, and floodplain interactions (Collins *et al.*, 2012; Thompson *et al.*, 2018a; CaBA, 2021). The seasonal growth of a diverse macrophyte mosaic can create localised reductions in flow velocity and increased fine sediment deposition within a patch, whilst increasing velocity and scour between patches. This can drive spatial and temporal habitat variability, enhancing community diversity and softening the impacts of perturbation (e.g. low flow; Wharton *et al.*, 2006; Gurnell *et al.*, 2006). Bioturbators can influence sediment dynamics. For example, the creation of redds by gravel spawning fish (e.g. brown trout) can enhance sediment transport and reduce the levels of fines within coarse substrates (Montgomery *et al.*, 1996; Acornley and Sear, 1999), whilst crayfish can increase bank erosion and sediment transport when moving and burrowing (e.g. signal crayfish, *Pacifastacus leniusculus;* Johnson *et al.*, 2011; Sanders *et al.*, 2021). Conversely, benthic macroinvertebrates (e.g. Hydropsychidae) can increase bedload stability when they create nets within sediment interstitial spaces (Statzner *et al.*, 1999; Albertson *et al.*, 2014).

2.3.3 Ecology

The physical and chemical conditions provided by chalk streams often offer an excellent environment for the formation of productive and diverse biotic communities (CaBA, 2021; see Mainstone (1999) for comprehensive list of species). Macrophytes benefit from the high water clarity and stable flow, forming diverse and abundant mosaics typically dominated by brook water crowfoot (*Ranunculus penicillatus ssp. pseudofluitans*), lesser water-parsnip (*Berula erecta*) and water starwort (*Callitriche sp.*) in spring and early summer, summer, and autumn, respectively (Ham *et al.*, 1982; Armitage *et al.*, 1994). These beds in turn provide heterogenous habitat and trap allochthonous detritus facilitating the development of diverse invertebrate communities, often with exceptionally high biomasses (Berrie, 1992; Bickerton *et al.*, 1993). Chalk streams are commonly dominated by Ephemeroptera, Plecoptera, Trichoptera (EPT) and crustacea (e.g. Gammaridae) and contain threatened species such as the Southern damselfly (*Coenagrion mercuriale;* Boudot, 2020) and white-clawed crayfish (*Austropotamobius pallipe;* Füreder *et al.*, 2010; O'Neill and Hughes, 2014). Habitat provided by ephemeral winterbournes can harbour internationally rare taxa specialised to cope with intermittent flow (Armitage and Bass, 2013; Bunting *et al.*, 2021).

Chalk streams are well renowned for their fish, particularly brown trout which constitute a primary target for the chalk stream-born practice of dry fly fishing (Kemp *et al.*, 2017). In addition to brown trout, other species including Atlantic salmon (*Salmo salar*), European bullhead (*Cottus gobio*) and sea (*Petromyzon marinus*), brook (*Lampetra planeri*) and river lamprey are found in chalk streams (12 species in Prenda, 1997; Mainstone, 1999). Chalk streams also constitute an important habitat for mammal and bird species such as European water voles (*Arvicola amphibius*), Eurasian otter (*Lutra lutra*) and common kingfisher (*Alcedo atthis*; Mainstone, 1999). Many chalk streams contain nationally and internationally protected species, and this constitutes a major reason behind the designation of seven and four rivers with SSSI (sites of special scientific interest; lower

Frome, Bere Stream, Test, Kennet, Nar, Hull headwaters, Crane) and SAC (special areas of conservation; Avon, Itchen, Wensum, Lambourne) status, respectively (in addition to rare habitats such as fen meadows; e.g. Itchen; Mainstone, 1999; Natural England, 2000; CaBA, 2021).

2.3.4 Contemporary importance to humans

Chalk streams are systems of significant economic and cultural value (CaBA, 2021). Chalk aquifers and their surface waters provide vital domestic, agricultural and industrial water supplies and source as much as 70% of the south-eastern population with drinking water (BGS, 2020), an asset suggested by O'Neill and Hughes (2014) to be worth billions. Additionally, businesses have exploited the high productivity of chalk streams through developing vast aquaculture schemes, especially watercress (*Nasturtium officinale*) and brown and rainbow trout (*Oncorhynchus mykiss*; Berrie, 1992; CaBA, 2021). Furthermore, internationally renowned recreational fly fisheries are widely distributed throughout chalk streams (i.e. especially the River Test and Itchen; Mainstone, 1999), contributing to the £1.4 billion spent on recreational freshwater fishing in England annually (Environment Agency, 2018a). Lastly, they provide additional services including transport, waste disposal and recreational value (Mainstone, 1999).

2.3.5 Chalk streams over time

Like most European rivers (Brown *et al.*, 2018) chalk streams have been linked with humans throughout history, with modern systems having been moulded by human intervention spanning millennia (Mainstone, 1999; CaBA, 2021). Appreciating the development timeline to this modern state is important in understanding current deterioration and how to direct restoration interventions (e.g. a reference state; Mainstone, 1999; CaBA, 2021). Despite this, the length of time over which chalk streams have been manipulated, both directly and indirectly, makes this difficult (Sear *et al.*, 1999; 2005). Moreover, individual rivers have unique histories and exhibit variability in modification timelines spatially and temporally, for example, depending on climate, economics and culture (e.g. River Test and Itchen have high fishing value, so were 'protected' from intensive agriculture; Wilkinson, 2003; French *et al.*, 2005; Brown *et al.*, 2013; CaBA, 2021). As a result, forming a single conceptual model for the history of all chalk streams is difficult (Wilkinson, 2003), however a broad summary of the most significant changes in chalk streams and their catchments are shown in Figure 2.3.

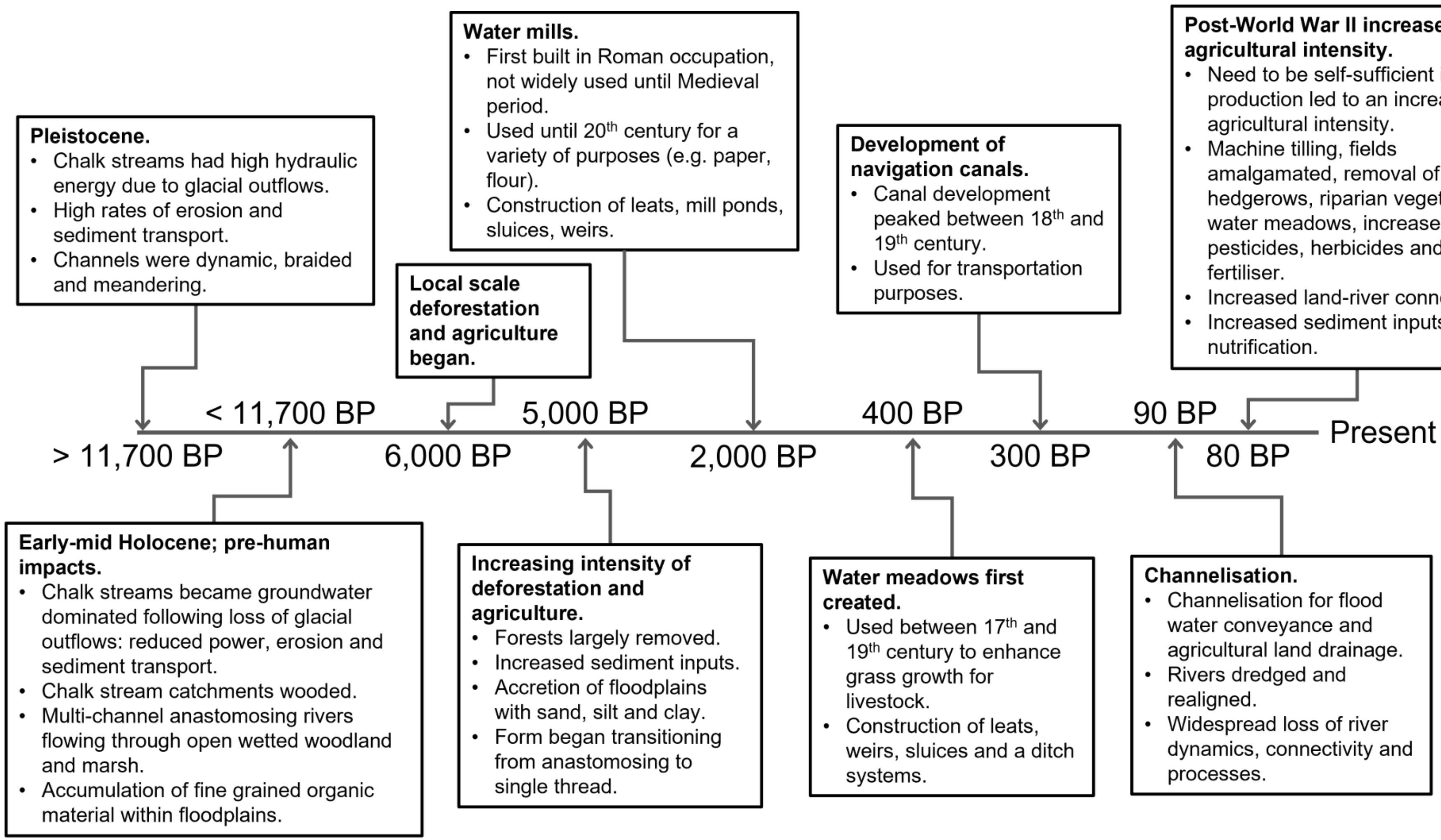


Figure 2.3 An approximate timeline for the occurrence of anthropogenic modifications of English chalk streams. BP = before present.

2.3.5.1 Pleistocene

During the Pleistocene (*ca.* 2.58 million – 11.7 ka), a geological epoch characterised by glacial formation and retreat, there were three main glacial episodes which collectively formed the British Irish Ice Sheets: the Anglian (480 - 430 ka), Wolstonian (300 - 130 ka) and Devensian (70 - 11.7 ka) glaciations (Gibbard and Clark, 2011). These glaciations and the associated geological processes played a significant role in sculpting the British landscape and chalk streams (Ballantyne and Harris, 1994; Sear *et al.*, 2005; Clark *et al.*, 2012). Whilst generalising the impacts of glaciation across chalk landscapes is difficult owing to variability in the spatial extent of different glacial episodes over time, generally, northern chalk was glaciated during the Pleistocene whilst the south was not (see Gibbard and Clark (2011) for an overview of glacial extents). Indeed, whilst parts of Norfolk, Lincolnshire and Yorkshire glaciated during the Devensian, south of London remained unglaciated throughout the Pleistocene (Gibbard and Clark, 2011). The result of this was that glaciated landscapes were subjected to subglacial processes including the fracturing of chalk and are overlain by unstratified boulder clay till (Marks *et al.*, 2004). Consequently, these systems tend to be relatively flashy compared to those unimpacted by subglacial processes, e.g. due to the influence of impermeable superficial deposits which slows aquifer recharge and enhances the levels of surface-derived flow (Ascott *et al.*, 2017; Barnsley *et al.*, 2021). Unglaciated landscapes were subjected to periglacial processes such as outwash flows, which were responsible for the formation of some of the defining features of chalk landscapes (Ballantyne and Harris, 1994). Meltwater derived from protracted freeze-thaw cycles formed high-energy river systems flowing over frozen grounds, carving out the soft chalk and contributing to the formation of the chalk downlands and dense distributions of dry valleys (Ballantyne and Harris, 1994; Whiteman and Haggart, 2018; CaBA, 2021). Flint, which is present within chalk but much harder, was crushed and redistributed across the valley floor, forming the characteristic gravel substrates found in chalk streams today (Murton and Belshaw, 2011; CaBA, 2021).

The impacts of glaciers on chalk streams is further complicated by the effects of marine incursions (Gibbard *et al.*, 2018). Following the retreat of the Devensian ice sheet, vast amount of freshwater entered the oceans resulting in a rise in global sea-level by around 100 m (Milne *et al.*, 2006). Concurrently, the loss of glaciers resulted in isostatic crustal readjustment across Great Britain; a process in which the Earth's crust deformed by glacial mass 'rebounds' following deglaciation (Peltier *et al.*, 2002). The effect of this is that Great Britain is in the process of tilting along an East-West axis, with southern England landscapes currently sinking (Bradley *et al.*, 2009). As a result, coastal chalk landscapes were further influenced by marine incursions, including the introduction of marine-derived deposits (Sear *et al.*, 2005) and loss of some rivers and valleys to the sea (e.g. River Solent, Hampshire; Allen and Gibbard, 1993). These further contribute to the heterogeneity of the British landscape and chalk streams, emphasising the need for restoration to take a system-specific approach considering antecedent conditions.

2.3.5.2 Early-mid Holocene; pre-human impacts

Following the loss of glacial outflows due to rapid changes in climate (Anderson *et al.*, 2013), chalk streams became groundwater dominated and exhibited an associated reduction in power, erosion and sediment transport (Collins *et al.*, 2006; Newell *et al.*, 2015). The retraction of glacial conditions allowed terrestrial vegetation species to colonise England from Europe (Hewitt, 1999). Indeed, evidence suggests that England, including chalk stream catchments, was largely wooded during this period (e.g. Waller and Hamilton, 2000; Collins *et al.*, 1996; 2006; Davies and Griffiths, 2005; although notably spatial and temporal variability in woodland presence exists, e.g. French *et al.*, 2005). This likely played an important role dictating river morphology, in addition to other ecosystem engineers such as Eurasian beavers (*Castor fiber;* Mainstone, 1999; Collins *et al.*, 2006; CaBA, 2021).

The Pleistocene-Holocene boundary has been associated with a switch in channel form from dynamic, gravel braided systems towards more stable multi-channel anastomosing rivers flowing through open wetted woodland and marsh with groundwater flooding and the accumulation of fine grained organic material within floodplains (e.g. Collins *et al.*, 1996; 2006; Davies and Griffiths, 2005; Newell *et al.*, 2015; Brown *et al.*, 2018). These habitats likely supported high biocomplexity due to the spatial and temporal heterogeneity in habitat patch mosaics (Brown *et al.*, 2018; e.g. Harper *et al.*, 1997). The communities supported by such habitats were likely very different from those in contemporary chalk streams. For example, the higher levels of shading would have largely restricted macrophyte communities to areas of woodland clearings (Mainstone, 1999).

2.3.5.3 Agriculture and deforestation

The earliest human manipulation of chalk streams and European lowland rivers started around 6,000 BP, when an increasing propensity for agriculture led to localised small-scale land clearances (e.g. Waller and Hamilton, 2000; CaBA, 2021). Larger and longer-term agricultural woodland clearances started during the Bronze Age (Waller and Hamilton, 2000; Collins *et al.*, 2006; Waller and Schofield, 2007) and continued in intensity throughout the Iron Age (Brown and Barber, 1985), and Roman (Bird, 2017) and Medieval Period (Campbell, 1988; Hopcroft, 1994; Macklin *et al.*, 2010). Most woodland was cleared by the 17-19th century (Sear *et al.*, 1999).

The impacts of such widespread changes in lowland river catchments on river morphology were considerable across Northern Europe (Brown *et al.*, 2018). The greatest changes were largely the result of agricultural-induced increases in sediment supply, which led to the accretion of floodplains by overbank deposition with sands, silts and clays and the transformation of the river channel from anastomosing to single thread (Brown *et al.*, 1994; 2013; 2018; Foulds and Macklin, 2006). For example, changes in floodplain sediments from largely organic material towards clays have been shown in the River Lambourne (Berkshire, United Kingdom) 4,000 years BP due to increasing agricultural activity (Newell *et al.*, 2015). On the River Frome (Herefordshire, United Kingdom), overbank sedimentation of fine sediments has accumulated up to five metres, resulting in a highly incised single channel (Brown *et al.*, 2013).

Following World War II, the intensity of agriculture further increased due to need to be self-sufficient in food production (Robinson and Sutherland, 2002; CaBA, 2021). Farmers were encouraged to maximise production (e.g. Agriculture Act of 1947); fields were amalgamated, hedgerows (~ 50% of hedgerows), riparian vegetation and water meadows were removed to enlarge areas for food growth, seed beds were tilled by heavy machinery, and the use of artificial fertilisers, pesticides and herbicides was increased (Robinson and Sutherland, 2002; Johannsen and Armitage, 2010; Mondon *et al.*, 2021). In terms of production this was a success, where despite a loss of 65% of farms, yield increased almost fourfold (Robinson and Sutherland, 2002). However, the impacts of such changes in agricultural practices on British rivers have been widespread. Indeed, the increased connectivity between land and river (i.e. due to farming on floodplains and removal or riparian vegetation) and intensification of land use (i.e. tilling, mechanisation) increased fine sediment inputs, physically, chemically and ecologically degrading the river ecosystem (reviewed by Mondon *et al.*, 2021). The extensive use of fertilisers increased phosphorus and nitrogen levels; enhancing the risk of eutrophication (Friberg *et al.*, 2010; Fones *et al.*, 2020; CaBA, 2021).

2.3.5.4 Water mills

The predominant water wheel design (i.e. with a vertical wheel, horizontal shaft) is thought to have been brought to England during the Roman occupation; however, it wasn't until the Medieval period that they were heavily used (Langdon, 2004; Downward and Skinner, 2005; Lewin, 2010; CaBA, 2021; Figure 2.4). For example, according to the Domesday book, 5,624 mills were recorded in England in the 11th century (Hodgen, 1939) and were often found in exceptionally high densities (e.g. River Wandle: 24 mills in 15 km of river; Downward and Skinner, 2005). Mills have been used throughout history for a variety of purposes, including flour, flax and paper production and whale bone grinding (Langdon, 2004; CaBA, 2021). They were typically operated by creating a mill pond by damming the main river (i.e. with a sluice controlled weir) and diverting flow down a shallow artificial channel known as a 'leat'. This ran along the floodplain until enough head height had been generated (i.e. dictated by slope gradient) which drove the mill. Water was returned to the main channel through a mill race (Downward and Skinner, 2005). Mills became largely redundant in the mid-20th century, although the structures and modifications persist on chalk streams and remain as a significant source of morphological (e.g. mill pond flow reduction, siltation) and ecological impacts (Downward and Skinner, 2005; CaBA, 2021). In some cases, the artificial leat has been transformed into the main channel, whilst the natural channel has dried and become lost (CaBA, 2021).

Figure 2.4 An example of a redundant mill situated on a leat on the River Test (Hampshire, United Kingdom).

2.3.5.5 Water meadows

Water meadows are areas of grassland subjected to controlled irrigation used primarily in southern England chalk valleys between the 17th and 19th century (Mainstone, 1999; Sear *et al.*, 1999; Cook, 2010; Historic England, 2017). The primary function of water meadows was to enhance the growth of grass swards for sheep in the spring, to prevent ground frosts and increase hay yield for winter feeding of livestock (Cook *et al.*, 2003). There were two main forms; (1) *catchworks*, which were used on hillslopes and diverted an uphill water source through a carrier on to a series of gutters, and (2) *bedworks*, which were formed adjacent to rivers with large, flat floodplains. A river was typically dammed with a weir, and a sluiced gate was used to control flow down a main carrier which fed water into a series of smaller carriers that overflowed to irrigate surrounding grass. Water was returned to the river through a series of drains (Cook *et al.*, 2003; Historic England, 2017). The use of water meadows began declining from the 1880s due to the labour and skill required to operate and changes to agricultural practices (e.g. artificial fertilisers; Mainstone, 1999; Historic England, 2017). As such, many water meadows were levelled to make way for more modern agricultural practices (Cook, 2010; Historic England, 2017). Today, remaining water meadows are often preserved for their ecological (i.e. wetland species habitat) and cultural value (Mainstone, 1999).

2.3.5.6 River engineering: channelisation

River channelisation includes modifications undertaken for the purposes of flood or erosion protection, agricultural land drainage and navigation (Brookes *et al.*, 1983; Hohensinner *et al.*, 2018). For example, straightening, dredging and embankment, levee and impounding infrastructure construction (e.g. weirs, locks). River channelisation has been carried out across the United Kingdom. For example, 8,504 km of major river work was undertaken between 1930 and 1980 (Brookes *et al.*, 1983). During the 18th/19th century, a large number of canals (4,800 miles by 1850) were constructed across the United Kingdom and Europe to facilitate transport and trade (Canals and River Trust, 2022). The 1930s saw an increase in channelisation projects aiming to improve floodwater conveyance and facilitate land drainage for agricultural practices (Brookes *et al.*, 1983). These projects typically involved straightening and dredging rivers; although the success of these in draining land and dispersing flood waters were overall low (CaBA, 2021). Such activities peaked in the 1970/80s, after which their impacts on river ecosystems were realised (CaBA, 2021). Channelisation is arguably one of the most pervasive modifications of rivers, fundamentally removing river dynamics, connectivity (e.g. lateral connectivity to floodplain) and habitat (Hohensinner *et al.*, 2018) with severe ecological consequences (e.g. Hansen, 1971; Horsák *et al.*, 2009).

2.3.6 Current threats

Chalk streams have been subjected to extensive anthropogenic manipulation throughout history which has resulted in highly degraded contemporary systems (O'Neill and Hughes, 2014; CaBA, 2021). Under the Water Framework Directive, all freshwater bodies in the

United Kingdom are required to achieve ‘good ecological status’ and ‘good chemical status’ by 2027 (EU Parliament Council, 2000). Despite this, in the most recent classification cycle (year: 2019), no chalk streams achieved good chemical status and only 15% were classified as good ecological status or above, with others classified as in ‘moderate’ (63%), ‘poor’ (16%) and ‘bad’ (6%) condition (Environment Agency, 2021b). Additionally, 37% of sites were classified as ‘heavily modified’ (physically altered by human activity and substantially changed in character; Environment Agency, 2009). The reasons for such poor conditions vary, but the major contributing factors for ecological element failures include physical modification (35%), low flow (10%), diffuse (23%) and point source pollution (17%) and invasive species (4%; Environment Agency, 2021a).

2.3.6.1 Channel modification

As described in section 2.3.5, almost all chalk streams have been extensively modified throughout history which has been retained in contemporary streams (O’Neill and Hughes, 2014). This is highlighted in the Test and Itchen River Restoration Strategy, where “the majority of both rivers were recorded to be subject to some kind of modification, with straightening and realignment being the most common” (Skinner, 2013; e.g. Figure 2.5). The impacts of channel modifications on riverine ecosystems can be pervasive. Indeed, they can impact natural river dynamics (e.g. sediment dynamics; Wyżga, 2001), abiotic conditions (Hansen, 1971), habitat (Rambaud *et al.*, 2009), connectivity (Kennedy and Turner, 2011) and restrict the ability of the river adjust to perturbation (Gurnell *et al.*, 2009). Channel modification can also severely degrade ecological communities (Hohensinner *et al.*, 2018). For example, channelisation has been associated with a decline in macrophyte (Rambaud *et al.*, 2009), macroinvertebrate (Horsák *et al.*, 2009; Kennedy and Turner, 2011) and fish (Hansen, 1971) diversity. Moreover, dredging has been shown to reduce macroinvertebrate abundance (Grygoruk *et al.*, 2015) and fish species richness (Freedman *et al.*, 2013). Opposing this, some have argued that some modifications may in fact improve ecological quality (Mainstone, 1999; Skinner, 2013). For example, drainage ditches have associated with a high wetland plant species richness (Meier *et al.*, 2017). Despite this, anthropogenic modification has been deemed one of the most influential factors currently threatening English chalk streams ecology (O’Neill and Hughes, 2014; CaBA, 2021). This is worsened by their reduced ability to easily reverse anthropogenic modification as a result of the low power and sediment supplies (Sear *et al.*, 1999).

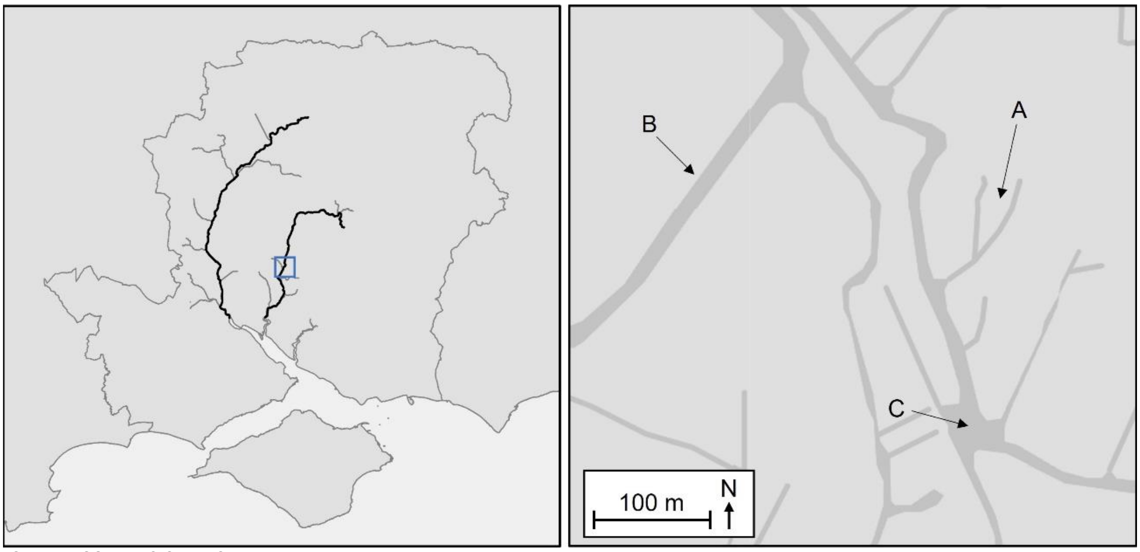


Figure 2.5 An example section of the River Itchen (Hampshire, United Kingdom) highlighting the extensive modification. This includes: (A) drainage channels; (B) channel straightening and widening; (C) flow diversion and impoundment. Location of the river section indicated by the blue box. Country/county and river network shapefiles were supplied from Ordnance Survey (2023) and Ordnance Survey (2022), respectively. Detailed map was edited from Google (2022).

2.3.6.2 Fine sediment

Increasing fine sediment (< 2 mm diameter) inputs have been highlighted as a key issue in chalk streams (Wood and Armitage, 1999; Heywood and Walling, 2003; Mondon *et al.*, 2021). Such an increase has been primarily attributed to changes in land-use (e.g. use of machinery in agriculture; Evans, 2017), particularly agricultural practices which contribute 72-76% of fine sediment inputs into English and Welsh rivers (Collins *et al.*, 2009; Zhang *et al.*, 2014). Additionally, aquaculture (Casey and Smith, 1994), livestock (Bond, 2012), damaged road verges (Collins *et al.*, 2010) and deforestation (Wood and Armitage, 1999) may contribute to increased inputs, whilst channel modification, infrastructure and abstraction may enhance deposition and retention (Bickerton *et al.*, 1993; Wood and Armitage, 1999; Mondon *et al.*, 2021).

High fine sediment loads may reduce light attenuation and dissolved oxygen (i.e. by increasing biological oxygen demand), increase scour, and ingress into interstitial spaces reducing surface-interstitial water transfer and burying larger particles (Kemp *et al.*, 2011). As a result, periphyton and macrophytes may be abraded and smothered, restricting growth, abundance and diversity (Izagirre *et al.*, 2009; Luce *et al.*, 2010). Fine sediment may impact macroinvertebrates in several ways. For example, by altering substrate suitability, increasing drift rates, reducing oxygen uptake (e.g. by damaging respiratory structures) and impacting feeding strategies (Wood and Armitage, 1999; Harrison *et al.*, 2007). Generally, it is expected that high fine sediment loads will reduce macroinvertebrate diversity, particularly sensitive EPT species (Kaller and Hartman, 2004; Harrison *et al.*, 2007). Investigations into the impacts of fine sediment on fish have primarily concentrated on salmonids due to its effects on reproduction, where silt can lower water permeability, waste removal and oxygen transportation to the egg and block alevin emergence (Greig *et al.*, 2005; Heywood and Walling, 2007; Kemp *et al.*, 2011). Despite the negative impacts associated with fine sediment, it is important to note that it is also a natural component of rivers which can be integral to the survival of many taxa, including protected species such as river lamprey (Aronsuu and Virkkala, 2014).

2.3.6.3 River infrastructure

Infrastructure such as weirs, culverts, bridges and mills have been constructed across chalk streams for millennia; forming a mosaic of impounded and regulated flows and widely impacting river connectivity (Berrie, 1992). Infrastructure has been constructed for a variety of reasons, including mechanical power, agriculture, navigation and flood defence. Today, infrastructure is often maintained in chalk streams for controlling water levels in recreational fisheries, flood defence and water storage, but many more remain redundant (O’Neill and Hughes, 2014).

The typical impacts of impounding infrastructure include the pooling of water upstream forming a ponded habitat (e.g. greater depth and fine sediment deposition, reduced velocity and dissolved oxygen), whilst restricted transportation of sediment and flow increases scour and produces unnatural lotic conditions downstream (e.g. dampening of natural flow variation, increase coarse substrates; Kemp, 2015). In response, upstream fish communities may become increasingly dominated by lentic taxa (Catalano *et al.*, 2007; Im *et al.*, 2020), whilst migratory species may decline due to reduced spawning and rearing habitat and restricted ability to longitudinally migrate (Moore *et al.*, 2013). Macroinvertebrates are largely influenced by substrate and flow conditions (Extence *et al.*, 1999; 2010), so upstream communities could be expected to comprise of more non-rheophilic, silt-tolerant taxa (e.g. Stanley *et al.*, 2002; Sharma *et al.*, 2005; Mueller *et al.*, 2011). Studies designed to assess the impacts of infrastructure on macrophytes are relatively scarce, although some have shown limited differences between upstream and downstream sections (e.g. Mueller *et al.*, 2011). Generally, it is expected that taxa unable to cope with fine sediment accumulation (e.g. *Ranunculus sp.*) would be at a lower abundance upstream than downstream due to the accumulation of silt and reduced flow velocity (Wood and Armitage, 1999; Kemp, 2015).

2.3.6.4 Abstraction

The over abstraction of surface and groundwater has been highlighted as one of the most pressing issues threatening chalk streams (Salter and Singleton-White, 2019; CaBA, 2021). Although chalk streams surface waters have been used for domestic and agricultural water supplies for millennia, aquifer abstraction increased rapidly in the second half of the 20th century due to the 1945 Water Act (CaBA, 2021). Presently, 70% of drinking water in southern and eastern England is supplied from chalk aquifers and this demand will likely increase due to a growing population (BGS, 2020). This, alongside poor river management, a climate change impacted hydrological cycle (Watts *et al.*, 2015) and high public water usage (e.g. Chilterns area use 155 l per person daily; CaBA, 2021) increases the risk of abstraction-induced impacts. A recent analysis of 55 chalk streams found abstraction took over 20% of the annual catchment recharge in 17 sites and 50% in five (CaBA, 2021).

The physical and ecological responses to a reduction in flow discharge has been thoroughly discussed within the literature (e.g. Bickerton *et al.*, 1993; Wood and Petts, 1994; Wood and Armitage, 1999). Typically, the worst-affected areas are within ephemeral winterbourne reaches, whereby over-abstraction may interfere with the natural flow-dry regime and move them further downstream (O'Neill and Hughes, 2014). Lowland perennial stretches can display reductions in flow, although this is often not enough to desiccate. The effects of flow reductions are wide-ranging and may include an increase in fine sediment deposition and algal-dominance, a reduction in wetted habitat, an altered ecological community (e.g. macrophytes and macroinvertebrates may take four and six years to recover from flow reduction, respectively; Westwood *et al.*, 2017) and a complete loss of aquatic habitat and species (Wood and Petts, 1994; Westwood *et al.*, 2017). Indeed, abstraction rates were so great in the 1980s that sections of the River Piddle, Darent and Misbourne dried completely (CaBA, 2021).

2.3.6.5 Nitrogen and phosphorus pollution

Nitrogen and phosphorus are crucial for all organisms (Hecky and Kilham, 1988) and under natural conditions are generally found in low concentrations (Limbrick, 2003; European Environment Agency, 2004). This is especially the case for phosphorus, which is often the limiting factor for floral growth (Hecky and Kilham, 1988; Vitousek *et al.*, 2010; Elser, 2012). Anthropogenic activities have increased the concentrations of phosphorus and nitrogen in many English rivers (CaBA, 2021; e.g. Bowes *et al.*, 2011; Fones *et al.*, 2020). For example, in the most recent assessment, 39% of chalk streams were attributed with high phosphorus, with sewage (60-80%) and agriculture (20-30%) being the main sources (CaBA, 2021). In the River Frome (Somerset, United Kingdom), nitrogen concentrations increased from 2.4 mg/l in the 1960s to 6.0 mg/l in 2008-2009, whilst phosphorus concentration decreased from 190µg/l in 1989 to 49 µg/l in 2007-2009 (i.e. due to phosphorus stripping at wastewater treatment plants; Bowes *et al.*, 2011). Sources for nitrogen and phosphorus include agricultural activities (Fones *et al.*, 2020), sewage treatment plants (Muscutt and Withers, 1996), household activities (e.g. dishwasher tablets; Richards *et al.*, 2015) and groundwater contamination (Strebel *et al.*, 1989). The most severe potential effect of nutrient enrichment is eutrophication, whereby high concentrations of nutrients, particularly phosphorus and nitrogen, lead to algal blooms which can reduce oxygen, impact water quality and degrade ecological communities (Friberg *et al.*, 2010). Additionally, water chemistry can directly influence ecological communities. For example, certain taxa, e.g. *Serratella ignita* (Everall *et al.*, 2018), are particularly sensitive to high phosphorus concentrations.

2.3.6.6 Invasive species

Invasive, non-native species are a major issue across British waterways and can severely impact habitat and ecological communities (Seeney *et al.*, 2019a; 2019b; Sanders *et al.*, 2021). Three notable examples in chalk streams include signal crayfish, Japanese knotweed (*Fallopia japonica*) and Himalayan balsam (*Impatiens glandulifera*; CaBA, 2021), although many others exist (e.g. American mink [*Neovison vison*], floating pennywort [*Hydrocotyle ranunculoides*]).

Signal crayfish were introduced to England in 1976 to fulfil a Scandinavian market and currently have a wide distribution across the United Kingdom (Holdich *et al.*, 2014). They are known to increase erosion and bank collapse when burrowing (Johnson *et al.*, 2011; Sanders *et al.*, 2021) and lower the abundance and diversity macroinvertebrates and fish through predation (Guan and Wiles, 1997; Crawford *et al.*, 2006; Galib *et al.*, 2021). They have been particularly detrimental to native white-clawed crayfish, in part due to their aggression (e.g. Usio *et al.*, 2001), but also because they act as a vector for the crayfish plague (*Aphanomyces astaci*; Holdich *et al.*, 2014).

Japanese knotweed and Himalayan balsam were initially transferred to the United Kingdom by Victorian naturalists in the 19th century (Perrins *et al.*, 1993; Beerling, 1994; Seeney *et al.*, 2019a). Currently, both species have a large presence in chalk streams, with Himalayan balsam being noted in 16% of chalk stream river habitat surveys and Japanese knotweed in 5% (O'Neill and Hughes, 2014). Both species outcompete native riparian vegetation, and may do so by light and pollinator competition as well as allelopathy (Siemens and Blossey, 2007; Murrell *et al.*, 2011; Thijs *et al.*, 2012; Seeney *et* *al.*, 2019a). They are also highly resistant to removal. Himalayan balsam disperses seeds explosively which allows rapid colonisation (Seeney *et al.*, 2019a), whilst Japanese knotweed can recover from seed banks and clonal rhizobium growth (Gowton *et al.*, 2016). The ecological impacts of these species can include the reduction of terrestrial plant diversity (Stoll *et al.*, 2012) and invertebrate abundance, diversity and morphodiversity (Stoll *et al.*, 2012; Tanner *et al.*, 2013; Seeney *et al.*, 2019a; 2019b). Additionally, the intolerance of Himalayan balsam to cold weather (Helmisaari, 2010) leads to winter diebacks, which can expose soil, increasing erosion and sediment inputs into the river system (Greenwood and Kuhn, 2014).

2.3.6.7 Management

Extensive management, such as by recreational fisheries, has become common within lowland chalk streams. Typically, managed chalk streams are characterised by a well-maintained, narrow (0.5–1.0 m) sedge margin with few trees and a mown lawn aimed at promoting angler access (Raven *et al.*, 1998). As a result, woody material inputs are often reduced and is typically removed prior to influencing the system (Skinner, 2013). Additionally, summer macrophyte and reed beds are extensively cut to promote habitat for salmonids, produce favourable fishing conditions and increase floodwater conveyance (Wood and Armitage, 1999; Old *et al.*, 2014). The impact of this can include the remobilisation of silt, increased bank erosion and over-widening, decline of macrophyte-associated species (e.g. *Brachycentrus subnubilus*) and the redistribution of fish (Swales, 1982; Dawson *et al.*, 1991; Wood and Armitage, 1999; Greer *et al.*, 2017). Despite the issues arising from excessive management, it is important to note that some management may maintain desirable attributes of contemporary chalk streams. For instance, excessive riparian shading may inhibit the growth of species rich macrophyte mosaics critical for habitat development (Gurnell *et al.*, 2006). Additionally, recreationally fisheries can increase the value of chalk stream habitats, which ultimately helps ‘protect’ them from other impactors (e.g. intensive agriculture; CaBA, 2021).

2.4 Chalk stream restoration

Given the widespread degradation and impacts caused by historic channel modification, alongside their poor ability to self-correct anthropogenic physical change (Sear *et al.*, 1999), restoration has become an integral management strategy in chalk streams (CaBA, 2021; River Restoration Centre, 2023b). Despite this, a limited number of studies appraising restoration in chalk streams means that its effectiveness remains poorly understood and a major source of uncertainty (Angelopoulos *et al.*, 2017; River Restoration Centre, 2023b). To help meet the aim of this thesis and guide the objectives and research chapters, this section aims to review: (1) recommended approaches to chalk stream restoration; (2) restoration activities in practice; (3) current literature monitoring ecological responses to English chalk stream restoration.

2.4.1 Chalk stream restoration: a recommended approach

Chalk streams are unique systems, and consequently require a system-specific approach to their restoration. Recognising this, the Chalk Stream Restoration Strategy was developed in collaboration with 28 experts with the aim of enhancing the condition and protection status of chalk streams (CaBA, 2021). The strategy is built around the concept of a "trinity of ecosystem health" relating to water quantity, water quality and habitat quality, and has produced over 30 recommendations including an implementation plan relating to these (CaBA, 2022). This includes encouraging monitoring and modelling (e.g. to understand water stressed regions), the wider adoption of phosphorus stripping processes in sewage treatment plants, sustainable farming incentives and promoting the sharing of data.

One of the key principles for the strategy is the restoration of historically modified habitat back toward a less impacted reference state (CaBA, 2021; 2022). Whilst this reference is difficult to acquire due to the long history of modification in chalk streams (Mainstone, 1999) and subject to system (e.g. differences in system geology; see section 2.3.2) and site specific variability, the reference state of a chalk stream is broadly defined as having the following characteristics (list modified from CaBA, 2021):

- Low drainage density / limited tributary network
- Low stream power relative to catchment area
- Relatively high width-to-depth ratios
- A mix of single, meandering channels with side channels and in lower reaches, anastomosed multiple channels

- Limited in-channel coarse sediment storage (bars or “riffles”)
- High residence time of large organic matter (woody materials)
- Presence of woody debris islands but few debris dams
- High-floodplain water tables leading to organic-rich floodplain soils
- Low rates of lateral channel adjustment
- Limited accumulation of fine sediments on bed surface in undisturbed catchments
- Tufa deposition and concretion of gravels at points of groundwater upwelling
- Long duration of bank-full / out-of-bank flows
- High density of aquatic macrophytes that facilitate flushing of fines
- Relatively open woodland with dominance of herbaceous plants due to high floodplain water tables
- Marsh habitat with open groundwater pools in floodplain where strong coupling with groundwater is evident
- Winterbourne, ephemeral reaches which dry naturally, usually in the summer, as the groundwater level and therefore the saturated zone of the valley recedes.

Whilst future work is required to provide further evidence of pre-restoration states (Seddon *et al.*, 2019; e.g. the strategy has helped secure funding for a PhD project relating to this; University of Southampton, 2023), these broad characteristics provide a useful base to help target restoration interventions.

The Chalk Stream Restoration Strategy strongly advocates the restoration of natural river processes degraded through historic modification. Indeed, a process based approach is especially vital in chalk streams to avoid unnatural restoration designs and just contributing another layer of anthropogenic modification (Beechie *et al.*, 2010). Moreover, restoring processes is crucial for promoting the sustainable self-development of habitat which varies across space and time, which ultimately helps promote resilience (Schindler *et al.*, 2015). Given the role of ecosystem engineers in chalk streams (see section 2.3.2 for overview), the need for restoration to target habitat requirements that ultimately allow them and the services they provide to flourish is highlighted. More specifically, several principles for effective chalk stream restoration were developed (CaBA, 2021; 2022):

- **Catchment scale interventions:** Given the top-down hierarchical nature of rivers (Frissell *et al.*, 1986), there is a need to tackle issues which operate over the catchment scale. More specifically, measures which restore natural water quantity and quality are required to support natural processes and ensure maximum benefits of physical restoration. This includes taking interventions to reduce nutrient run-off, fine sediment inputs and encourage sustainable abstraction.

- **Dredged channels:** Chalk streams have been extensively dredged over the past several centuries (Brookes *et al.*, 1983). This pervasive form of modification has widely degraded river dynamics, connectivity, habitat and ecological communities (Horsák *et al.*, 2009; Hohensinner *et al.*, 2018), including removing much of the natural flint gravel substrates which characterise chalk streams (Berrie, 1992). Given the low gravel production and transport ability of chalk streams, natural substrates will not return without additional interventions. Consequently, there is a need to restore these substrates to enable the development of more naturalised habitat, processes and ecological communities (e.g. gravel augmentation). Importantly, these substrates must be of a suitable size and specification for the river, e.g. due to preferences of salmonid spawning substrates (Kondolf and Wolman, 1993), and so over or undersized, graded and non-fluvial derived substrates are not appropriate (CaBA, 2021). Often, substrates are available 'as dug' adjacent to the river, which ensures suitable properties and can be a more financially desirable option to importing.

- **River-bed gradient:** The natural gentle gradient of chalk streams has been widely subjected to 'staircasing' through a multitude of channel diversions (e.g. mill leats) and river infrastructure (CaBA, 2021). As a result, natural habitat, longitudinal connectivity and processes (e.g. sediment transport) have been widely impacted with knock on effects to ecology. For example, the reduction in longitudinal connectivity through river infrastructure can lead to a decline in migratory salmonids (Welters *et al.*, 2001; Moore *et al.*, 2013) and the associated clearing of fine sediments from gravels during redd production (Montgomery *et al.*, 1996). Furthermore, siltation and a reduction in flow can alter instream plant communities (e.g. decline in Ranunculus; Brookes, 1986), impacting the production of a diverse macrophyte mosaic and the habitat forming benefits these can ensue (Gurnell *et al.*, 2006). Circumnavigating or removing channel diversions and river infrastructure is therefore key for restoring ecology, habitat and processes.

- **Channel planform:** A naturalised chalk stream typically exhibits single thread meandering and anastomosing form, which have historically been straightened to provision transportation and floodwater conveyance. Recovering historic planforms can reinvigorate processes and dynamics which support healthy habitat and ecological communities (CaBA, 2021). This can often be achieved by reinstating historic channels through excavating and diverting flow from the contemporary river (e.g. River Restoration Centre, 2013).

- **Working with trees and macrophytes:** Woody materials and macrophytes are a fundamental for accelerating processes and habitat development in chalk streams (Wharton *et al.*, 2006; Collins *et al.*, 2012). For example, a felled tree can influence river habitat for decades, increasing floodplain connectivity, enhancing sediment deposition by pooling water upstream, funnelling flow downstream increasing scour, and diversifying ecological communities (Thompson *et al.*, 2018a; CaBA, 2021). Moreover, diverse macrophyte mosaics can locally increase scour and deposition between and within patches, respectively, enhancing habitat heterogeneity (Gurnell *et al.*, 2006). The strategy therefore advocates the exploitation of these ecological engineers within restoration projects, e.g. through recovering normative woody material inputs and more naturalised in-stream habitat (CaBA, 2021).

- **River-floodplain interaction:** River-floodplain interactions are an important component of natural chalk stream functioning (CaBA, 2021), for example due to their role in energy and nutrient transfer (Venterink *et al.*, 2003), sediment dynamics (Walling *et al.*, 1998), ability to reduce the impacts of land run-off (e.g. pollutants; Haycock and Burt, 1993), and as a heterogeneous habitat supporting many organisms (e.g. fish; Copp, 1989). Where possible, reinstating floodplains, marsh, wet woodland and the features within these (e.g. ponds) can help recover processes. This can be achieved, for example, through embankment and infrastructure removal, bank reprofiling and the placement of woody materials/tree hinging (e.g. Clilverd *et al.*, 2013)

By implementing restoration addressing these issues at an appropriate scale (e.g. by integrating reach-scale projects within a catchment plan where needed), the strategy encourages the reinvigoration of ecological processes and ecosystem engineers which facilitate the formation of self-sustaining spatially and temporally heterogeneous chalk stream habitat (CaBA, 2021). It is important to note, that given the characteristics of chalk streams and use of a process-based approach, these interventions could take decades or centuries to realise (CaBA, 2021). As such, effective communication with stakeholders to manage expectations is required.

2.4.2 Chalk stream restoration in practice

To understand current approaches to restoration in chalk streams, projects listed on the River Restoration Centre's NRRI database (River Restoration Centre, 2023b) were analysed. This database contains self-reported information on over 5,000 restoration projects across the United Kingdom, including a description and details such as the location and whether monitoring was conducted. For more specific information that could not be accurately determined from the NRRI database (e.g. specific restoration methodologies), more detailed case studies reported on the River Restoration Centre (River Restoration Centre, 2023a) and RESTORE (RESTORE, 2023) website were analysed.

A total of 398 restoration projects have been recorded within chalk streams in the NRRI database. The majority of these took place within the Thames river basin district (136; e.g. River Kennet), followed by Anglian (94; e.g. River Wensum), South East (79; e.g. River Itchen), South West (75; e.g. River Piddle) and Humber (14; e.g. West Beck). The most widely stated motivator for restoration was habitat and biodiversity improvements (85.9%; Figure 2.6), likely largely driven by the biodiversity-orientated objectives set out in the Water Framework Directive (Smith *et al.*, 2014). In addition, fisheries enhancement was a major motivator for restoration (43.5%). This is potentially due to the widespread presence of recreational fisheries in chalk streams (e.g. River Test and Itchen; Skinner, 2013), as well as the frequent acquisition of funding through fisheries and rod licence fees (*Personal knowledge*). Further exploring fisheries motivated projects highlighted many were orientated towards socio-economically important salmonid species (34.7%; e.g. Mitchell, 2016). In addition, some projects included ecosystem services motivations such as flood protection (e.g. floodplain reconnection; 13.8%) and societal goals (e.g. recreational use, aesthetics; 8.5%), in part likely to assist in acquiring project funding (e.g. to gain access flood alleviation funds; *Personal knowledge*). Projects which were motivated by reversing deterioration in water quality (4.8%), low flow (3.8%) and land-use issues (e.g. livestock poaching; 3.0%) were comparatively rare.

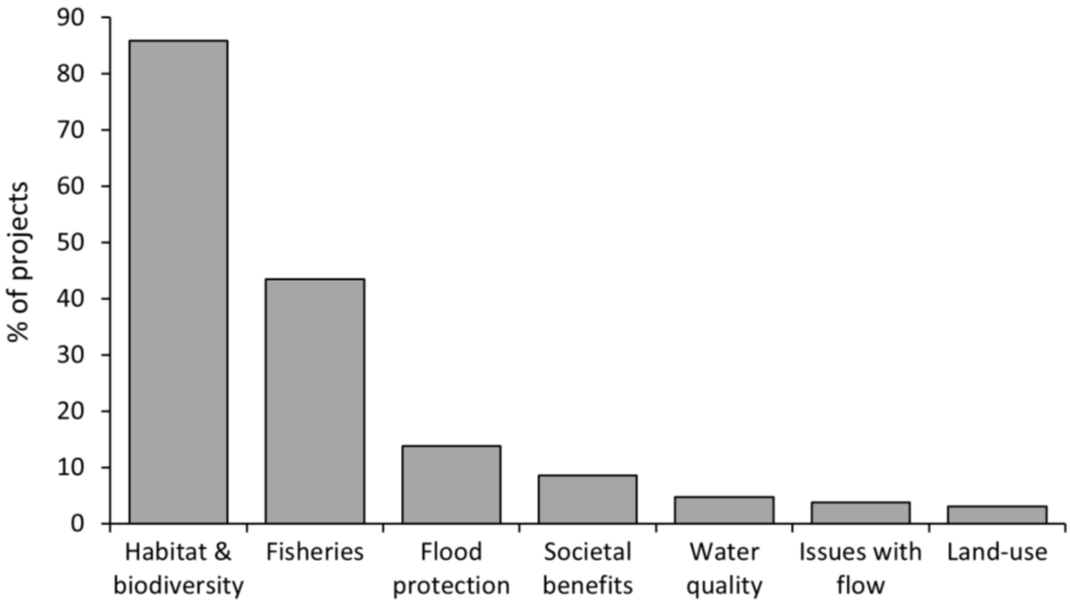


Figure 2.6 The percentage of chalk stream restoration projects listed in the NRRI database (n = 398; River Restoration Centre, 2023b) with each motivation.

The majority of the case study restoration projects (n = 57) were implemented at the reach-scale (91.2%; mean length ± standard deviation [SD] = 753.2 m ± 607.2) and often restored river form and features (e.g. geomorphic features such as riffles and pools; 44.2%). Five (8.8%) case studies described several reach-scale projects which were integrated within a wider catchment-scale plan, which were often motivated by improving local habitat and catchment-scale issues (e.g. sediment inputs, water quality). Across the case study projects, the most common restoration method was gravel augmentation (43.9%; Figure 2.7), followed by the creation of geomorphic features (e.g. pools, riffles; 40.4%), large woody material placement (31.6%) and channel or bank reprofiling (28.1%).

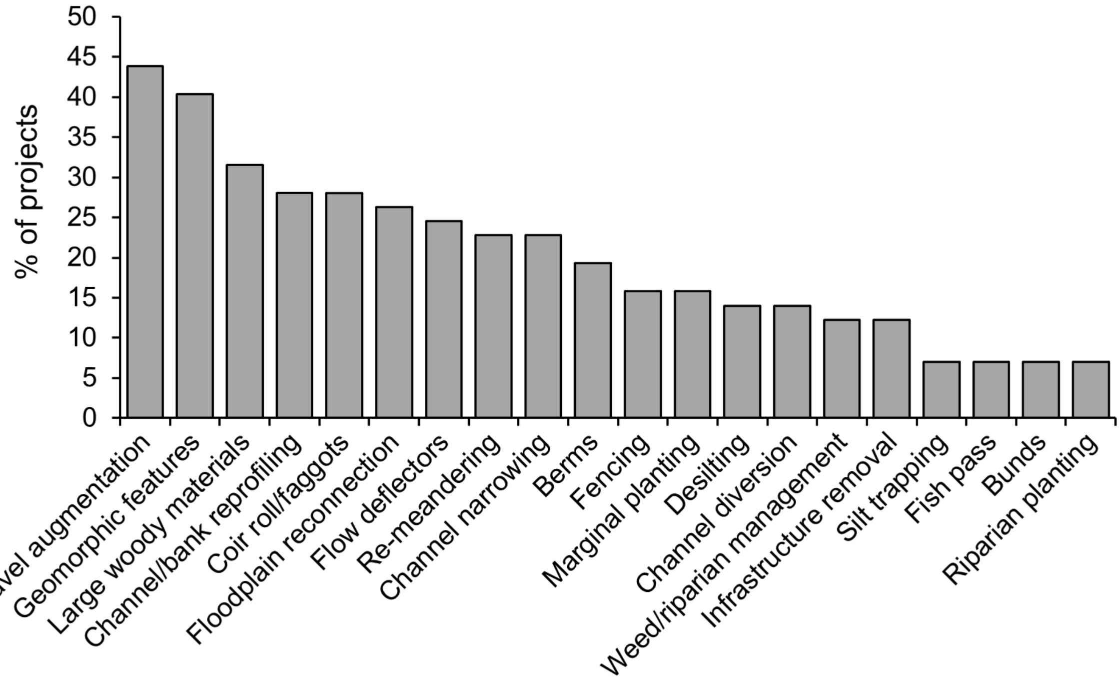


Figure 2.7 The percentage of case study chalk stream restoration projects (n = 57) employing each technique.

Out of the 398 projects described on the NRRI database, only 108 (27.1%) conducted any monitoring (River Restoration Centre, 2023b). Such a low amount is fitting with the wider restoration literature, and emphasises the need for further appraisals to gain a fuller understanding of its effectiveness (Smith *et al.*, 2014; England *et al.*, 2020). By far the most common form of monitoring was fixed point photography (17.6%), likely due to the low cost of equipment and ease of implementation (Figure 2.8). Despite this, whilst photography can inform managers on general changes occurring following restoration (England *et al.*, 2020), the data captured may be of restricted value for assessing ecological outcomes against project aims. The next most common form of monitoring was fish (10.5%) and physical habitat surveys (e.g. River Habitat [8.8%] and River Corridor [8.8%] surveys). Given that 85.9% and 43.5% of projects aimed to alter habitat and fisheries, respectively, this highlights the limited appraisal of projects in relation to their goals. Despite playing integral roles within the ecosystem (e.g. Wallace and Webster, 1996), the responses of macrophytes (1.5%), macroinvertebrates (1.3%), marginal/riparian vegetation (0.25%) and mammals (e.g. water vole surveys; 0.25%) were rarely considered.

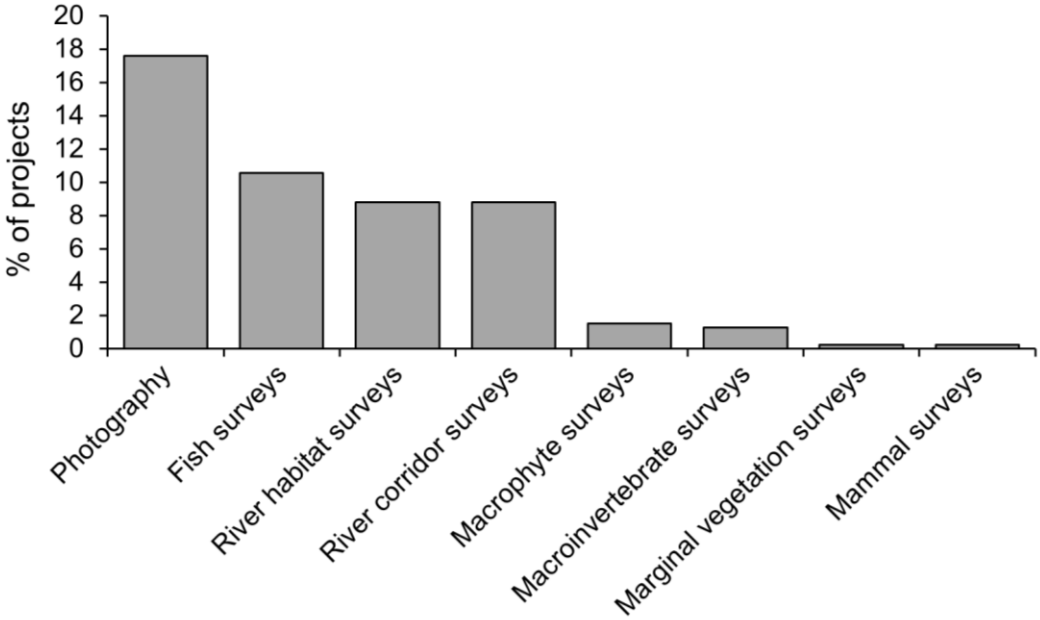


Figure 2.8 The percentage of chalk stream restoration projects listed in the NRRI database (n = 398; River Restoration Centre, 2023b) carrying out each form of monitoring.

2.4.3 Chalk stream restoration research

In total, 11 studies (9 research papers and two PhD theses) monitoring ecological responses to restoration in English chalk streams were found and analysed (Table 2.1). Within these studies, a total of 39 individual restoration projects were assessed. However, the scale of each project and monitoring efforts varied highly from point measurements at patch-scale gravel augmentation projects (Mitchell, 2016) towards longer-term responses at larger reach-scale schemes (Summers *et al.*, 2008; ~ 1 km length). The majority of projects were conducted within the Anglian basin district (53.8%), followed by Thames (25.6%), South West (10.3%), Humber (7.7%) and South East (2.6%). Such data highlights several issues in chalk stream restoration research. Firstly, too few studies have appraised restoration in chalk streams, providing a limited evidence base for its effectiveness and best practice in these unique systems. Where studies have been conducted, there is an area bias towards rivers within the Anglian and Thames basin districts, despite the fact that many restoration projects have taken place in southern streams (38.7% according to the NRRI database). Chalk streams in different areas are subject to variation in geology (e.g. chalk fracturing; MacDonald and Allen, 2001), land-use pressures (e.g. urbanisation; Government Office for Science, 2021) and historical modification (e.g. mills; Downward and Skinner, 2005) which can influence methodological approaches and physical and ecological responses to restoration. For example, the influence of superficial deposits from glacial drift varies highly across chalk landscapes (see section 2.3.5.1 for overview of the influence of glaciation) and has been shown to impact the effectiveness of natural flood management methods, with more permeable basins (e.g. Test and Itchen) tending to respond less positively than less permeable basins (e.g. River Nar; Barnsley *et al.*, 2021). Moreover, macroinvertebrates downstream of dam removals have been shown to respond more positively (e.g. enhanced density) in systems with greater discharges and levels of catchment disturbance (Carlson *et al.*, 2018). As such, it is important that future efforts are directed to appraising restoration projects within chalk streams, especially understudied regions, to better understand its effectiveness.

Table 2.1 Studies assessing ecological responses to physical habitat restoration in English chalk streams.

Study	**River**	**Restoration**	**Monitored**
Summers *et al.* (2008)	Piddle & Devil's Brook	Livestock fencing.	Physical habitat, fish, macrophytes.
		Livestock fencing, pool creation, flow deflectors.	
England and Wilkes (2018)	Mimram and Rib	Weir lowering, channel narrowing, gravel augmentation.	Physical habitat, macroinvertebrates, macrophytes.
England *et al.* (2019)	Bulbourne	Large woody material, bank regrading, fencing, channel narrowing.	MoRPH survey, physical habitat, vegetation, public perception.
Harvey *et al.* (2018)	Bure	Large woody material.	Physical habitat, macrophytes.
Thompson *et al.* (2018a)	Test, Loddon, Lyde, Wensum & Bure	Large woody material.	Physical habitat, chemistry, diatoms, macroinvertebrates, fish.
England *et al.* (2021b)	Kennet	Weir removal, channel narrowing.	Physical habitat, macroinvertebrates.
Robertson *et al.* (2021)	Lambourne	Weir notching, channel narrowing, planform reprofiling, gravel reworking.	Physical habitat, benthic and hyporheic macroinvertebrates.
Champkin *et al.* (2018)	Glaven	Embankment removal, re-meandering.	Physical habitat, fish.
England and Peacock (2010)	Chess	Weir removal.	Macroinvertebrates (Riverfly Partnership).
Mitchell (2016)	Stiffkey	Gravel augmentation.	Physical habitat, fish.
Angelopoulos (2013)	Driffield Beck	Bed reprofiling, coir mattresses.	Physical habitat and fish.
	Lowthorpe	Channel narrowing.	
	Stiffkey	Gravel augmentation, flow deflectors.	

An array of different methodological approaches to restoration have been assessed within the chalk stream literature, but rarely in isolation of other methods. The most common methods were channel narrowing (n = 5 studies), followed by infrastructure removal/modification (n = 4), large woody material placement, gravel augmentation and the creation of geomorphic features (n = 3), fencing, flow deflectors and planform reprofiling (n = 2), and coir mattresses, embankment removal and bank regrading (n = 1). Although the overall number of studies are low, these widely cover the techniques most commonly applied in English chalk streams (Figure 2.7).

To determine the effectiveness of restoration in chalk streams, there is a need to appraise the efficacy of the suite of different methods used in these systems. It is argued here, however, that two techniques in particular require further investigation, infrastructure removal and gravel augmentation:

- **Infrastructure removal:** given the high numbers of structures across England (Jones *et al.*, 2019) and Europe (Belletti *et al.*, 2020), alongside their often deteriorated state (Ding *et al.*, 2019), infrastructure removal presents a valuable opportunity to restore processes, connectivity, habitat and ecological communities (Bednarek, 2001). Consequently, infrastructure removal has become a widely adopted practice, with 325 structures removed across Europe in 2022 alone (Dam Removal Europe, 2022). However, this form of restoration can also be complex and risky (e.g. Orr *et al.*, 2008b; East *et al.*, 2015), with the impacts of infrastructure and benefits of their removal varying highly with environmental and structural characteristics (e.g. discharge, sediment accumulated and the ability of the river to transport these; Csiki and Rhoads, 2010; Carlson *et al.*, 2018). Given their low power and ability to mobilise sediments, chalk streams may be particularly susceptible to deterioration following infrastructure removal due to a poor ability to clear accumulated sediments (i.e. sediment pulse; Renöfält *et al.*, 2013), creating a need to assess its effectiveness.

- **Gravel augmentation:** gravel augmentation is widely used in chalk streams (> 40% of projects) but has been rarely investigated. Where studies have been carried out, they tend to concentrate on the responses of fish, especially salmonids (e.g. Angelopoulos, 2013; Mitchell, 2016; but see England and Wilkes, 2018). Despite this, gravel augmentation can lead to spatially and temporally variable responses (e.g. Pulg *et al.*, 2013; 2022; Mueller *et al.*, 2014) and impact ecological groups less often considered in appraisals (e.g. macrophytes and macroinvertebrates; Merz and Ochikubo Chan, 2005; Albertson *et al.*, 2011; Mueller *et al.*, 2014). Hence, there is a need to provide additional information on the effectiveness of gravel augmentation in chalk streams, with those assessing multiple ecological groups being particularly valuable.

Both infrastructure removal and gravel augmentation are recommended by the Chalk Stream Restoration Strategy (CaBA, 2021). Thus, gaining a better understanding of the physical and ecological responses to these can help to reduce uncertainties and provide the evidence needed to support future restoration efforts.

All studies but one (England and Peacock, 2010) monitored physical habitat. This is important not only in that it reflects a primary motivator for restoration (85.9% in NRRI dataset) but also because it acts as a template upon which biological communities are formed (e.g. Duan *et al.*, 2008; 2009). In terms of biotic components, benthic macroinvertebrates and fish were monitored most (five studies), though several studies concentrated on the responses of brown trout (e.g. Summers *et al.*, 2008). Several studies also monitored macrophytes (four studies), but only Harvey *et al.* (2018) assessed in more detail than the percentage cover of broad groups (e.g. submerged, emergent). Other components of habitat and ecology monitored included water chemistry, biofilms and hyporheic macroinvertebrates (1 study). Most studies appraised using single ecological indicators (e.g. Champkin *et al.*, 2018). One notable exception is Thompson *et al.* (2018a), who quantified the responses of fish, benthic macroinvertebrates and biofilms to restoration with large woody materials and found complex interactions between each level. This study highlights the added value of monitoring multiple ecological indicators (Pander and Geist, 2013). Indeed, such an approach can provide information on food web dynamics (Thompson *et al.*, 2018a), interactions between groups (e.g. abundance of macroinvertebrate taxa in response to changes in macrophyte cover; Pedersen *et al.*, 2007) and intra- and inter-group variation in responses (Mueller *et al.*, 2014), providing a more holistic understanding of chalk stream restoration effectiveness (Pander and Geist, 2013).

Quantifying longer term responses to restoration using strong study designs has long been deemed crucial for assessing restoration effectiveness (England *et al.*, 2008; Smokorowski and Randall, 2017; Lu *et al.*, 2019). In English chalk stream restoration research, study design included a mixture of before-after-control-impact (BACI; e.g. England and Wilkes, 2018), before-after (BA; e.g. England and Peacock, 2010) and control-impact (CI; e.g. Mitchell, 2016). The total length of monitoring ranged from 1 to 12 years, with pre- and post-restoration monitoring ranging from 1 month - 5 years and 8 months - 9 years, respectively. Given the low power of chalk streams, they will naturally take longer to respond physically and ecologically to restoration compared with more powerful systems (Sear *et al.*, 1999), exemplifying the importance of robust longer term studies to better understand its effects.

2.4.4 Data collection constraints

Despite being a motivator for 43.5% of chalk stream restoration projects on the NRRI database (River Restoration Centre, 2023b), only 10.5% actually monitored the effects of restoration on fish. In part, this low-level of monitoring may be due to constraints with traditional fish data collection methods. For instance, restoration projects are regularly funded by recreational fisheries, who can prohibit physical capture methods due to concerns with fish injury, mortality and disturbance (*Personal knowledge*). Furthermore, physical capture methods can be restricted when in the presence of protected species and habitat (e.g. SSSI or SACs) or within sensitive time periods (e.g. spawning seasons; Environment Agency, 2022a). Environmental characteristics such as high flow, depth and siltation can negatively influence the catch efficiency of traditional methodologies (e.g. Allard *et al.*, 2014; Neufeld *et al.*, 2016), which may impact the robustness of the data and conclusions drawn (*Personal knowledge*). Moreover, traditional capture methods often require expensive equipment, several sufficiently trained team members (Kristensen *et al.*, 2020) and have inherent safety concerns (e.g. electrocution), increasing survey costs and limiting the number of projects which can be appraised. Together, these factors reduce the number of projects which can be effectively monitored in chalk streams.

2.5 Summary

River ecosystems are hierarchically structured and naturally dynamic, shaped by processes and disturbances which creates a shifting habitat mosaic key for biocomplexity and ecological resilience. River restoration has become integral in efforts to return degraded habitat and ecological communities towards a more naturalised state; however, a lack of and bias in project monitoring restricts the development of sound restoration practice. Chalk streams exhibit unique characteristics and can support diverse biological communities, but anthropogenic modification over millennia has led to widespread degradation. Restoration has become an integral approach for desirably changing habitat and ecology in chalk streams, but its effectiveness remains poorly understood. The analysis of the wider and chalk stream restoration literature highlighted that: (1) the effects of restoration are typically not monitored; (2) in projects which are monitored, these are typically limited in temporal scope and focus on single ecological groups; (3) there is a need for further investigation into the effects of infrastructure removal and gravel augmentation; (4) social, economic and environmental factors can inhibit monitoring of fish using traditional data collection methods, potentially reducing the number of projects which can be appraised. Considering these points, a finalised set of objectives was created (Chapter 3).

CHAPTER 3 Finalised aim and objectives

The aim of this thesis is:

- To develop understanding of the effects of restoration on physical habitat and ecology in English chalk streams.

To achieve this aim, an initial objective was formed:

1) Review current literature on fluvial and ecological theory, river restoration, chalk streams and their restoration to identify issues, knowledge gaps and bias in research and restoration practice.

After an in-depth literature review, the following objectives and research chapters were developed to achieve the overall aim set out in this thesis (Figure 3.1).

2) Quantify physical and ecological responses to a variety of restoration techniques in chalk streams.

3) Determine the influence of time since restoration on these responses and implications for determining 'success'.

4) Take a multi-taxa approach to determine variation in responses to restoration between ecological groups.

5) Develop a passive methodological approach for monitoring fish populations in chalk streams.

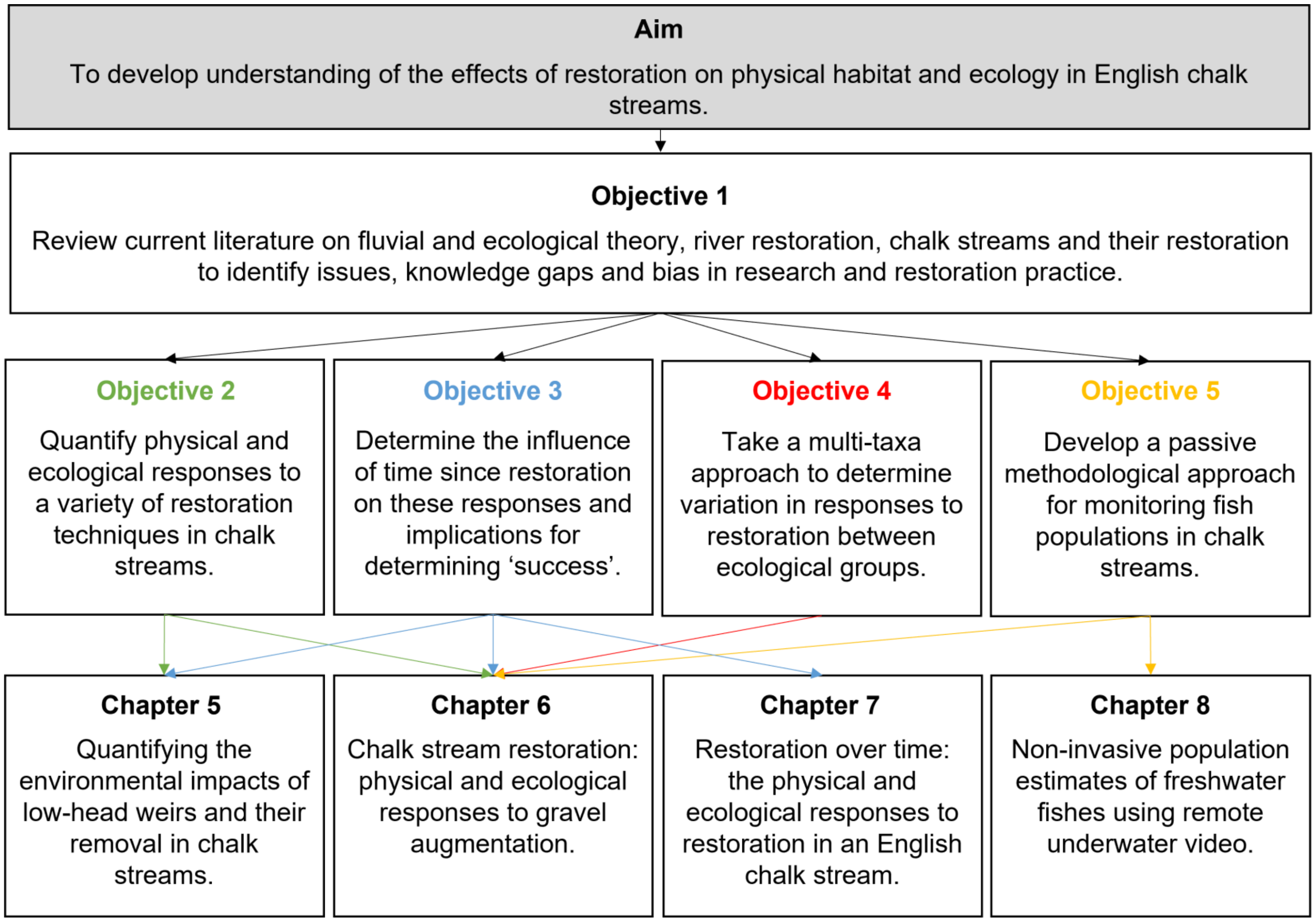


Figure 3.3.1 Schematic summarising the thesis aims and objectives and the results chapters which were undertaken to meet these.

CHAPTER 4 Study sites

The restoration monitoring chapters of this thesis (Chapters 5 - 7) focussed on two classic slope faced chalk streams in southern England; the River Test and Itchen (Hampshire, United Kingdom; Figure 4.1). The River Test has a main channel length of 50 km and catchment area of 1,260 km^2. It rises near Ashe; flowing through Leckford, Longstock and Romsey before entering the sea at Southampton port. Several tributaries join the Test along this route, including the River Anton, Dun and Dever, Bourne Rivulet, Wallop Brook and Blackwater. The River Itchen is slightly shorter (~ 45 km) and has a smaller catchment than the Test (470 km^2). It rises near the village of Cheriton before flowing through Winchester, Eastleigh, and finally joining the River Test at Southampton Port. Tributaries of the Itchen include Candover and Cheriton Stream and Alre (Skinner, 2013).

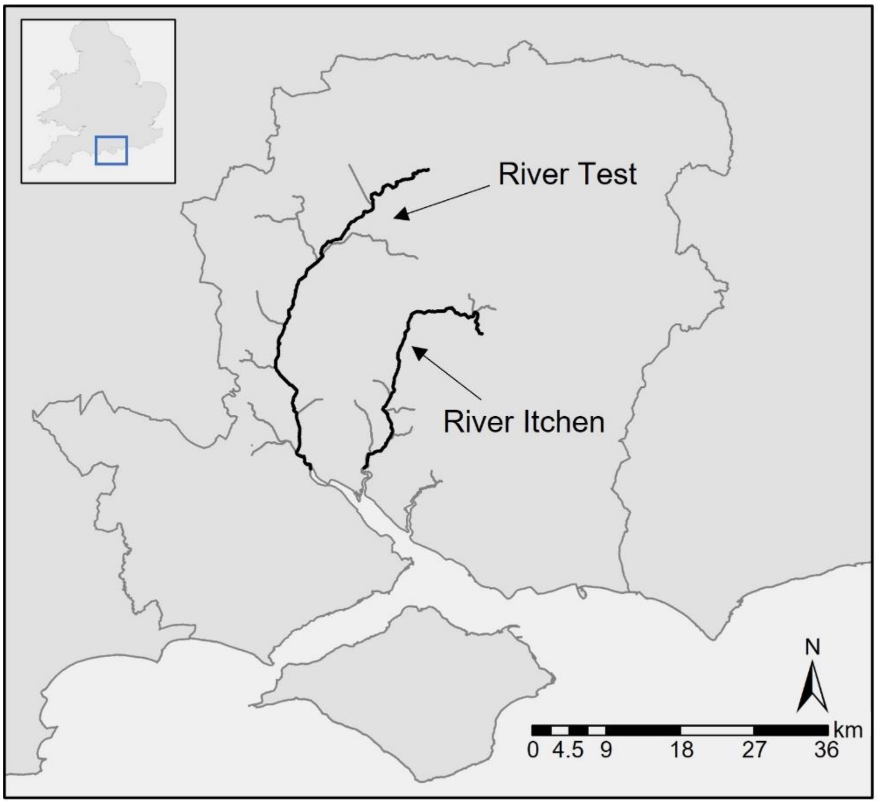


Figure 4.1 Hampshire county and the River Test and Itchen (solid black line) and their main tributaries (grey line). Country/county and river network shapefiles were supplied from Ordnance Survey (2023) and Ordnance Survey (2022), respectively.

Both rivers rise from and derive the majority of their flow from Cretaceous chalk aquifers (> 0.9 base flow index; NFRA, 2023). A large portion of the River Test (90% total chalk outcrops) and Itchen (80% total chalk outcrops) catchment are underlain by upper chalk deposits, with small sections of lower and middle chalk cropping near the upper Test and Winchester (Skinner, 2013). In the south of the catchment, tertiary clay and sand deposits overlie the chalk geology leading to greater surface run-off and more reactive hydrographs (WCSRT, 2016; NFRA, 2023). Land-use primarily consists of pasture, typically concentrated in the south and adjacent to the watercourse, and arable land (80% of overall catchment; Blincow and Sykes, 2019), but becomes increasingly urbanised going downstream (AEDA, 2013). Highly urbanised regions include Southampton, Winchester, Romsey, Totton and Eastleigh. Given the high contribution of aquifer-derived flow, both rivers typically display dampened hydrographs, peaking in the early spring and troughing in late summer as a result of fluctuations in rainfall (mean yearly rainfall: Test = 375 mm, Itchen = 612 mm; CaBA, 2021), temperature, vegetation growth and aquifer recharge (Berrie, 1992; Mainstone, 1999; DEFRA, 2021; Figure 4.2).

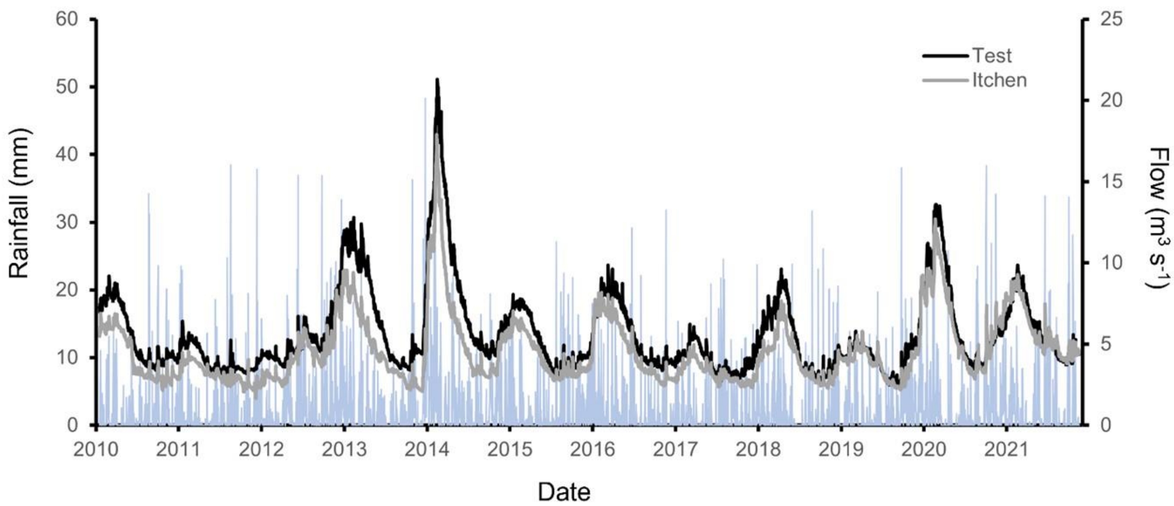


Figure 4.2 Long-term discharge on the River Test and Itchen in relation to rainfall. Flow data from Chilbolton (Test) and Highbridge (Itchen) gauging stations. Rainfall is in blue and represents the daily mean across Portswood, Testwood, Romsey, Bishops Waltham and Andover gauging stations (DEFRA, 2021). Contains public sector information licensed under the Open Government Licence v3.0.

The River Test and Itchen are renowned for their diverse and abundant biological communities (Skinner, 2013). Both rivers hold SSSI status for the habitat (e.g. classic chalk stream habitat, fen meadow), flora (water crowfoot; *Ranunculus spp.*) and fauna (e.g. brook lamprey, Atlantic salmon) they contain (Natural England, 1996; 2000). In addition, the Itchen holds a SAC status for Habitat Directive (92/43/EEC; European Communities, 1992) Annex I habitats ('Water courses of plain to montane levels with the *Ranunculion fluitantis* and Callitricho-Batrachion vegetation') and Annex II species (Southern damselfly and European bullhead; JNCC, 2023). In addition to these qualifying features, both rivers are characterised by rich macrophyte communities (e.g. > 100 species in River Test), typically dominated several water crowfoot species (e.g. *Ranunculus penicillatus var. pseudofluitans*), blunt-fruited water-starwort (*Callitriche obtusangula*), fools water cress (*Apium nodiflorum*) and lesser water-parsnip (Natural England, 1996; 2000; Poynter, 2013). Macroinvertebrate communities are exceptionally abundant and diverse (Environment Agency, 2023b), with records identifying over 232 and 210 taxa in the Test and Itchen, respectively. Both rivers are especially rich in molluscs (e.g. *Pisidium tenuilineatum*), Crustacea (e.g. *Gammarus pulex*) and Ephemeroptera (e.g. *Ephemera danica*; Natural England, 1996; 2000). Fish communities are comprised of 'typical chalk stream species' (CaBA, 2021), including brown trout, European grayling (*Thymallus thymallus*), European bullhead, European eel, northern pike (*Esox lucius*), European chub (*Leuciscus cephalus*) and common dace (*Leuciscus leuciscus*; Environment Agency, 2023b). The River Test and Itchen also constitutes an important habitat for many mammal (e.g. otter, water vole) and bird (e.g. kingfisher) species (Natural England, 1996; 2000).

The rivers provide significant cultural and economic value to the local human population (Skinner, 2013). Both surface and ground water sources are heavily abstracted (CaBA, 2021), acting as a key resource for domestic, agricultural and industrial consumption (Cox and Özdemiroğlu, 2018). They also provide valuable wastewater disposal services (Southern Water, 2020), with 11 (64% remove phosphorus) and four (100% remove phosphorus) sewage treatment plants currently operating on the Test and Itchen, respectively (CaBA, 2021). Historically, both rivers were used for transportation (Skinner, 2013; Langdon and White, 2017). For instance, a 10.4 mile navigation channel was constructed on the Itchen in 1710, acting as an important trade route between Winchester and Southampton port until its decommission in 1869 (SCS, 2021). The rivers were also widely manipulated to provide power for industry in the form of mills, which largely remained in use until the mid-20th century (Downward and Skinner, 2005; Langdon and White, 2017). Both the River Test and Itchen are internationally renowned salmonid fisheries and support numerous recreational dry fly angling enterprises (e.g. National

Rivers Authority, 1992). They also provide excellent conditions for fish and water cress aquaculture, which are widely distributed across each river and contribute to the local economy (National Rivers Authority, 1992; Skinner, 2013).

The Test and Itchen have long been subjected to anthropogenic manipulation which has widely impacted biotic communities (WCSRT, 2016; S&TC, 2018). In 2019, 35% of the River Test and 14% of the Itchen Water Framework Directive monitoring sites were considered heavily modified, and only 48% and 50% of sites achieved 'good ecological status', respectively. All sites had a poor 'chemical status' (Environment Agency, 2021b). The primary reasons for the failure to achieve good ecological status were physical modification, diffuse and point source pollution, low flow (i.e. abstraction) and invasive species (Table 4.1; Environment Agency, 2021a).

Table 4.1 Reasons for the failure of River Test and Itchen Water Framework Directive monitoring units to achieve good ecological status. Sites with 'suspect data' and 'natural deterioration' are not included (Environment Agency, 2021a).

Reason for failure	**Test (% of sites)**	**Itchen (% of sites)**
Physical modification	75	42
Point pollution	5	17
Diffuse pollution	5	25
Low flow	5	8
Invasive species	5	0

Point and diffuse pollution: Point and diffuse pollution have contributed to the degradation of water and ecological quality in the Test and Itchen for decades (National Rivers Authority, 1992; Skinner, 2013; WCSRT, 2016). A myriad of anthropogenic pollutants have been recorded in each river, including phosphates, organic chemicals (e.g. nitrates), hazardous substances (e.g. mercury), pharmaceuticals (e.g. 2-ethylhexyl 4-methoxycinnamate), plant protection products (insecticides, fungicides; e.g. atrazine) and industrial compounds (e.g. fluoranthene; DEFRA, 2022a; Robinson *et al.*, 2023). This chemical cocktail is likely having a major impact on the ecological communities of both rivers (e.g. Environment Agency, 2022b), although their cumulative impacts have been underexplored (Robinson *et al.*, 2023). Phosphorus pollution and fine sediment accumulation is of a particular concern, and have been associated with degraded ecological communities in both rivers (Acornley and Sear, 1999; WCSRT, 2016; S&TC, 2018).

Low flow: Like many chalk streams, the surface and groundwater of the River Test and Itchen are heavily abstracted (Test = 63.3 Ml/d, Itchen = 55.4 Ml/d based on 2017-2019 data; Le Quesne *et al.*, 2011; Southern Water, 2020; CaBA, 2021). This is especially the case for the Itchen, where current abstraction rates are 6.9% of the total aquifer recharge (Test = 2.9%; CaBA, 2021). This rate of abstraction has been shown to impact the habitat (e.g. fine sediment deposition) and ecology (e.g. Atlantic salmon spawning success; see section 2.3.6.4 for overview of impacts) of the Itchen, especially during years of naturally low flow (WCSRT, 2016; Cox and Özdemiroğlu, 2018; S&TC, 2018). Given the high demand for water and a shifting climate, the frequency and impacts of low flows are predicted to worsen (Wilby, 2010; Le Quesne *et al.*, 2011), as evidenced by long-term ecological datasets (e.g. WCSRT, 2016) and modelling (Cox and Özdemiroğlu, 2018). To safeguard future water supplies, several management strategies have been implemented (e.g. Southern Water, 2014; Environment Agency, 2019b).

Invasive species: Both rivers are impacted by many common non-native species (e.g. Porteus *et al.*, 2012), including Canadian waterweed (*Elodea canadensis*), Japanese knotweed, Himalayan balsam, New Zealand mudsnail (*Potamopyrgus jenkinsi*), topmouth gudgeon (*Pseudorasbora parva*) and American mink (Pinder and Gozlan, 2003; Porteus *et al.*, 2012; Environment Agency, 2023b). A series of local (e.g. Test and Itchen Invasive Non Native Species Project; Wessex River Trust, 2022) and national (e.g. Environment Agency, 2019a) eradication projects have been implemented in both rivers.

Physical modification: As with most chalk streams, the Test and Itchen have been extensively modified over millennia (see section 2.3.5 and 2.3.6.1 for modification timeline and impacts, respectively; Skinner, 2013; Langdon and White, 2017). For instance, both rivers have been straightened, dredged and managed (e.g. large woody material removal) for flood water conveyance, land drainage and transportation (National Rivers Authority, 1992; Blincow and Sykes, 2019). Artificial channels were constructed across the Test and Itchen (e.g. mill leats for mechanical power), resulting in a system dominated by bifurcation (Langdon and White, 2017; DEFRA, 2022a). Infrastructure such as weirs were widely constructed for agricultural water supplies and to divert water into mill leats and water meadows (Natural England, 2000). Many of these structures remain to this day (e.g. 670 and 379 structures on Test and Itchen in 2013, respectively), sometimes in use (e.g. to maintain water levels in recreational fisheries) but more often redundant (Skinner, 2013). The legacy of such modifications remain to this day, with almost all channels having been deviated from their natural state (Skinner, 2013; Environment Agency, 2021a).

In 2012, the Test and Itchen Restoration Strategy (Environment Agency) was developed with the aim of returning both rivers to a more favourable condition (RESTORE, 2020). The strategy has three main objectives: "(1) determine the impacts of physical modification on the geomorphology and ecology of each river; (2) provide an outline restoration plan for each river on a reach by reach basis; (3) identify potential delivery mechanisms to help achieve this" (RESTORE, 2020). Since its launch, the strategy has worked with 28 landowners and funded (i.e. 50% match funding with the landowner) restoration projects across 15 km of river (Leman, 2020). Such projects include the removal of 13 river structures (e.g. Cain Bio Engineering, 2022), addition of > 20,000 tonnes of coarse substrates and numerous other measures (e.g. channel planform re-profiling and large woody materials; Leman, 2020). The strategy has been deemed highly successful, winning the River Restoration Centre's 'Catchment Scale UK Rivers Prize' in 2020 (Leman, 2020). The results of this thesis supports this strategy by contributing to an evidence base towards the effectiveness of restoration in chalk streams (RESTORE, 2020).

This thesis specifically focusses on two recreational fisheries; Bossington Estate (River Test) and East Lodge (River Itchen; Figure 4.3; 4.4). Bossington Estate is found in the mid-reaches of the Test near Stockbridge, directly below the confluence with Wallop Brook. Several projects have taken place on the estate since 2013 to mitigate the impacts of historic modification and improve ecological quality. These include weir removal (Cain Bio Engineering, 2022) and gravel augmentation sites alongside other projects employing a variety of methods (e.g. gravel augmentation, woody materials, narrowing; e.g. Cain Bio Engineering, 2020; 2023). ICER at the University of Southampton holds monitoring datasets collected during undergraduate student research from several of these projects, starting in 2013. This offers an ideal opportunity to deliver several of the objectives set out in this thesis over a greater timescale than the PhD duration would have permitted (i.e. three years of data collection). East Lodge is found in the mid-reaches of the River Itchen near Colden Common. In 2019, at the same time as on Bossington Estate, a reach-scale gravel augmentation project took place to restore substrates and salmonid spawning habitat removed by historic dredging (R. J. Bull, 2023). This project presents a valuable extra case study to meet Objective 2 - 4. The individual projects appraised within this thesis are described in greater detail in each chapter.

Figure 4.3 Hampshire county, the River Test and Itchen (black line) and their main tributaries (grey line) with the location of Bossington Estate and East Lodge shown in the black and red box, respectively. More detailed maps of Bossington Estate and East Lodge show the (A) weir removal (Chapter 5) and (B) gravel augmentation sites (Chapter 6) and (C) projects used to assess longer-term responses to restoration (Chapter 7). Blue arrows show flow direction. Country/county and river network shapefiles were supplied from Ordnance Survey (2023) and Ordnance Survey (2022), respectively.

(A) Chapter 5: Weir removal site (upstream)


III


IV

(A) Chapter 5: Weir removal site (downstream)

(B) Chapter 6: Gravel augmentation study (Home Stream)

(B) Chapter 6: Gravel augmentation study (East Lodge)

(C) Chapter 7: Time study (Old Station Beat)

(C) Chapter 7: Time study (Old Stews Beat)

Figure 4.4 Photographs of the study sites monitored in this thesis. Chapter 5: upstream and downstream of the weir removal restoration site pre (I – II) and post-restoration (III – IV, V – VI). Chapter 6: Home Stream and East Lodge gravel augmentation sites pre (VIII) and post-restoration (VII, IX). Chapter 7: Old Station and Old Stews Beat pre (X, XIII) and post-restoration (XI, XII). Photographs I, II, X and XIII were kindly supplied by Cain Bio Engineering.

CHAPTER 5 Quantifying the environmental impacts of low-head weirs and their removal in chalk streams

5.1 Summary

Low-head weir (< 5 m height) removals are common globally, but the environmental benefits of this practice are poorly understood due to limited information on initial impacts and responses once removed. Using English chalk streams as a model for low stream power systems, this study quantified the effects of low-head weirs and their removal on habitat and macroinvertebrate communities. The impact of weirs on macroinvertebrates was quantified through a coarse scale desk-based analysis by collating online datasets immediately upstream and downstream of weirs and at control sites. Additionally, a fine scale field study monitoring habitat and macroinvertebrates prior to (2 years; including a control for one year) and following (4 years) a weir removal and restoration (e.g. gravel augmentation, silt dredging) project was conducted. The coarse scale analysis showed no differences in macroinvertebrate metrics upstream or downstream of weirs when compared to controls, possibly reflecting high variation in impacts between structures or challenges with using existing open source data not originally intended for this purpose. In the fine scale study, most pre-restoration weir impacts were upstream, illustrated by the reach being deep, silt-dominated, slow flowing, and supporting a community containing few rheophilic, silt-intolerant taxa and lower abundances of EPT when compared with the control and downstream. Following restoration, upstream habitat became shallower, faster flowing, and coarse substrate dominated. Macroinvertebrates communities were represented by more rheophilic, silt-intolerant taxa and greater EPT abundance. The additional restoration techniques alongside closely situated source populations likely facilitated rapid habitat recovery and colonisation, respectively. Overall, it was shown that weirs can degrade local habitat and ecological condition and that their removal can initiate rapid ecological change, even in systems with relatively low stream power.

5.2 Introduction

Impounding infrastructure, such as dams and weirs, have been developed in river systems across the globe and are considered a major source of ecological deterioration (Grill *et al.*, 2019; Reid *et al.*, 2019; Belletti *et al.*, 2020). The impacts of infrastructure, particularly high-head dams (> 5 m in height), on local upstream and downstream habitat and ecology have been well studied, both theoretically (e.g. serial discontinuity concept; Ward and Stanford, 1983; 1995) and empirically (e.g. Rehn, 2009; Santos *et al.*, 2013). Typical impacts include the impounding of water upstream which creates a more lentic habitat, whilst the restricted transportation of sediment and flow increases scour and creates unnatural lotic conditions downstream (Kemp, 2015). The modification of habitat, processes and fluvial connectivity can alter biological communities either side of infrastructure. For example, as benthic macroinvertebrates are largely influenced by substrate (Extence *et al.*, 2010) and flow (Extence *et al.*, 1999), upstream sites are likely to contain fewer silt-intolerant and rheophilic taxa compared to downstream (e.g. Stanley *et al.*, 2002; Sharma *et al.*, 2005; Mueller *et al.*, 2011).

The removal of infrastructure has been gaining traction across Europe and North America as a cost-effective method for tackling safety (e.g. aging infrastructure failure), financial (e.g. saving maintenance costs) and/ or environmental goals (Lovett, 2014; Grabowski *et al.*, 2018; Ding *et al.*, 2019). When successful, the removal of infrastructure can restore pre-impoundment river processes, dynamics and connectivity, and can facilitate large changes in habitat and biological communities (Bednarek, 2001; Bellmore *et al.*, 2019). This is especially the case in upstream locations, where the transition from more ponded back to free-flowing conditions and redistribution of trapped fine sediments can transform communities from a predominantly lentic to a lotic one (e.g. Stanley *et al.*, 2002; Hansen and Hayes, 2012a; Kil and Bae, 2012). The timely recovery of habitat and ecological communities following infrastructure removal, however, is not guaranteed, with several studies reporting altered channel morphology and declines in benthic populations associated with the redistribution of previously trapped sediments (i.e. sediment pulse, e.g. Orr *et al.*, 2008a; Renöfält *et al.*, 2013; East *et al.*, 2015). Consequently, there is a need to understand the factors which drive responses following infrastructure removal to inform effective practice (e.g. Carlson *et al.*, 2018).

Low-head weirs (< 5 m high) are globally abundant. For example, of the roughly 200,000 weirs which have been recorded across Europe, 95% of these are < 5 m in height (AMBER, 2023). Weirs are described as structures without active water regulation and heights that do not exceed the natural bank, and, unlike most high-head impounding structures, typically create small reservoirs with short water retention times (minutes-hours) and allow the passage of more sediment (Csiki and Rhoads, 2010; Pearson and

Pizzuto, 2015). Despite these less obvious physical impacts, the high density of weirs means that their cumulative impact may be considerable (e.g. Davies *et al.*, 2021). Consequently, weirs are commonly targeted for removal globally (Ding *et al.*, 2019). Despite this, fundamental understanding of the impacts of these structures and the benefits of their removal remains limited, in part due to low levels of monitoring (Garcia de Leaniz, 2008). This has contributed to widespread uncertainties and discrepancies regarding ecological outcomes to weir removals, with both positive (e.g. Stanley *et al.*, 2002) and negative (e.g. Thomson *et al.*, 2005) responses reported. These mixed results may in part relate to differences in the initial state of degradation and/ or the speed of recovery following removal, both of which may be effected by the environmental context of the structure (Major *et al.*, 2017; Bellmore *et al.*, 2019).

River power is likely an important characteristic influencing the impacts caused by low-head weirs and the degree and rate of recovery following removal (Csiki and Rhoads, 2010; Carlson *et al.*, 2018). Rivers with low power (typically shallow sloped with low flow discharge and a more dampened hydrology), such as groundwater dominated chalk streams, tend to exhibit low rates of erosion and sediment transport (Sear *et al.*, 1999). Consequently, when faced with river infrastructure, they are likely to display high rates of sedimentation (Csiki and Rhoads, 2010) and a long persistence of modification (Mainstone, 1999). Moreover, the spatial extent of the impacts of weirs, such as the relative size of an associated reservoir or impounded reach, are likely to be negatively related to gradient, leading to high habitat fragmentation and strong ecological discontinuities upstream and downstream of the structure. Such rivers are also likely to be slow to recover following weir removal as there is limited natural means to redistribute sediment and recreate natural geomorphological features (Doyle *et al.*, 2005; Carlson *et al.*, 2018). Therefore, the impacts of infrastructure in rivers with low power are predicted to be relatively high, and recovery following removal is likely slow. However, more information is needed to better determine the dynamics of restoration in these systems so that management efforts can be adapted to optimise benefits relatives to costs.

This study aimed to quantify the effects of low-head weirs and their removal on physical habitat and ecology within river systems with low power. Using English chalk streams as a model system, a coarse scale, desk-based approach utilising online infrastructure and macroinvertebrate databases was used to quantify the effects of low-head weirs on upstream and downstream communities. Additionally, a fine scale field study following a case study weir removal and restoration (e.g. dredging, gravel augmentation, reprofiling) was used to quantify (a) the pre-restoration impacts of the weir on physical habitat and macroinvertebrates by assessing differences between upstream, downstream and a control site, and (b) the responses of habitat and macroinvertebrates to restoration over time. It was predicted that (1) sites upstream of weirs would be deeper, slower and more dominated by fine sediment (fine scale analysis only), and that macroinvertebrate communities would be lower in abundance and taxon richness, both in total and of EPT, and be comprised of more non-rheophilic, silt-tolerant taxa (coarse and fine scale analysis). Differences between downstream reaches and controls were expected to be comparatively smaller. (2) Following the weir removal and restoration (fine scale study), upstream and downstream habitat and macroinvertebrate communities were predicted to become more similar over time. More specifically, upstream depth and velocity was expected to reduce and increase immediately following restoration, respectively. The poor ability of the river to redistribute sediments was expected to result in an increase in the cover of fine substrates immediately downstream of the weir (i.e. sediment pulse) and impacted macroinvertebrate communities in both reaches (e.g. reduction in abundance, taxon richness, silt-intolerant taxa). As fine sediments were slowly redistributed and macroinvertebrate communities recovered over time, it was expected that the cover of coarse substrates, abundance, taxon richness (both total and of EPT) and the contribution of rheophilic and silt-intolerant taxa would increase upstream compared to pre-restoration. Comparatively, downstream was expected to have shown little change overall.

5.3 Methods

5.3.1 Coarse scale analysis

Publicly available data was used to quantify the impacts of low-head weirs in upstream and downstream reaches in English chalk streams at a coarse scale. The coordinates of (a) low-head weirs (< 5 m in height) and (b) all other structures (e.g. weirs > 5 m in height, dams, sluices, mills) within English chalk streams were collated using the infrastructure database presented in Jones *et al.* (2019). Next, the coordinates and accompanying information (e.g. site slope and sampling dates) of macroinvertebrate datasets in these chalk streams, collected between 2000 and 2022, were collated from the ‘Ecology and Fish Data Explorer’ (Environment Agency, 2023b). These datasets, which contain macroinvertebrate samples taken from across England over several decades, are mostly from routine monitoring and used for purposes such as Water Framework Directive waterbody assessment. Coordinates were used to generate a map of infrastructure and macroinvertebrate dataset locations using Google’s ‘My Maps’ (Google, 2023).

Each low-head weir mapped was inspected for the presence of macroinvertebrate datasets within 300 m upstream or downstream of its location. Filtering criteria were applied, and to be included in further analysis the macroinvertebrate sample needed to: (a) not be in close proximity to side channels unaffected by the weir; (b) not have other infrastructure in closer proximity; and (c) be collected using a standard 3 minute kick sample and 1 minute hand search. Additionally, for each weir a proxy for the distance of impact was calculated as the river slope (metre change in elevation per horizontal metre; where not supplied in the focal macroinvertebrate dataset this was sourced from another nearby sample) divided by the weir height (m). Macroinvertebrate data was only included in the analysis if it was within half of this value (upstream or downstream). If all criteria were met, the full dataset (i.e. site information, macroinvertebrate metrics and raw macroinvertebrate data for all sampling dates) was extracted. Each dataset in proximity to a low-head weir was paired with a dataset from a control site, the closest available that had (i) similar sampling dates (< 40 days apart) and (ii) no infrastructure within 500 m upstream or downstream of the sample location (based on distances in Kil and Bae, 2012; Robertson *et al.*, 2021). Additionally, the distance of impact was also calculated (i.e. as per above) for all structures on the same channel 1,000 m upstream and downstream from each control sample. No control datasets fell within this impact zone suggesting they were not directly impacted by river infrastructure. Where only a subset of the sampling dates between the impacted and control were similar then these were selected for inclusion in the analysis.

To standardise taxonomic classification, macroinvertebrates were considered to family or the lowest possible level. For each sample, the abundance, taxon richness, abundance (EPT abundance) and taxon richness (EPT richness) of EPT, Lotic Index for Flow Evaluation (LIFE; Extence *et al.*, 1999) and Proportion of Sediment sensitive Invertebrates (PSI; Extence *et al.*, 2010) was calculated. EPT are commonly used as an indicator in biological monitoring programmes, and were assessed due to their sensitivity to a range of environmental stressors (Lenat and Crawford, 1989) and the important roles they regularly play within freshwater ecosystems (e.g. fish prey; Montori *et al.*, 2006), including chalk streams (CaBA, 2021). LIFE and PSI metrics were developed to understand flow and silt pressures based on the tolerances of different macroinvertebrate taxa, with lower values suggesting a more lentic, silt-tolerant community (Extence *et al.*, 1999; 2010). These metrics, in combination with the abundance and taxon richness, thus provide a useful indication of the level of habitat degradation and the effectiveness of restoration in mitigating this. As each dataset contained between one and 20 samples taken between 2000 and 2022, the mean of each metric was taken across the data series to produce a single value.

5.3.2 Fine scale field study

To assess the impacts of low-head weirs and their removal on physical habitat and ecology on a fine scale, this study monitored a case study weir removal and restoration (dredging, gravel addition and planform reprofiling) on the River Test (Figure 5.1). Information on the River Test can be found in Chapter 4. Prior to restoration, the study site was impacted by a 1.5 m high, 8.8 m long weir that impounded approximately 400 m of channel. In addition, both upstream and downstream reaches had been historically subjected to modification, including dredging and straightening. In October 2017, a restoration project commenced with the aim of improving habitat quality, connectivity and salmonid spawning habitat (Cain Bio Engineering, 2022). This included the removal of the weir in addition to fine sediment dredging and gravel augmentation (5,500 tonnes of site won, mixed sized coarse substrates for bed raising) and planform reprofiling across an 800 m stretch of river (including upstream and downstream of the weir and a closely located side channel; Figure 5.1; Cain Bio Engineering, 2022; Environment Agency, 2018b).

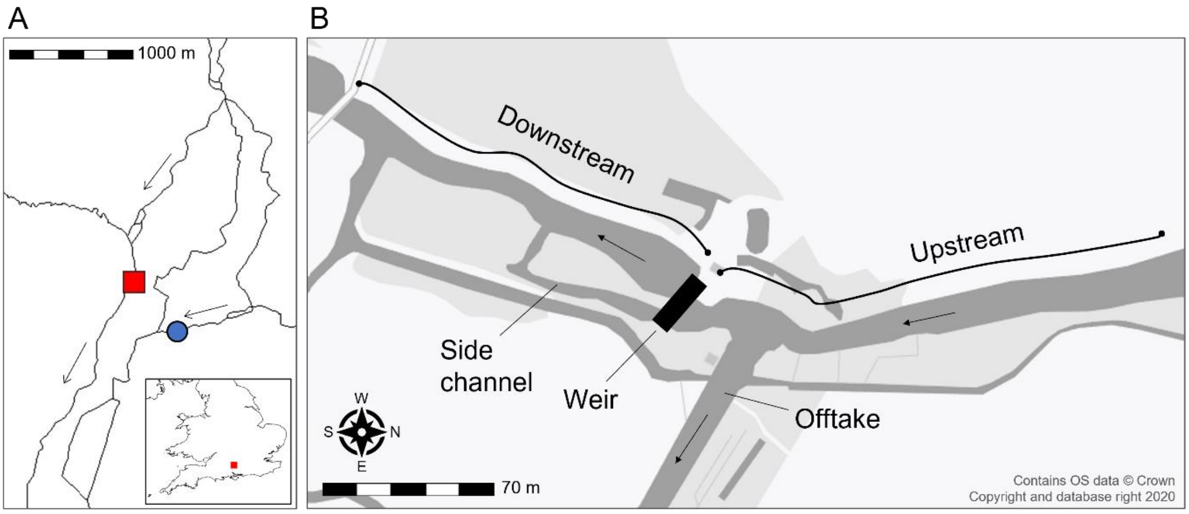


Figure 5.1 (A) Locations of a weir removal site (red square) and pre-restoration control site (blue circle) on the River Test (Hampshire). The inset map indicates the location of the River Test in the south of England. (B) Fine scale details of the reaches upstream and downstream of the focus weir. The sites were monitored to assess physical habitat and ecological (macroinvertebrates) response to the weir removal. Black arrows illustrate direction of flow. River and United Kingdom shapefile used in 'A' was obtained from Ordnance Survey (2022) and GADM (2023), respectively, and plotted using the R package 'raster' (Hijmans, 2022). Map in 'B' was obtained from Ordnance Survey (2016)

Physical habitat and ecological monitoring was conducted pre- (August 2017) and post-restoration (July/August 2018, 2019, 2020, 2021) along 20 transects spaced 20 m apart; ten moving upstream in a 200 m reach commencing 10 m upstream (upstream site) and ten moving downstream in a 200 m reach starting 10 m downstream of the weir (downstream site). In September 2016, six transects were surveyed for macroinvertebrates, 20, 60 and 100 m above and below the weir. Additionally, in August 2017, physical habitat and ecological data were collected at ten transects at a nearby control site, which was unimpacted by river infrastructure and considered to be in ‘good physical condition’. Data between 2016 and 2018 was collected as a part of undergraduate student research projects.

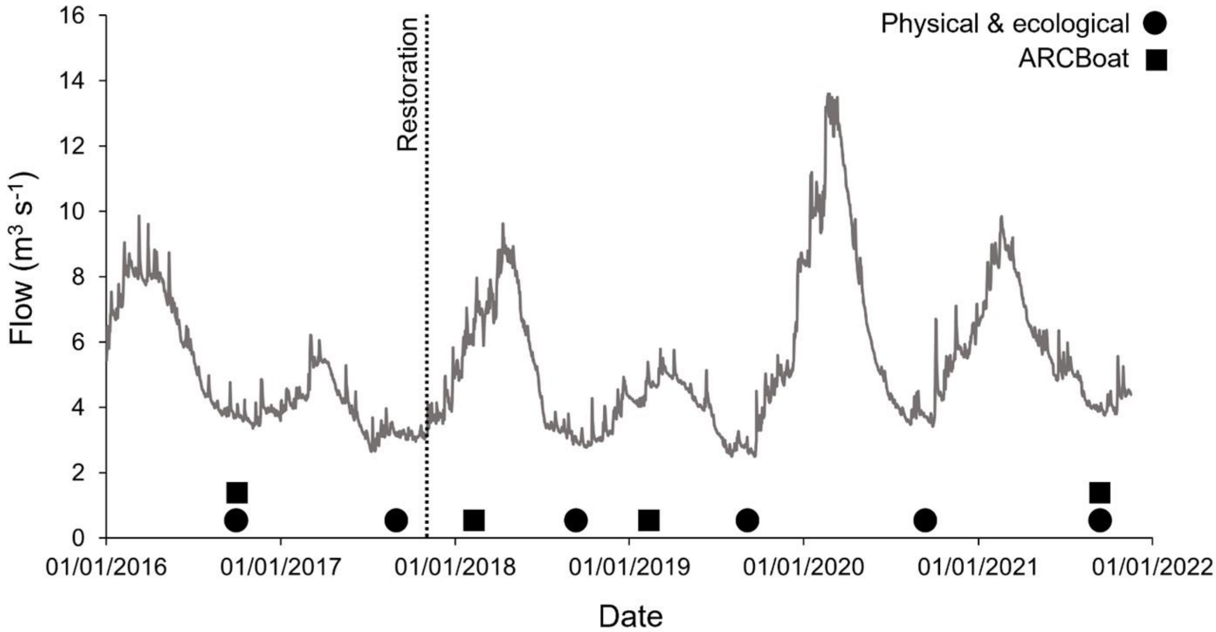


Figure 5.2 River flow during a weir removal and river restoration study conducted on the River Test, Hampshire. Symbols on the x-axis indicate data collection periods for physical habitat and ecology metrics (circles; in 2016 macroinvertebrate data was collected only and in 2017 a control site was included) and ARCboat surveys (squares). Dashed line indicate the dates of weir removal and restoration. Flow data from Chilbolton flow gauging station (DEFRA, 2021). Contains public sector information licensed under the Open Government Licence v3.0.

Along each transect (aside from 2016), depth (m), water velocity (m s^{-1}; mean of ten readings at 60 % depth from the substrate to surface using a Valeport Model 801 electro-magnetic flow meter) and percentage cover of substrate (estimated within a 0.5 m^2 quadrat and categorised as silt [0.0039-0.123 mm], sand [0.125-2 mm], gravel [2-64 mm] or cobble [> 64 mm]) and macrophytes (% cover estimated within a 0.5 m^2 quadrat; not recorded in 2018) were assessed by taking the mean of three measurements equally spaced along each transect in 2017 and 2018 and five measurements in 2019, 2020 and 2021. To supplement manual measurements, an acoustic Doppler current profiler and GPS (Leica Viva GS14 Global Navigation Satellite System) attached to an ARCboat (HR Wallingford, 2022) was used to collect coordinate-tagged depth and velocity measurements in September 2016, February 2018 and 2019, and August 2021. During data collection, the ARCboat was remotely driven slowly in a zig-zag pattern upstream through the study reaches, and where it was too shallow to collect data (< 0.3 m), manual coordinate-tagged velocity and depth measurements were recorded. The river boundary was recorded using a handheld GPS, aside from in 2016 where coordinates were extracted from Google satellite maps (Google, 2022). To visualise spatial variability in depth and velocity, ARCboat data were interpolated using inverse distance weighting within the restored reaches using ArcMap (10.8; ArcGIS, 2020).

At each transect, macroinvertebrates were collected with a 0.25 m^2 square-frame net with 1 mm mesh using a 3 minute kick/sweep sampling method (WFDUK, 2022), aside from in 2017 where 30 s samples were collected (i.e. due to data being collected for different undergraduate studies). In sections that were too deep to wade, samples were collected using a sweep sampling method from a boat. The sample duration was divided proportionally between habitats (e.g. different substrate compositions, depths) to ensure equal representation. After collection, samples were placed into individual 1.2 L sealable buckets and fixed in 70% methylated spirit. Prior to identification, the contents of each bucket were poured through a 30 µm sieve and washed lightly with tap water to remove methylated spirit. Individual samples were then transported to a white tray with water and sorted using tweezers, collecting all macroinvertebrates present. Macroinvertebrates were identified to family level (aside from Oligochaeta and Nematomorpha that were classified as such) using a compound microscope (Motic ST-30) and identification guide (Dobson, 2012). For each sample, the abundance, taxon richness, EPT abundance, EPT richness, LIFE and PSI was calculated.

To assess comparability between kick sample durations (30 second in 2017 versus 3 minutes during other periods), 20 paired 3 minute and 30 s kick samples (separated ~ 1 m longitudinally on the river) were taken in August 2019 and compared using a paired sample t-test or paired Wilcoxon test when the assumption of normality (tested with

Shapiro-Wilk statistic) was violated. When 30 s sample abundances were multiplied by two, invertebrate metrics (aside from PSI) did not statistically differ between sampling durations (Appendix A; Table A1). Therefore, invertebrate metrics in 2017 were calculated using doubled abundances of each individual macroinvertebrate family and included in subsequent analysis. When PSI values calculated from 30 s samples were multiplied by two (mean ± SD; 69.68 ± 8.47), they were on average 4.45 lower than 3 minute samples (74.13 ± 7.62). Therefore, 4.45 was added to PSI values calculated from 2017 (with abundance multiplied by two) invertebrate samples and the data used in subsequent analysis.

5.3.3 Statistical analysis

5.3.3.1 Coarse scale analysis

Paired-sample t-tests were used to assess the differences in macroinvertebrate metrics collected at sites upstream and downstream of weirs with their control in the coarse-scale study. All metrics met assumptions of normality, checked by using Shapiro Wilk tests. Where extreme outliers were observed, results were confirmed using paired-sample Wilcoxon tests that are robust to outliers. Results did not differ between methods employed.

5.3.3.2 Fine scale field study

As the number of transect sampling points differed between some years, the mean habitat values for each transect was used in subsequent analysis. As cobble cover was low throughout the study it was combined with gravel to comprise a ‘coarse substrates’ category.

To assess the impact of the case study weir, habitat and macroinvertebrate metrics were compared between upstream, downstream and at the control prior to its removal (2017 data only) using a one-way ANOVA. Where required, the dependent variable was square-root (sand cover) or log (abundance, EPT abundance) transformed to meet parametric assumptions. Where transformation failed, and assumptions of normality (Shapiro Wilk) or homogeneity of variance (Levene’s Test) continued to be violated, Kruskal-Wallis tests were used (velocity, coarse substrate cover, silt cover). Where results were significant, post-hoc pairwise comparisons between locations were conducted using TukeyHSD (one-way ANOVA) or Dunn tests (Kruskal-Wallis).

To assess the change in physical habitat and macroinvertebrate metrics following weir removal, generalised linear (GLMM; taxon richness and EPT richness; Poisson distribution and log link function) and linear (LMM; all other metrics) mixed models fitted under restricted maximum likelihood were used. 'Sampling year', 'location' (upstream or downstream reach) and their interaction were included as fixed factors, and 'transect number' was considered a random effect to account for repeated measures. The significance of each independent variable was assessed using likelihood ratio tests comparing the full model against one with the focal variable removed. Where significant main effects were found, post-hoc TukeyHSD pairwise comparisons were conducted to investigate these further. Multicollinearity between fixed effects was assessed using variance inflation factor applied to full models (excluding the interaction). Model assumptions were assessed visually using box, Q-Q and fitted vs residuals plots. Where required, data was square-root (velocity) or log (abundance, EPT abundance) transformed to meet test assumptions.

To test for differences in community structure between sampling years and locations, permutational multivariate analysis of variance (PERMANOVA) models were created in 'PRIMER-e (V7)' and the 'PERMANOVA+' package (PRIMER, 2022). Specifically, Bray-Curtis dissimilarity was calculated from square-root transformed macroinvertebrate data (i.e. to reduce the influence of highly abundant groups). Samples from 2016 were excluded to maintain a balanced design and ensure high robustness of the test to differences in group dispersion (Anderson and Walsh, 2013). PERMANOVAs (999 permutations) were then used to test for differences in community structure between 'location', 'sampling year' and their interaction. 'Transect' nested within 'location' was considered a random variable to account for repeated measures. Significant differences between sampling years were further assessed using the pairwise comparisons function within PRIMER-e. To visualise changes in macroinvertebrate community structure, non-metric multidimensional scaling (NMDS) ordination plots ($k = 2$) were created using the same Bray-Curtis dissimilarity values.

5.3.3.3 Statistical software and packages

Analyses and data visualisation were carried out in PRIMER-e V7 (PRIMER, 2022), R Studio (R Studio Team, 2020) and the R packages patchwork (Pedersen, 2020), ggplot2 (Wickham, 2016), Lme4 (Bates *et al.*, 2015), lmerTest (Kuznetsova *et al.*, 2015), R Commander (Fox, 2005), glmmTMB (Brooks *et al.*, 2017), FSA (Ogle *et al.*, 2022), performance (Lüdecke *et al.*, 2020) and lsmeans (Lenth, 2016). For all statistical tests, significance was assessed at $p < 0.05$.

5.4 Results

5.4.1 Coarse scale analysis

Macroinvertebrate data was collated at 8 and 13 sites directly upstream and downstream of low-head weirs (heights ± SD: upstream = 1.60 m ± 0.79, downstream = 1.39 m ± 0.68) and paired-controls sites, respectively (Appendix A: Table A2 for site information). No differences in macroinvertebrate metrics in upstream or downstream sites compared to the control were found (Table 5.1; Figure 5.3).

Table 5.1 Results of paired-sample t-tests comparing macroinvertebrate metrics directly upstream or downstream of low-head weirs in English chalk streams with unimpacted control sites in a coarse scale analysis.

Location	Term	*t*	*df*	*p*
Upstream	Abundance	1.09	7	0.312
	Taxon richness	0.946	7	0.376
	EPT abundance	0.853	7	0.422
	EPT richness	1.231	7	0.258
	LIFE	0.259	7	0.805
	PSI	0.168	7	0.871
Downstream	Abundance	-1.509	12	0.157
	Taxon richness	1.549	12	0.147
	EPT abundance	-1.981	12	0.071
	EPT richness	1.102	12	0.292
	LIFE	-0.53	12	0.606
	PSI	-0.536	12	0.602

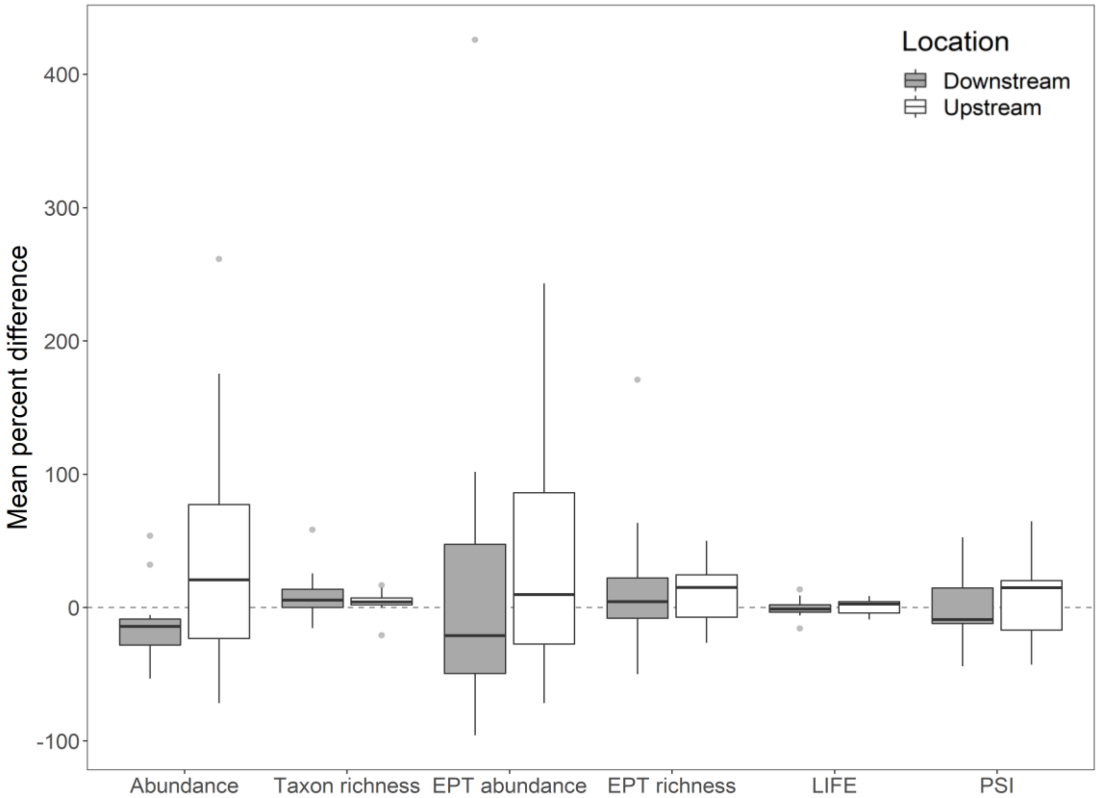


Figure 5.3 The mean percent difference between macroinvertebrate metrics found upstream and downstream of chalk stream low-head weirs compared to paired-control sites. Black bar and boxes show median and 25th and 75th percentile, respectively. Whiskers represent minimum and maximum values excluding outliers. Dots show outliers (values > 1.5 x the interquartile range).

5.4.2 Fine scale field study

Prior to the weir removal and restoration habitat and macroinvertebrate communities differed between upstream, downstream and the control site (Table 5.2). Physically, upstream had a greater depth and silt cover and a lower velocity and cover of coarse and sand substrates compared to downstream and the control. Downstream was deeper than the control. Upstream and downstream macroinvertebrate communities were less dominated by rheophilic (LIFE) and silt-intolerant (PSI) taxa compared to the control. Upstream LIFE and PSI was lower than the downstream site. EPT abundance was lower upstream compared to downstream and the control. The three most abundant macroinvertebrate taxa upstream, downstream and at the control were Sphaeriidae (mean abundance per sample ± SD: 30.8 ± 18.6), Chironomidae (28.2 ± 24.7) and Hydrobiidae (23.2 ± 35.7); Gammaridae (82.0 ± 74.7), Elmidae (61.2 ± 75.9) and Ephemeridae (33.0 ± 52.1), and Gammaridae (178.4 ± 183.6), Elmidae (143.0 ± 174.2) and Oligochaeta (41.2 ± 50.4), respectively.

Table 5.2 Statistical results comparing physical habitat and macroinvertebrate metrics between a control site and reaches immediately upstream and downstream of a low-head weir on the River Test (Hampshire, United Kingdom) prior to removal and restoration. Significant results are boldened.

Variable	F/X2	df	p	Upstream (U)		Downstream (D)		Control (C)		Post-hoc		
				Mean	SD	Mean	SD	Mean	SD	D-C	U-C	U-D
Depth	**42.09**	**2, 27**	**< 0.001**	1.28	0.15	0.78	0.24	0.51	0.15	**< 0.01**	**< 0.001**	**< 0.001**
Velocity	**11.55**	**2**	**< 0.01**	0.15	0.08	0.44	0.33	0.37	0.14	0.542	**< 0.01**	**< 0.05**
Coarse substrate cover	**16.12**	**2**	**< 0.001**	8.00	5.57	54.50	29.12	52.30	21.16	0.980	**< 0.001**	**< 0.001**
Sand cover	**5.51**	**2, 27**	**< 0.01**	15.00	11.40	34.50	22.58	39.70	22.29	0.813	**< 0.05**	**< 0.05**
Silt cover	**19.33**	**2**	**< 0.001**	77.00	16.00	11.00	24.68	8.00	7.48	0.536	**< 0.001**	**< 0.001**
Abundance	2.74	2, 27	0.082	208.60	118.88	329.60	208.40	475.40	297.21	NA	NA	NA
Taxon richness	0.04	2, 27	0.965	15.20	4.42	14.80	4.53	14.70	3.52	NA	NA	NA
EPT abundance	**4.75**	**2, 27**	**< 0.05**	34.00	28.64	97.40	63.71	75.00	45.48	0.952	**< 0.05**	**< 0.05**
EPT richness	1.70	2, 27	0.202	4.60	2.65	5.90	2.26	6.50	1.69	NA	NA	NA
PSI	**28.26**	**2, 27**	**< 0.001**	33.19	10.83	55.45	12.21	70.31	8.19	**< 0.05**	**< 0.001**	**< 0.001**
LIFE	**26.78**	**2, 27**	**< 0.001**	6.71	0.26	7.43	0.45	7.97	0.36	**< 0.05**	**< 0.001**	**< 0.001**

Following the weir removal and restoration, the upstream reach became shallower, quicker, less dominated by silt and more dominated by coarse substrates compared to before and downstream (Table 5.3; Figure 5.4; Figure 5.5 for spatial variability in depth and velocity; Appendix A: Table A3 – A5 for post-hoc statistical outputs). Downstream depth, velocity and silt and coarse substrate cover did not change over time. For terms with significant interactions between 'location' and 'year', upstream and downstream conditions differed prior to but not after restoration. Macrophyte cover was overall higher downstream and changed across both sites over time; it was lower in 2017 compared to 2019 ($t = -2.753$, $p < 0.05$) and 2021 ($t = -4.281$, $p < 0.001$), and in 2020 compared to 2021 ($t = -3.818$, $p < 0.01$).

Table 5.3 Results of GLMM and LMMs assessing the effect of year, location (upstream or downstream reach) and their interaction on physical habitat and macroinvertebrate metrics. Statistics calculated via likelihood ratio tests between full models and those with the focal term removed. Significant terms are boldened.

Term	Interaction			Location			Year		
	X2	*df*	*p*	*X2*	*df*	*p*	*X2*	*df*	*p*
Depth	**45.154**	**4**	**< 0.001**	0.128	1	0.721	**54.212**	**4**	**< 0.001**
Velocity	**21.134**	**4**	**< 0.001**	0.332	1	0.577	7.631	1	0.106
Coarse substrate cover	**29.330**	**4**	**< 0.001**	0.077	1	0.781	**35.496**	**4**	**< 0.001**
Sand cover	8.071	4	0.089	2.767	1	0.096	6.664	4	0.155
Silt cover	**55.502**	**4**	**< 0.001**	0.937	1	0.333	**22.458**	**4**	**< 0.001**
Macrophyte cover	0.992	3	0.803	**4.467**	**1**	**< 0.05**	**21.863**	**3**	**< 0.001**
Abundance	4.395	5	0.494	0.585	1	0.444	**44.228**	**5**	**< 0.001**
Taxon richness	1.954	5	0.855	0.117	1	0.732	**74.666**	**5**	**< 0.001**
EPT abundance	**19.690**	**5**	**< 0.01**	0.004	1	0.952	**69.457**	**1**	**< 0.001**
EPT richness	3.471	5	0.628	0.524	1	0.469	**65.484**	**5**	**< 0.001**
LIFE	**35.455**	**5**	**< 0.001**	**4.141**	**1**	**< 0.05**	**46.118**	**5**	**< 0.001**
PSI	**46.200**	**5**	**< 0.001**	0.654	1	0.419	**76.843**	**5**	**< 0.001**

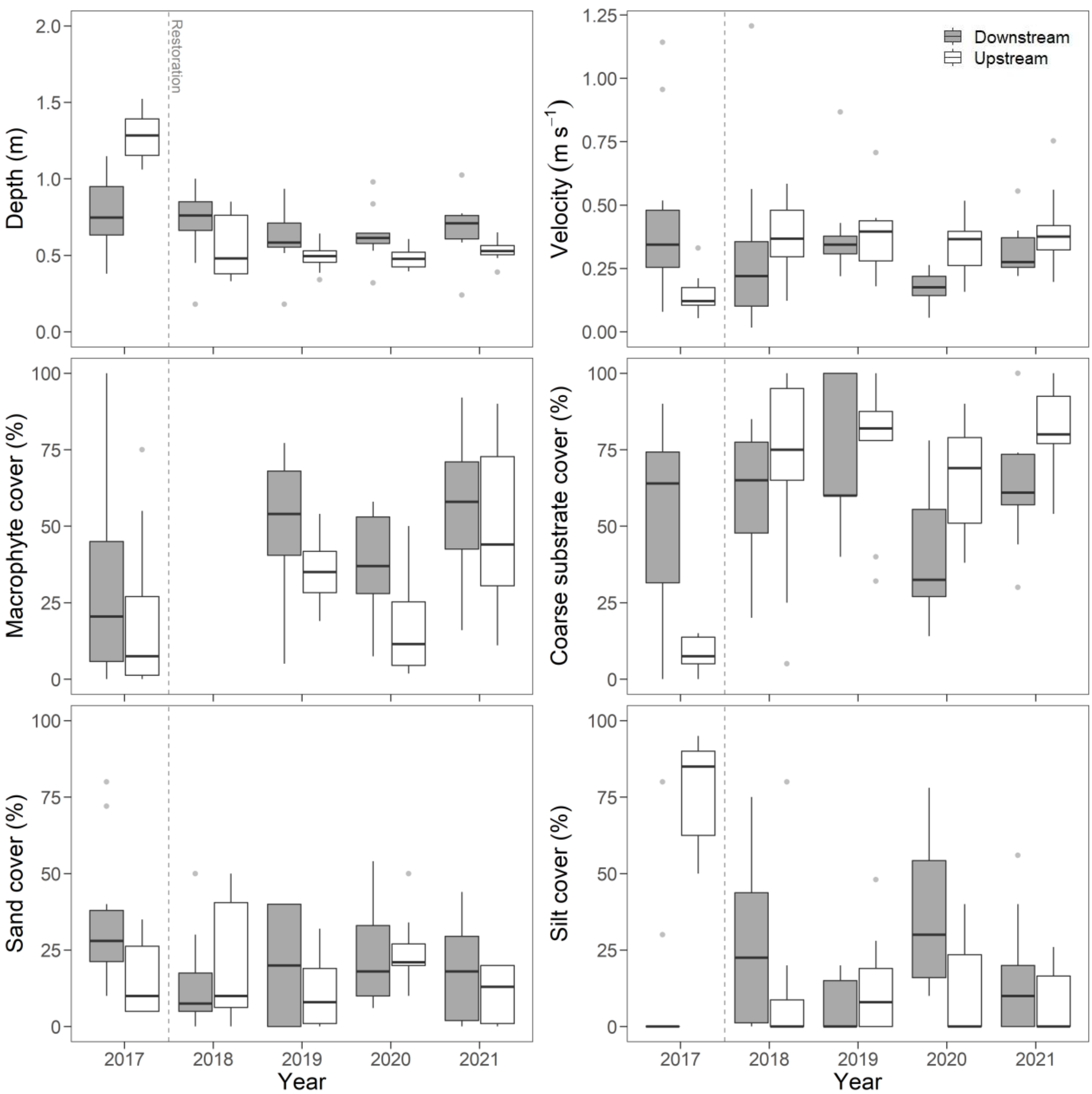


Figure 5.4 Boxplots showing the median depth (m), velocity (m s^{-1}), macrophyte cover (%) and the cover of coarse, sand and silt substrates (%) in sites upstream and downstream of the Bossington Estate weir removal over a five year period. Black bar and boxes show median and 25th and 75th percentile, respectively. Whiskers represent minimum and maximum values excluding outliers. Dots show outliers (values > 1.5 x the interquartile range). Dashed line shows the point of weir removal and restoration.

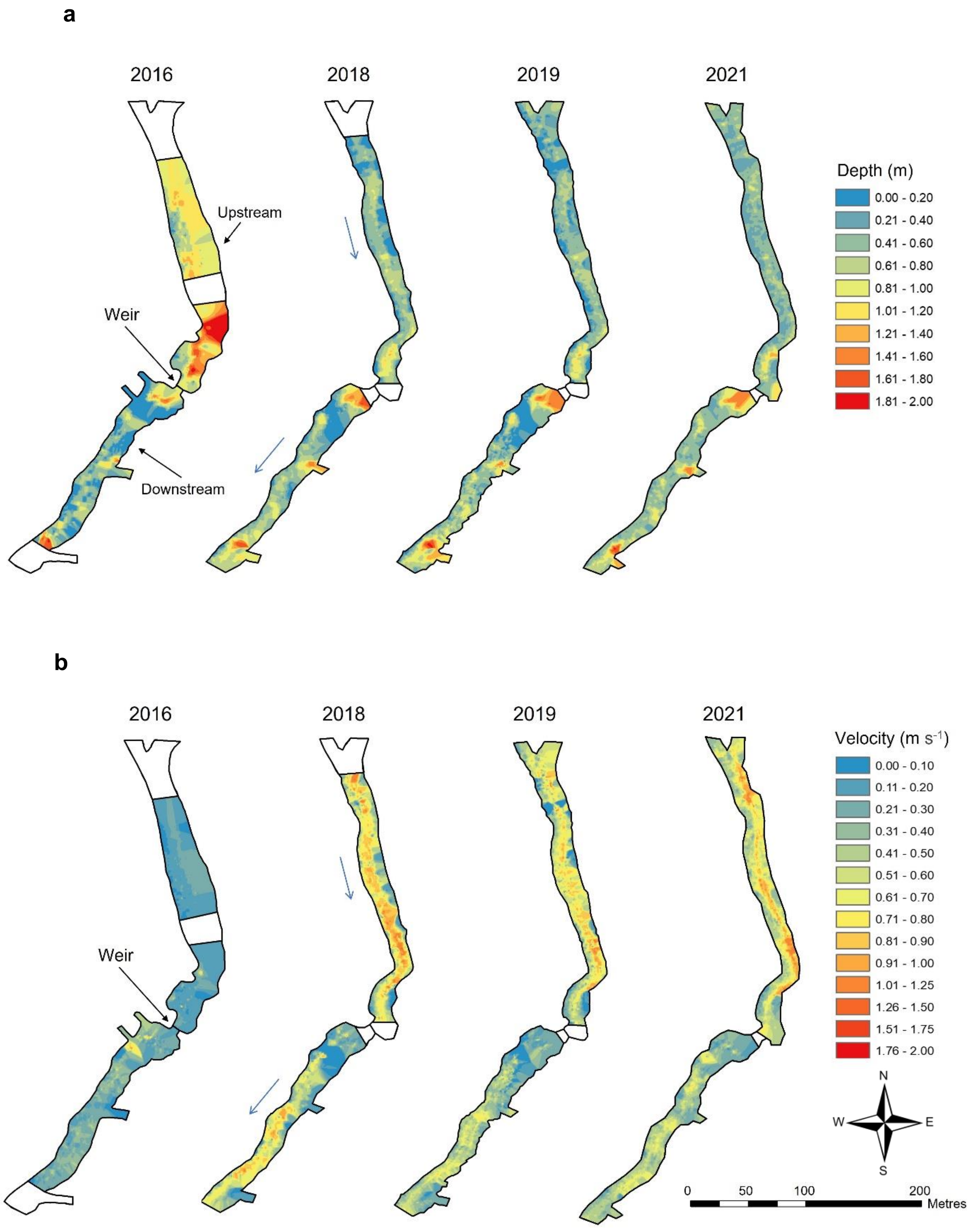


Figure 5.5 Spatial variability in (a) depth (m) and (b) velocity (m s^{-1}) at Bossington Estate pre- (2016) and post-weir removal and restoration (2018, 2019, 2021). River flow direction shown with blue arrow. White areas show those with no data.

In total, 40,834 individuals belonging to 80 different macroinvertebrate groups were found. Macroinvertebrate metrics changed considerably throughout the study period. There was an interaction between 'location' and 'year' for EPT abundance, LIFE and PSI, where values increased more upstream compared to downstream following restoration (Table 5.3; Figure 5.6). Upstream, most pre- (2016 and 2017) and post-restoration values differed (aside from: EPT abundance 2016-2020, 2016-2021; LIFE 2016-2018, 2016-2020; PSI 2016-2018). Downstream, the only pre- and post-restoration differences were a lower EPT abundance in 2016 and 2017 compared to 2018, and lower PSI in 2017 compared to 2019. Upstream, PSI continued to develop throughout the study, with values in 2019, 2020 and 2021 being higher than 2018. Abundance, taxon richness and EPT richness changed over time. Compared to pre-restoration, EPT richness was higher over both sites ≥ 2 years post-restoration. Abundance and taxon richness was lower in 2016 than all other years, and in 2017 compared to all post-restoration years (aside from abundance in 2017-2020 and taxon richness 2017-2018 and 2017-2019). No differences in abundance, taxon or EPT richness were found between 2019, 2020 and 2021. Dominant taxa in 2021 differed from 2017 (reported in pre-restoration comparisons) and were similar between upstream and downstream reaches: Baetidae (upstream: 59.0 ± 21.5, downstream: 47.3 ± 30.1), Gammaridae (upstream: 125.3 ± 79.0, downstream: 95.5 ± 73.8) and Simuliidae (upstream: 124.3 ± 123.2, downstream: 47.5 ± 93.3).

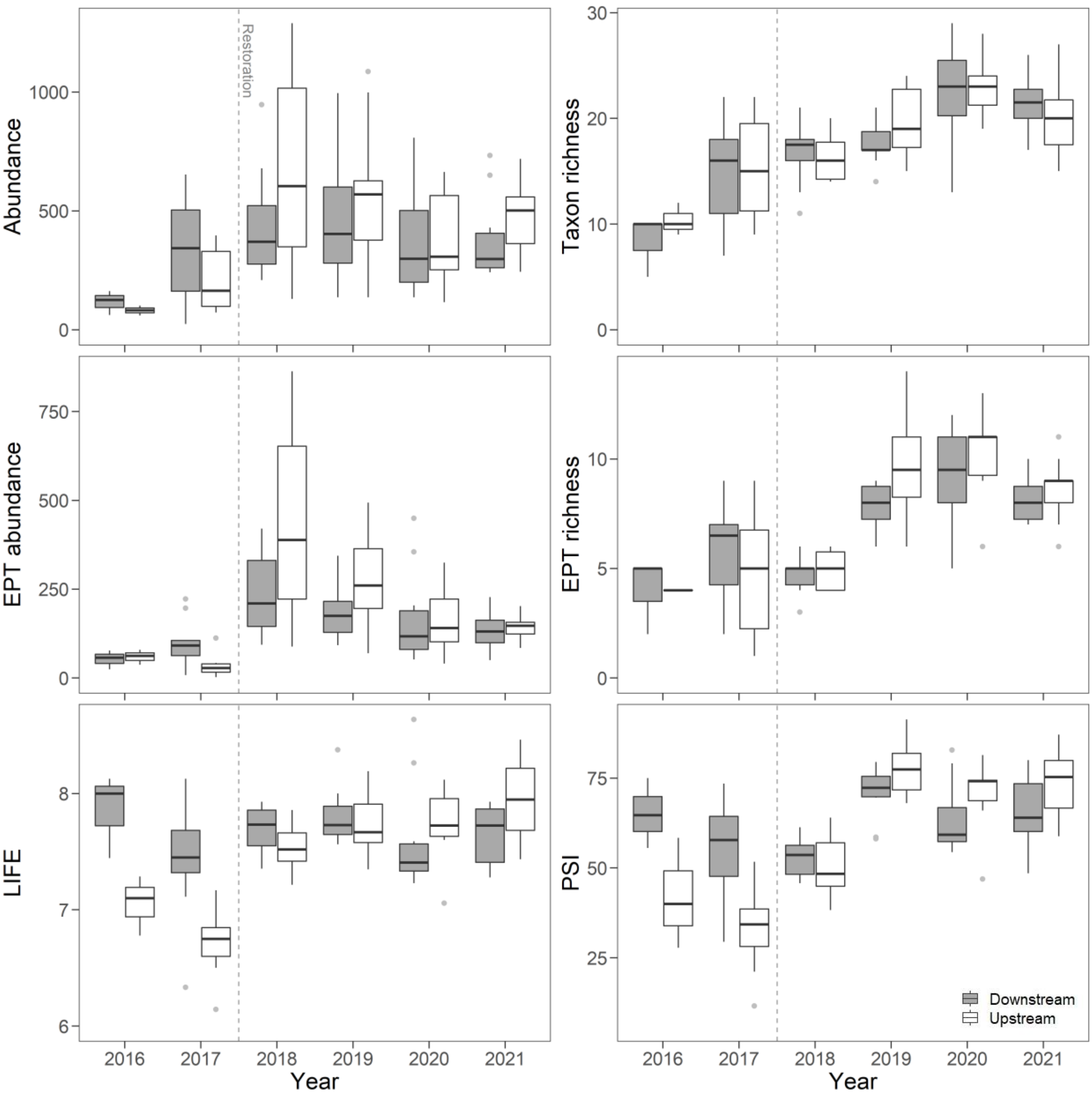


Figure 5.6 Boxplots showing the median abundance, taxon richness, EPT abundance, EPT richness, LIFE and PSI for macroinvertebrate samples collected in sites upstream and downstream of the Bossington Estate weir removal over a six year period. Black bar and boxes show median and 25th and 75th percentile, respectively. Whiskers represent minimum and maximum values excluding outliers. Dots show outliers (values > 1.5 x the interquartile range). Dashed line shows the point of weir removal and restoration.

Macroinvertebrate community structure changed considerably in both upstream and downstream reaches following restoration (Figure 5.7). An interaction between location and sampling year ($F_{4, 72}$: 3.309, < 0.001) was found. More specifically, post-hoc analysis suggested that upstream and downstream communities differed in all years, although these differences were largest in 2017 (Appendix A: Table A6). Looking at each location, differences in community were found between all years, although notably, following the 2018 sample the differences in communities between sequential years became gradually smaller (as indicated by the 't' statistic).

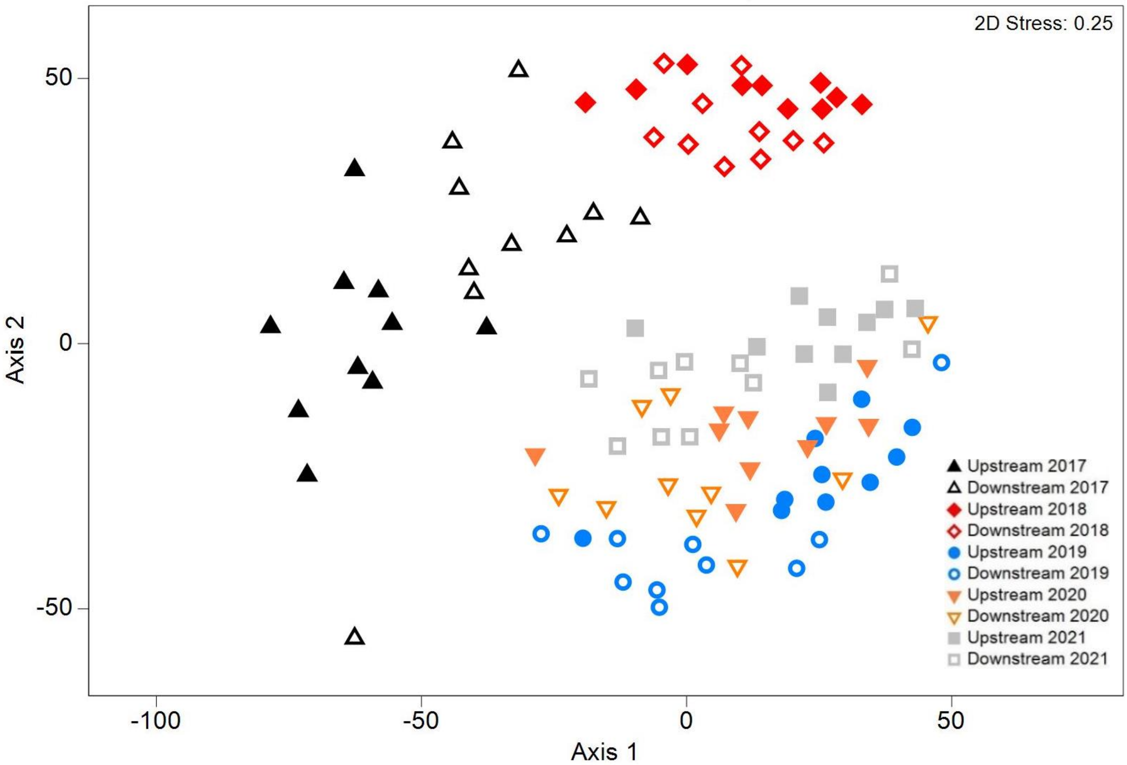


Figure 5.7 NMDS representation of macroinvertebrate communities upstream and downstream of a low-head weir removal project on the River Test pre (2017) and post-restoration (2018 - 2021). Samples clustered by Bray-Curtis distance matrices calculated from square-root transformed macroinvertebrate abundances (k = 2).

5.5 Discussion

River infrastructure removal has become integral in efforts to restore habitat and ecology (Ding *et al.*, 2019). However, the effects caused by low-head weirs and their removal remains poorly understood, inhibiting the development of sound restoration practice (Csiki and Rhoads, 2010). This is especially the case in systems with low power, which may exacerbate initial impacts and delay recovery following restoration owing to a reduced ability to mobilise sediments (Csiki and Rhoads, 2010; Carlson *et al.*, 2018). Whilst no impacts of low-head weirs on macroinvertebrate communities were shown in the coarse scale study, the fine scale field study demonstrated that weirs can degrade habitat and ecological communities, supporting the first prediction. Indeed, most impacts were confined to the upstream reach, which exhibited more lentic characteristics (e.g. higher silt cover, fewer rheophilic taxa) than downstream and the control. Supporting the second prediction, responses to weir removal and restoration were predominantly observed in the upstream reach (e.g. reduced depth and silt cover, more silt-intolerant taxa), which resulted in upstream and downstream becoming more similar. Recovery was unexpectedly rapid, with little indication of impacts associated with the inability of the river to quickly redistribute sediments (i.e. sediment pulse). However, analysis indicated that macroinvertebrate communities were still adjusting four years following weir removal, highlighting the need for monitoring to take place at commensurate scales to fully elucidate responses to restoration.

Going against the first prediction, no effects of low-head weirs on macroinvertebrate communities were detected using the coarse scale approach. One possibility is that this reflects the high variation in hydrogeomorphological impacts between structures. For example, differences in structural characteristics (e.g. sediment trapping ability; Stanley *et al.*, 2002; Roberts *et al.*, 2007), operation (e.g. sluice boards), river conditions and land-use (Csiki and Rhoads, 2010; Mueller *et al.*, 2011) are all known to influence the magnitude of impact of river infrastructure on the local environment. This could explain why substantial variability was detected between impacted and control sites for some metrics (e.g. abundance). Furthermore, the lack of an effect could reflect the prominence of catchment-scale pressures in chalk streams (CaBA, 2021). Indeed, if these pressures exerted a greater level of impact on macroinvertebrate communities compared to the reach-scale effects of the weirs (Kail and Wolter, 2013), this may have reduced differences between impacted and control sites. Another explanation may be attributable to the coarse scale approach taken. For example, river infrastructure datasets are often incomplete (for the United Kingdom see Jones *et al.*, 2019; for Europe see Belletti *et al.*, 2020), meaning that unrecorded structures may have unknowingly impacted the macroinvertebrate data either directly (e.g. through impoundment) or indirectly (e.g. altering sediment regimes). Moreover, the macroinvertebrate data analysed were mostly collected for routine monitoring purposes, and so are potentially biased towards sites that are more easily surveyed. The implication for this study is that macroinvertebrates are unlikely to have been sampled from deep, silty sites (i.e. conditions often characteristic of impounded reaches) that are difficult to survey via kick sampling. Finally, despite the high quantity of available data, few met the criteria for inclusion in this study resulting in a low sample size and statistical power to detect effects. The exploitation of publicly available datasets to answer ecological questions at a coarse scale has become common (e.g. O'Hare *et al.*, 2020) and offers many potential benefits. This includes negating the need for resource intensive field-based data collection and enabling analysis over greater spatial and temporal scales. Yet, this study suggests some caution as existing data may not always be appropriate for addressing specific ecological questions, highlighting the value of finer-resolution investigations for ensuring confidence in the data and results obtained.

In contrast to the coarse scale study and in support of the first prediction, the fine scale study weir clearly degraded local physical habitat and ecology. Most impacts were observed upstream, which was deeper, slower, more dominated by silt, and supported a community comprised of fewer rheophilic, silt-intolerant taxa and EPT. Downstream habitat and macroinvertebrates were more similar to the control, but was also deeper and contained fewer rheophilic, silt-intolerant taxa. The discontinuity between reaches were further emphasised through the most abundant families, in which upstream and downstream were dominated by more lentic (e.g. Sphaeriidae, Chironomidae) and lotic taxa (e.g. Gammaridae; Elmidae), respectively (Extence *et al.*, 1999; 2010). Unexpectedly, no evidence of an impact of the weir on diversity metrics were found (e.g. Mueller *et al.*, 2011), possibly because drift from upstream reaches allowed the persistence of small populations of ill-adapted taxa in each reach (i.e. mass effects; e.g. Baetidae; Waters, 1966). The effects found here are similar to those in other studies, including those which focussed on systems with ‘flashier’ hydrological regimes (e.g. Stanley *et al.*, 2002; Mueller *et al.*, 2011; Kil and Bae, 2012). Thus, the results from other systems appear comparable to chalk streams. Whilst the effects shown here are perhaps not surprising, the high variation in impacts caused between individual structures (Csiki and Rhoads, 2010; Mueller *et al.*, 2011) underscores the importance of pre-restoration evaluations such as these to fully comprehend the extent of deterioration and optimise restoration efforts. Indeed, such evidence is crucial for acquiring stakeholder and financial support, setting appropriate restoration objectives, estimating timelines for recovery, and to ensure the prioritisation of restoration efforts and funding towards structures with the greatest opportunity for remediation (O’Hanley, 2011; King *et al.*, 2017; Barry *et al.*, 2018).

The weir removal and restoration was expected to result in an initial decline in several macroinvertebrate metrics (e.g. abundance) associated with a sediment pulse (e.g. Kil and Bae, 2012). Opposing this, an immediate reduction in silt cover upstream and no change downstream was found. Macroinvertebrate metrics in both reaches either exceeded or did not differ from the pre-restoration sample < 11 months following weir removal, suggesting limited impacts of the restoration and silt redistribution (supported by

PSI). In the context of other studies, this recovery was rapid. For example, weir removals have been associated with enhanced levels of downstream fine sediments 18 months following restoration (Thomas *et al.*, 2015), whilst macroinvertebrate density typically takes around 15 months to recover to pre-restoration baselines (Carlson *et al.*, 2018). It is likely that the recovery was enhanced by the additional restoration methods employed. For example, coarse substrates within the heavily dredged upstream reach would have likely failed to recover without gravel augmentation owing to the naturally low levels of sediment recruitment and transportation in chalk streams (CaBA, 2021). Moreover, silt removal combined with gravel augmentation likely aided the rapid removal/redistribution of fine sediments, reducing the impacts associated with a sediment pulse. The timely recolonisation of habitat was likely facilitated by migration from nearby reaches in 'good condition', including previously restored sites located < 1 km away. Supporting this, mobile (e.g. Gammeridae; Baumgartner and Robinson, 2017) and drifting (e.g. Baetidae; Waters, 1966) taxa were observed in high abundances 11 months following restoration. Whilst the role of species pools and dispersal mechanisms for recolonisation has been well studied (e.g. Tonkin *et al.*, 2014), the situations in which additional measures are required to help facilitate recovery following infrastructure removal is under investigated (e.g. silt management; Carlson *et al.*, 2018). Despite this, when used to complement the reestablishment of natural processes through infrastructure removal these methods may be important for achieving the rapid responses desired. This is likely especially the case for low-powered systems such as chalk streams, where timelines for recovery when relying exclusively on natural dynamics may be long (Sear *et al.*, 1999; CaBA, 2021). Future studies should aim to develop knowledge on the importance of these methods for assisting recovery following infrastructure removal, potentially helping to facilitate system-specific optimisation of restoration designs.

The restoration was expected to result in greater similarity between upstream and downstream reaches over time, driven by changes to habitat and macroinvertebrates within the upstream reach. As predicted, the majority of effects were found upstream, which included an increase in velocity, coarse substrate cover and a reduction in depth. In response to these changes, macroinvertebrate communities became comprised of more rheophilic, silt-intolerant taxa with greater abundances of EPT. These outcomes are comparable to other studies (e.g. Stanley *et al.*, 2002; Maloney *et al.*, 2008; Kil and Bae, 2012) and demonstrate the benefits that can be brought about through infrastructure removal. An increase in abundance, taxon richness and EPT richness was also found across both reaches, likely driven by an increase in riverbed and structural complexity. Indeed, gravel augmentation and the enhancement of depth and velocity heterogeneity (as illustrated in Figure 5.5) likely increased occupiable space (e.g. sediment voids) and niches, facilitating a greater abundance and diversity of macroinvertebrates (Gayraud and

Philippe, 2003; Mueller *et al.*, 2014; Staentzel *et al.*, 2018a). Whilst the responses observed were generally rapid, analyses indicated that communities were still developing four years following restoration, albeit, slowing down over time. Assuming community change is slowing, the rates of recovery shown here are similar to those in other infrastructure removal projects, and goes against the expectation that the low-power of chalk streams will result in a delayed recovery. For example, long-term (40 years) assessments of the effects of dam removals (< 5.5 m heights) on macroinvertebrates found taxon richness typically recovered within 3-7 years (Hansen and Hayes, 2012b). The changes over time shown here could reflect habitat development (e.g. macrophyte mosaics) or the time taken for rarer/less mobile taxa to colonise (e.g. Nepidae was first found in 2021; Tonkin *et al.*, 2014), and highlights the need for appraisals to take place at appropriate timescales to fully elucidate ecological responses (England *et al.*, 2021a). Despite this, long-term monitoring is often difficult to achieve, hampered by short-term funding, stakeholder expectations and other external influences (e.g. further restoration; Borgström *et al.*, 2016). Long-term appraisals are therefore likely best achieved by focussing efforts and funding into the robust appraisal of exemplar case studies (England *et al.*, 2021a), which can serve as useful examples to help guide and inspire future restoration efforts.

This study found that weirs have the potential to degrade chalk streams physically and ecologically, especially within upstream reaches. However, these impacts are not necessarily universal and may vary considerably between sites, e.g. with sediment retention ability. Consequently, the fine scale assessment of weirs on a case by case basis to identify the most impactful structures is needed to maximise restoration benefits. The removal of low-head weirs can result in rapid changes in habitat and ecological communities in low powered systems such as chalks streams, and may represent somewhat of a ‘low hanging fruit’ considering their abundance and often deteriorated state. However, the underlying role of additional restoration methods, for example to help manage fine sediment loads and mitigate the impacts of a sediment pulse, is poorly understood and in need of future investigation. These methods may be especially important in systems such as chalk streams due their low power and typical delayed response to physical alteration. Future studies comparing recovery to infrastructure removal projects with and without additional methods in systems with varying levels of power would be especially valuable to help facilitate system-specific optimisation of restoration designs. Ensuring appraisals take place at commensurate scales to fully capture responses to restoration is crucial, and should represent a priority for upcoming studies to help provide robust evidence of restoration effectiveness. These appraisals will be particularly important to guide forthcoming restoration efforts by allowing the avoidance of common pitfalls and highlighting best practices.

CHAPTER 6 Chalk stream restoration: physical and ecological responses to gravel augmentation.

6.1 Summary

This study quantified immediate (0-1 years) and short-term (1-2 years) physical and ecological responses to gravel augmentation at two English chalk stream restoration sites: Home Stream (HS; River Test) and East Lodge (EL; River Itchen). Habitat (depth, velocity, substrate composition), the cover of different macrophytes, and macroinvertebrate (before-after-control-impact) and fish (control-impact) abundance and communities were assessed. At both sites, depth reduced and gravel cover increased due to restoration. Cross-sectional variation in velocity increased 1-2 years post-restoration in HS. Total macrophyte cover did not change, but the cover of filamentous green algae in HS decreased during both post-restoration periods compared to the control. Macroinvertebrate communities were dominated more by silt-intolerant taxa 0-1 and 1-2 years post-restoration while taxon richness and abundance increased [HS only] 1-2 years post-restoration. Fish communities in the HS restored reach were more abundant and species rich than the control 0-1 years post-restoration, and supported more Eurasian minnow (*Phoxinus phoxinus*). Observations of wild brown trout per minute were higher in the EL restored reach compared to the control. Responses varied across sites, post-restoration time periods and ecological groups. More and longer-term case studies are required to inform on the ubiquity and longevity of ecological responses to chalk stream restoration.

6.2 Introduction

For centuries, humans have intensively modified rivers for agriculture, navigation, flood defence, industrial and domestic water supply and energy generation (Lenders *et al.*, 2016; Gibling, 2018). As a consequence, rivers have been dammed, channelised, dredged, and cut-off from their flood plains, disrupting natural hydrogeomorphological regimes (Piqué *et al.*, 2016; Galia *et al.*, 2021), reducing fluvial connectivity (Foster *et al.*, 2021) and homogenising habitat (Im *et al.*, 2020). Extensive river modification has reduced biodiversity (Wang *et al.*, 2020), modified ecological communities (Graf *et al.*, 2016) and degraded ecological quality (Grizzetti *et al.*, 2017), contributing to global threats to fresh waters and associated potential for humanitarian crisis (Albert *et al.*, 2021).

Localised depletion of river sediments through direct (e.g. dredging and mining; Freedman *et al.*, 2013; Rentier and Cammeraat, 2022) and indirect (e.g. interruption of sediment regime by dams; Brenna *et al.*, 2020) mechanisms threatens morphological and ecological fluvial integrity (Kondolf, 1997; Koehnken *et al.*, 2020). Morphologically, sediment depletion can promote channel incision, bank instability and armouring of the river bed (Kondolf, 1997; Koehnken *et al.*, 2020), reduce habitat heterogeneity (Brown *et al.*, 1998) and inhibit channel dynamics (Draut *et al.*, 2011; Marren *et al.*, 2014). Ecologically, it can negatively impact biodiversity, communities and food web dynamics (Paukert *et al.*, 2008; Freedman *et al.*, 2013), habitat suitability for substrate-spawning taxa (Cote *et al.*, 1999; Mingist and Shewit, 2016), and has been associated with a greater presence of non-native species (Paukert *et al.*, 2008). Globally, there has been increased efforts to mitigate the negative impacts associated with sediment depletion through rehabilitation measures, including gravel augmentation, one of the more common substrate restoration techniques (Kondolf *et al.*, 2014; Staentzel *et al.*, 2020; Mörtl and De Cesare, 2021).

The artificial addition of gravels to degraded rivers has been widely employed in several regions, with examples from North America (United States [Sellheim *et al.*, 2016], Canada, [Kasahara and Hill, 2007]), Europe (United Kingdom [England and Wilkes, 2018], Germany [Pulg *et al.*, 2013], Norway [Pulg *et al.*, 2022]) and Asia (Japan; Matsushima *et al.*, 2018). This practice helps facilitate the regeneration of natural processes (e.g. sediment transport) and can be used to restore riverbed structure (e.g. redistributing silt) and features over a range of scales. Those operating at the reach-scale tend to focus on re-naturalising riverbed structure and features (e.g. to create riffles [Pretty *et al.*, 2003] and gravel bars [Merz and Ochikubo Chan, 2005]) and improving ecological utility (e.g. salmonid spawning habitat quality; Zeug *et al.*, 2014). At larger scales, efforts are directed at re-establishing dynamic processes, for example the formation and evolution of geomorphic features (Gaeuman, 2014). However, logistical constraints (e.g. land ownership), costs of implementation and monitoring can result in bias (e.g. in publication; Mueller *et al.*, 2014; Pulg *et al.*, 2022) in favour of the more common reach-scale gravel augmentation projects (Bannister *et al.*, 2005).

Despite the widespread use of gravel augmentation to help restore rivers (Staentzel *et al.*, 2020), the ecological responses observed are often variable and remain poorly understood (Mueller *et al.*, 2014). On one hand, the addition of gravel can enhance fish habitat, particularly for gravel spawning taxa (Palm *et al.*, 2007; Mueller *et al.*, 2014; Zeug *et al.*, 2014; Pulg *et al.*, 2022), macroinvertebrate diversity (Staentzel *et al.*, 2018a) and density (Merz and Ochikubo Chan, 2005; Mueller *et al.*, 2014), and macrophyte species richness (Staentzel *et al.*, 2018b). On the other, several studies have indicated limited (e.g. fish [Pretty *et al.*, 2003], macroinvertebrates [Harrison *et al.*, 2004; McManamay *et al.*, 2013]), temporary (e.g. fish [Pulg *et al.*, 2013], vegetation [Bauer *et al.*, 2018]), mixed (e.g. fish; Romanov *et al.*, 2012) and negative effects (e.g. reduced macroinvertebrate abundance and biomass [Albertson *et al.*, 2011], reduced macrophyte diversity, biomass and cover [Mueller *et al.*, 2014]). A lack of understanding of the mechanisms that underpin the ecological responses observed may be attributed to multiple factors, including limited monitoring (Pander and Geist, 2013), insufficient time-scales of appraisal (Kail *et al.*, 2015), and the potential for catchment scale processes to overshadow reach scale outcomes (Pretty *et al.*, 2003; Polvi *et al.*, 2020). Moreover, the general focus on single ecological indicators, especially salmonids (Pulg *et al.*, 2022), and the bias towards certain regions and river types (Merz and Ochikubo Chan, 2005; Albertson *et al.*, 2011; Albertson *et al.*, 2013; Staentzel *et al.*, 2020), may constrain understanding of the value of gravel augmentation as an effective restoration strategy.

Chalk streams have been modified over many centuries (Mainstone, 1999; Mondon *et al.*, 2021), including dredging and impoundment, which has contributed to their widespread degradation (CaBA, 2021; see section 2.3.5 for overview). Physical habitat degradation, such as that due to infrastructure, alongside intensive water abstraction and land use practices, have widely disrupted natural sediment regimes of chalk streams (Bickerton *et al.*, 1993; Mondon *et al.*, 2021). Due to their stable hydrogeomorphology and naturally low levels of sediment recruitment and bedload mobilisation (Acornley and Sear, 1999; Sear *et al.*, 1999), alongside impoverished baseflows and highly modified channels, the natural regeneration of sediment is difficult without appropriate intervention. Consequently, the replenishment of gravels has become an important management strategy in the restoration of chalk streams (CaBA, 2021; River Restoration Centre, 2023b). However, few studies have evaluated the ecological consequences of gravel augmentation in these systems, and those that have tend to focus on single ecological indicators (e.g. macroinvertebrates; England and Wilkes, 2018).

This study quantified physical and ecological responses to gravel augmentation at two case study chalk stream restoration sites in southern England. Restoration was predicted to have: (1) an immediate effect on physical habitat and that this would be maintained throughout the duration of the study period (two years post-restoration). Specifically, when compared with the conditions prior to restoration and at a control site, the restored sections were expected to be characterised by greater velocity and depth variability, higher velocities and shallower water depth, and higher coarse-substrate cover. These physical responses were predicted to result in: (2) changes to the stream ecology, considered in terms of enhanced richness, abundance and/ or cover of aquatic fauna and flora, and shifts in community composition towards those considered characteristic of chalk stream environments (e.g. greater presence of rheophilic and silt-intolerant taxa such as *Ranunculus* spp. and brown trout and EPT; Mainstone, 1999; CaBA, 2021). Finally, it was expected that: (3) time would play an influential role in the ecological response, with limited or potentially negative changes associated with the immediate disturbance of habitat in the year following restoration (especially for benthic groups), followed by a shift to the aforementioned outcomes thereafter. To test these predictions, this study focused on three ecological groups: (a) macrophytes (total macrophyte cover and cover of different macrophyte types); (b) macroinvertebrates (abundance, taxon richness, percentage of abundance [EPTA] and taxon richness [EPTN] comprised of EPT, PSI and LIFE); and (c) fish (species richness and abundance). To investigate the influence of time, the physical and ecological response were monitored throughout the year immediately after (immediate response) and between one and two years (short-term) post-restoration.

6.3 Methods

6.3.1 Study sites

This study monitored the physical and ecological responses of two gravel augmentation restoration projects on the Rivers Test (HS) and Itchen (EL; Figure 6.1), Hampshire, United Kingdom. Details on both rivers can be found in Chapter 4. At each study site, a reach of river approximately 200 m in length was restored in October 2019 with the goal of increasing in-river habitat heterogeneity and enhancing biodiversity and conditions for *Ranunculus* spp. and gravel spawning salmonids. Approximately 1,500 and 3,000 tonnes of washed gravel substrates were deposited along the HS (natural gravel excavated on site; predominantly 2-64 mm but with some finer and coarser grain sizes) and EL (predominantly 16-30 mm imported washed river gravel) reaches, respectively. This was intended to reduce depth, remobilise silt, reprofile the planform, recover a more naturalised riverbed and processes and create geomorphic features (e.g. pools). Localised cobble sized substrate was also placed at EL. Additionally, at each site, a limited number of felled trees (1 to 2 structures) were secured at the riverbank to form low velocity, sheltered habitats and *Ranunculus* spp. were sparsely 'seeded' (approximately one plant per 5 m^2) throughout the reaches via translocation from unrestored areas nearby.

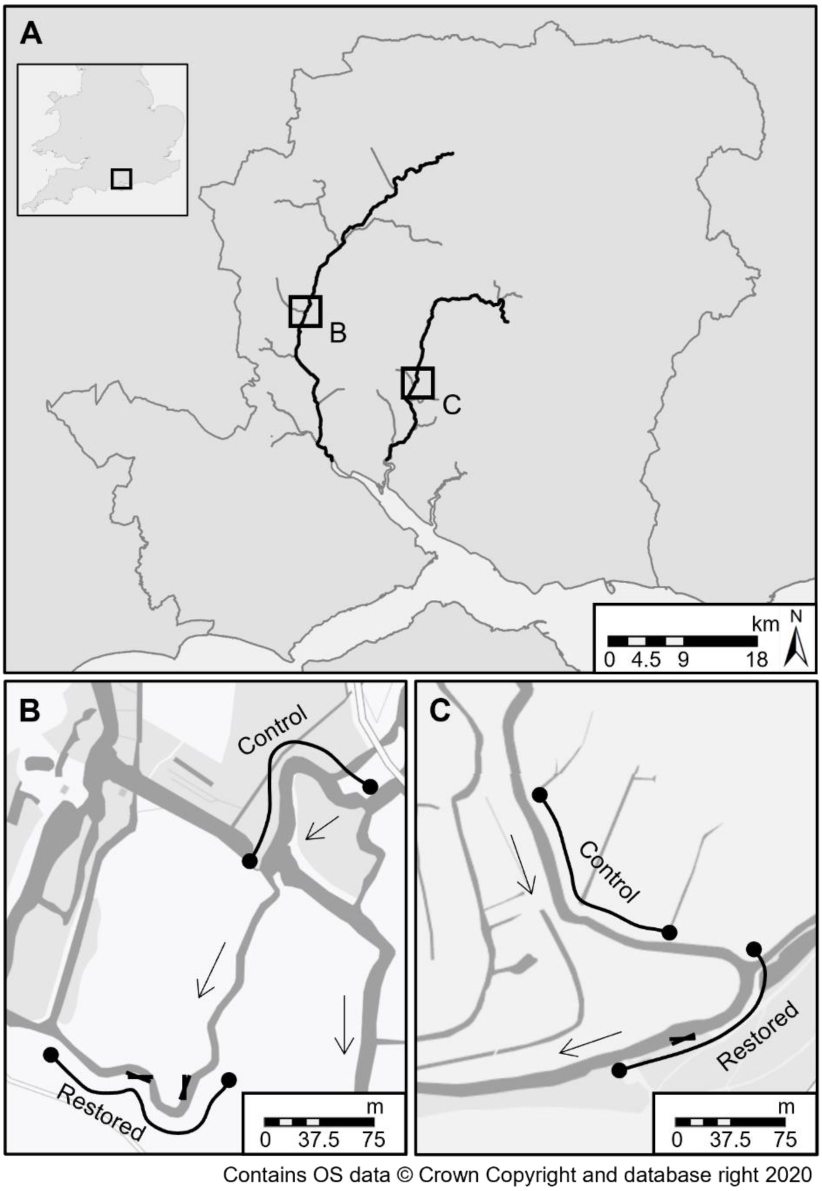


Figure 6.1 (A) Location of study sites on the Rivers Test and Itchen in Hampshire, (United Kingdom), with greater detail provided for (B) HS (51.07296, -1.51685) and (C) EL (51.00047, -1.32551). The arrows, black lines and crosses respectively indicate flow direction, extent of restored and control reaches and positions where felled trees were secured. Country/county and river network shapefiles were supplied from Ordnance Survey (2023) and Ordnance Survey (2022), respectively. Detailed maps (B and C) were supplied from Ordnance Survey (2016).

A single restored reach paired with a control (150 m length) were monitored at both restoration sites (Figure 6.1). Control reaches were selected based on their proximity and similarity to the restored sites prior to the rehabilitation work. To prevent downstream effects of the interventions the control sites were located 200 m and 150 m upstream of the restored sections at HS and EL, respectively. At HS, the only suitable control was located upstream of a 1.1 m high weir. A BACI study design was used to quantify changes in physical habitat, macrophytes and macroinvertebrates. It was not possible to collect fish data prior to restoration so a CI approach was adopted.

6.3.2 Physical habitat

Physical habitat was measured at five equidistant points across 16 transects located at 10 m intervals during five surveys per restoration project (one pre-restoration and four post-restoration; see Figure 6.2 for a summary of data collection periods and the flow conditions under which surveys were conducted). At each point, depth (cm), velocity ($m\ s^{-1}$; mean taken over 10 secs at 1 Hz and 60% depth using a Valeport Model 801 flow meter) and the dominant surface substrate (silt [0.0039-0.123 mm], sand [0.125-2 mm], gravel [2-64 mm], cobble [> 64 mm]) within a 0.5 m^2 quadrat was recorded. Wetted widths (m) were measured at each transect, although for some sampling periods and transects this was not possible due to excessive riparian growth and safety concerns. Depth (DCSV) and velocity (VCSV) cross sectional variability, a measure of habitat heterogeneity, was calculated by taking the standard deviation of the five depths and velocity measurements across each transect.

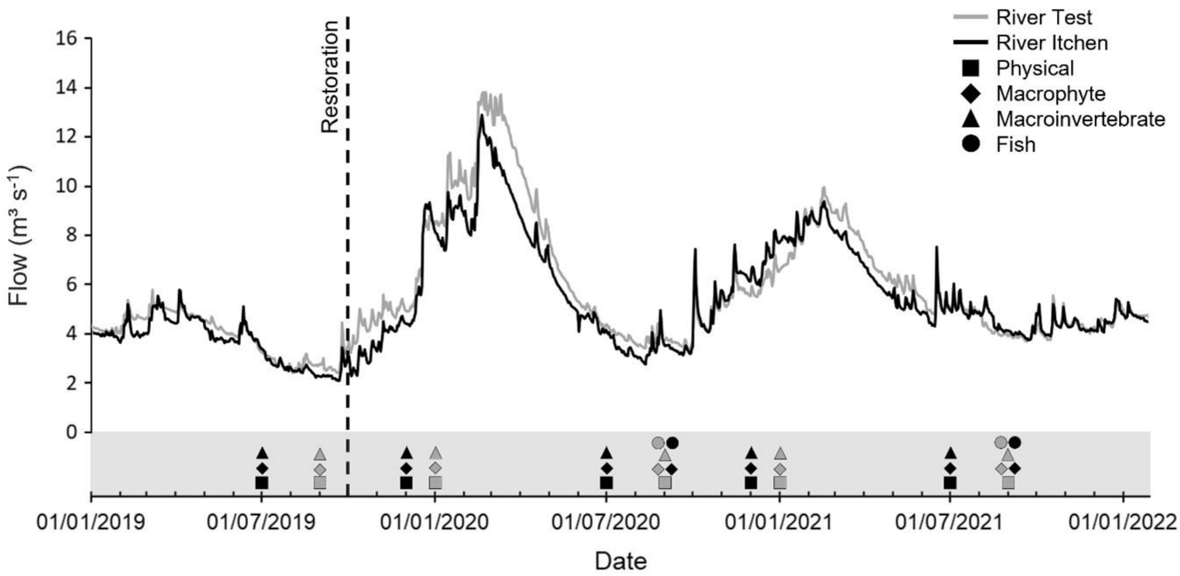


Figure 6.2 River discharge (m^3 s^{-1}) for the River Test and Itchen during a study to quantify physical and ecological response to gravel augmentation. Symbols in grey shaded area show the months during which data was collected at HS (River Test, grey symbols) and EL (River Itchen, black symbols). Flow data was obtained from Chilbolton (River Test) and Highbridge (River Itchen) gauging stations, approximately 10 km upstream and 2 km downstream of the restored sites, respectively (DEFRA, 2021). Contains public sector information licensed under the Open Government Licence v3.0.

Total macrophyte cover and submerged macrophyte group cover were quantified on five and seven occasions at HS and EL, respectively. Using the same transects as for the physical habitat metrics, total macrophyte cover was assessed by estimating the percentage cover (including emergent and submerged plants) within a 0.5 m^2 quadrat at each point (five per transect). Additionally, at the same transects, the cover of five submerged macrophyte groups (Table 6.1) was calculated (eight transects were conducted in the EL restored reach during the pre-restoration period). The overall macrophyte cover within a prescribed area (1 m length spanning the width of the river) was estimated using the mean of the five total macrophyte cover and wetted width measurements at each transect. The amount of overall cover comprising each macrophyte group was estimated for each transect (Appendix B: Figure B1 for example of calculation). To control for limited accuracy of estimates of group cover in HS when turbidity was high, further analysis was restricted to data obtained during September when turbidity was low. Where wetted widths were not recorded (EL September 2020 and 2021, HS control September 2019), widths measured during the other sampling periods under similar flow conditions were used.

Table 6.1 Groups of macrophytes recorded across transects to monitor ecological change following gravel augmentation. Examples of common species found within each group are provided. The groups were selected as they encompass the typical dominant taxa found in each river (e.g. Poynter, 2013).

Group	Description	Typical species
Water crowfoot	Any species from the *Ranunculus* genus.	*Ranunculus penicillatus ssp. pseudofluitans*
		Ranunculus aquatilis
Water starwort	Any species from the *Callitriche* genus.	*Callitriche obtusangula*
		Callitriche platycarpa
Broad leaved macrophytes	Any submerged macrophytes deemed to have broad leaves.	*Berula erecta*
		Apium nodiflorum
Filamentous green algae	Any submerged filamentous green algae.	*Cladophora glomerata*
Tape grass	Submerged macrophytes with long, flattened leaves splitting at the base of the plant.	*Schoenoplectus lacustris*
		Sparganium emersum

6.3.4 Macroinvertebrates

Macroinvertebrate samples were collected at every second transect (20 m intervals) using a standard 3 minute kick sample (250 mm^2 net, 1 mm mesh), or sweep sample from a boat if depth restricted wading (WFDUK, 2022). This was followed by a 1 minute hand search for macroinvertebrates not likely to be found in the kick sample, such as those residing under larger substrate or located on the surface (WFDUK, 2022). To ensure standardised sampling, the technique (i.e. kick or sweep sample) used during the first sampling period was maintained throughout the study. Over the 3 minute kick sampling period, substrates and all habitat types (e.g. macrophytes) were sampled in estimated proportion to their occurrence in the respective transect to provide appropriate representation of invertebrates from each microhabitat. Following collection, samples were placed in 1.2 L sampling pots and fixed with 70% methylated spirit.

Samples were sorted and macroinvertebrates identified within one month of collection. Each sample was poured through a 30 μm sieve and washed lightly with tap water to remove methylated spirit, before being placed into a tray with water and evenly distributed throughout. Samples were sub-sampled by dividing the area of the tray in half and sorting a random half by hand, collecting any macroinvertebrates present. These were identified by a single Freshwater Biological Association trained practitioner to the family level (Oligochaeta was classified as such) using a compound microscope (Motic ST-30) and identification guide (Dobson, 2012). Following identification, the abundance, taxon richness, EPTA, EPTN, LIFE and PSI was calculated.

6.3.5 Fish

Fish abundance and species richness was assessed using a single remote underwater video (RUV) camera (GoPro Hero 6, wide frame setting, at a minimum of 60 frames per second, 1080 p mounted to a brick, 200 x 100 x 50 mm) during September 2020 and 2021. The camera was rotated between the eight transect locations as described for the macroinvertebrate surveys. Single video samples of 30 minute duration were collected for each transect. The RUV camera was submerged facing 45° downstream towards the centre of the channel in an area where macrophyte cover was absent to maximise the field of view. The RUV was placed in the channel from a position on the bank to minimise disturbance of sediments and fauna and flora. After this the river was left undisturbed for 30 minutes before the camera was retrieved and moved to the next transect where recording recommenced after approximately 10 minutes. Video recordings were collected between 8 am and 6 pm by working in an upstream direction to reduce disturbance.

The first three minutes of each video recording was designated a settling period and excluded from analysis. The maximum number of individuals per species observed in a single frame for each remaining minute ($n = 27$) of video footage was quantified. In the event that fish exited the field of view and were immediately (approximately < 2 secs) replaced by others from the opposite side of the frame, indicating they must have been different individuals (e.g. Appendix B: Figure B2), then the total sum of fish observed were counted. Stocked farm-reared, triploid brown trout were distinguished from wild trout based on their larger size and fin condition, which were typically damaged due to conditions experienced during hatchery rearing under high densities (example in Appendix B: Figure B2). Those deemed to be stocked trout were excluded from further analysis as their presence was independent of the restoration and they could not contribute to the population due to the inability to reproduce. For each recording, the (1) maximum number of individuals per species observed instantaneously across the 27-minute period (NMax),

(2) the mean of the maximum number of individuals observed for each species per minute (NMean), (3) species richness, and (4) the total abundance (sum of all NMax values across all species per video) were calculated.

6.3.6 Statistical analysis

To evaluate the influence of time since restoration on physical habitat and ecological responses, the analysis was divided into two periods: immediate (0-1 years) and short-term (1-2 years) post-restoration. Separate statistical models were created for EL and HS as a direct comparison between the two sites was not the focus of this study. Each dominant substrate type was summed across each transect and VCSV was square-root transformed. Analyses were carried out in R Studio (R Studio Team, 2020) and the packages Lme4 (Bates *et al.*, 2015), LSmeans (Lenth, 2016), performance (Lüdecke *et al.*, 2020), ggplot2 (Wickham, 2016), patchwork (Pedersen, 2020), nparLD (Noguchi *et al.*, 2012) and nparcomp (Konietschke *et al.*, 2015).

Physical habitat (excluding substrate cover) and macroinvertebrate metrics were analysed using GLMMs (macroinvertebrate abundance [HS] and taxon richness [HS and EL]) with Poisson error distribution and log-link function and LMMs (all other physical and macroinvertebrate metrics). Models encompassed the terms 'sampling period' (pre-restoration, 0-1, 1-2 years post-restoration), 'location' (restored or control site) and the 'interaction between sampling period x location'. 'Sampling date' and 'sampling point/transect' were considered random effects to account for pseudoreplication. In these models, significant sampling period x location interactions suggest an effect of the restoration. The significance of each variable was assessed using likelihood ratio tests by comparing full models with one with the focal terms removed. For all LMMs and GLMMs, multicollinearity and model assumptions were checked using variance inflation factor and QQ and fitted vs residual plots, respectively. TukeyHSD pairwise comparisons were performed post-hoc when sampling period or sampling period x location interactions were significant.

Diagnostic plots suggested mixed models were not appropriate for fish, macrophyte or substrate metrics. Therefore, a non-parametric rank-based repeated measures (NPM) approach was conducted using 'nparLD' (Noguchi *et al.*, 2012). This package does not require any distribution assumptions, is considered robust to small and variable samples sizes and outliers, and provides an 'ANOVA-type' statistic (ATS; Noguchi *et al.*, 2012). Where multiple samples were taken within a sampling period, a single value for each sampling point/transect was calculated by taking the mean across each period. Models were created with the same terms as for the parametric analysis. Where sampling period or sampling period x location interactions were significant for macrophyte and substrate metrics, post-hoc pairwise comparisons were conducted in 'nparcomp' and using the function 'mctp.rm' with TukeyHSD corrections (Konietschke *et al.*, 2015). For significant interactions, pairwise comparisons were used to test differences between sampling periods on separate models for restored and control reaches.

6.4 Results

6.4.1 Physical habitat

Interactions between sampling period and location were observed for depth, VCSV and the cover of sand and gravel substrates in HS (Table 6.2; Figure 6.3, 6.4). Depth and sand cover was lower, and gravel cover higher during both post-restoration periods in the restored reach compared to pre-restoration (see Appendix B: Table B1 – B3 for all post-hoc statistical tests). Compared to pre-restoration, VCSV was higher 1-2 years post-restoration in the restored reach. No difference in metrics between periods was observed for the control site.

In EL, interactions between sampling period and location were observed for depth, velocity, and cover of silt, sand, gravel and cobble. In the restored reach, silt cover was lower, and gravel and cobble cover higher, during both post-restoration periods compared to pre-restoration. Gravel cover was higher 0-1 years compared to 1-2 years post-restoration. Compared to pre-restoration, sand cover and depth was lower 0-1 years but not 1-2 years post-restoration in the restored reach. Velocity in the restored reach was lower than the control 0-1 years post-restoration. Aside from higher gravel cover 1-2 years post-restoration than the pre-restoration period, there was no change in physical habitat metrics over time in the control site.

Table 6.2 GLMM, LMM and NPM results assessing the responses of physical habitat and ecological metrics to gravel augmentation. Significant p-values are highlighted in bold. Location = control or restored reach, Sampling period = pre-restoration, 0-1 or 1-2 years post-restoration (0-1 and 1-2 years only for fish). TMC = total macrophyte cover, FGA = filamentous green algae; BL = broad leaved.

Site	Type	Term	Test	Sampling period x Location		Location		Sampling period	
				X2/ATS	p	*X2*/ATS	p	*X2*/ATS	p
HS	Physical	Depth	LMM	28.142	**< 0.001**	63.439	**< 0.001**	7.260	**< 0.05**
		Velocity	LMM	0.013	0.994	0.087	0.768	4.901	0.086
		DCSV	LMM	5.713	0.057	21.219	**< 0.001**	2.097	0.351
		VCSV	LMM	6.939	**< 0.05**	4.106	**< 0.05**	7.699	**< 0.05**
		Silt cover	NPM	1.507	0.223	0.763	0.383	3.439	**< 0.05**
		Sand cover	NPM	12.999	**< 0.001**	7.030	**< 0.01**	5.429	**< 0.01**
		Gravel cover	NPM	26.222	**< 0.001**	2.985	0.084	18.349	**< 0.001**
		Cobble cover	NPM	0.290	0.674	0.572	0.450	5.055	**< 0.05**
	Macrophytes	TMC	NPM	2.586	0.077	11.682	**< 0.001**	10.770	**< 0.001**
		FGA	NPM	4.490	**< 0.05**	0.674	0.412	6.070	**< 0.01**
		Water crowfoot	NPM	0.125	0.833	62.135	**< 0.001**	6.507	**< 0.01**
		BL macrophyte	NPM	0.505	0.593	3.085	0.079	0.444	0.630
		Tape grass	NPM	0.433	0.640	31.397	**< 0.001**	4.878	**< 0.01**

		Water starwort	NPM	0.410	0.658	3.258	0.071	0.431	0.645
	Macroinvertebrates	Abundance	GLMM	158.070	**< 0.001**	2.117	0.146	4.861	0.088
		Taxon richness	GLMM	13.994	**< 0.001**	1.547	0.214	4.682	0.096
		EPTA	LMM	3.706	0.157	21.854	**< 0.001**	3.120	0.210
		EPTN	LMM	6.542	**< 0.05**	5.208	**< 0.05**	3.758	0.153
		PSI	LMM	13.803	**< 0.01**	5.166	**< 0.05**	8.722	**< 0.05**
		LIFE	LMM	6.259	**< 0.05**	4.803	**< 0.05**	1.034	0.596
	Fish	Total abundance	NPM	4.044	**< 0.05**	3.968	**< 0.05**	0.991	0.319
		Species richness	NPM	10.140	**< 0.01**	0.442	0.506	19.102	**< 0.001**
		NMax minnow	NPM	2.964	0.085	4.627	**< 0.05**	0.643	0.423
		Nmax chub	NPM	11.667	**< 0.001**	11.667	**< 0.001**	11.667	**< 0.001**
		Nmean chub	NPM	11.475	**< 0.001**	11.475	**< 0.001**	11.475	**< 0.001**
		Nmax stickleback	NPM	0.345	0.557	4.187	**< 0.05**	0.345	0.557
		Nmean stickleback	NPM	0.305	0.582	4.183	**< 0.05**	0.305	0.582
EL	Physical	Depth	LMM	51.031	**< 0.001**	19.547	**< 0.001**	7.088	**< 0.05**
		Velocity	LMM	7.377	**< 0.05**	16.214	**< 0.001**	5.871	0.053
		DCSV	LMM	3.301	0.192	28.812	**< 0.001**	0.871	0.647
		VCSV	LMM	0.145	0.930	0.566	0.452	2.450	0.294
		Silt cover	NPM	3.987	**< 0.05**	2.590	0.108	7.139	**< 0.001**
		Sand cover	NPM	6.226	**< 0.01**	7.114	**< 0.01**	8.284	**< 0.001**

		Gravel cover	NPM	9.908	**< 0.001**	0.136	0.712	18.402	**< 0.001**
		Cobble cover	NPM	3.852	**< 0.05**	6.643	**< 0.01**	13.931	**< 0.001**
	Macrophytes	TMC	NPM	1.077	0.329	2.642	0.104	13.876	**< 0.001**
		FGA	NPM	1.900	0.157	1.967	0.161	10.657	**< 0.001**
		Water crowfoot	NPM	3.297	0.053	0.244	0.621	15.012	**< 0.001**
		BL macrophyte	NPM	3.742	**< 0.05**	1.000	0.317	26.202	**< 0.001**
		Tape grass	NPM	3.625	**< 0.05**	0.300	0.584	0.697	0.478
		Water starwort	NPM	0.964	0.376	0.915	0.339	0.532	0.574
	Macroinvertebrates	Abundance	LMM	2.628	0.269	0.000	0.991	1.890	0.389
		Taxon richness	GLMM	7.570	**< 0.05**	3.720	0.054	9.452	**< 0.01**
		EPTA	LMM	5.780	0.056	0.392	0.532	0.912	0.634
		EPTN	LMM	3.145	0.208	0.906	0.341	8.577	**< 0.05**
		PSI	LMM	7.862	**< 0.05**	3.103	0.078	8.264	**< 0.05**
		LIFE	LMM	1.522	0.467	3.429	0.064	6.797	**< 0.05**
	Fish	NMean brown trout	NPM	0.339	0.560	4.784	**< 0.05**	15.084	**< 0.001**

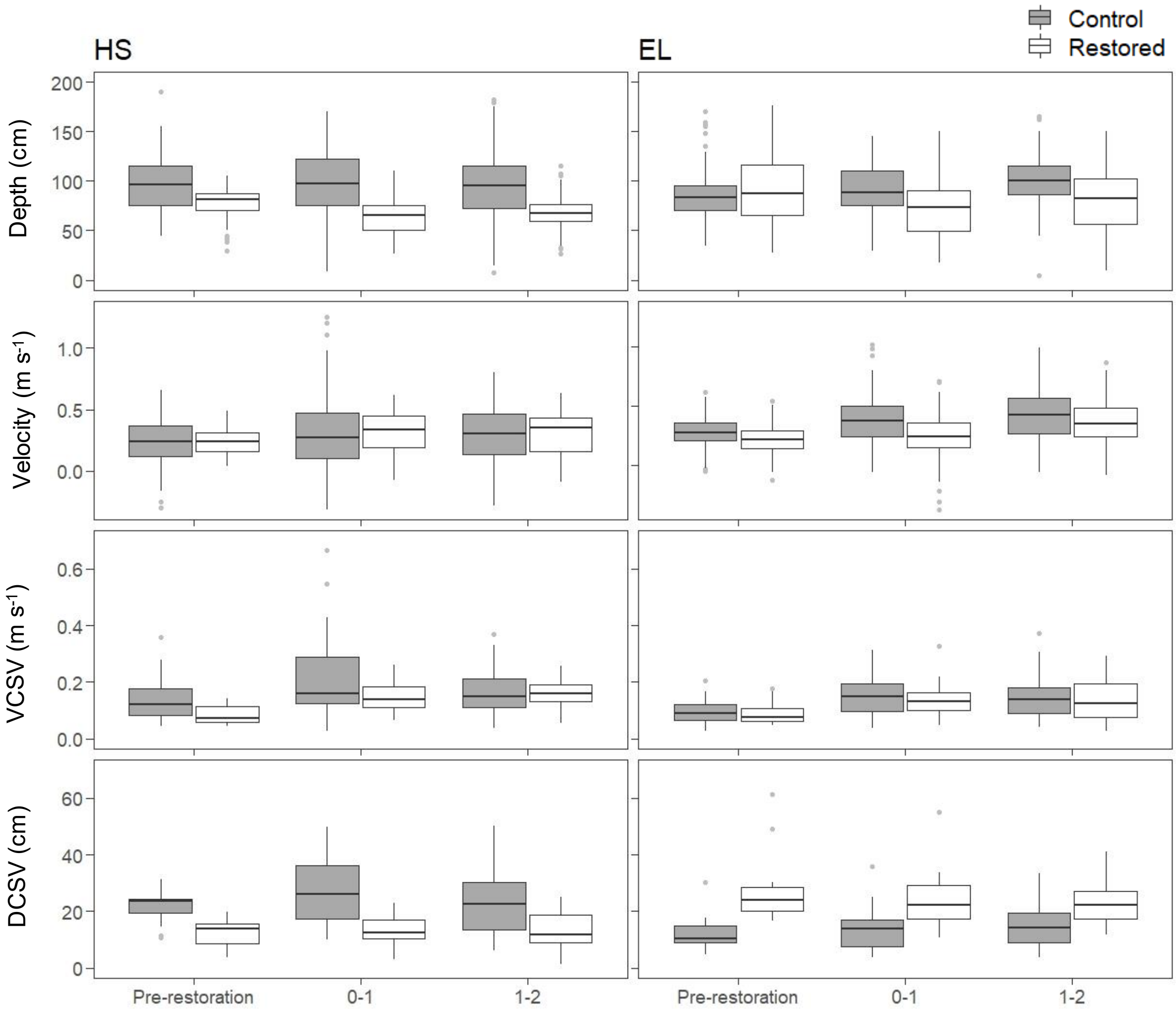


Figure 6.3 Changes in physical habitat metrics in HS and EL restored and control sites prior to and 0-1 and 1-2 years post gravel augmentation. Black bars and boxes indicate median and 25th and 75th percentiles, respectively. Whiskers represent minimum and maximum values excluding outliers. Dots show outliers (values > 1.5 x the interquartile range).

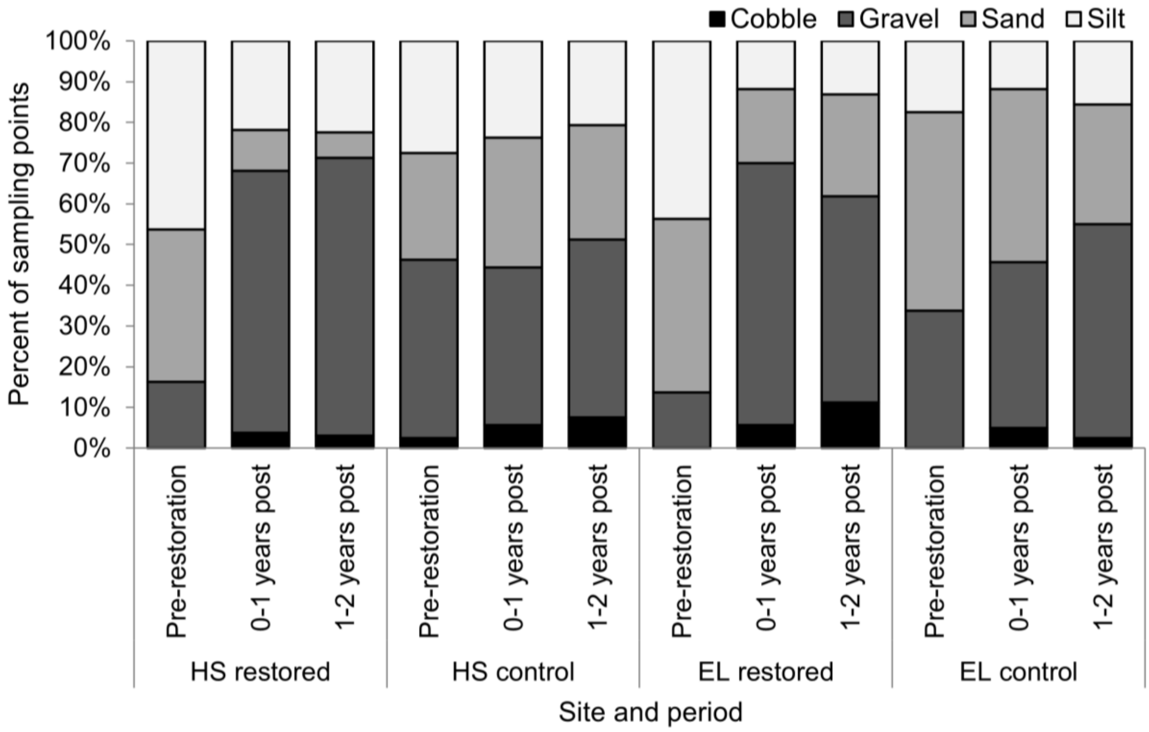


Figure 6.4 Substrate composition in restored and control reaches in HS and EL prior to and 0-1 and 1-2 years post gravel augmentation.

6.4.2 Macrophytes

Total macrophyte cover in HS and EL was influenced by sampling period, and in the case of HS also by location (Table 6.2; Figure 6.5). There was no interaction between sampling period and location. Total macrophyte cover was higher prior to restoration compared to 0-1 and 1-2 years post-restoration in HS, and higher 1-2 years post-restoration compared to pre- and 0-1 years post-restoration in EL. In HS, total macrophyte cover was higher overall in the restored reach.

In HS, an interaction between sampling period and location for filamentous green algae indicated lower cover in the restored reach during both post-restoration periods compared to pre-restoration, while there was no difference over time for the control reach. In EL, an interaction between sampling period and location was observed for broad leaved macrophytes and tape grass. However, this was marginal and post-hoc comparisons indicated the overall responses of these groups did not differ between the restored and control reach.

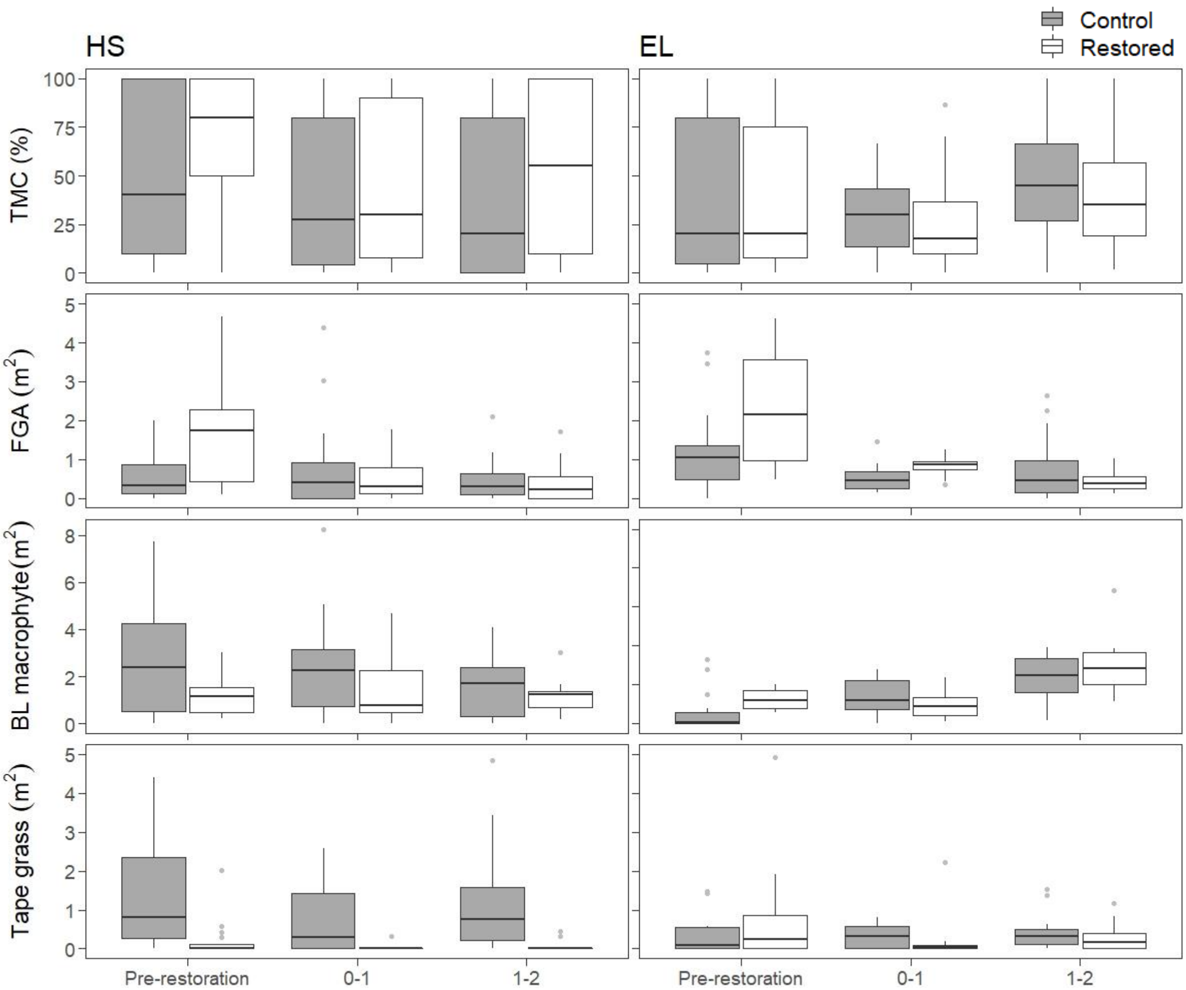


Figure 6.5 The changes in macrophyte metrics in HS and EL restored and control sites prior to and 0-1 and 1-2 years post-restoration with gravel augmentation. Black bars and boxes indicate median and 25th and 75th percentiles, respectively. Whiskers represent minimum and maximum values excluding outliers. Dots show outliers (values > 1.5 x the interquartile range). TMC = total macrophyte cover, FGA = filamentous green algae.

6.4.3 Macroinvertebrates

In total, 11,963 and 18,835 individual macroinvertebrates representing 66 and 63 families were sampled in HS and EL, respectively. Prior to restoration, dominant families were Gammaridae (mean abundance ± SD = 22.3 ± 18.4), Ephemeridae (8.6 ± 6.0) and Aphelocheiridae (7.6 ± 9.6) in HS, and Gammaridae (28.5 ± 31.5), Ephemerellidae (28.5 ± 18.3) and Bithyniidae (21.5 ± 16.5) in EL. One year after the initial survey in HS (11 months post-restoration), Gammaridae (51.4 ± 30.1) and Ephemeridae (25.6 ± 15.0) remained the most abundant families, but Valvatidae (19.4 ± 17.3) exhibited increasing numbers. Likewise, in EL (9 months post-restoration), Gammaridae (113.1 ± 47.8) and Ephemerellidae (90.3 ± 55.7) remained most abundant, but Baetidae (31.4 ± 31.4) became increasingly more frequent. The most abundant taxa remained similar (23 and 21 months post-restoration for HS and EL, respectively) at the end of the study period, although the abundance did vary. Indeed, Gammaridae (65.1 ± 22.9), Valvatidae (17.8 ± 9.4) remained abundant, but Baetidae (38.9 ± 24.7) replaced Ephemeridae as the second most abundant taxa in HS. Gammaridae (40.5 ± 34.1), Ephemerellidae (36.0 ± 25.8) and Baetidae (38.9 ± 20.8) were most abundant in EL.

In HS and EL, interactions between sampling period and location were observed for taxon richness and PSI (Table 6.2; Figure 6.6). Compared to pre-restoration values, the restored sites had a higher PSI in both post-restoration periods and a higher taxon richness 1-2 years post-restoration. Taxon richness was also lower for both sites 0-1 years compared to 1-2 years post-restoration. In HS, an interaction between sampling period and location was also observed for abundance, LIFE and EPTN. Abundance in the restored reach was higher 1-2 years post-restoration compared to pre-restoration. Post-hoc comparisons did not indicate a change in LIFE or EPTN across periods in the restored or control reach, although LIFE was lower in the restored compared to the control reach prior to restoration. In both HS and EL, there was no change in macroinvertebrate metrics between periods in the control reach.

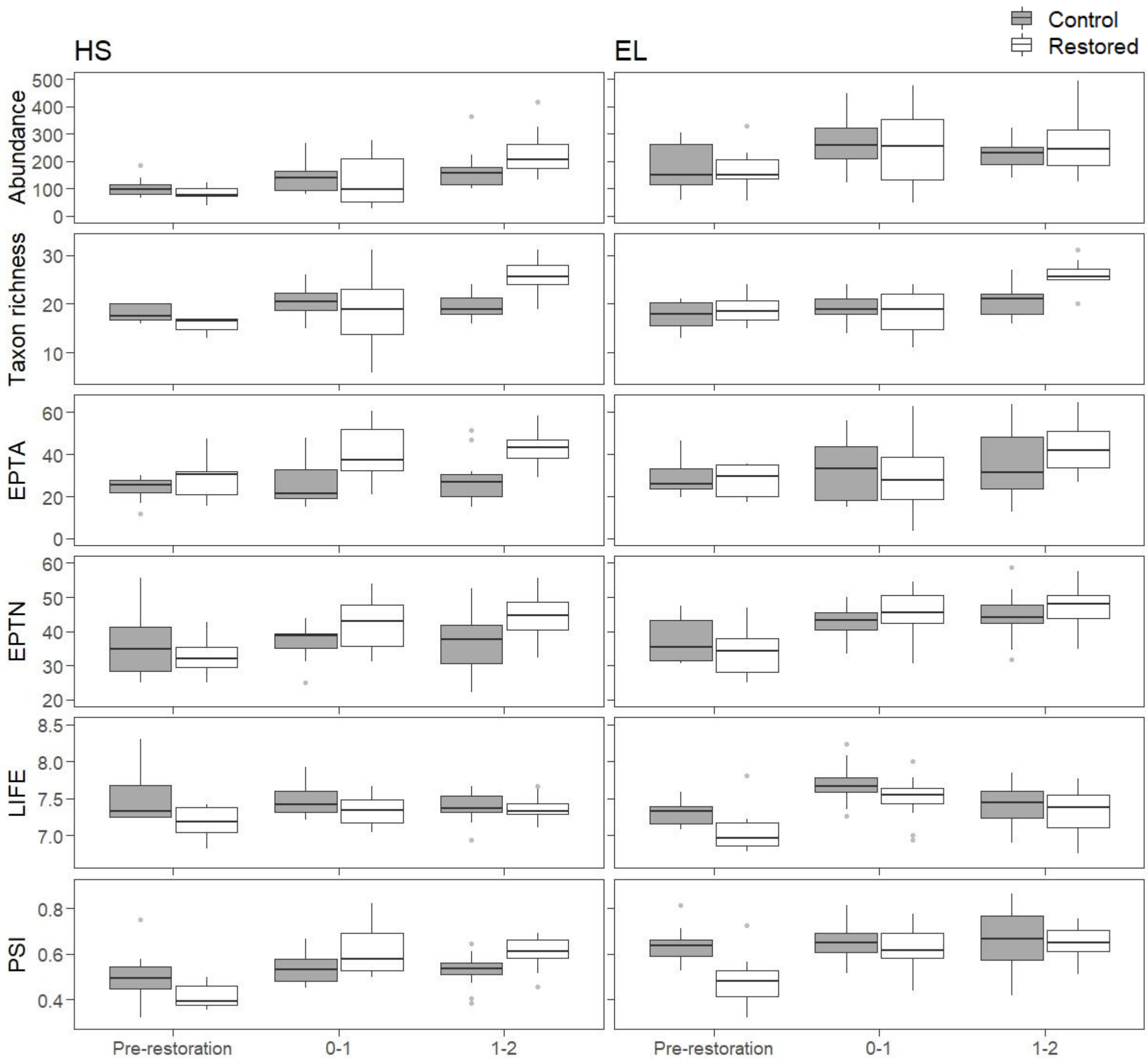


Figure 6.6 The changes in macroinvertebrate metrics in HS and EL restored and control sites prior to and 0-1 and 1-2 years post-restoration with gravel augmentation. Black bars and boxes indicate median and 25th and 75th percentiles, respectively. Whiskers represent minimum and maximum values excluding outliers. Dots show outliers (values > 1.5 x the interquartile range).

6.4.4 Fish

In total, 902 and 706 individual fish, representing eight species, were observed in EL and HS, respectively. The most common species was Eurasian minnow, which accounted for 90.2% of individuals in EL and 95.2% in HS. Brown trout (EL: 3.9%, HS: 1.0%), grayling (EL: 4.1%, HS: 1.7%), European chub (EL: 0.3%, HS: 0.7%), stone loach (*Barbatula barbatula*; EL: 0%, HS: 0.3%), European eel (EL: 0.1%, HS: 0%), three-spined stickleback (*Gasterosteus aculeatus*; EL: 0.7%, HS: 0.7) and European bullhead (EL: 0.7%, HS: 0.4%) were also observed. European eel and stone loach were exclusively observed in EL and HS, respectively.

In HS, interactions between sampling period (0-1 years and 1-2 years post-restoration only) and location for total abundance and species richness indicated higher values in the restored reach compared to the control 0-1 years post-restoration, but similar 1-2 years after (Table 6.2; Figure 6.7). In HS, both the NMax and NMean of European chub and stickleback was higher in the control and restored reach, respectively. Despite this, the occurrence of both European chub and stickleback were low (n = 5) and they were observed exclusively within these reaches. An interaction between sampling period and location for European chub indicated that individuals were only observed in the control site 1-2 years post-restoration. Furthermore, compared to the controls the restored reach exhibited a higher NMax for Eurasian minnow in HS and NMean for brown trout in EL.

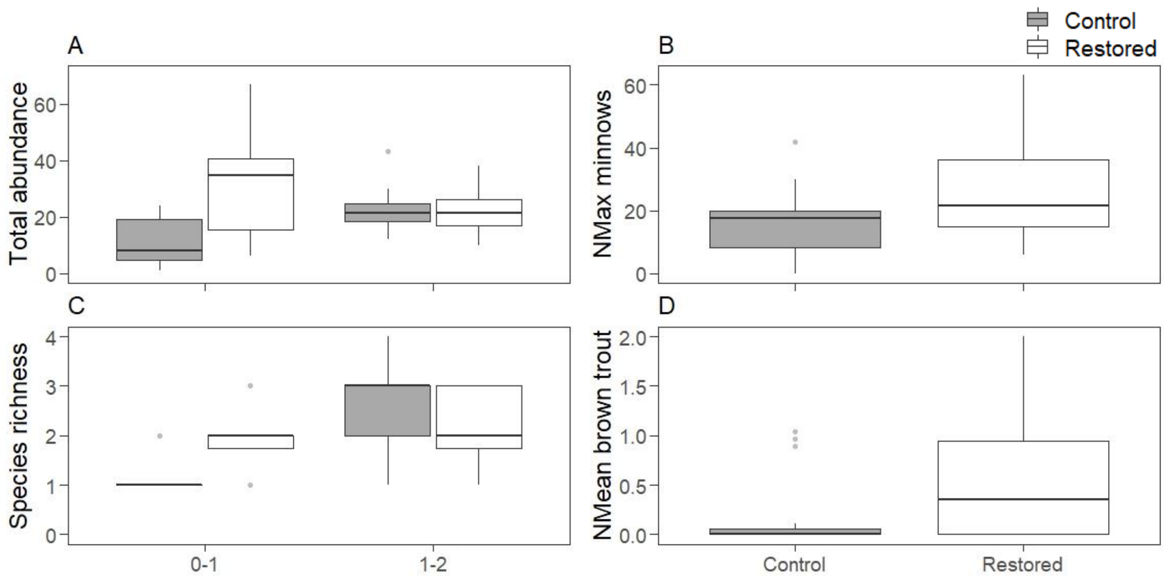


Figure 6.7 The changes in HS (A) total abundance, (B) NMax minnow, (C) species richness and (D) EL NMean brown trout in restored and control sites 0-1 and 1-2 years post-restoration with gravel augmentation. Black bars and boxes indicate median and 25th and 75th percentiles, respectively. Whiskers represent minimum and maximum values excluding outliers. Dots show outliers (values > 1.5 x the interquartile range).

6.5 Discussion

Although gravel augmentation is commonly used to improve the physical and ecological condition of sediment depleted rivers (Staentzel *et al.*, 2020), the impact on different ecological groups remains poorly understood. This study investigated the physical and ecological responses to gravel augmentation at two chalk stream restoration sites in southern England. In support of the first prediction, changes in physical habitat metrics were often immediate (e.g. increased gravel cover) and remained so for the duration of the study. However, other factors (e.g. velocity) showed little change. Likewise, and in support of the second prediction, the consequent ecological response could be considered to be mostly positive in light of the restoration goals (e.g. increase in biodiversity and improved conditions for salmonids), but also varied between sites and ecological groups. For example, whilst there was little change in macrophytes following restoration, clearer responses were observed for macroinvertebrates (e.g. enhanced dominance of silt-intolerant taxa) and fish (e.g. increased presence of brown trout and Eurasian minnow), especially in HS. Furthermore, in support of the third prediction the ecological response was often influenced by time. For example, an increase in macroinvertebrate abundance (HS only) and taxon richness was only observed 1-2 years post-restoration.

When applied at the reach scale, as in this study, the addition of gravel to a degraded river represents a feature-based restoration approach intended to enhance localised physical habitat (Mörtl and De Cesare, 2021), although it may also help re-establish more natural hydrogeomorphological processes over larger scales (Beechie *et al.*, 2010). Such interventions are hoped to result in a desired outcome related to improvement in some measure of ecological condition (e.g. ecological status: Water Framework Directive [EU Parliament Council, 2000]; biodiversity net gain: United Kingdom Environment Act [UK Government, 2021]). In chalk streams, which tend to be highly engineered, managed and hydrogeomorphological stable, it was predicted that changes to physical habitat would be immediate, and predominantly relate to a reduction in depth, and increased velocity, habitat heterogeneity and coarse substrate cover. This expectation was partially realised. At both sites, restored reaches became shallower (in EL 0-1 years post-restoration only), more gravel-dominated, and velocity became more heterogeneous in HS (1-2 post-restoration only). Conversely, mean velocity showed little change (lower 0-1 years post-restoration in the restored reach compared to the control at EL only). Furthermore, although gravel cover increased following restoration, at EL, cover was lower 1-2 compared to 0-1 years post-restoration, possibly because fine sediment input (Skinner, 2013) confounded the influence of gravel addition the year following restoration. Continued fine sediment deposition might smother introduced coarse substrates and compromise the long-term success of such an approach (Pulg *et al.*, 2013; Mitchell, 2016), illustrating the potential for the benefits of reach-scale interventions to be confounded by catchment-scale deterioration in processes (Beechie *et al.*, 2010; Bernhardt and Palmer, 2011). This problem is especially relevant in chalk streams, which typically exhibit stable flow regimes and limited stream power to redistribute fine sediments (Acornley and Sear, 1999). This emphasises the need to understand the underlying root causes of degradation and for restoration actions to take place over commensurate scales (Beechie *et al.*, 2010). Due to differences in the perception of river restoration of those involved in the United Kingdom context, and consequent willingness of riparian landowners to participate, holistic catchment-scale targets are more likely to be achieved if the planning process is based on pragmatic opportunism that embraces what may first appear to be a rather piecemeal approach. As such, reach-scale interventions that may represent feature-based approaches when viewed in isolation, may also enable the reestablishment of hydrogeomorphological processes over greater spatial and temporal scales, perhaps representing a reverse process to that which occurred over centuries when rivers were degraded through engineering.

Gravel augmentation was predicted to bring about desirable ecological change in line the restoration goals (e.g. enhanced salmonid abundance). For the most part this prediction was realised, although responses varied considerably between ecological groups and sites. Indeed, macroinvertebrates responded strongly to restoration, becoming more abundant (HS only), taxon rich and silt-intolerant taxa dominated, likely due to an increase in occupiable microhabitat formed within the interstitial spaces of the coarser substrates added (Duan *et al.*, 2008; 2009) and redistribution fine sediments. Likewise, gravel spawning brown trout and Eurasian minnow were more commonly observed in the restored reaches, supporting the observations of others (e.g. minnow [Mueller *et al.*, 2014], trout [Pedersen *et al.*, 2009]) and likely achieved through a variety of mechanisms (e.g. improved spawning conditions and young survival, migration; Roni, 2018). In contrast, the response of macrophytes to restoration was comparatively weak. Only a reduction in HS filamentous green algae was observed, potentially due to the redistribution of nutrients within fine sediment (Jones *et al.*, 2012) or because Cladophora are mid to late successional species (Dodds and Gudder, 1992) and require a longer colonisation time than provided in this study. Ecological responses to restoration are complex and can vary between systems and ecological groups as a result of a plethora of interacting factors. For example, catchment size (Carlson *et al.*, 2018) and degradation (Pulg *et al.*, 2013), substrate mobility (Albertson *et al.*, 2011) and recolonisation potential (e.g. species pools; Sundermann *et al.*, 2011) can all influence recovery, whilst differences in organism group (e.g. benthic versus open water groups), species (e.g. salmonid versus lamprey substrate requirements; Aronsuu and Virkkala, 2014; Pulg *et al.*,

2022) and life-stage (Mitchell, 2016) habitat preferences can further complicate the prediction of outcomes. Gaining a deeper comprehension of the factors that contribute to variation in response is crucial for minimising uncertainties and developing effective restoration practices. To achieve this, there is a need to promote the wider adoption of monitoring and its timely dissemination as a key component of the restoration process. This includes the reporting of results which show limited or negative effects and/ or go against the study predictions, which have historically been biased against within the restoration literature (Reid *et al.*, 2018a) but can provide valuable insights and allow for the avoidance of common pitfalls when implementing future projects (e.g. failing to consider overarching catchment scale issues; Pulg *et al.*, 2013).

The manipulation of river habitat through restoration can lead to localised ecological disturbance that may delay the realisation of desirable outcomes as communities recover (Biggs *et al.*, 1998; Merz and Ochikubo Chan, 2005; Hansen and Hayes, 2012b). For this reason, many have argued that the time-scales over which monitoring should occur must be sufficient to capture the response investigated (e.g. Kail *et al.*, 2015); in many studies this is not the case (Wohl *et al.*, 2005). It was predicted that the ecological response may be limited or even negative (e.g. decline in abundance and taxon richness) when measured within one-year of restoration and that desirable outcomes (e.g. increased abundance and taxon richness) may take longer to accrue. In this study, negative impacts were limited, with most metrics showing either positive responses (e.g. increased observations of Eurasian minnow and brown trout at HS and EL, respectively, and PSI) or no change. As predicted, positive responses in several metrics (e.g. macroinvertebrate taxon richness and abundance [HS only]) became apparent only between one and two years after restoration, likely reflecting the time required for colonisation of the restored sites (Tonkin *et al.*, 2014). Conversely, some of the ecological responses observed tended to be relatively short-lived. For example, the greater abundance and species richness of fish in HS was observed only immediately after restoration. The lack of sufficient monitoring evidenced in many studies is perhaps unsurprising considering the costs of doing so relative to the overall budget available for individual projects, particularly those that are relatively small (Roni *et al.*, 2018). One approach to resolve this challenge is to develop collaborative and co-ordinated river restoration networks to share resources and strategically plan programmes in which representative (flag-ship) projects are selected for robust monitoring over appropriate spatial and temporal scales (England *et al.*, 2021a). This will advance the collection of appropriate evidence on which future decision making can be based, learning lessons from both successes and failures.

This study indicates that gravel augmentation can positively benefit degraded chalk stream habitat and ecology, at least over limited spatial and temporal scales. However, responses to such interventions can be variable due to a multitude of factors, including physical and chemical attributes of the site, the ecological group considered, and the time since restoration. In addition to ensuring strategically selected projects are rigorously monitored using appropriate scientific techniques and field study design over appropriate spatial and temporal scales, there is also a need to adopt more holistic approaches that consider community level response, moving away from a single target species bias that typically focuses on fish (Staentzel *et al.*, 2020). The use of feature-based approaches, not in isolation, but as part of a spatially and temporally broader and integrated strategy to reinstate process-based river re-naturalisation is likely to yield benefits in the long-term. Just as rivers were degraded through engineering practices over many centuries, their regeneration will take time and likely depend on opportunistic reach-scale projects apparently conducted in a piecemeal fashion in a resource limited environment. However, the effectiveness of such may be enhanced if applied within a strategic catchment scale management framework that recognises the false dichotomy between the relative values of feature versus process based restoration.

CHAPTER 7 Restoration over time: the physical and ecological responses to restoration in an English chalk stream.

7.1 Summary

The ecological responses to river restoration often deviate from expectations. A reason for this may relate to the timescales over which projects are monitored, with a tendency for short-term monitoring (e.g. over a few years) where the initial disturbance from restoration is captured or the river ecosystem has not had time to adjust to physical alterations. To better understand restoration effectiveness, this study quantified habitat (depth, velocity, substrate composition) and macroinvertebrates at two restoration projects on the River Test (United Kingdom) over an 8-9 year period using a before-after repeated measures study design. Restoration involved gravel augmentation, bankside tree hinging/ woody material placement and planform reprofiling. At both sites, restoration enhanced habitat heterogeneity (e.g. cross sectional variability in depth) and the cover of coarse substrates (e.g. cobbles). Macroinvertebrate communities became more abundant and diverse in both projects and dominated by non-rheophilic taxa in one, likely due to an increase in habitat structure. Following the initial response, the macroinvertebrate metrics studied remained relatively stable across the study period, with the exception of a study-wide decline in several metrics (e.g. abundance and taxon richness) one/ three years post-restoration (year: 2016). The reason behind this was unclear, possibly reflecting a local disturbance (e.g. river management) or inter-surveyor variability, but demonstrates the value in carrying out longer-term appraisals with multiple temporal replicates to comprehend restoration effects more fully. Overall, this study provides evidence towards the effectiveness of restoration in chalk streams and highlights the benefits and challenges of implementing longer term monitoring with strong study designs. It is recommended that funding and efforts are directed towards the robust, long-term appraisal of a network of flagship case studies to help provide the evidence and guidance required to implement effective restoration strategies.

7.2 Introduction

River restoration has become a global priority to mitigate the impacts associated with historic physical modification (United Nations, 2023; European Commission, 2000). Typically, these projects have focussed on the enhancement of habitat for specific biotic groups/ species (e.g. salmonids; Zeug *et al.*, 2014) or more broadly target diversity and river function (Addy *et al.*, 2016), and may use a variety of form (e.g. woody material placement, flow deflectors, e.g. Pretty *et al.*, 2003) and/ or process-based (e.g. infrastructure removal; e.g. Stanley *et al.*, 2002) approaches. Whilst the number of restoration projects and appraisals are growing (RESTORE, 2023; Web of science, 2023), inter-project variability in ecological responses has remained high (Friberg *et al.*, 2016). For example, whilst some studies report desirable ecological outcomes as expected (e.g. increased macroinvertebrate and macrophyte diversity: Staentzel *et al.*, 2018a), others have found limited (e.g. fish: Pretty *et al.*, 2003; macroinvertebrates: Harrison *et al.*, 2004), temporary (e.g. Pulg *et al.*, 2013) and even negative effects (e.g. decreased macroinvertebrate density; Orr *et al.*, 2008a). Several factors potentially contribute to these mixed responses, including the targeting of restoration at inappropriate scales (Polvi *et al.*, 2020), poor goal setting (Suding, 2011), the failure to address the root cause of degradation (Pulg *et al.*, 2013; Wolff *et al.*, 2021), a poor site recovery potential (e.g. a lack of species pools for recolonisation; Sundermann *et al.*, 2011), inadvertent impacts of the restoration (Albertson *et al.*, 2011) and low-levels of monitoring (Pander and Geist, 2013) conducted over insufficient temporal scales to adequately capture ecological response (Feld *et al.*, 2011; Kail *et al.*, 2015).

Understanding the physical and ecological responses to restoration over a sufficiently long timescale is key for the development of sound restoration practice (Lu *et al.*, 2019; England *et al.*, 2021a). Indeed, whilst the time since restoration has been shown to be a key predictor of ecological response (e.g. Kail *et al.*, 2015), trajectories can also be non-linear (e.g. the reversal of initial benefits due to gradual silt ingression; Pulg *et al.,* 2013) and vary with site characteristics (e.g. river discharge; Carlson *et al.*, 2018), colonisation potential (Langford *et al.*, 2009), the ecological group of interest (Thompson *et al.*, 2018b) and restoration approach taken (Gilvear *et al.*, 2013; Al-Zankana *et al.*, 2020). As such, longer-term appraisals are needed to develop a more comprehensive understanding of project effectiveness, recovery times, adaptive management requirements and the influence of environmental variables and perturbation (e.g. flood events; England *et al.*, 2008; Weber *et al.*, 2018). Ultimately, these appraisals reduce the uncertainties surrounding restoration and contributes to an evidence base that can guide future restoration design, with the view of maximising the probability of achieving intended outcomes.

Despite the importance of longer-term appraisals, they remain rare. This is in part due to the limited funding typically allocated toward appraisal, in addition to the resource intensiveness of robust monitoring, challenges with implementation (e.g. when focal sites are subjected to further manipulation) and the desire for immediate results to satisfy stakeholders (Palmer *et al.*, 2007; Smith *et al.*, 2014; Borgström *et al.*, 2016). For example, a review of 74 restoration appraisals found monitoring was conducted for a median duration of 2.5 years (Feld *et al.*, 2011). Gauging the timescale of monitoring required to sufficiently capture responses following restoration is difficult and requires consideration of an array of factors. For example, systems with lower stream power may lack the ability to mobilise bedload sediments, consequently relying more upon ecological processes to generate complexity and potentially extending the time taken to respond to restoration (CaBA, 2021). Furthermore, rivers with degraded water quality may have experienced widespread ecological extirpation, and thus contain limited species pools for recolonisation slowing the rate of recovery (Langford *et al.*, 2009). In these instances, short-term monitoring may lead to misleading conclusions, highlighting the need for longer-term appraisals to accurately understand project effectiveness.

This study quantified the responses of physical habitat and benthic macroinvertebrates over an 8-9 year period at two case study restoration projects (e.g. gravel augmentation, bankside tree hinging, woody material placement) on the River Test (Hampshire, United Kingdom). It was predicted that the restoration would: (1) enhance velocity, the cover of coarse substrates and depth and velocity heterogeneity whilst reducing depth and silt cover. (2) Increase macroinvertebrate abundance and taxon richness and the contribution of EPT, silt-intolerant and rheophilic taxa to the community. Additionally, (3) the ecological responses to restoration were predicted to change over time. More specifically, based on the responses observed in Chapter 5 and Chapter 6, macroinvertebrates were expected to rapidly respond to the restoration, as with prediction 2. Over time, the abundance, taxon richness and contribution of EPT to the community was predicted to increase, e.g. as rarer taxa recolonised, reproduction/migration increased population size and habitat developed (e.g. macrophyte mosaics, woody materials inputs).

7.3 Methods

7.3.1 Study sites

This study monitored physical habitat and macroinvertebrate communities at two restoration sites, Old Station Beat (OSTN) and Old Stews Beat (OSTW), at Bossington Estate, a recreational dry fly fishery on the River Test (see Chapter 4 for background on the River Test; Figure 7.1). Prior to restoration, both reaches were straightened, widened, dredged and silted and deemed to be in a deteriorated ecological condition (Cain Bio Engineering, 2020; 2023). As part of the Test and Itchen Restoration Strategy, 450 m of OSTN and 250 m of OSTW was restored in October 2013 and September 2015, respectively (Environment Agency, 2015). The aim of the projects were broadly to create a more 'naturalised' chalk stream habitat and community. Both projects involved bed raising and the creation of geomorphic features (e.g. pools) using site-won washed mixed size coarse substrates (OSTN = 1,600 tonnes, OSTW = 2,500 tonnes), bank and planform reprofiling, bankside tree hinging/ woody material placement and channel narrowing. In OSTN, the restoration additionally involved creating several backwater scrapes. In 2019, two approximately 1 m diameter pools were created in OSTN using a long-reach excavator (see Figure 7.1 for position of scrapes and pools). Overall, this was expected to have a limited impact on the rest of the reach.

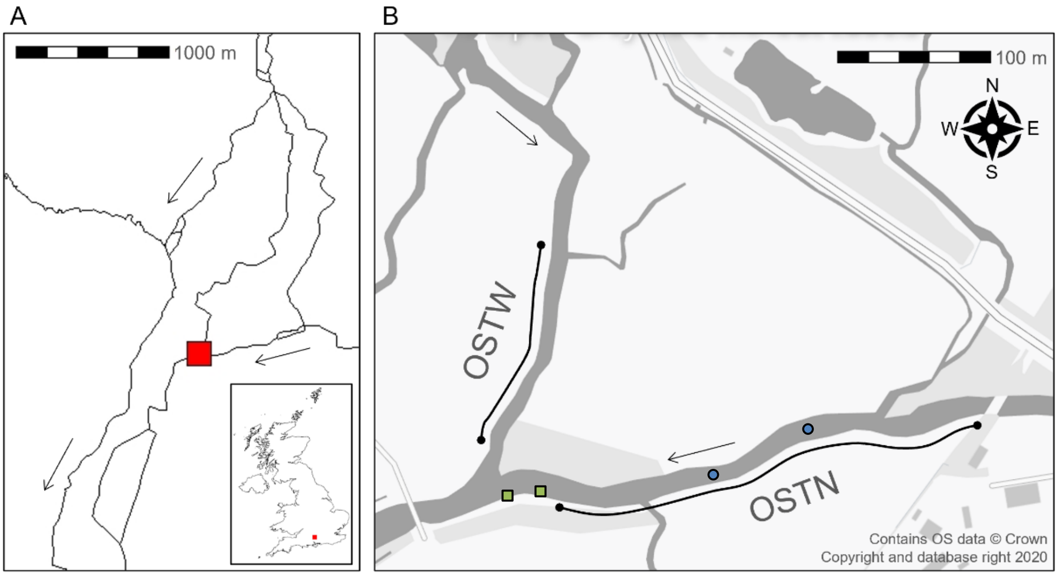


Figure 7.1 (A) Location of the restoration sites (red box) studied on the River Test (Hampshire, United Kingdom) with greater detail for (B) OSTN and OSTW monitoring sites. Arrows show direction of flow. Blue dots and green squares show the approximate location of the small pools created in 2019 and backwater scrapes, respectively. River and United Kingdom shapefile used in 'A' was obtained from Ordnance Survey (2022) and GADM (2023), respectively. Map in 'B' was obtained from Ordnance Survey (2016).

Data was collected as part of several undergraduate student research projects (data in 2020 and 2021 was collected as a part of this thesis) in a before-after, repeated measures study design across 300 m of OSTN and 140 m of OSTW. The original intention was that OSTW would represent a control to better enable the quantification of responses in OSTN. However, the subsequent restoration of this reach meant two restored sites were monitored in a before-after design. Measurements were taken at 16 and eight transects situated at 20 m intervals across OSTN and OSTW, respectively. Surveys were carried out in September 2013 (OSTN only) and July/August 2014, 2016, 2020 and 2021 (Figure 7.2). As such, one pre- and three (OSTW) or four (OSTN) post-restoration surveys were conducted. Available data collected for Water Framework Directive monitoring in the local area showed physio-chemical, hydromorphological and macroinvertebrate classifications remained consistent between 2013 and 2019 (DEFRA, 2022b). The area was impacted moderately by copper and lead in 2014, and by mercury and polybrominated diphenyl ethers in 2019, but this did not alter macroinvertebrate classifications (DEFRA, 2022b).

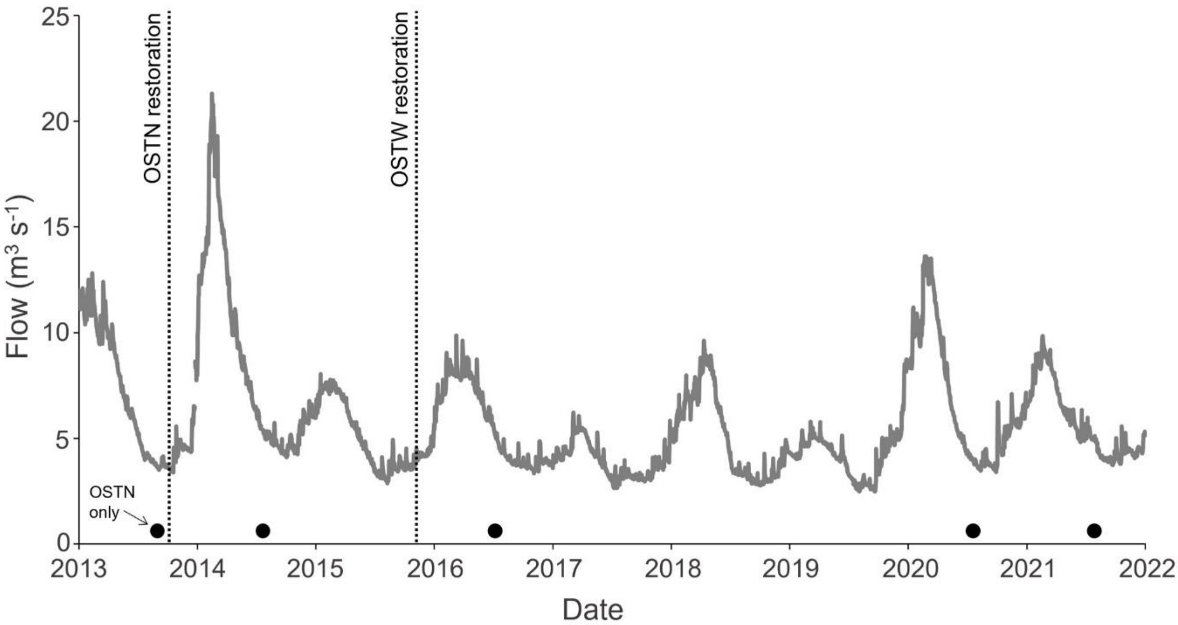


Figure 7.2 Flow on the River Test throughout the study period. Circles on the x-axis and dashed lines show data collection periods and the dates of restoration for OSTN and OSTW, respectively. Flow data from Chilbolton flow gauging station (DEFRA, 2021). Contains public sector information licensed under the Open Government Licence v3.0.

7.3.2 Physical habitat

Depth (cm), velocity (m s^{-1}; mean of ten readings over 10 secs at 1 Hz at 60 % depth from the substrate to surface using a Valeport Model 801 flow meter) and dominant substrate (silt [0.0039-0.123 mm], sand [0.125-2 mm], gravel [2-64 mm], cobble [> 64 mm] in a 50 cm^2 quadrat) was assessed at three equidistant points across each transect. DCSV and VCSV was calculated as the standard deviation of the three measurements taken across each transect. To visualise spatial changes in depth, velocity and dominant substrate, interpolation maps were created in ArcMap 10.8 (ArcGIS, 2020) using river boundary and sampling point coordinates collected from Google (2022) and inverse distance weighting.

7.3.3 Macroinvertebrates

Macroinvertebrates were sampled using a standard 3 minute kick sample and 1 minute hand search (e.g. water surface, beneath larger substrates) with a 250 mm^2 square-framed net (1 mm mesh; WFDUK, 2022). Samples were collected from nine dedicated sampling points across each site throughout the study. After collection, samples were stored in labelled 1.2 L sampling pots in 70% methylated spirit. All samples were identified within a month of collection. Samples were poured through a 30 µm sieve, washed lightly with tap water, and placed in a white tray with water. The sample was sorted by hand using tweezers, collecting all macroinvertebrates observed. Macroinvertebrates were identified to the family level, aside from Oligochaeta and Nematomorpha which were classified as such, using a compound microscope (Motic ST-30) and identification guide (Dobson, 2012). Following identification, the abundance, taxon richness, EPTA, EPTN, LIFE (Extence *et al.*, 1999) and PSI (Extence *et al.*, 2010) was calculated for each sample.

7.3.4 Macroinvertebrate control datasets

Natural fluctuations in macroinvertebrates across time were controlled for by collating datasets from Environment Agency (Environment Agency, 2023b) and Salmon and Trout Conservation group (SmartRivers, 2023) databases. Macroinvertebrate datasets collected using standard 3 minute kick samples from the River Test and its tributaries (e.g. River Anton) between 2013 and 2021 were taken. To help control for differences between seasons, only data collected between May and October was extracted. Where multiple datasets were taken in the same location in a year, the mean of the metrics for each sample was used. To ensure sites had not been previously effected by restoration, the

River Restoration Centre's NRRI (River Restoration Centre, 2023b) was checked, and any datasets potentially influenced by restoration were excluded. Direct statistical analyses were not possible due to the lack of sites and samples in certain years (i.e. 2020/2021). Therefore, metrics were plotted which allowed a visual assessment of the background level of variability in metrics over time.

7.3.5 Statistical analysis

Each restoration site was analysed separately. Prior to analysis, macroinvertebrate abundance was log transformed. Statistical analysis was carried out in R Studio (R Studio Team, 2020) and the packages ggplot2 (Wickham, 2016), Lme4 (Bates *et al.*, 2015), LSmeans (Lenth, 2016), performance (Lüdecke *et al.*, 2020), patchwork (Pedersen, 2020), nparLD (Noguchi *et al.*, 2012) and nparcomp (Konietschke *et al.*, 2015).

To quantify the responses of physical habitat and macroinvertebrate metrics to restoration over time, GLMMs (taxon richness) with a Poisson error distribution and log-link function and LMMs (all other metrics aside from substrate cover) were created. As with Chapter 6, NPMs, which are free of distributional assumptions and robust to small sample sizes and outliers (Noguchi *et al.*, 2012), was used to assess changes in substrate cover. Models included the term 'year' as a fixed factor and 'transect/sampling point' as a random/subject factor to account for repeated measures. For mixed models, the significance of year was assessed using likelihood ratio tests by comparing full and null models (i.e. not containing 'year') and model assumptions were checked using QQ and fitted vs residual plots. For all models, significant effects of year were further investigated using TukeyHSD pairwise comparisons. For the non-parametric analysis, these were carried out using the 'mctp.rm' function in 'nparcomp' (Konietschke *et al.*, 2015).

7.4 Results

7.4.1 Physical habitat

Differences between sampling years were found for all physical habitat metrics in OSTN (Table 7.1; Figure 7.3; 7.4, 7.5a). Compared to the pre-restoration sample in 2013, depth was greater in all post-restoration samples, DCSV was higher in 2014 and 2016, velocity was lower in 2016 and 2020, and VCSV was higher in 2014 (Appendix C: Table C1 for physical metrics post-hoc statistics). Additionally, the cover of cobble was higher and sand lower in 2020 and 2021, and silt cover was higher in 2020. Compared to immediately after restoration in 2014, velocity and VCSV was lower in 2016, 2020 and 2021, DCSV and gravel cover was lower and cobble cover higher in 2020 and 2021, and silt cover was higher in 2020. Compared to three years post-restoration in 2016, sand cover was lower and silt higher in 2020 and cobble cover was greater in 2020 and 2021.

Table 7.1 Results of GLMMs, LMMs and NPMs assessing the responses of physical habitat and ecological metrics to restoration in OSTN and OSTW. Significant p values are in bold.

Variable	Model	OSTN			OSTW		
		X2/ATS	*df*	*p*	*X2/ATS*	*df*	*p*
Depth	LMM	**42.833**	**4**	**< 0.001**	**11.437**	**3**	**< 0.01**
Velocity	LMM	**36.817**	**3**	**< 0.001**	**14.027**	**3**	**< 0.01**
DCSV	LMM	**27.341**	**4**	**< 0.001**	**32.817**	**3**	**< 0.001**
VCSV	LMM	**15.104**	**4**	**< 0.01**	0.578	3	0.901
Cobble	NPM	**8.259**	**2.5**	**< 0.001**	**6.258**	**2.3**	**< 0.01**
Gravel	NPM	**5.766**	**3.5**	**< 0.001**	1.473	2.6	0.225
Sand	NPM	**6.220**	**3.3**	**< 0.001**	**3.892**	**2.0**	**< 0.05**
Silt	NPM	**4.141**	**3.5**	**< 0.01**	1.467	2.3	0.229
Abundance	LMM	**55.567**	**4**	**< 0.001**	**27.902**	**3**	**< 0.001**
Taxon richness	GLMM	**61.640**	**4**	**< 0.001**	**65.222**	**3**	**< 0.001**
EPTA	LMM	9.008	4	0.061	**8.314**	**3**	**< 0.05**
EPTN	LMM	**14.070**	**4**	**< 0.01**	5.742	3	0.125
PSI	LMM	**21.359**	**4**	**< 0.001**	6.796	3	0.079
LIFE	LMM	**25.849**	**4**	**< 0.001**	1.035	3	0.793

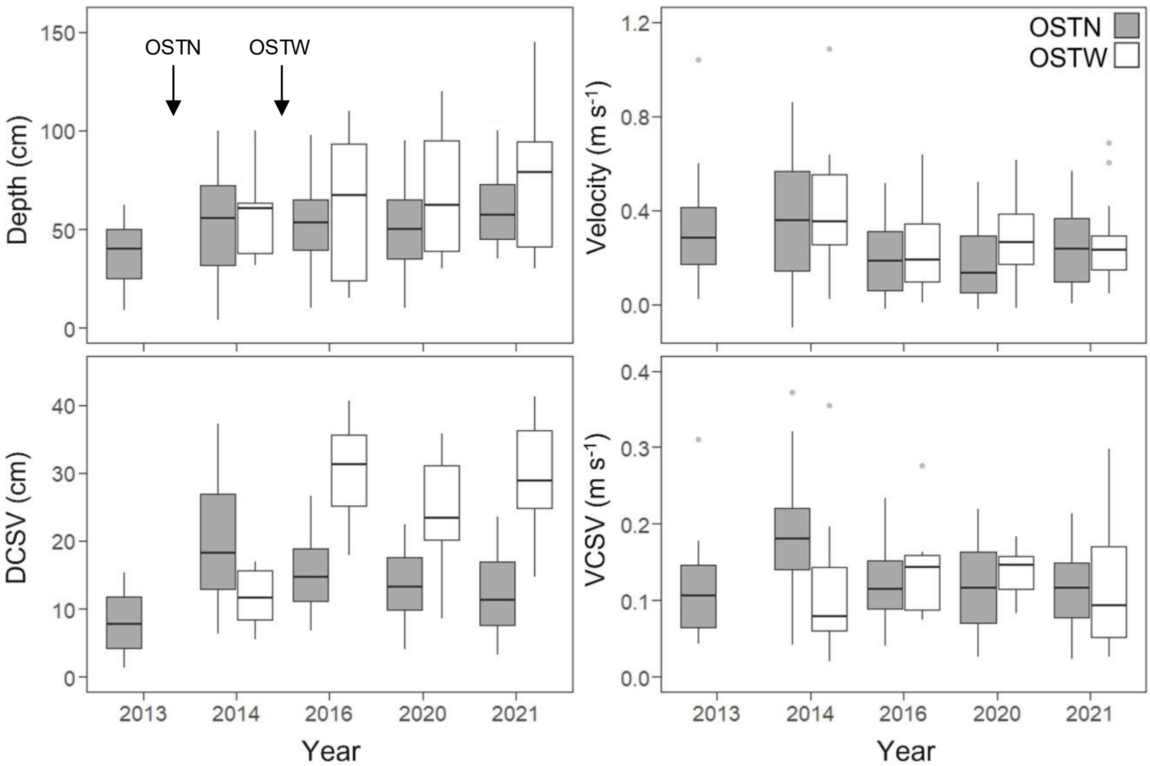


Figure 7.3 Physical habitat metrics in OSTN and OSTW across years. Arrows show point of restoration. Black bar and boxes show median and 25th and 75th percentile, respectively. Whiskers represent minimum and maximum values excluding outliers. Dots show outliers (values > 1.5 x the interquartile range).

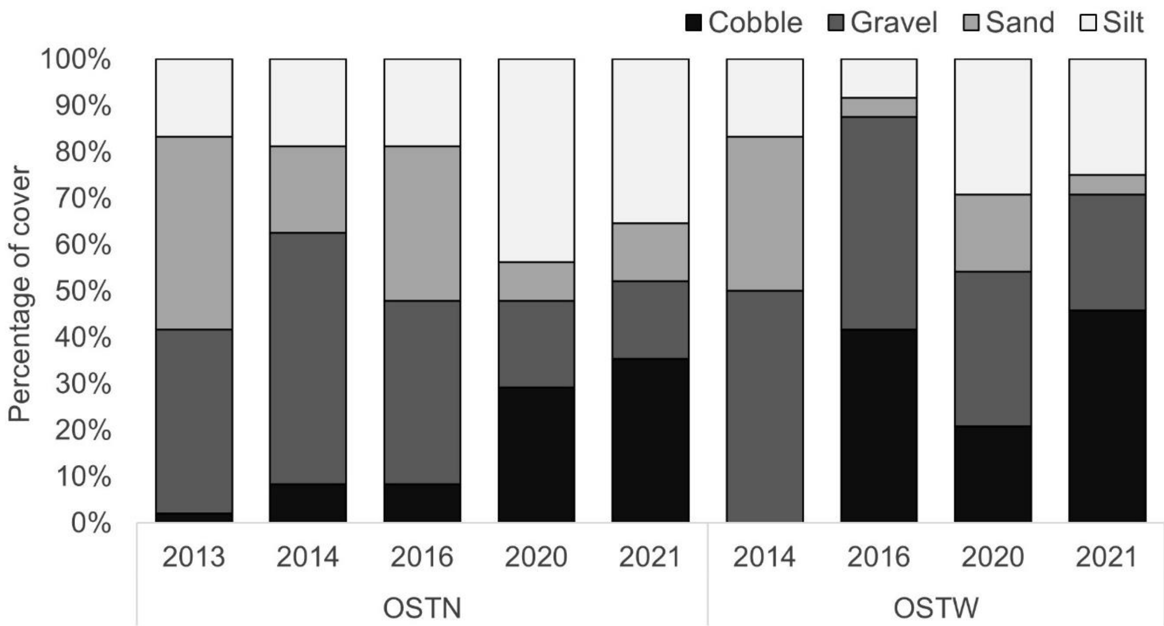


Figure 7.4 The percentage of sampling points in OSTN and OSTW in which each substrate was dominant.

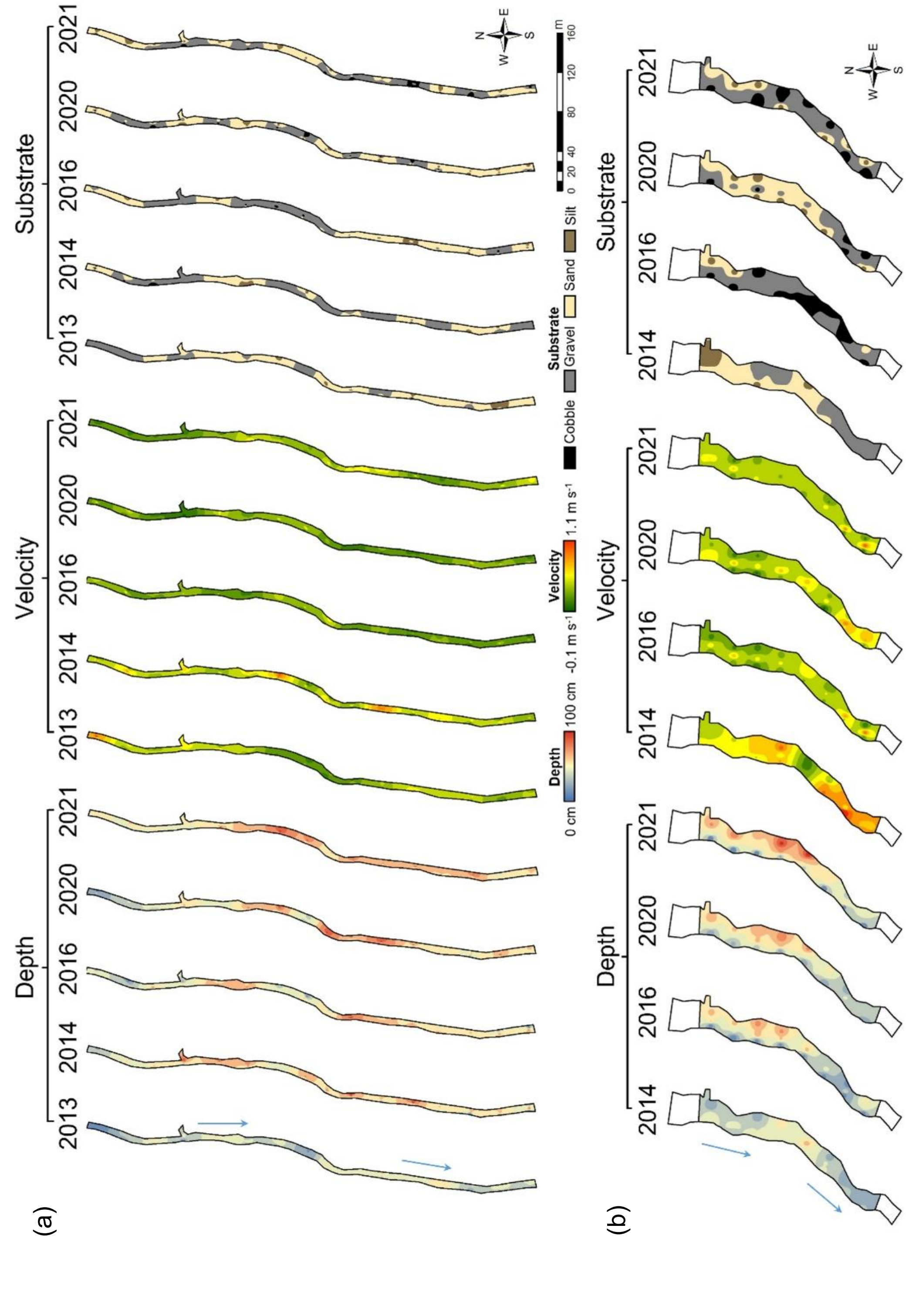


Figure 7.5 Spatial variability in depth, velocity and substrate cover across the study period for (a) OSTN and (b) OSTW. Blue arrows indicate flow direction.

In OSTW, an effect of year was found for depth, velocity, DCSV and cobble and sand cover (Table 7.1; Figure 7.3; 7.4, 7.5b). All differences were between the 2014 pre-restoration and post-restoration samples. Compared to 2014, DCSV was higher in all post-restoration sampling years, velocity was lower and cobble cover higher in 2016 and 2021, and depth was higher in 2021. No differences between years were found for sand cover in the post-hoc analysis.

7.4.2 Macroinvertebrates

Visualisation of routine macroinvertebrate monitoring data collected away from restoration sites within the River Test catchment, used here as a control for potential catchment scale effects, showed low levels of variation over time (Appendix C: Figure C1). The greatest variation was between 2019-2021 and likely reflects the low number of samples available.

In OSTN, 11,236 individuals belonging to 60 different families were found. Prior to restoration, Gammaridae (mean abundance ± SD = 23.0 ± 24.0), Elmidae (21.0 ± 18.8) and Ephemeridae (20.4 ± 11.0) were dominant. In the year following restoration, Gammaridae (70.1 ± 44.6) remained the most common taxa, but Planorbidae (57.1 ± 75.6) and Philopotamidae (24.0 ± 40.7) were increasingly dominant. Gammaridae (19.3 ± 26.6), Planorbidae (6.8 ± 4.3) and Ephemeridae (6.7 ± 9.0) were most common in 2016. In 2020 and 2021, Gammaridae (2020 = 193.9 ± 168.2, 2021 = 102.1 ± 56.4) and Ephemerellidae (2020 = 91.6 ± 51.0, 2021 = 65.4 ± 52.1) were the most abundant taxa, followed by Elmidae (35.4 ± 37.5) and Baetidae (38.3 ± 31.2) in 2020 and 2021, respectively.

An effect of year was found for abundance, taxon richness, EPTN, LIFE and PSI in OSTN (Table 7.1; Figure 7.6). Abundance and taxon richness were higher in 2014, 2020 and 2021 compared to pre-restoration (2013) and 2016 (Appendix C: Table C2 for macroinvertebrate metrics post-hoc statistics). No differences in abundance or taxon richness were found between 2014, 2020 and 2021. LIFE was greater in 2013 compared to 2014, 2016 and 2021, and 2020 compared to 2014 and 2016. EPTN was higher in 2013 compared to 2016. PSI was lower in 2016 compared to 2020 and 2021.

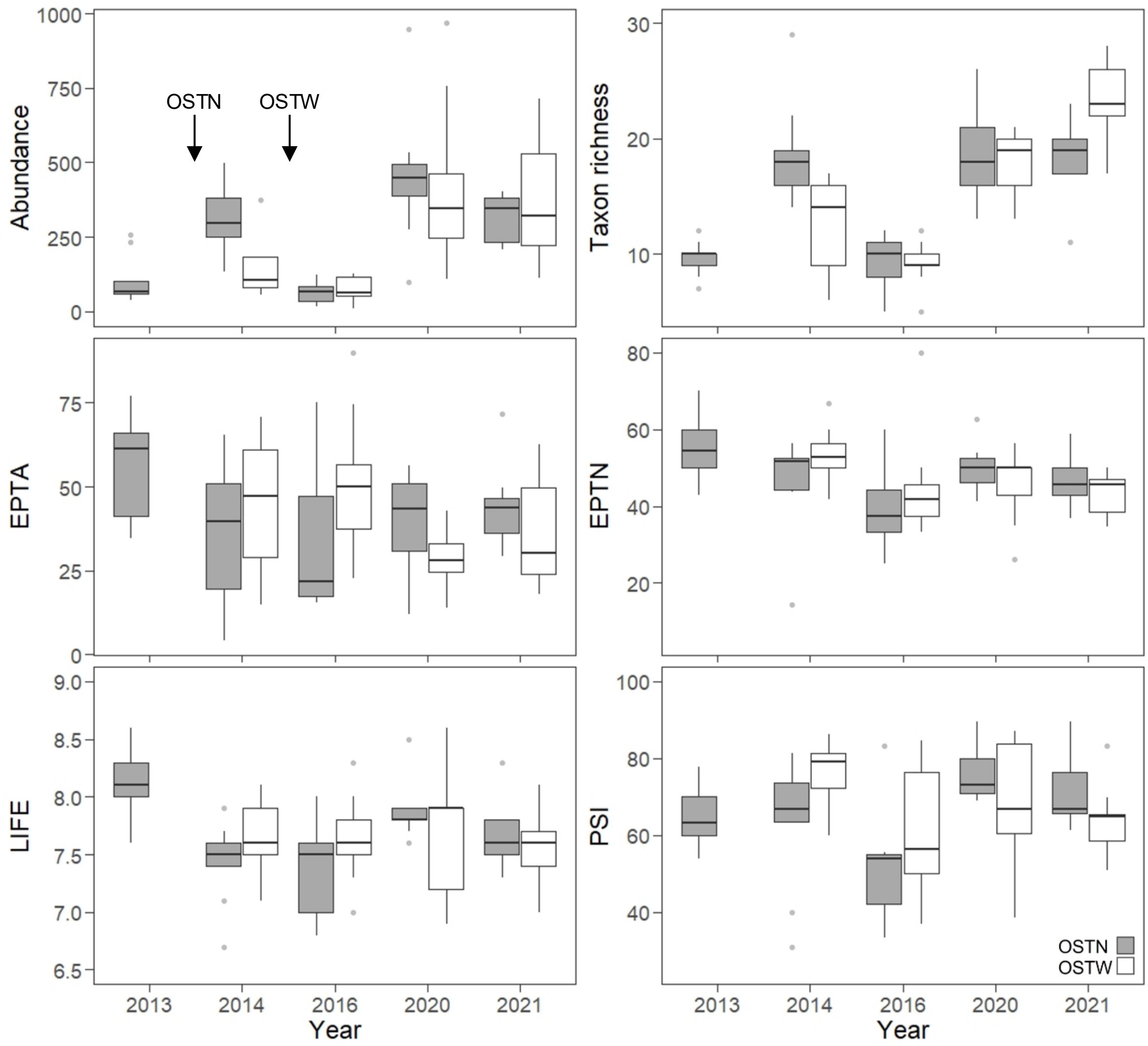


Figure 7.6 Changes in macroinvertebrate metrics in OSTN and OSTW across years. Arrows show point of restoration. Black bar and boxes show median and 25th and 75th percentile, respectively. Whiskers represent minimum and maximum values excluding outliers. Dots show outliers (values > 1.5 x the interquartile range).

A total of 8,976 macroinvertebrate individuals belonging to 65 different families were found in OSTW. Prior to restoration, OSTW was dominated by Elmidae (25.9 ± 17.3), Goeridae (25.6 ± 33.0) and Neritidae (12.4 ± 13.2). In 2016, the dominant taxa shifted to Gammaridae (19.4 ± 18.5), Ephemerellidae (14.1 ± 14.9) and Ephemeridae (11.1 ± 9.8). Gammaridae (2020 = 239.9 ± 235.4, 2021 = 127.4 ± 108.0) and Ephemerellidae (2020 = 58.2 ± 43.1, 2021 = 45.1 ± 58.6) remained dominant in 2020 and 2021, whilst Chironomidae (20.8 ± 18.8) and Baetidae (35.6 ± 49.8) were the third most abundant taxa in 2020 and 2021, respectively.

An effect of year was found for abundance, taxon richness and EPTA in OSTW (Table 7.1; Figure 7.6). Macroinvertebrate abundance and taxon richness was lower in 2014 and 2016 compared to 2020 and 2021. No difference in abundance or taxon richness were found between 2014 and 2016 samples. No differences between years were found in the post-hoc analysis for EPTA.

7.5 Discussion

Restoration can play an important role in mitigating the impacts associated with historic river modification (United Nations, 2023). Despite this, the effectiveness of these interventions often deviate from expectations (e.g. Orr *et al.*, 2008a), in part due to a lack of monitoring and poor understanding of longer-term effects (Pander and Geist, 2013; England *et al.*, 2021a). This study assessed physical habitat and macroinvertebrates at two chalk stream restoration projects over an 8-9 year period. Partially in support of the first prediction, several physical elements clearly adjusted to the restoration (e.g. increased DCSV), whilst others unexpectedly showed little response (e.g. VCSV). Likewise, whilst several macroinvertebrate metrics were enhanced by the restoration (e.g. abundance, taxon richness), others did not change (e.g. PSI). Little evidence was found in support of the third prediction that macroinvertebrate metrics would change over time as populations and habitat recovered. However, a notable decline in several metrics in 2016 (e.g. abundance) highlighted the value in longer-term monitoring to attain a fuller understanding of restoration effectiveness.

Both projects were intended to revitalise historically modified and degraded channels back towards a more ‘naturalised’ state, which was expected to enhance prospects for local ecology (e.g. biodiversity). This was expected to be realised through a reduction in depth and increase in velocity, coarse substrate cover and habitat heterogeneity (DCSV, VCSV). This prediction was partially met for both projects. For instance, DCSV increased immediately in both sites, likely driven by the construction of geomorphic features such as pools. The cover of larger (cobble) substrates also increased, although in OSTN this was not realised until seven years after restoration suggesting habitat continued to develop throughout the study. A notable event was a period of flood in 2014, which occurred several months following the OSTN restoration and likely facilitated the rapid restructuring of sediments, e.g. by transporting new substrates into the reach (Kil and Bae, 2012; Arnaud *et al.*, 2017). This possibly explains why little change was found to sediment composition immediately following the restoration of OSTN, despite introducing coarse substrates. Environmental stochasticity represents a major source of 'aleatoric' uncertainty in restoration, and may influence the predicted timeframe and/ or magnitude of physical and ecological response (van Asselt and Rotmans, 2002; Wheaton *et al.*, 2008). Unlike other sources of uncertainty, which may be accounted for by developing a deeper knowledge base, i.e. 'epistemic' uncertainty (e.g. Applestein *et al.*, 2021), stochastic events are often impossible to predict or eliminate (Yoe *et al.*, 2010), and so should be embraced within the restoration process. For example, it is possible to account for some potential impacts associated with stochasticity within design phase modelling (van Vuren *et al.*, 2016). Furthermore, by clearly communicating the risks and range of possible outcomes of restoration to stakeholders and adequately monitoring to facilitate adaptive management, it is possible to reduce the severity of backlash if outcomes deviate from expectations (Downs and Kondolf, 2002; Wheaton *et al.*, 2008).

Manipulation of the physical condition of both reaches was predicted to bring about changes in ecological community, realised through an increase in macroinvertebrate abundance, taxon richness and the contribution of EPT, rheophilic and silt-intolerant taxa to the community. In support of this prediction, macroinvertebrate abundance and richness increased in both sites across all post-restoration data collection periods, except 2016. It is likely this response was driven by an increase in occupiable space and niches through the enhancement of riverbed structure (Duan *et al.*, 2008; Barnes *et al.*, 2013), as well as the connectivity of the site to nearby species pools to facilitate recolonisation (Sundermann *et al.*, 2011). A reduction in LIFE in OSTN indicated that the community also became comprised of more non-rheophilic taxa. This was unexpected, but may reflect an enhancement in habitat structure (e.g. woody materials) which can offer refuge to taxa less tolerant to high flows (e.g. Mathers *et al.*, 2022). Whilst the ecological responses observed here were generally positive in light of the restoration goals and supported (e.g. Merz and Ochikubo Chan, 2005; England *et al.*, 2021b), they are not universal, with other chalk stream restoration projects exhibiting contrasting outcomes (e.g. little change in benthic macroinvertebrates; Harrison *et al.*, 2004; Robertson *et al.*, 2021). The reasons behind these variable responses are often poorly understood and complex. For example, studies have shown when regional habitat quality is low or high, it plays a greater role in structuring communities than localised habitat due to insufficient propagules for colonisation and mass effects, respectively (Stoll *et al.*, 2016). In this case, the River Test may have offered an intermediate regional habitat quality, providing sufficient propagule pressure to facilitate recovery but not offset local sorting processes. This theory is supported in that only 48% of River Test Water Framework Directive classification sites were ‘good ecological status’ or above (Environment Agency, 2021b). Developing a greater understanding of the factors which drive inter-project variability in response is key for enhancing the capacity to predict restoration outcomes (Brudvig and Catano, 2021). One way to achieve this is through the implementation of meta or coarse scale analyses specifically designed to determine causal drivers behind project failures (Kail *et al.*, 2015; Carlson *et al.*, 2018). To facilitate this, there is therefore a need to not only to ensure projects are adequately monitored, but that all data, regardless of the result, is swiftly disseminated.

Following the initial response, it was expected that several macroinvertebrate metrics would adjust over time, e.g. as rarer taxa recolonised or habitat developed (Lorenz, 2021; Sinclair *et al.*, 2023). There was little evidence in support of this prediction, with the initial changes in OSTN macroinvertebrates remaining relatively consistent across the study period, aside from in 2016. In OSTW, changes over time were difficult to quantify due to what appears to be a study wide decline in several metrics the year following restoration (e.g. taxon richness), which likely overshadowed the assessment of initial response. The speed and longevity of ecological response in OSTN shows similarities with other chalk stream projects (e.g. England and Peacock, 2010) and may have been influenced by an array of factors including the proximity of species pools (Sundermann *et al.*, 2011) and patch connectivity (Tonkin *et al.*, 2014). In chalk streams, which typically respond slowly to physical modification (Sear *et al.*, 1999), process-based approaches may take years or even decades to attain sought after changes (CaBA, 2021). Therefore, the use of what could be considered traditionally as feature-based approaches, e.g. large woody material addition, to kick-start habitat development, dynamics and supplement the longer-term self-maintenance of habitat through the recovery of processes, may have been key for achieving the timely but longer-term responses observed. For example, whilst restoring normative rates of woody material inputs through tree hinging may take many years to realise (e.g. Beechie *et al.*, 2000), complementing this through the addition of large woody materials to encourage habitat development likely enhanced the short-term ecological effectiveness of this project. When timelines of habitat recovery are expected to be slow, taking such an approach to increase the brevity of change may assist in maintaining stakeholder support and willingness to participate in restoration activities (e.g. when restoration is funded by recreational fisheries).

In 2016, a decline in abundance and taxon richness in OSTN compared to all other post-restoration years was observed. The cause of this remains unclear, but may represent a site-wide impactor given the lack of a response to restoration observed in OSTW (i.e.

compared to OSTN). The control metrics (Appendix C: Figure C1) and waterbody classifications (DEFRA, 2022b) provided no evidence of a decline in macroinvertebrates nor water quality during this period, suggesting this could have been caused by a localised impact such as a weed cut. However, no notable events which may have impacted local ecology were identified (i.e. confirmed by the site river keeper). Moreover, weed cuts are regularly carried out in both reaches and the impacts of these on macroinvertebrates have been shown to be limited (Armitage *et al.*, 1994), making this explanation unlikely. Another possibility could be that these difference reflect sampler bias, e.g. due to differences in surveyor experience and kicking ability (Furse *et al.*, 1981). This finding demonstrates that longer-term appraisals conducted with sufficient temporal replication can be important for fully elucidating the responses to restoration. For example, a short-term appraisal may have suggested that the OSTN and OSTW restoration only provided short-term benefits or was ineffective, respectively. It was only by monitoring over a longer duration and with sufficient replication that a fuller understanding of restoration effectiveness was developed.

The use of existing routine monitoring data provides confidence that most responses identified were driven by the restoration. However, study design could be improved by adopting a stronger BACI approach (England *et al.*, 2021a). In this study, a BACI approach would have been particularly valuable as data was collected by multiple surveyors, which may have contributed to data variability, and the long-term design increases opportunity for catchment-scale environmental change (e.g. water quality) and perturbations (e.g. flooding) to influence the results. Whilst BACI designs are often hailed as a 'gold standard' (England *et al.*, 2021a), they are also difficult to implement in longer-term studies. For example, restoration projects are often carried out opportunistically with little warning, which can restrict the collection of pre-restoration baselines and interfere with control sites (e.g. when subjected to restoration or management). Moreover, monitoring is often conducted in an ad hoc manner (e.g. student projects) and not tied into a wider project, creating data compatibility (e.g. differences in methodologies, data not collected at control site; Chapter 5) or quality (e.g. number of transects monitored; Chapter 5) issues which can weaken study robustness and the conclusions that can be drawn (e.g. Albertson *et al.*, 2013). Provided that the limitations are acknowledged, studies implemented with sub-optimal designs can contribute important conclusions to the restoration literature (Albertson *et al.*, 2013). For example, Harrison *et al.* (2004) demonstrated that the effects of instream rehabilitation measures can be overarched by wider catchment scale deterioration (e.g. water quality) using a control-impact study design. However, to better facilitate the delivery of robust long-term appraisals widely quoted as key for the development of the field (e.g. Lu *et al.*, 2019; England *et al.*, 2021a), there is a need to improve the implementation of high-quality monitoring. As noted in

Chapter 5 and 6, this is likely best achieved through the funding and implementation of monitoring at specifically selected case study restoration projects (e.g. CaBA, 2022). These can simplify the delivery of robust appraisals collected using a more optimised approach (e.g. over a sufficient timescale, assessing multiple ecological groups), guiding and inspiring future efforts and contributing evidence towards restoration effectiveness (England *et al.*, 2021a).

This study provides evidence that restoration can be an effective management strategy for altering the habitat and ecology of chalk streams. In addition, the benefits of conducting longer-term appraisals to identify responses and their longevity was highlighted. Despite this, there are inherent difficulties in implementing robust long-term studies due to the opportunistic nature of restoration and monitoring efforts that can impact study design, data and introduce uncertainties to the conclusions drawn. There is a need for continued efforts to provide these appraisals to gain a deeper understanding of the long-term effectiveness of restoration. These studies will be particularly valuable for understanding recovery times, factors driving inter-project variability in outcome, and for providing the much needed evidence required to strengthen future restoration strategies.

CHAPTER 8 Non-invasive population estimates of freshwater fishes using remote underwater video.

8.1 Preamble

One of the greatest obstacles in implementing effective restoration in chalk streams is the lack of robust evidence describing project effectiveness. For instance, according to the River Restoration Centre's NRRI database only 10.5% of projects assessed the responses of fish, despite the fact that 43.5% of projects had 'fisheries enhancement' objectives (River Restoration Centre, 2023b). In part, the lack of monitoring of chalk stream restoration projects is due to the vast challenges of its implementation. For example, traditional fish surveys (e.g. electrofishing, seine netting) can be financially costly and labour intensive (Kristensen *et al.*, 2020), restricted under certain conditions (e.g. in spawning seasons, landowner restrictions) and have a low efficiency in deep and silty environments (Neufeld *et al.*, 2016) which are commonly the target of restoration interventions in chalk streams. To enhance the delivery of robust evidence, there is a need to improve monitoring capabilities in chalk streams.

Remote underwater video (RUV) offers a potentially useful non-invasive alternative to physical capture methods for assessing fish populations at chalk stream restoration sites. Indeed, using RUV, it was possible to collect valuable data on fish populations in Chapter 6 where electrofishing was restricted (i.e. due to landowner restrictions) or ineffective (i.e. due to depth and siltation). Despite the advantages of this technique (e.g. deployable in a range of habitats, no risk of injuring fish, less resource intensive), RUV is not commonly used to study the effects of restoration. In part, this may be due to limitations in the metrics which can be acquired from RUV and the lack of evidence of its effectiveness. This chapter therefore takes the form of a methodological study aiming to develop the utility of RUV by allowing the creation of non-invasive population estimates. Ultimately, this indirectly contributes to the aim of this thesis by enhancing monitoring capabilities at chalk stream restoration sites and the delivery of robust evidence, with which, more effective restoration strategies can be developed.

8.2 Summary

Accurate population estimates are needed to implement effective management strategies aimed at mitigating the loss of freshwater fish. Typically, such estimates are made using data derived from physical capture and marking methods. As there is potential for these to cause pain, distress and lasting harm to target and non-target fish, or be restricted at certain times of year, locations or under certain conditions, non-invasive methods could represent a desirable alternative. This study evaluated the efficacy of using unique identifiable features (UIF; e.g. spots) and morphometrics to identify individual brown trout and Eurasian minnow from photographs on a measuring board and underwater video in an aquarium. Where successful, it was assessed whether these could be combined with remote underwater video (RUV) and mark-recapture equations to form accurate non-invasive estimates of fish population size in a large tank. It was possible to identify more minnow (86.9% and 79.3% from photographs and underwater video, respectively) and trout (100% and 96.0%) from UIF than morphometrics (minnow = 27.7% and 10.3%; trout = 12.1% and 4.8%). Reidentification was more successful when using photographs than images from video, likely due to the uncontrollability of body positioning in the latter (e.g. bending). Between species, reidentification using UIF and morphometrics was greater for trout and minnow, respectively, likely reflecting inter-specific differences in patterns (e.g. clarity, variability, number) and body shape heterogeneity. When UIF were combined with underwater video and mark-recapture equations, population estimates closely matched actual population sizes and did not differ between species. This study demonstrates the utility of individual identification using UIF, which when combined with underwater video, may serve as a useful alternative to more invasive methods typically used in freshwater systems. Compared with traditional methods, there could be practicality, ethical and safety benefits of the approach tested with useful applications for those working in research, conservation and industry. This may hold particular value in chalk stream restoration monitoring given the clarity of water and widespread factors inhibiting the use of traditional methodologies (e.g. landowner restriction, non-optimum pre-restoration environmental conditions). Future challenges include automation of individual identification, refining methods of data collection and validating population estimates in situ.

8.3 Introduction

Freshwater ecosystems only cover around 0.01% of the globe's surface, but contain at least 9.5% of described animal species including a third of vertebrates (Balian *et al.*, 2008) and over 18,000 fish species (Fricke *et al.*, 2023). They are also imperative for human survival, providing vital food (McIntyre *et al.*, 2016), water (Wada *et al.*, 2010) and energy resources (Couto and Olden, 2018). The loss of freshwater biodiversity is occurring at an alarming rate globally (WWF, 2016). Indeed, a third of freshwater fishes are currently threatened by extinction (WWF, 2021), and megafauna (> 30 kg mass) have experienced population declines of up to 88% (He *et al.*, 2019). Designing and implementing effective conservation and management strategies is crucial for curbing the loss of freshwater biodiversity (Strayer and Dudgeon, 2010; Tickner *et al.*, 2020). To do this, there is often a need to generate reliable estimates of population size, e.g. for understanding the scope and type of restoration required and its effectiveness once deployed.

Traditionally, freshwater fish population sizes have been estimated using physical capture methods. These include timed (i.e. catch per unit effort) and depletion electric-fishing surveys (e.g. Reid *et al.*, 2009; Habera *et al.*, 2010), seine netting (Reid and Hogg, 2014) and/ or marking (e.g. fin clipping or electronic tagging; Vander Haegen *et al.*, 2005) and recapturing individuals on multiple occasions (e.g. Gresswell *et al.*, 1997; Feunteun *et al.*, 2000). Although such methods have been employed for decades (e.g. Kipling and Le Cren, 1984) several issues can restrict their use. These include low efficacy under certain environmental conditions (e.g. sites with high depth, silt loads and flow; Allard *et al.*, 2014; Neufeld *et al.*, 2016), prohibited use within certain sites (e.g. recreational fisheries, protected sites; *Personal knowledge*) and sensitive time periods (e.g. spawning seasons; Environment Agency, 2022a), the requirement for several sufficiently trained individuals and expensive equipment (Kristensen *et al.*, 2020), and the potential to cause physical and psychological harm to target (Dolan and Miranda, 2004; Kanigan *et al.*, 2019) and non-target organisms (Grant *et al.*, 2004). When tagging fish, there is also the potential for poor tag retention (e.g. Pierce and Tomcko, 1993) and impacted movement, growth and survival (Jepsen *et al.*, 2015). In the context of river restoration, these issues can restrict the implementation (e.g. due to cost, restricted access) and reduce the effectiveness (e.g. poor data quality) of monitoring, impeding the number of projects which can be appraised and lesson learnt.

Using RUV to study freshwater fish populations (e.g. Ebner and Morgan, 2013) offers several advantages over physical capture methods. For example, RUV does not cause physical or psychological harm to the fish (Ellender *et al.*, 2012), which is especially beneficial when studying protected/ threatened species or within restricted areas and seasons (Environment Agency, 2022a). They can also be collected using small teams with relatively inexpensive equipment (Schmid *et al.*, 2016) and within a broad range of habitats (Ebner and Morgan, 2013), including those where traditional methods may be deemed unsafe or ineffective (e.g. Ebner *et al.*, 2015; Frehse *et al.*, 2020). RUV has been previously used to assess fish abundance (calculated as the NMax; Wilson *et al.*, 2014), behaviour (e.g. Ebner *et al.*, 2009), habitat use (Trinci *et al.*, 2020), and community composition and diversity (e.g. Ebner and Morgan, 2013). However, using RUV to generate population estimates in freshwater ecosystems remains underexplored and a weakness inhibiting its wider-scale adoption.

To generate population estimates using RUV, it is essential that individual fish can be identified. UIF (e.g. scales, spots) can be effectively used to identify individuals for an array of species (e.g. Huntingford *et al.*, 2013; Hirsch and Eckmann, 2015; Al-Jubouri *et al.*, 2018). For example, by assessing stripes and body plates, 88% of Sumatran Barbs (*Puntigrus tetrazona*; Bekkozhayeva *et al.*, 2021) and > 97% of armoured catfish (*Rineloricaria aequalicuspis*; Dala-Corte *et al.*, 2016) were successfully identified. Moreover, studies have shown UIF can remain stable over time, allowing long-term re-identification (Bekkozhayeva and Cisar, 2022). For example, 93% of Atlantic salmon were reidentified over a 10 month period using spots on the operculum (Stien *et al.*, 2017). UIF may provide an effective method of identifying individuals from RUV images, enabling population estimates to be made by adopting existing mark-recapture equations. Indeed, population estimates of northern pike made using photographs of spots taken by anglers were more comprehensive compared to gill net surveys (Kristensen *et al.*, 2020). Despite the potential of RUV combined with UIF for generating estimates of freshwater fish populations, this method will likely only be accurate for species with clear and distinguishable markings. Levels of accuracy for species with less obvious or variable markings/ features may compromise the validity of this approach.

Morphometrics, the analysis of body shape, has previously been used for image-based species identification (e.g. Strachan *et al.*, 1990), but applications for identifying individuals are poorly understood. Fish morphology varies with age (Letcher, 2003), environment (Perazzo *et al.*, 2018), condition (Greenway *et al.*, 2016), sex (Schutz *et al.*, 2022), life history (Billman *et al.*, 2014) and genetics (Toline and Baker, 1997), and can also vary within populations. For example, populations of Eurasian minnow, European perch (*Perca fluviatilis*) and Prussian carp (*Carassius gibelio*) have been found to be morphologically heterogeneous (Baranov, 2020; 2021; Khan *et al.*, 2022); although notably this variability varied across populations likely due to differences in habitat complexity (e.g. Funk and Reckendorfer, 2008). By taking advantage of intra-population variability, image-derived morphometrics may facilitate short-term re-identification of individuals sufficient for the production of mark-recapture population estimates.

This study aimed to assess whether RUV could be used in combination with UIF or morphometrics to identify individual fish and generate accurate estimates of population size. To do this, two common stream-dwelling species were used: brown trout and Eurasian minnow. Objective 1 quantified the accuracy with which individuals could be identified based on UIF and morphometrics from photographs taken when the fish was out the water under optimal conditions (e.g. good lighting, fish still and lying flat; hereafter ‘photographs’) and from video of the fish swimming in a small tank. It was predicted that reidentification accuracy would be higher: (1) when using UIF compared to morphometrics because they are likely to be less susceptible to error from random bending/ angling of the body; (2) for trout than minnow due to their greater size and pattern array complexity; (3) from photographs compared to images collected from underwater video which are expected to be of better quality. Objective 2 assessed whether UIF or morphometrics could be used to accurately predict the population size of a group of fish within an artificial (large tank) setting from images collected using RUV. It was predicted that: (4) estimates would closely match actual population size in both species (assessed as correlation values > 0.9), but overall be more accurate in trout than minnow.

8.4 Methods

8.4.1 Fish capture and husbandry

Eurasian minnow (*n* = 130; standard length ± SD: 5.82 cm ± 0.69) and brown trout (*n* = 141; 21.22 cm ± 1.27) were caught with seine nets in the River Itchen (United Kingdom; 50.934502, -1.375119) and procured from a local fish farm, respectively, in several batches (minnow: 30 [01/06/2021], 35 [07/06/2021], 65 [11/06/2021]; trout: 69 [21/03/2022], 72 [31/03/2022]). Fish were transported in aerated 50 L (minnow) or 290 L (trout) fish transportation tanks to the ICER facility (University of Southampton, United Kingdom). Upon arrival, fish were visually checked for obvious signs of injury or disease before being acclimated (> 3 hours, i.e. to water temperature) and transferred to a holding tank (150 x 100 x 80 cm) containing 1,200 L of filtered and aerated water. Fish were given a 48 hr acclimation period before trials commenced. Ammonia, nitrite, nitrate, pH and temperature were checked daily and remained within the limits of what is considered good water quality. Approximately 30% water changes were conducted between batches. Minnow and trout were fed a commercial flake and pellet, respectively.

8.4.2 Experimental protocol

Experiments were conducted between 01/06/2021 – 17/06/2021 for Eurasian minnow and 21/03/2022 – 08/04/2022 for brown trout. For each species, the study objectives were met by conducting the experiment in three phases, with phase 1 and 2 relating to objective 1, and phase 3 relating to objective 2.

During phase 1, each fish was individually removed from the holding tank and placed on a white plastic measuring board with their left flank facing upwards. The measuring board was wetted, fitted with a 30 cm ruler, and labelled with a unique identification number for each individual. A ca. 25 cm diameter white LED ring light was placed 40 cm above the measuring board to create uniform lighting. A Canon EOS 250D (automatic settings) fitted with a 50 mm lens (Canon f/1.8 STM) and set on a tripod 45 cm above the fish was used to capture at least two photographs per fish.

In phase 2, each fish was individually transferred from the holding tank to a recording area (minnow: 18 x 6 x 9 cm, trout: 65 x 18 x 18 cm) within a glass aquarium filled with holding tank water (depth: minnows = 9 cm, trout = 18 cm). The recording area was constructed using four white polystyrene sheets secured to the bottom, back, and each side of the aquarium, leaving one side open to allow video recording, and illuminated with a white LED light. A GoPro Hero 6 (1080p, 120 fps, linear setting) placed 10 (minnow) or 20 cm (trout) from the aquarium recorded each fish for five minutes. To assist subsequent analysis, a unique identification number was presented to the camera immediately prior to each five minute recording. A 50% water change was conducted between each recording.

During phase 3, 30 trials per species were conducted using four separate batches of 30 individuals (7-8 trials per batch). In each trial, 10 – 30 randomly selected individuals were placed in a (290 L) acclimation tank and drip-acclimated to the water in an experimental tank for at least 30 minutes using an airline hose (0.6 cm diameter). The experimental tank (150 x 100 x 80 cm) was identical to the holding tank, with the exception that it was filled to a depth of approximately 30 cm and contained 15 pebbles (width ~ 15 cm) and several air diffuser stones to encourage exploration. After acclimation, the fish were released into the experimental tank and allowed to settle for 10 minutes. A GoPro Hero 6 (1080p, 120 fps, linear setting) located inside the experimental tank then recorded for 40 minutes before the trial concluded. At the end of each trial, additional fish were added to the experimental tank to increase the "population size" and the next trial commenced after another 10 minute settling period. This sequential method of testing each batch, from the lowest (10) through to the highest (30) population size, was an ethical requirement to avoid excessive handling of fish. Once phase 3 was completed, minnow and trout were returned to the river at the point of capture, in agreement with the Environment Agency, and humanely euthanised according to Schedule 1 of the Animals (Scientific Procedures) Act (1986), respectively.

8.4.3 Image collation

Two images of the left flank of each fish from phase 1 and phase 2 were collated into an electronic database. Images from phase 2 were extracted from video footage and selected based on clarity and the visibility of spots and morphometric landmarks. For trout and minnow, it was not possible to collect images in phase 2 for 17 (12%) and 14 (11%) individuals, respectively. In phase 3, images of all individuals displaying their left flank within the first five (minnow) or 15 (trout) minutes (capture 1) and last five (minnow) or 15 (trout) minutes (capture 2) of each trial were extracted and collated into an electronic database. A lower time was used for minnow due to their tendency to shoal directly in the view of the camera, enabling more images to be collated per unit time. Three minnow trials (consisting of "populations" of 12, 14 and 22 individuals) from phase 3 were excluded from analysis as it was not possible to collect enough images for mark-recapture estimates to be made (i.e. > 1 'recapture'). Where required, image clarity was improved by adjusting brightness and/ or contrast in Windows image editor.

8.4.4 Morphometric calculation

Morphometric data were extracted from images using the Click Coordinates Tool in ImageJ (ImageJ, 2022). For all images, the width of the eye was used as a standardised unit for measurements. Eye width was used rather than taking actual measurements to avoid inaccuracies associated with the distance of the individual to the camera. The coordinate tool was used to obtain the XY coordinates of 15 landmark points (Figure 8.1). The distance between each XY coordinate, calculated using Pythagoras Theorem, enabled a total of 43 measurements per image to be extracted (Figure 8.1). The measurements were chosen as it was expected they would be less susceptible to changes with fish position (i.e. bending). For images of trout captured in phase 2, measurements between points 11 and 12 were excluded as the landmarks could not be clearly identified.

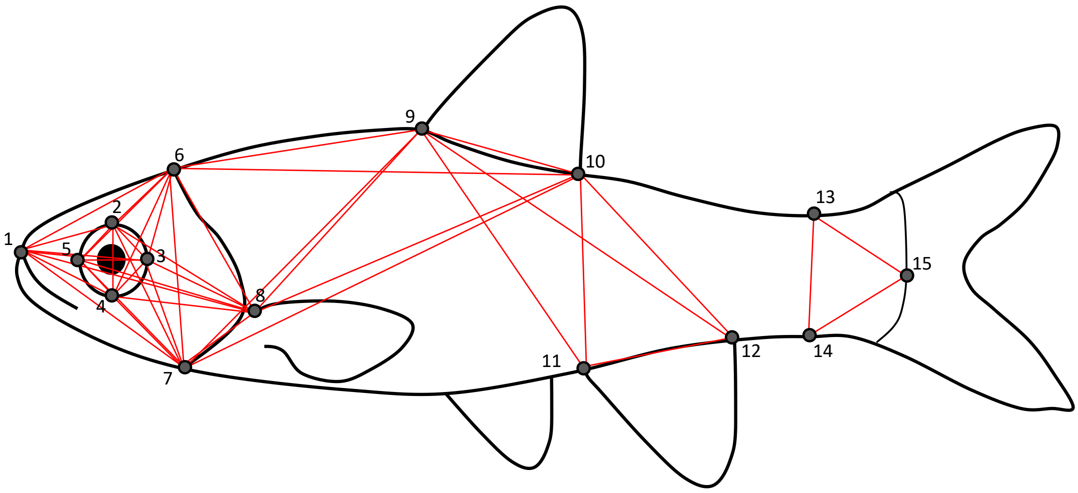


Figure 8.1 Morphometric landmarks (numbered grey circles) and the 43 measurements made between them (red lines). Point 3-5 was used as a standardised unit for all measurements (i.e. 1 unit). Points 13 and 14 represent the narrowest part of the tail.

Morphometric measurements of known fish (the first image taken during phase 1 and 2) were compiled into separate reference databases. Then, morphometric measurements of unidentified individuals (the second image taken during phase 1 and 2) were compared to the database and a similarity score calculated between all known and unidentified individuals as the sum of the absolute difference between each measurement. Unidentified fish with the greatest similarity (lowest score) to known fish were then paired before the identity of the unidentified fish was revealed (i.e. using the file name), enabling the proportion of fish accurately identified to be determined.

8.4.5 Unique identifiable features calculation

Spots below the lateral line and stripes were used as UIF for trout and minnow, respectively. These features were analysed using I^{3}S Spot (Version 4.02; Reijns, 2020), a free pattern analysis software which can be used to record a “fingerprint” of UIF and identify individuals from an inbuilt reference database. I^{3}S Spot was chosen because of the manual method of image analysis and ability to adjust “fingerprints” based on the shape and size of UIF, rather than just position. This was expected to maximise the identification accuracy for the test species which have variable sized/ shaped spots and stripes.

To compare the UIF of unidentified and known individuals, separate ‘reference databases’ were created in I^{3}S Spot using the first images taken in phase 1 and 2, and the first sighting of an individual in phase 3. Separate databases were created for each trial in phase 3. Specifically, the identification number (not available in phase 3), reference image and a “fingerprint” of spot/stripe patterns for all individuals were included. For each individual, the fingerprint of UIF were created by firstly selecting 3 reference points on the fish (points 1, 8 and 9; Figure 8.1), which allowed for differences in angle between images to be corrected (Den Hartog and Reijns, 2016). Following this, between 12 and 30 spot/ stripe patterns were manually mapped and added to the reference database. Where minnow did not have enough UIF to fulfil the minimum 12 points required by I^{3}S, landmark 2 on Figure 8.1 was selected as many times as required to meet the minimum number. This reference database allowed comparison of future images, where the identification of the individual was not known (i.e. second image in phase 1 and 2 and unknown individuals in phase 3), with individuals in the database. Specifically, a ranking of the top 50 matches based on a similarity score was automatically generated and the identity of the individual, or whether the individual had not yet been observed was determined.

8.4.6 Statistical analysis

In phase 1 and 2, the percentage of successfully identified individuals in each species was recorded for UIF and morphometrics. Chi squared tests were used to assess whether identification success differed between species. Due to lack of independence in the data, mid-p McNemar tests were used to assess whether identification success differed between identification methods (UIF versus morphometrics) and image collection methods (photographs versus video-derived images; Fagerland *et al.*, 2013). As the McNemar test requires paired data, 17 trout and 14 minnow were excluded from analysis because it was not possible to extract multiple images in phase 2.

UIF extracted from images from phase 3 were used to test whether accurate mark-recapture population estimates could be made using RUV. Morphometric data was not used due to a low identification accuracy obtained during phase 1 and 2. For each trial, UIF for fish in each image collected during 'capture 1' (i.e. first 5/15 minutes of each trial) and 'capture 2' (i.e. last 5/15 minutes of each trial) were mapped. If it was deemed the fish had not previously been identified, they were given an identification number and added to the reference database. If the individual had been previously identified, the ID number and time of sighting was noted. After all images of fish had been identified, Lincoln-Peterson mark-recapture population estimates were calculated for each trial as;

$$Population\ estimate = \frac{N1 * N2}{Number\ of\ individuals\ found\ in\ both\ N1\ and\ N2}$$

where 'N1' and 'N2' are the number of individuals observed in the 'capture 1' and 'capture 2', respectively.

One-tailed Pearson's correlation tests were used to relate estimated with actual population sizes for both species. Normality of residuals for both actual and predicted population sizes were tested with Shapiro-Wilk tests. To assess whether the accuracy of estimated population sizes differed between species, the difference between actual and estimated population sizes were compared using a two sample Wilcoxon test. Homogeneity of variance was assessed using a Levene's test. Analysis and data visualisation was carried out in R Studio (R Studio Team, 2020) using the packages 'Rcmdr' (Fox, 2005) and 'ggplot2' (Wickham, 2016).

8.5 Results

Reidentification success was higher using UIF than morphometrics in both species and phases (Table 8.1; $p < 0.001$). Reidentification was higher for trout than minnow when using UIF in both phase 1 ($X^2 = 19.673$, $p < 0.001$) and 2 ($X^2 = 15.654$, $p < 0.001$). More minnow than trout were identified using morphometrics in phase 1 ($X^2 = 10.511$, $p < 0.01$) but not phase 2 ($X^2 = 2.619$, $p = 0.106$). Reidentification success was higher in phase 1 than 2 for trout identified using UIF ($p < 0.05$) and minnow with morphometrics ($p < 0.001$). No differences were found between phases for trout identified using morphometrics ($p = 0.210$) and minnow with UIF ($p = 0.230$).

Mark-recapture population estimates calculated using UIF were strongly associated with the actual population size for minnow ($t_{28} = 12.534$, $p < 0.001$, correlation = 0.927) and brown trout ($t_{28} = 14.542$, $p < 0.001$, correlation = 0.940; Figure 8.2). No differences in the accuracy of estimated population sizes were detected between species ($W = 428.5$, $p = 0.713$).

Table 8.1 The percent of brown trout and Eurasian minnow successfully identified using UIF and morphometrics from images taken when the fish was out the water on a measuring board under optimal conditions (phase 1) and from video with the fish free swimming within an aquarium (phase 2).

Species	Method	Phase	Correct ID (%)
Brown trout	UIF	1	100
		2	96
	Morphometrics	1	12.1
		2	4.8
Eurasian minnow	UIF	1	86.9
		2	79.3
	Morphometrics	1	27.7
		2	10.3

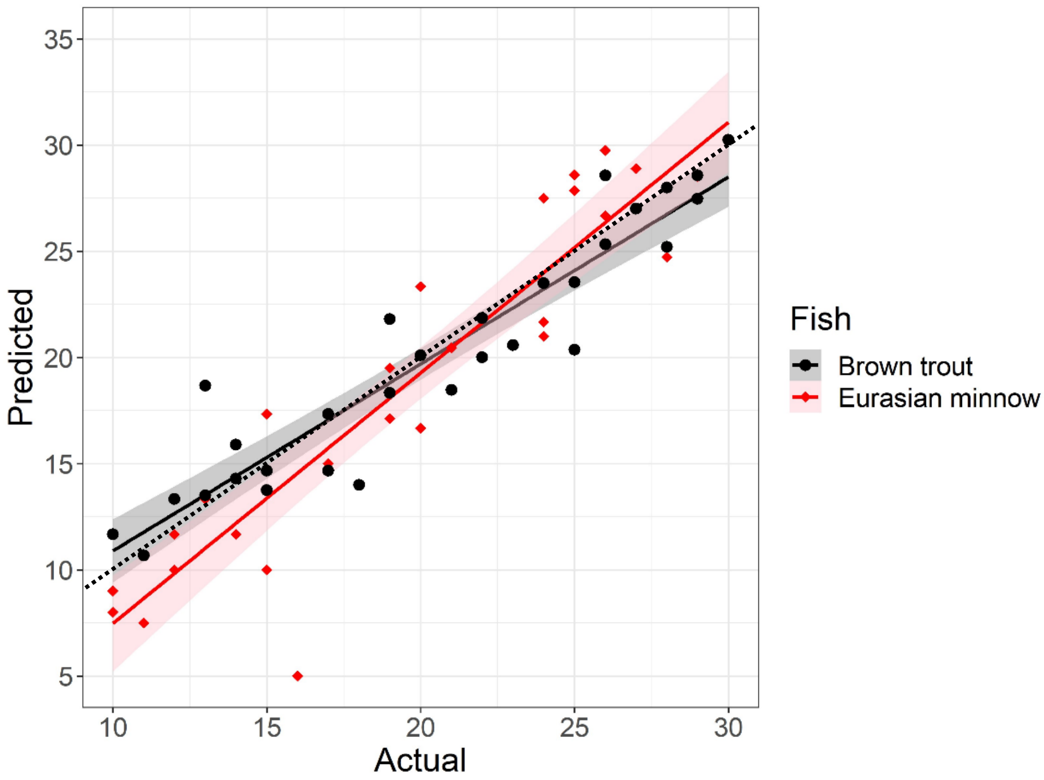


Figure 8.2 Relationship between predicted population sizes of brown trout and Eurasian minnow, calculated using mark-recapture equations using RUV and UIF, and actual population sizes in a large experimental tank. The relationship is fitted with a linear regression line. Dashed line shows 1:1 slope. Shaded areas show 95% confidence intervals.

8.6 Discussion

Being able to accurately estimate population size is important for implementing effective management strategies aimed at limiting freshwater biodiversity loss (WWF, 2021). For fish, invasive capture and marking procedures are typically used; however, ethical concerns, practicality issues and restrictions can make these methods inappropriate. This study evaluated the efficacy of using UIF and morphometrics to identify individual fish from images, and whether these could be incorporated with RUV methodologies and mark-recapture equations to form accurate population estimates. Using UIF, it was possible to identify most individuals of each species and at significantly more success when compared to the use of morphometrics. Reidentification accuracy also differed between image collection methods and species, where accuracy was at times lower from video-derived images than photographs (e.g. when identifying minnow using morphometrics) and higher for trout compared to minnow when using UIF. Identifying fish from RUV allowed the creation of accurate non-invasive population estimates for both minnow and trout under controlled conditions. This research demonstrates that UIF can serve as a useful method for identifying individual fish and to create population estimates from underwater video. This may serve as a valuable alternative to traditional physical capture and tagging methods and provides numerous practicality, safety and ethical benefits.

Supporting the growing body of literature demonstrating the utility of UIF-based identification, it was possible to identify individual brown trout and Eurasian minnow from body markings at levels comparable to that of other studies (Dala-Corte *et al.*, 2016; Stien *et al.*, 2017). Reidentification using UIF was more successful than morphometrics, supporting the first prediction. This is likely the result of greater intra-individual variability in markings than body shape and the ability to accurately detect these differences using purpose created software (e.g. by accounting for fish positioning within I^3S). Minnow were more difficult to identify from UIF, supporting the second prediction, and likely reflected the lower number, clarity (e.g. contrast with skin) and variation in patterns compared to trout. Indeed, I^3S recommends that at least 12 features are mapped for accurate identification (Reijns, 2020), which was not possible for several minnow. Whilst this finding demonstrates that this approach may not be appropriate for all species, technological advances that improve identification of taxa with less clear markings may permit a greater future success. For example, studies have shown zebrafish (*Danio rerio*) and common carp (*Cyprinus carpio*) can be accurately identified using texture and Hue/Saturation/Value colour models (Al-Jubouri *et al.*, 2018) and scale patterns (Bekkozhayeva and Cisar, 2022), respectively. Likewise, whilst reidentification was at times lower from video than photographs, reflecting the lower image quality (e.g. due to insufficient frame rates to capture rapidly moving fish) and a greater variability in fish positioning (e.g. bending), the development of more sophisticated camera systems (e.g. stereo-camera set-ups; Boldt *et al.*, 2018) will likely improve identification accuracy in the future. Whilst future advancements are required, UIF offers many potential benefits and opportunities for research and conservation. For example, fish population size can be established using images collected from anglers, reducing the need for physical surveys which can be financially costly, disturb habitat and lead to unintentional fish mortality (Kristensen *et al.*, 2020). Moreover, eliminating the need to surgically implant electronic tags may reduce ethical “severity” (e.g. degree of distress or harm to obtain similar data) and technical and legal restrictions (e.g. training, licensing, protected sites).

Reidentification using morphometrics was low for both species, especially trout. This may be because the focal populations exhibited low body shape diversity. Whilst populations can exhibit high morphological variation, others have been shown to be relatively uniform which reflects differences in genetics, pressures (e.g. parasites) and habitat diversity (Taylor, 1986; e.g. Khan *et al.*, 2022). The trout used in this study were sourced from aquaculture, and so were reared under physically homogenous conditions with high food availability, and would be the same age and of low genetic variability. Moreover, whilst minnow were sourced from the wild, this habitat was anthropogenically modified and homogeneous (silted, channelised). Consequently, it is likely an overall low morphological diversity decreased the ability to differentiate between individuals. This may also explain why minnow, which were shaped by the pressures of a wild environment (e.g. predation and variability in food resources), were identified more successfully than trout. Low reidentification rates could also relate to insufficient precision of landmarks selection due to image quality and fish position relative to the camera. This theory is supported in that significantly fewer minnow were reidentified from video compared to photographs. Studies that collect morphometric data often anesthetise or euthanise fish to facilitate the manipulation of body position and ensure high image quality (e.g. Baranov, 2020). Here, fish were conscious, reflecting common fieldwork conditions under which this method would be used. For example, fish would be quickly photographed while being measured on a board, or from RUV deployed in-situ and images of free swimming fish extracted afterwards. As incapacitating the fish is not possible or desirable in the present application of morphometrics, it is likely that its use for non-invasive reidentification is currently limited. The accuracy of this method could be higher if assessing smaller population sizes and may be useful if used in combination with UIF (i.e. to narrow the range of possible individuals).

Population estimates using UIF data extracted from images from RUV were highly accurate (correlation > 0.9) and did not differ between species. This suggests it could be a useful non-invasive alternative to obtain population estimates in a range of species, which may be especially useful when traditional methodologies are restricted (e.g. site and time restrictions). Whilst this study demonstrates the potential for using RUV to estimate population size under controlled experimental conditions, when deployed in situ, there are several additional factors that require consideration and should be the focus of future research. Firstly, to adequately sample a wild population, footage would likely need to be collected over greater timescales and at several locations, e.g. to capture enough images of fish and ensure representative sampling of different habitat in a reach. Depending on the number of fish present, the high manual processing times required to analyse this footage would be impractical. Therefore, automated processing techniques that capture images and accurately identify individuals would greatly increase utility. Several studies have shown that automation of images for individual identification is possible under controlled situations (e.g. Bekkozhayeva *et al.*, 2021; Cisar *et al.*, 2021), but few have attempted this in uncontrolled environments (e.g. Zhang *et al.*, 2021). Secondly, it is important that RUV methodological approaches are honed to facilitate the capture of high-quality images adequate for analysis. Experimenting with RUV set-ups (e.g. Rizzo *et al.*, 2017) and gaining a better understanding of the effects of attractants (e.g. baits; Schmid *et al.*, 2016), environmental characteristics (e.g. Wilson *et al.*, 2014) and fish behaviour (e.g. Dunlop *et al.*, 2015) will all help improve quality/ quantity of images captured and subsequent population estimates. Finally, there is a need to compare RUV population-estimates with traditional physical capture methods in-situ to determine the costs, benefits, trade-offs and effectiveness of underwater video for quantifying fish populations (e.g. Ebner and Morgan, 2013).

This study demonstrates the potential for using UIF to non-invasively identifying individual fish, which when combined with underwater video, can allow the calculation of accurate estimates of population size. Such an approach has numerous potential safety, practicality and ethical benefits over traditional physical capture and tagging methodologies. For instance, the non-invasive nature of RUV negates ethical concerns and can allow data collection at previously restricted sites or times (e.g. spawning seasons). Underwater video can be safely collected under a broad range of conditions which would otherwise inhibit the use of traditional methods, e.g. deep and highly silted habitats which are frequently found prior to restoration. Given the widespread ownership of submersible cameras (e.g. GoPro), ease of video collection and potential future automation of video processing and analysis (e.g. Bekkozhayeva *et al.*, 2021), it may also prove a cost-effective citizen science method. In the context of chalk stream restoration, this technique may be especially valuable given the excellent water clarity and often limited potential to conduct traditional fish surveys (e.g. because of the desire to not compromise use by recreational anglers or injure stocked fish, highly modified conditions inhibiting fish capture), enabling a more widespread monitoring of projects, delivery of evidence, and helping to facilitate the development of sound practice.

CHAPTER 9 Discussion

Habitat has been extensively degraded in lotic systems, leading to widespread ecological decline and a growing risk of humanitarian crisis (WWF, 2021). Consequently, there has been an increasing urgency to implement effective management strategies in rivers, of which, the physical restoration of habitat has emerged as a key player (Kail *et al.*, 2015). Despite this, the effectiveness of restoration is poorly understood and often goes against expectations (e.g. Albertson *et al.*, 2011). In part, this is due to the limited amount and scope of monitoring, especially in rarer river types (Kaiser *et al.*, 2020; England *et al.*, 2021a). English chalk streams have been extensively modified over millennia, and these alterations have been highlighted as the leading source of failures to achieve good ecological status under the Water Framework Directive (Environment Agency, 2021a). Consequently, restoration has become a major management strategy for restoring the physical and ecological condition of degraded chalk streams (CaBA, 2021). Despite this, a lack of robust appraisals currently constrains our understanding of the value of restoration in these unique systems. The aim of this thesis was to develop understanding of the effects of restoration on physical habitat and ecology in English chalk streams. To achieve this, this thesis addressed four main objectives, which were to assess: (1) the physical and ecological effects of different techniques, focussing on weir removal and gravel augmentation; (2) the influence of time since restoration on physical and ecological responses; (3) the effects of restoration on different ecological groups. Additionally, (4) a passive methodological approach for monitoring fish populations was developed, which indirectly contributes to the aim of this thesis by improving monitoring potential at chalk stream restoration sites. This chapter discusses the findings of this body of research in relation to these objectives, as well as future research needs, management advice and limitations to the approach taken.

9.1 The effectiveness of different restoration techniques

The first objective of this thesis was to quantify physical and ecological responses to a variety of restoration techniques in chalk streams. More specifically, weir removal (Chapter 5) and gravel augmentation (Chapter 6) were focussed on due to their widespread adoption (River Restoration Centre, 2023b) and advocated use by experts as key for restoring more naturalised chalk stream habitat, ecological communities and processes (CaBA, 2021).

9.1.1 Weir removal

Low-head weirs are highly abundant in chalk streams and considered a major source of their deterioration (Skinner, 2013; Environment Agency, 2021a). Given their frequent redundant and deteriorated state, their removal can often represent a 'low-hanging fruit' for restoration (Grabowski *et al.*, 2018). However, as the impacts of river infrastructure (Csiki and Rhoads, 2010) and benefits and speed of recovery following their removal (Carlson *et al.*, 2018) depend in part on river power and the system's ability to drive natural physical processes (e.g. sediment transport to redistribute accumulated silt; Major *et al.*, 2017), there is a need to appraise its utility in systems with lower energy, such as chalk streams.

Chapter 5 supports a growing body of literature demonstrating the effectiveness of infrastructure removal for recovering lost habitat, ecological communities and processes (Bellmore *et al.*, 2019). Indeed, the effect of restoration was particularly pronounced in the former reservoir, which became more lotic (e.g. increase velocity) and exhibited rapid changes to ecological communities (e.g. EPT abundance). Downstream unexpectedly displayed little indication of impacts associated with a sediment pulse, as shown in other studies (e.g. Orr *et al.*, 2008a). The results observed here show similarities with other appraisals in chalk streams. For example, in the River Kennet (England *et al.*, 2021b) and Chess (England and Peacock, 2010), macroinvertebrate communities became more dominated by rheophilic and coarse-substrate associated taxa and contained more EPT and Gammaridae (indicated by River Fly Partnership's Angling Monitoring Initiative score), respectively. Other studies which assessed projects involving weir lowering (England and Wilkes, 2018) and notching (Robertson *et al.*, 2021) in chalk streams found limited/inconsistent changes to benthic macroinvertebrate communities. This may suggest that the scale of the restoration was not sufficient to overcome the impacts of the weir, or that these projects failed to tackle the primary source of degradation (e.g. water quality). Despite finding similarities between studies, the timely recovery of habitat and ecology following weir removal is not guaranteed (Thomson *et al.*, 2005) and requires further investigation to consolidate knowledge. Notably, England and Peacock (2010) and England *et al.* (2021b) did not differentiate between upstream and downstream reaches. Thus, further research which quantifies responses to weir removal above and below the structure is needed to assess the potential for sediment pulse induced impacts and recovery. Furthermore, the additional restoration methods used in this project were likely vital for accelerating recovery in this low power river. Therefore, research assessing the value of these methods, especially in relation to the sediment transport ability of the river, would be useful for site-specific optimisation of restoration designs. Finally, research aiming to better understand the deterioration caused by river infrastructure in chalk streams would be valuable to help optimise structure removal.

9.1.2 Gravel augmentation

Chapter 6 demonstrated that gravel augmentation can rapidly and desirably (i.e. in light of the restoration goals) alter habitat (e.g. reduce depth) and ecology (e.g. enhanced macroinvertebrate diversity) over the short-term. Considering other appraisals in chalk streams and further afield, the ecological responses shown here are both supported and opposed. For example, Merz and Ochikubo Chan (2005) and Albertson *et al.* (2011) demonstrated an enhancement in macroinvertebrate density and reduction in abundance following gravel augmentation, respectively. Even in this study, which took place in rivers with similar characteristics, settings (e.g. climate) and pressures (S&TC, 2018) and using comparable restoration methodologies, inter-project discrepancies in outcomes were found. This highlights the high level of uncertainty surrounding restoration outcomes (Wheaton *et al.*, 2008) and the need to better understand the factors which drive response to reduce this. This can be achieved, for example, through the development of meta-analyses designed to identify barriers inhibiting recovery (e.g. Kail *et al.*, 2015; Carlson *et al.*, 2018). As such, the dissemination of all results, including those perceived as 'negative' (i.e. going against the study predictions or project objectives), should be actively encouraged to facilitate these analyses. With this understanding, river managers are provided with the information required to make informed decisions and optimise restoration effectiveness (e.g. targeting root cause of deterioration and understanding catchment-scale limitations; Polvi *et al.*, 2020). It is important to note, however, that whilst this information can reduce uncertainties, it is not possible to remove them all (e.g. aleatoric uncertainties caused by a stochastic environment; Chapter 7). Therefore, uncertainties should be effectively communicated with stakeholders to manage expectations and be embraced within the restoration process (Wheaton *et al.*, 2008).

Whilst the gravel augmentation projects assessed in Chapter 6 were shown to be effective over the short-term, the on-going issues of fine sediment inputs and deposition (S&TC, 2018) means that the long-term success of such restoration projects remains precarious. Indeed, as sediment inputs remain high (e.g. Zhang *et al.*, 2017), it is possible that silt ingression and the eventual smothering of augmented substrates will occur. Supporting this, in the River Stiffkey (Mitchell, 2016) and Moosach (Pulg *et al.*, 2013), rehabilitation gravels were expected to represent unsuitable brown trout spawning habitat in under 10 years due to silt ingression. Whilst gravel augmentation is clearly required to restore a more naturalised chalk stream riverbed (e.g. due to the inability to recover naturally under current hydrology; CaBA, 2021), there is a need to combine these interventions with a catchment-wide programme of measures designed to reduce sediment inputs (e.g. buffer zones, wetlands, agricultural management advice; Mitchell, 2016). Likewise, restoration should focus on the re-establishment of the processes and ecosystem engineers which facilitate temporally and spatially dynamic habitats (i.e. a shifting habitat mosaic) vital for the self-maintenance of silt-free gravel patches (e.g. Brown *et al.*, 2023). Trees and macrophytes are crucial in this regard (e.g. for altering flow patterns, deposition and scour; Roni *et al.*, 2015), and should represent a priority in chalk stream restoration (CaBA, 2021). In many situations, this may be achieved passively through encouraging landowners to cease woody material and macrophyte (e.g. 'weed cuts') clearance and embrace natural processes as a crucial component of river functioning. Additionally, the recovery of riparian vegetation and wet woodland, as well as the re-establishment of Eurasian beaver (Law *et al.*, 2016), will further support the development of naturally dynamic, self-sustaining habitat which supports biocomplexity and ecological resilience.

9.2 The influence of time since restoration

Supporting a number of publications calling for appraisals to be conducted at appropriate temporal scales (e.g. Kail *et al.*, 2015; England *et al.*, 2021a), Chapter 5 - 7 demonstrated the time since restoration was a key determinant for the effects found. In Chapter 6, the analysis of immediate (0-1 years post-restoration) versus short-term (1-2 years post-restoration) responses showed many physical and ecological effects could not be detected until at least a year had passed, i.e. due to recovery following disturbance. Likewise, despite finding a rapid response following weir removal in Chapter 5, macroinvertebrate communities were still developing four years following restoration. These delayed responses possibly reflect the time taken for habitat to develop or rarer taxa to colonise from distant species pools (Tonkin *et al.*, 2014). Chapter 7 demonstrated that whilst responses to restoration can be rapid and persist over a relatively long timeframe, longer-term appraisals can be crucial for accurately describing these. Indeed, a short-term analysis would have led to potentially misleading conclusions that the projects made little difference or only provided short-term benefits owing to the macroinvertebrate decline in 2016. It is for this reason that monitoring not only needs to be conducted over a sufficiently long timescale, but gathered with an adequate number of replicates to detect these events (England *et al.*, 2021a). From a river manager perspective, this is also crucial for providing advanced warning for the need of adaptive management (Downs and Kondolf, 2002).

To truly capture responses to restoration and accurately determine 'success', appraisals need to be conducted over an sufficiently long timescale (England *et al.*, 2021a). However, determining this period can be difficult. For example, the length of time required can be system specific, varying with factors such as the rates of hydrogeomorphological processes (e.g. erosion; Major *et al.*, 2017), catchment size (Carlson *et al.*, 2018) and species pools for recolonisation (Tonkin *et al.*, 2014). Likewise, the restoration measure and scale at which this is applied can influence recovery, with techniques which cause high levels of perturbation potentially requiring longer to recover than those causing less disturbance (Gilvear *et al.*, 2013). Differences in the life history of ecological indicators can also impact recovery periods, with taxa with a greater dispersal ability and rapid turnover generally being expected to recover more quickly (Thompson *et al.*, 2018b). Given the low power and sediment supplies of chalk streams and a heavy reliance on ecosystem engineers to develop heterogeneous habitat, when restored using a process-based approach, the true effectiveness of interventions may take decades to realise (CaBA, 2021). This herein lies one of the difficulties in understanding the effectiveness of restoration in chalk streams, and highlights the need to enhance the levels of appraisal funding and for monitoring to be considered as a continuous process rather than a discrete, time-bound one.

9.3 The effect of restoration on different ecological groups

To assess the effects of restoration on different ecological groups, a multi-taxa approach was taken in Chapter 6. Gravel augmentation projects were specifically chosen for this approach due to the widespread use of the technique to enhance salmonid populations (i.e. through spawning habitat; Mitchell, 2016) and often little consideration to other fish species or ecological groups (Albertson *et al.*, 2011). The study demonstrated that restoration can lead to significant inter-group variation in responses, where changes in fish (i.e. more brown trout, Eurasian minnow) and macroinvertebrates (e.g. enhanced diversity) were not reciprocated in macrophytes. It is possible these variable responses reflect differences in colonisation times, including the ability to disperse and establish in new habitat (Padial *et al.*, 2014). Moreover, biotic resistance may have played an important role if space and resource competition excluded the establishment of new macrophytes (Barrett *et al.*, 2021). It is also possible that the restoration simply did not alter habitat and niches in a way which effected macrophytes. Indeed, studies have shown river widening/ re-meandering projects tend to elicit a greater response from macrophytes, whereas instream restoration measures such as gravel augmentation tend to more greatly effect macroinvertebrates and fish (Kail *et al.*, 2015). Where funds and resources allow, conducting appraisals with a multi taxa approach can allow for a fuller and more holistic understanding of restoration effectiveness (England *et al.*, 2021a). For example, these approaches can provide crucial information on 'winners and losers' to assess project cost-benefits (Mueller *et al.*, 2014), food web dynamics (Thompson *et al.*, 2018a) and may provide mechanistic explanations for the responses observed (e.g. linking the responses of macrophytes and macroinvertebrates; Pedersen *et al.*, 2007).

9.4 Monitoring fish using remote underwater video

Traditional physical capture methods hold many potential limitations which can at times restrict the ability of researchers to effectively monitor fish (e.g. Neufeld *et al.*, 2016). For example, landowner restrictions (e.g. due to fear of injuring recreationally important fish) and suboptimal conditions (i.e. high depth, siltation and flow) in Chapter 6 constrained the use of electric-fishing and seine netting. Hence, RUV was trialled as an alternative and proved to be a simple yet effective method for assessing fish communities at chalk stream restoration sites. Aiming to develop the utility of RUV further, Chapter 8 was developed and demonstrated the capacity for generating reliable estimates of fish population size. The potential applications of RUV to assess chalk stream restoration, alongside other research questions (e.g. Schmid *et al.*, 2016) and in different systems (e.g. Wilson *et al.*, 2014), are wide spanning. For example, as well as offering a non-invasive, adaptable technique to assess community and population size, RUV can provide information on fine scale habitat use (Trinci *et al.*, 2020) and behaviour (e.g. Ebner *et al.*, 2009) which may further enhance understanding of chalk stream restoration effects. Furthermore, the application of RUV as a citizen science method is interesting and warrants further investigation. Indeed, with the potential simplicity of the method, widespread ownership of submersible cameras and technological advancements enabling computer-aided individual (Bekkozhayeva *et al.*, 2021; Zhang *et al.*, 2021) and species (Marrable *et al.*, 2022) identification, RUV may provide a useful way to engage communities whilst contributing meaningful data to the body of restoration evidence (i.e. as with other citizen science methods; e.g. England and Peacock, 2010; England *et al.*, 2019). There is a need for future research to assess and develop the utility of RUV methodologies. More specifically, future studies should aim to: (1) provide more in-situ trials, with those comparing against traditional methods being particularly valuable (e.g. Ebner and Morgan, 2013). (2) Refine methodological approaches to enable capture of more and higher quality images (e.g. stereo-camera set-ups; Boldt *et al.*, 2018). (3) Assess the value of RUV, especially as a citizen science method, for monitoring and answering research questions including assessing the effectiveness of restoration.

9.5 Advice for effective chalk stream restoration and monitoring

This thesis supports the Chalk Stream Restoration Strategy's calls for a focus on the recovery of the processes and ecosystem engineers which facilitate the self-maintenance of spatially and temporally heterogeneous habitat, biocomplexity and ecological resilience (CaBA, 2021). To have the best chance of initiating change, recovery should be targeted at a sufficiently large scale (i.e. in respect to the scale of the deteriorated process; Beechie *et al.*, 2010). In the case of chalk streams, which often have a large number of landowners and differences in willingness to participate in restoration schemes, this is likely best achieved through the opportunistic implementation of reach-scale interventions tied into an overarching catchment strategy (e.g. Test and Itchen Restoration Strategy; RESTORE, 2020). Developing a clear set of quantifiable objectives for both this strategy and the smaller-scale interventions which feed into this is an often forgotten step (e.g. Chapters 5 – 7), but crucial for maintaining a clear project direction and to enable the quantification of 'success' (Morandi *et al.*, 2014). These objectives should be developed using a 'SMART approach' (specific, measurable, achievable, realistic and time-bound; ECRR, 2019) and consider socio-economic (e.g. urbanised areas) and environmental constraints (e.g. species distributions), including potential future changes (e.g. climate change; Addy *et al.*, 2016; England *et al.*, 2021a).

In the planning stage, developing an understanding of the system (e.g. through a scoping report; Skinner, 2013) to identify river/ site recovery potential (e.g. species pools for recolonisation; Sundermann *et al.*, 2011), the sources and scale of deterioration and a reference condition (e.g. a historical reference, extant 'pristine' site) is important for directing interventions and to avoid common pitfalls (e.g. failing to address the cause of degradation [Pulg *et al.*, 2013], inappropriate or vague objectives [Friberg *et al.*, 2016]). Integrating ecological theory at this stage can provide further insight into the potential effects and appropriateness of different interventions (Patrick *et al.*, 2021). For example, metacommunity theory posits that ecological communities are more likely to be controlled by local habitat when at an intermediate propagule pressure (i.e. 'species sorting'), and suggests that it is under these conditions in which restoration will be most effective (see section 2.1.2.2; Leibold *et al.*, 2004; Patrick *et al.*, 2021). As dispersal (i.e. 'mass effects') and local processes (e.g. competition, i.e. 'patch dynamics') play a greater role in shaping ecological communities when at high and low propagule pressure, respectively, we might expect to see a weaker ecological response to restoration under these conditions (Patrick *et al.*, 2021). With this understanding, more effective restoration strategies can be developed. For example, where propagule pressure is low, projects which increase patch connectivity (e.g. infrastructure removal) or, where appropriate, translocate species may be more effective (Stoll *et al.*, 2016). Measures should be of an appropriate scale in regard to the deteriorated process and used to tackle the source of the issue rather than a symptom of it (Beechie *et al.*, 2010; Feld *et al.*, 2020). Thus, where overarching issues with water quality or hydrology may inhibit the recovery of processes, habitat and ecology (e.g. fine sediment inputs; Pulg *et al.*, 2013), directing measures at these prior to physical restoration may be crucial for optimising restoration benefits and longevity (Polvi *et al.*, 2020). In many cases, interventions may be used to tackle multiple issues concurrently. For example, the re-establishment or wetted/ riparian woodland can restore habitat, processes and ecosystem engineers whilst acting as a buffer to diffuse pollutants (Feld *et al.*, 2011; Turunen *et al.*, 2021).

A recurring conclusion in this thesis is the need for more comprehensive monitoring to provide the robust evidence required to understand chalk stream restoration effectiveness. In an ideal situation, this monitoring should be conducted for an appropriately long timescale with sufficient temporal and spatial replication considering an integrated ecosystem approach (i.e. monitoring physical habitat and multiple ecological groups) with a strong study design (e.g. BACI) and over multiple restoration sites to discern intra-project variability. However, this thesis has also highlighted the widespread difficulties in implementing this ideal. For example, the limited amount and timescale of funding (Borgström *et al.*, 2016; Roni *et al.*, 2018), resource intensiveness and ad-hoc nature of data collection and external pressures (e.g. when control sites are subjected to manipulation) can all impact appraisal robustness. Given the constraints in monitoring, detailed appraisals are probably best achieved through the investment in flagship case studies specifically selected to represent the range of techniques used in these systems. These can provide important evidence towards restoration effectiveness and serve as exemplars to guide and inspire future efforts (Addy *et al.*, 2016; England *et al.*, 2021a). Supporting this, the Chalk Stream Restoration Strategy is currently forming a national network of catchment-scale case study projects with the aim of supporting the uptake of restoration under the strategy’s guidance (CaBA, 2022). Whilst detailed appraisals are often not appropriate for less well funded or resourced projects, monitoring with simple, cost-effective but reliable techniques (e.g. PRAGMO; River Restoration Centre, 2023c) with a strong study design to quantify success, allow intra-project comparison (Weber *et al.*, 2018), understand adaptive management requirements and to contribute to the body of evidence is invaluable (Downs and Kondolf, 2002; Addy *et al.*, 2016). The potential of citizen science to support this is considerable (Huddart *et al.*, 2016) and requires further investigation (e.g. the application of remote underwater video). In all cases of monitoring and regardless of the result, the raw data, methodology and findings should promptly be disseminated either within an open-access journal or public database (e.g. EU RiverWiki; RESTORE, 2023). This will help to provide the evidence required to support the development of effective chalk stream restoration strategies.

9.6 Future research directions

In chalk streams, the general lack of research assessing restoration means that any robust studies monitoring its effectiveness are valuable. However, some broad future research directions that would greatly improve our understanding of/ capabilities to undertake restoration in chalk streams include:

- Studies focussed on enhancing our understanding of **chalk stream reference states** to provide a greater picture of how humans have modified chalk streams, restoration potential and what can be expected from these interventions.
- Monitoring studies employing an '**integrated ecosystem approach'**. Specifically, those which assess the responses of physical habitat, processes and multiple different ecological groups to provide a more holistic understanding of restoration effects and mechanistic driving factors causing the response observed.
- Robust monitoring studies which have been carried out over a **long timescale** to provide information on the longevity of responses and trajectories. This is particularly crucial when implementing process-based restoration given the typical slow rate of change in chalk streams.
- Studies which assess the utility of **citizen science** for monitoring restoration projects and providing the data required to answer research questions.
- Studies aiming to understand the utility and develop the capabilities of **remote underwater video** to monitor and answer research questions would be valuable. Given the clarity of water and potential inhibited use of traditional physical capture methods in chalk streams, this may be particularly useful for restoration monitoring.

9.7 Study constraints and limitations

Whilst this body of research fulfils its aim of developing understanding of the effectiveness of chalk stream restoration, several constraints and limitations were identified and should be considered in future studies.

- **Case studies:** Whilst the fine scale case studies presented in this thesis provide useful, detailed information which contributes to the body of evidence describing restoration effectiveness, it is important to note that these are individualistic cases and the effects observed are not necessarily universal (e.g. Chapter 6). Whilst limited resources may constrain the number of sites and detail at which they are appraised, quantifying effects over a greater number of projects within the same analysis (i.e. qualitative sampling or coarse scale analyses) can provide information on the variability of responses and factors which drive or inhibit these (e.g. Sundermann *et al.*, 2011). The development of meta-analyses to gain a broader understanding of restoration effectiveness in chalk streams would be valuable, although are possibly constrained by the low number of detailed studies published. Another possibility is to exploit the data collected as a part of monitoring as noted in the NRRI database (River Restoration Centre, 2023b). However, challenges with accessing the data, methodological consistency and study design may create difficulties in this approach.

- **Data limitations:** Part of the data used in some monitoring chapters (Chapter 5 and 7) existed from previous (undergraduate) research projects and provided a good opportunity to quantify responses over a longer timescale than this PhD would have permitted (~ 3 years). However, it also created difficulties with study design (e.g. lack of a control in Chapter 7) and methodological consistency (e.g. number of points sampled in Chapter 5), an issue common across the restoration field (e.g. due to ad hoc nature of data collection; Albertson *et al.*, 2013). In addition, the data at times restricted the analyses which could be performed. For example, the identification of macroinvertebrates to the family level restricted the information which could be extracted regarding functional groups, which can provide important information for determining restoration effectiveness. Indeed, some have found functionality is comparatively more difficult to change than structural metrics (e.g. due to functional redundancy; England and Wilkes, 2018) and these may elucidate mechanistic factors driving response (Kail *et al.*, 2015). Whilst utilising pre-existing data can at times be a useful way to understand longer term responses, especially when resources are limited, recognising the limitations in this data is crucial for assessing its appropriateness for answering the question at hand (e.g. Albertson *et al.*, 2013).

9.8 Research impact

This thesis contributes much needed evidence towards the effectiveness of restoration in chalk streams. Additionally, it identified key issues in current restoration practice and monitoring and utilised/ developed novel approaches to appraise its effectiveness:

- **Chapter 2:** A literature review was conducted on chalk streams and restoration to identify current issues and research gaps. The lack of comprehensive monitoring of restoration projects in chalk streams was highlighted as a key issue. Analysis of River Restoration Centre datasets and case studies provided a useful quantitative overview of current chalk stream restoration practice. A review of chalk stream restoration literature identified several research gaps which required further exploration, including assessing certain techniques (e.g. weir removal) and the need for longer-term and more holistic appraisals.

- **Chapter 5:** This chapter provided insights into the impacts of weirs in chalk streams using a fine scale field study and novel coarse scale approach. The fine scale study demonstrated that weirs can degrade local habitat and ecological communities, especially upstream. However, the potential for variability in impacts between structures highlights the need for impact assessments to optimise restoration targets. The appraisal of a case study weir removal and restoration contributed evidence towards the effectiveness of this technique in chalk streams. The novelty of this study came from monitoring both upstream and downstream of the structure, providing insight into the potential for sediment-pulse related impacts in chalks streams. The restoration rapidly altered habitat and macroinvertebrates towards a more naturalised state, especially in the upstream reach. However, the role of the additional restoration methods to facilitate rapid recovery in low powered rivers, particularly the redistribution of silt, was identified as potentially key and in need of future investigation. Furthermore, the need for monitoring to take place at commensurate scales to adequately capture ecological response was highlighted. The results from this chapter will be submitted imminently to the journal *River Research and Applications* as Dolman *et al.,* "*Quantifying the environmental impacts of low-head weirs and their removal in chalk streams*".

- **Chapter 6:** This chapter contributed evidence towards the effectiveness of gravel augmentation restoration in chalk streams. The value of this study came from taking a 'multi-taxa approach' by assessing several ecological groups, something rarely considered in previous chalk stream restoration studies. It was demonstrated that whilst the effects of restoration were overall positive in light of the project goals, the responses varied considerably between sites, ecological groups and time periods, highlighting the need to better understand the drivers of variability in response. Furthermore, the conclusion of the need for monitoring to be conducted at sufficiently long timescales considering multiple sites and ecological groups emphasised the need for flagship case studies to provide the robust evidence required. To my knowledge, this study is the first to use remote underwater video to assess the responses of freshwater fish to habitat modification. The results from this chapter will be submitted imminently to the journal *PLOS ONE* as Dolman *et al.,* "*Chalk stream restoration: physical and ecological responses to gravel augmentation*". The results were disseminated at the 2021 British Ecological Society and River Restoration Centre conference.

- **Chapter 7:** This chapter provided one of the longest assessments of the physical and ecological effects of restoration in chalk streams. The value of monitoring over a longer timescale and with sufficient replication to accurately describe restoration effects was demonstrated. Furthermore, the need for and difficulty in carrying out long-term appraisals using robust monitoring strategies was highlighted, supporting the need to fund exemplar case studies. The role of and need to embrace unpredictable uncertainty in the restoration process was also shown. This chapter will be disseminated as Dolman *et al.,* "Restoration over time: the physical and ecological, responses to restoration in an English chalk stream".

- **Chapter 8:** This study was the first to empirically test the utility of RUV and UIF to form accurate, non-invasive population estimates in freshwater fish. It holds potentially wide spanning implications to an array of research disciplines and systems, but may be especially useful for monitoring chalk stream restoration projects due to its adaptability (e.g. to river conditions) and non-invasive nature (e.g. to avoid landowner restrictions). The results from this chapter will be submitted imminently to the journal *Methods in Ecology and Evolution* as Dolman *et al., "Non-invasive population estimates of freshwater fishes using remote underwater video".* The results were disseminated at the 2023 Fisheries, Biodiversity and Geomorphology conference (Environment Agency). Additionally, we are currently collaborating with computer scientists to help develop computer-aided approaches to allow automated individual identification from underwater video. This may be particularly valuable for developing remote underwater video as citizen science methodology.

APPENDIX A Chapter 5 supplementary material

Table A1 Results of paired sample t-tests and paired Wilcoxon tests comparing metrics calculated from paired 30 second (multiplied abundance of each macroinvertebrate by two) and 3 minute kick samples. Significant results are boldened.

Term	Test	T/V	df	p
Taxon richness	t-test	-0.779	19	0.446
Abundance	Wilcoxon	91	NA	0.888
EPT abundance	t-test	0.137	19	0.892
EPT richness	Wilcoxon	54	NA	0.477
LIFE	t-test	1.610	19	0.124
PSI	t-test	**-2.247**	**19**	**< 0.05**

Table A2 Descriptions and locations of the weir sites, impacted and control macroinvertebrate datasets used within the coarse scale analysis of the impacts on low-head weirs on upstream and downstream macroinvertebrate communities. DFW = distance from weir. U = Upstream, D = downstream.

Location	River	Weir				Macroinvertebrate sample					Control sample		
		ID	Height (m)	Latitude	Longitude	ID	Latitude	Longitude	DFW (m)	Samples	ID	Latitude	Longitude
U	Piddle	953	0.999	50.750213	-2.344368	9043	50.750274	-2.344918	40	4	9069	50.7531417	-2.3571726
	Misbourne	11547	0.89499	51.577734	-0.516191	34011	51.578143	-0.516317	47	7	183928	51.5660923	-0.4873324
	Thet	10971	0.891	52.492066	0.9387848	55912	52.492828	0.9393738	90	2	55921	52.4763752	0.9199408
	Lark	10118	2.6	52.326425	0.5783797	55974	52.326093	0.5787533	45	10	55966	52.308887	0.6225881
	Cam	10362	2.341	52.134582	0.1419868	56087	52.13458	0.1423067	20	1	56111	52.157238	0.0882779
	Nar	10960	2.849	52.678046	0.5478418	56341	52.67857	0.549177	120	10	165184	52.6776527	0.5269174
	Test	13933	1.188	51.144753	-1.464089	146221	51.144713	-1.459736	300	1	151182	51.1613965	-1.4495407
	Great Stour	14380	1.008	51.15608	0.8275518	147909	51.156144	0.8274716	10	3	159856	51.1524667	0.8367142
D	Allen	1387	1.36	50.80581	-1.989631	8526	50.805513	-1.988403	100	3	190615	50.8206389	-1.9939925
	Tarrant	1466	1.376	50.85851	-2.0867	8639	50.858169	-2.087276	55	4	85963	50.847176	-2.0922696
	Wylye	1919	2.032	51.186695	-2.183311	9201	51.187201	-2.18375	70	12	9198	51.1482884	-2.1972347
	Elmswell Beck	5924	1.296	54.004187	-0.461832	76041	54.003989	-0.460905	80	13	142	53.9969288	-0.4473436
	Gypsey Race	6721	0.616	54.090527	-0.219682	166	54.090604	-0.218669	65	2	145610	54.0946009	-0.2596332
	Little Ouse	10950	2.984	52.387037	0.7789722	55938	52.386954	0.7783461	45	16	55932	52.3878123	0.8983216
	Loddon	11627	2.12	51.318693	-1.020501	36035	51.319939	-1.021058	200	9	36034	51.2926001	-1.0163912
	Colne	11847	0.49499	51.628597	-0.493901	34318	51.627793	-0.494037	100	6	34319	51.5837905	-0.4930524
	Gade	12104	1.497	51.759938	-0.476204	184607	51.759603	-0.476107	50	8	185665	51.7724553	-0.4832971
	Darent	12116	0.82399	51.388279	0.2346846	101602	51.388859	0.2353729	75	1	161420	51.3684059	0.202251
	Wey (Thames)	13073	1.613	51.169938	-0.920583	35829	51.169821	-0.919869	50	9	35569	51.1547919	-0.957226
	Itchen	14726	0.505	50.990317	-1.335557	82504	50.989896	-1.333984	120	4	82501	50.9841031	-1.3352923
	Great Stour	14751	1.392	51.258114	1.0307525	43751	51.258707	1.0316384	90	20	43435	51.2553284	0.9934025

Table A3 Post-hoc TukeyHSD pairwise comparisons to test LMMs assessing physical habitat characteristics with significant interactions between location (U = Upstream, D = Downstream) and sampling years before (2017) and after (2018-2021) the removal of a low-head weir. Significant tests are boldened.

Contrast	Depth		Velocity		Coarse substrate cover		Silt cover	
	t	p	t	p	t	p	t	p
2017 D - 2017 U	**-6.209**	**< 0.001**	**3.492**	**0.023**	**4.601**	**< 0.001**	**-7.470**	**< 0.001**
2018 D - 2018 U	1.928	0.650	-1.478	0.898	-0.980	0.993	1.641	0.825
2019 D - 2019 U	1.486	0.895	0.005	1.000	-0.257	1.000	-0.724	0.999
2020 D - 2020 U	1.903	0.667	-2.436	0.316	-2.464	0.300	2.886	0.122
2021 D - 2021 U	1.841	0.708	-0.898	0.996	-1.583	0.854	0.951	0.994
2017 D - 2018 D	0.934	0.995	1.874	0.686	-0.455	1.000	-1.698	0.794
2017 D - 2019 D	2.164	0.489	0.194	1.000	-1.929	0.649	0.566	1.000
2017 D - 2020 D	1.880	0.682	3.098	0.074	1.365	0.934	-2.841	0.139
2017 D - 2021 D	1.312	0.948	0.890	0.996	-1.118	0.982	-0.521	1.000
2018 D - 2019 D	1.230	0.965	-1.680	0.804	-1.474	0.899	2.264	0.423
2018 D - 2020 D	0.946	0.994	1.224	0.967	1.821	0.721	-1.143	0.979
2018 D - 2021 D	0.378	1.000	-0.984	0.993	-0.663	1.000	1.177	0.974
2019 D - 2020 D	-0.284	1.000	2.904	0.120	**3.295**	**< 0.05**	-3.407	0.032
2019 D - 2021 D	-0.852	0.997	0.696	1.000	0.811	0.998	-1.087	0.985
2020 D - 2021 D	-0.568	1.000	-2.208	0.459	-2.483	0.292	2.320	0.387
2017 U - 2018 U	**9.131**	**< 0.001**	-3.211	0.055	**-6.035**	**< 0.001**	**7.413**	**< 0.001**
2017 U - 2019 U	**9.916**	**< 0.001**	**-3.374**	**< 0.05**	**-6.787**	**< 0.001**	**7.312**	**< 0.001**
2017 U - 2020 U	**10.052**	**< 0.001**	-2.966	0.103	**-5.699**	**< 0.001**	**7.515**	**< 0.001**
2017 U - 2021 U	**9.421**	**< 0.001**	**-3.601**	**< 0.05**	**-7.302**	**< 0.001**	**7.900**	**< 0.001**
2018 U - 2019 U	0.785	0.999	-0.162	1.000	-0.752	0.999	-0.102	1.000
2018 U - 2020 U	0.921	0.995	0.245	1.000	0.336	1.000	0.102	1.000
2018 U - 2021 U	0.290	1.000	-0.390	1.000	-1.266	0.958	0.487	1.000
2019 U - 2020 U	0.136	1.000	0.407	1.000	1.088	0.985	0.204	1.000
2019 U - 2021 U	-0.495	1.000	-0.228	1.000	-0.514	1.000	0.589	1.000
2020 U - 2021 U	-0.631	1.000	-0.635	1.000	-1.603	0.843	0.385	1.000

Table A4 Post-hoc TukeyHSD pairwise comparisons to test LMMs assessing macroinvertebrate metrics with significant interactions between location (U = Upstream, D = Downstream) and sampling years before (2016, 2017) and after (2018-2021) the removal of a low-head weir. Significant tests are boldened.

Contrast	EPT abundance		LIFE		PSI	
	t	p	t	p	t	p
2016 D - 2016 U	-0.382	1.000	3.109	0.092	3.254	0.063
2017 D - 2017 U	**3.741**	**< 0.05**	**5.045**	**< 0.001**	**5.246**	**< 0.001**
2018 D - 2018 U	-1.676	0.875	1.224	0.986	0.579	1.000
2019 D - 2019 U	-1.174	0.990	0.346	1.000	-1.603	0.904
2020 D - 2020 U	-0.194	1.000	-0.946	0.998	-1.694	0.867
2021 D - 2021 U	-0.368	1.000	-2.083	0.636	-1.848	0.788
2016 D - 2017 D	-1.057	0.996	2.083	0.636	1.533	0.928
2016 D - 2018 D	**-3.510**	**< 0.05**	0.788	1.000	1.967	0.714
2016 D - 2019 D	-3.074	0.102	0.295	1.000	-1.071	0.995
2016 D - 2020 D	-2.469	0.371	1.240	0.984	0.155	1.000
2016 D - 2021 D	-2.320	0.469	1.023	0.997	-0.161	1.000
2017 D - 2018 D	**-3.694**	**< 0.05**	-1.949	0.726	0.661	1.000
2017 D - 2019 D	-3.038	0.114	-2.689	0.248	**-3.963**	**< 0.01**
2017 D - 2020 D	-2.127	0.605	-1.268	0.981	-2.097	0.626
2017 D - 2021 D	-1.903	0.754	-1.595	0.907	-2.577	0.307
2018 D - 2019 D	0.657	1.000	-0.741	1.000	**-4.623**	**< 0.001**
2018 D - 2020 D	1.568	0.916	0.681	1.000	-2.758	0.215
2018 D - 2021 D	1.791	0.819	0.354	1.000	-3.237	0.068
2019 D - 2020 D	0.911	0.999	1.421	0.957	1.866	0.777
2019 D - 2021 D	1.134	0.992	1.095	0.994	1.386	0.964
2020 D - 2021 D	0.223	1.000	-0.326	1.000	-0.480	1.000
2016 U - 2017 U	1.986	0.702	1.615	0.900	1.132	0.993
2016 U - 2018 U	**-4.176**	**< 0.01**	-2.287	0.492	-1.806	0.811
2016 U - 2019 U	**-3.397**	**< 0.05**	**-3.379**	**< 0.05**	**-6.421**	**< 0.001**
2016 U - 2020 U	-2.120	0.610	-3.316	0.053	**-5.260**	**< 0.001**
2016 U - 2021 U	-2.092	0.630	**-4.308**	**< 0.05**	**-5.687**	**< 0.001**
2017 U - 2018 U	**-9.282**	**< 0.001**	**-5.871**	**< 0.001**	**-4.470**	**< 0.001**
2017 U - 2019 U	**-8.107**	**< 0.001**	**-7.513**	**< 0.001**	**-11.493**	**< 0.001**
2017 U - 2020 U	**-6.185**	**< 0.001**	**-7.418**	**< 0.001**	**-9.728**	**< 0.001**
2017 U - 2021 U	**-6.142**	**< 0.001**	**-8.911**	**< 0.001**	**-10.377**	**< 0.001**
2018 U - 2019 U	1.174	0.990	-1.642	0.889	**-7.023**	**< 0.001**
2018 U - 2020 U	3.097	0.098	-1.547	0.923	**-5.257**	**< 0.001**
2018 U - 2021 U	3.140	0.088	-3.040	0.113	**-5.906**	**< 0.001**
2019 U - 2020 U	1.923	0.742	0.095	1.000	1.766	0.832
2019 U - 2021 U	1.966	0.715	-1.398	0.961	1.117	0.993
2020 U - 2021 U	0.043	1.000	-1.493	0.939	-0.649	1.000

Table A5 Post-hoc TukeyHSD pairwise comparisons to test GLMM or LMMs assessing macroinvertebrate metrics with a significant effect of sampling years. Significant tests are boldened.

Contrast	Abundance		Taxon richness		EPT richness	
	t	p	t	p	t	p
2016 - 2017	**-2.946**	**< 0.05**	**-3.282**	**< 0.05**	-1.166	0.852
2016 - 2018	**-5.809**	**< 0.001**	**-3.919**	**< 0.05**	-0.845	0.958
2016 - 2019	**-5.690**	**< 0.001**	**-4.836**	**< 0.001**	**-3.572**	**< 0.01**
2016 - 2020	**-4.600**	**< 0.001**	**-6.283**	**< 0.001**	**-4.111**	**< 0.001**
2016 - 2021	**-5.352**	**< 0.001**	**-5.603**	**< 0.001**	**-3.399**	**< 0.05**
2017 - 2018	**-4.334**	**< 0.001**	-1.117	0.873	0.506	0.996
2017 - 2019	**-4.154**	**< 0.001**	-2.791	0.068	**-4.135**	**< 0.001**
2017 - 2020	-2.503	0.133	**-5.569**	**< 0.001**	**-5.136**	**< 0.0001**
2017 - 2021	**-3.643**	**< 0.01**	**-4.243**	**< 0.001**	**-3.819**	**< 0.01**
2018 - 2019	0.180	1.000	-1.681	0.548	**-4.616**	**< 0.001**
2018 - 2020	1.830	0.451	**-4.487**	**< 0.001**	**-5.605**	**< 0.001**
2018 - 2021	0.691	0.983	**-3.145**	**< 0.05**	**-4.305**	**< 0.001**
2019 - 2020	1.650	0.568	-2.829	0.062	-1.066	0.894
2019 - 2021	0.511	0.996	-1.472	0.683	0.336	0.999
2020 - 2021	-1.139	0.864	1.363	0.749	1.402	0.726

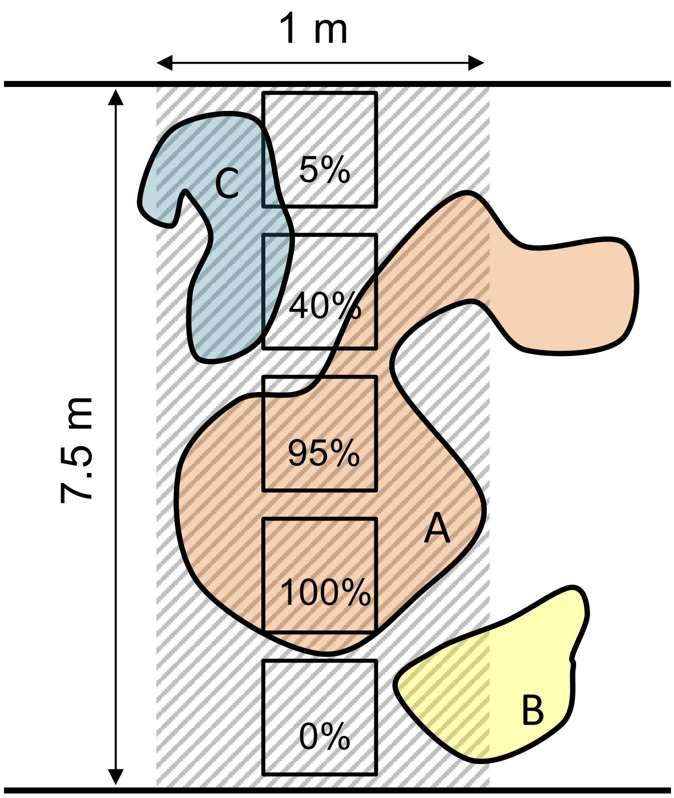
Table A6 Results of post-hoc analysis assessing differences in macroinvertebrate community structure between (a) sampling years in upstream and downstream sites, and (b) between upstream and downstream sites across each year. UP = 'unique permutations'. Significant tests are boldened.

Groups	Upstream			Downstream		
	t	p	UP	t	p	UP
2017 - 2018	**4.3557**	**0.001**	**998**	**3.029**	**0.001**	**998**
2017 - 2019	**4.3736**	**0.001**	**999**	**2.6226**	**0.001**	**999**
2017 - 2020	**4.1759**	**0.001**	**998**	**2.4909**	**0.001**	**999**
2017 - 2021	**4.2498**	**0.001**	**999**	**2.4536**	**0.001**	**999**
2018 - 2019	**5.5085**	**0.001**	**999**	**4.411**	**0.001**	**997**
2018 - 2020	**4.831**	**0.001**	**998**	**4.2286**	**0.001**	**997**
2018 - 2021	**5.064**	**0.001**	**999**	**4.1476**	**0.001**	**999**
2019 - 2020	**2.3901**	**0.001**	**999**	**1.6558**	**0.009**	**998**
2019 - 2021	**3.3489**	**0.001**	**999**	**2.2669**	**0.001**	**998**
2020 - 2021	**1.9665**	**0.001**	**998**	**1.5054**	**0.021**	**997**

(b)

Term	t	p	UP
2017	**2.1406**	**0.001**	**990**
2018	**1.6785**	**0.012**	**994**
2019	**1.9544**	**0.007**	**996**
2020	**1.4983**	**0.028**	**994**
2021	**1.6041**	**0.028**	**994**

APPENDIX B Chapter 6 supplementary material



1) Calculate macrophyte cover over 1 m² area across transect:

- Transect area (**7.5 m²**)
- Mean percent TMC cover (0 + 100 + 95 + 40 + 5/5 = **48%**)
- Estimated transect macrophyte cover (7.5 m²/100 * 48 = **3.6 m²**)

2) Estimate the percentage of cover made of a macrophyte group:

- Percentage of total cover in transect made of Macrophyte A (**75%**)

3) Calculate actual cover:

- Actual cover of Macrophyte A (3.6 m²/100 * 75 = **2.7 m²**)

Figure B1 Example calculation of the cover of macrophyte groups across each transect in a study to assess physical and ecological responses to gravel augmentation. Thick lines show river boundary. Hashed area shows the 1 m area across the transect which was assessed. Boxes show the five percent total macrophyte cover (TMC) estimates made across each transect. Letters and coloured areas represent different macrophyte groups.

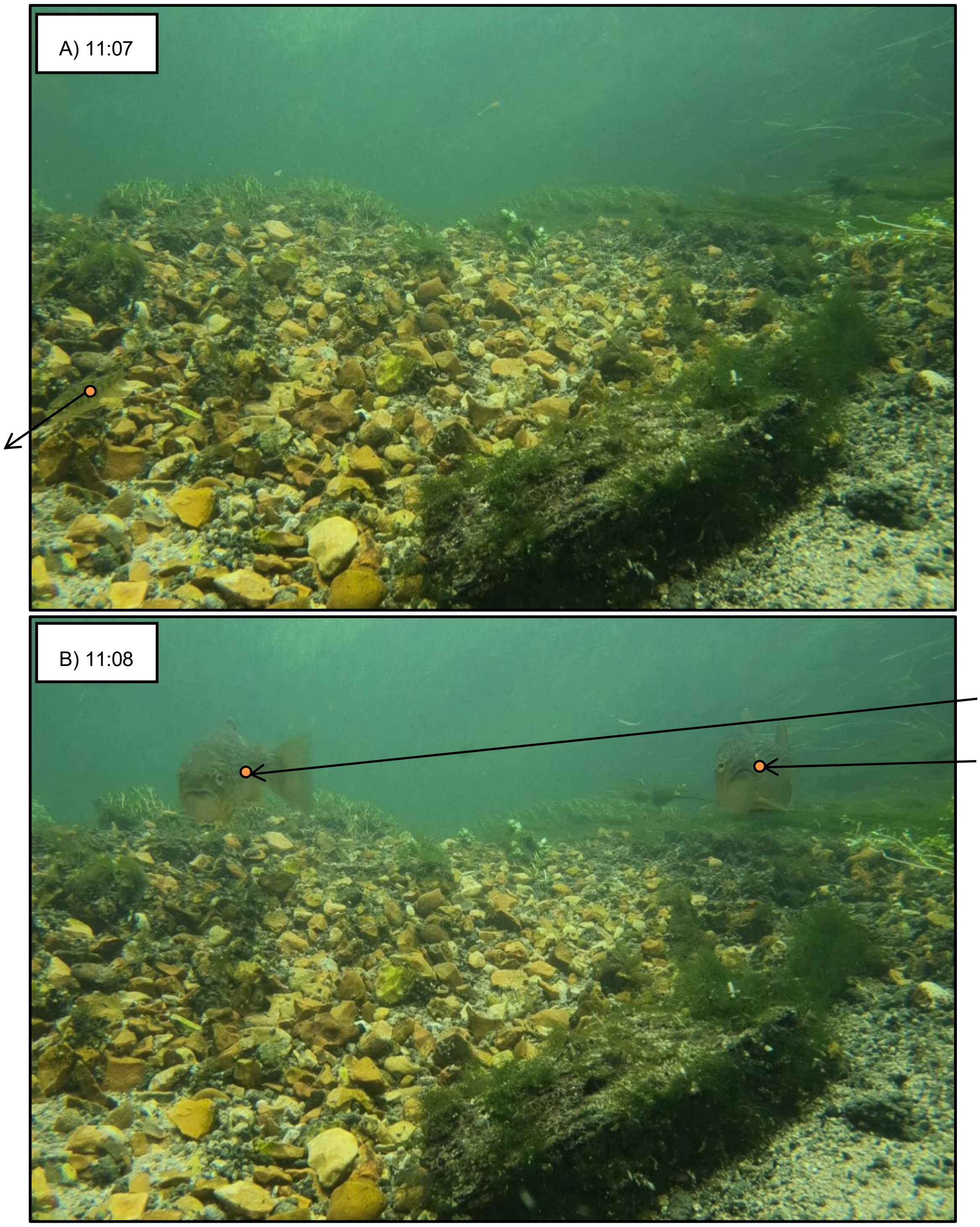


Figure B2 Images showing an example of how remote underwater videos were analysed. In image A, a single brown trout is within the frame. This individual leaves the frame to the left and one second later in image B, two brown trout enter the frame from the right. Here, the maximum abundance of brown trout would be scored as three. Number in the top left of each image shows the time. Orange dot shows fish position. Arrows show the direction of travel for each fish. In the actual analysis, wild brown trout (image A) and stocked brown trout (image B) were distinguished based on their size and fin condition and the latter was not included in the analysis.

Table B1 Results of Tukey pairwise comparison post-hoc tests following significant BA x CI interactions in GLMM and LMM. Significant comparisons are boldened. FGA = filamentous green algae; TMC = total macrophyte cover.

Contrast	HS														EL							
	Depth		VCSV		Abundance		Taxon richness		EPTN		LIFE		PSI		Depth		Velocity		Taxon richness		PSI	
	t	p	t	p	z	p	z	p	t	p	t	p	t	p	t	p	t	p	z	p	t	p
pre-control - pre-restored	4.00	**< 0.001**	2.39	0.17	2.88	**< 0.05**	1.10	0.88	1.07	0.89	3.13	**< 0.01**	2.29	0.21	-1.21	0.83	1.79	0.47	-0.64	0.99	3.28	**< 0.05**
0-1 control - 0-1 restored	9.80	**< 0.001**	2.52	0.13	0.75	0.98	1.17	0.85	-1.82	0.46	1.51	0.66	-2.70	0.09	5.43	**< 0.001**	4.89	**< 0.001**	0.82	0.96	0.53	0.99
1-2 control - 1-2 restored	7.60	**< 0.001**	0.23	1.00	-4.18	**< 0.001**	-3.59	**< 0.05**	-2.71	0.09	0.34	1.00	-2.81	0.07	5.35	**< 0.001**	2.86	0.05	-3.18	0.02	0.14	1.00
0-1 control - pre-control	1.51	0.67	2.30	0.23	0.76	0.97	0.86	0.96	0.17	1.00	-0.49	1.00	0.65	0.99	1.20	0.83	1.38	0.74	0.93	0.94	0.19	1.00
1-2 control - pre-control	0.10	1.00	1.00	0.91	1.58	0.61	0.67	0.98	0.09	1.00	-1.31	0.77	0.47	1.00	3.14	0.05	2.16	0.31	1.50	0.66	0.45	1.00
0-1 control - 1-2 control	1.72	0.56	1.59	0.61	-1.01	0.91	0.23	1.00	0.09	1.00	1.01	0.90	0.21	1.00	-2.37	0.21	-0.96	0.92	-0.71	0.98	-0.31	1.00
0-1 restored - pre-restored	-6.00	**< 0.01**	2.65	0.12	1.50	0.67	1.12	0.88	2.14	0.29	1.96	0.43	4.28	**< 0.01**	-4.44	**< 0.01**	0.39	1.00	-0.47	1.00	3.62	**< 0.05**
1-2 restored - pre-restored	-4.24	**< 0.05**	3.23	**< 0.05**	3.77	**< 0.01**	3.66	**< 0.01**	2.59	0.12	2.19	0.33	4.18	**< 0.01**	-2.44	0.19	1.90	0.44	3.28	**< 0.05**	4.21	**< 0.05**
0-1 restored - 1-2 restored	-2.17	0.34	-0.71	0.98	-2.79	0.06	-3.23	**< 0.05**	-0.56	0.99	-0.29	1.00	0.13	1.00	-2.45	0.19	-1.86	0.47	-4.68	**< 0.001**	-0.72	0.97

Table B2 Results of Tukey pairwise comparison post-hoc tests following significant BA x CI interactions in Non-parametric models (NPMs). Significant comparisons are boldened. FGA = filamentous green algae; TMC = total macrophyte cover, BL = broad leaved.

Contrast	HS						EL											
	Sand		Gravel		FGA		Silt		Sand		Gravel		Cobble		BL macrophyte		Tape grass	
	ATS	p	ATS	p	ATS	p	ATS	p	ATS	p	ATS	p	ATS	p	ATS	p	ATS	p
0-1 restored - pre-restored	-4.54	**< 0.01**	5.78	**< 0.001**	-3.11	**< 0.05**	-4.20	**< 0.01**	-3.95	**< 0.01**	5.47	**< 0.001**	3.47	**< 0.01**	-1.01	0.59	-1.38	0.39
1-2 restored - pre-restored	-4.38	**< 0.01**	5.46	**< 0.001**	-4.02	**< 0.01**	-3.80	**< 0.01**	-2.36	0.08	3.83	**< 0.01**	4.80	**< 0.001**	5.12	**< 0.01**	-0.67	0.78
0-1 restored - 1-2 restored	-0.55	0.85	0.33	0.94	-0.82	0.70	0.32	0.95	2.18	0.11	-3.67	**< 0.01**	2.08	0.13	5.04	**< 0.01**	1.28	0.44
0-1 control - pre-control	0.98	0.59	-0.46	0.88	0.26	0.96	-0.71	0.76	-0.36	0.93	0.67	0.77	2.22	0.10	2.32	0.08	1.54	0.30
1-2 control - pre-control	0.55	0.85	0.15	0.99	-0.69	0.77	-0.20	0.98	-2.25	0.09	2.90	**< 0.05**	2.19	0.10	5.11	**< 0.001**	1.76	0.21
0-1 control - 1-2 control	-0.71	0.76	0.84	0.65	-0.82	0.70	0.57	0.84	-2.58	0.05	2.18	0.10	-0.13	0.99	3.54	**< 0.01**	0.23	0.97

Table B3 Results of Tukey pairwise comparison post-hoc tests following significant BA interactions in GLMM, LMM and NPMs. Significant comparisons are boldened.

Contrast	HS										EL									
	Silt		Cobble		TMC		Water crowfoot		Tape grass		TMC		FGA		Water crowfoot		EPTN		LIFE	
	ATS	p	ATS	p	ATS	p	ATS	p	ATS	p	ATS	p	ATS	p	ATS	p	t	p	t	p
Pre-restoration - 0-1 post-restoration	-1.78	0.19	3.07	**< 0.05**	-4.44	**< 0.001**	-3.12	**< 0.01**	-3.35	**< 0.01**	-1.54	0.27	-2.81	**< 0.05**	1.45	0.32	2.48	0.07	2.40	0.08
Pre-restoration - 1-2 post-restoration	-2.10	0.10	3.48	**< 0.01**	-2.83	**< 0.05**	-2.12	0.10	-1.48	0.32	2.94	**< 0.05**	-2.83	**< 0.05**	5.13	**< 0.001**	2.94	**< 0.05**	1.02	0.58
0-1 - 1-2 years post-restoration	-0.34	0.94	0.27	0.96	1.59	0.25	1.82	0.18	1.58	0.27	7.33	**< 0.001**	-0.92	0.62	4.45	**< 0.001**	-0.55	0.85	1.69	0.25

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Table C1 Results of Tukey HSD post-hoc comparison analysis for physical metrics following a significant effect of ‘year’ in main tests.

Site	Contrast	Depth		Velocity		DCSV		VCSV		Cobble		Gravel		Sand		Silt	
		t	p	t	p	t	p	t	p	ATS	p	ATS	p	ATS	p	ATS	p
OSTN	2013 - 2014	**-4.678**	**< 0.001**	-1.962	0.289	**-5.536**	**< 0.001**	**-3.238**	**0.016**	1.354	0.624	1.261	0.709	-2.380	0.132	0.275	0.999
	2013 - 2016	**-4.387**	**< 0.001**	**3.037**	**0.023**	**-3.213**	**0.017**	-0.186	1.000	1.357	0.622	0.000	1.000	-0.891	0.892	0.275	0.999
	2013 - 2020	**-4.691**	**< 0.001**	**3.430**	**0.007**	-2.424	0.121	-0.078	1.000	**3.755**	**0.004**	-2.102	0.231	**-4.352**	**0.001**	**2.877**	**0.044**
	2013 - 2021	**-6.535**	**< 0.001**	1.486	0.573	-2.132	0.219	-0.065	1.000	**4.734**	**< 0.001**	-2.667	0.072	**-3.413**	**0.010**	2.128	0.220
	2014 - 2016	0.291	0.998	**4.999**	**< 0.001**	2.323	0.150	**3.052**	**0.026**	0.000	1.000	-1.470	0.579	1.544	0.525	0.000	1.000
	2014 - 2020	-0.013	1.000	**5.392**	**< 0.001**	**3.113**	**0.022**	**3.160**	**0.019**	**3.484**	**0.008**	**-3.988**	**0.002**	-1.703	0.427	**3.251**	**0.017**
	2014 - 2021	-1.857	0.344	**3.448**	**0.006**	**3.404**	**0.010**	**3.173**	**0.019**	**3.210**	**0.017**	**-4.181**	**0.001**	-0.903	0.888	1.733	0.417
	2016 - 2020	-0.304	0.998	0.393	0.995	0.789	0.933	0.108	1.000	**2.843**	**0.043**	-2.465	0.113	**-3.266**	**0.016**	**3.028**	**0.030**
	2016 - 2021	-2.148	0.204	-1.551	0.531	1.081	0.816	0.122	1.000	**3.025**	**0.027**	-2.513	0.102	-2.462	0.111	1.823	0.366
	2020 - 2021	-1.844	0.352	-1.944	0.298	0.292	0.998	0.014	1.000	0.595	0.970	-0.256	0.999	0.704	0.951	-0.850	0.910
OSTW	2014 - 2016	-0.753	0.875	**3.420**	**0.006**	**-6.891**	**< 0.001**	NA	NA	**3.993**	**0.003**	NA	NA	-2.549	0.071	NA	NA
	2014 - 2020	-1.707	0.327	2.587	0.055	**-4.589**	**0.001**	NA	NA	2.476	0.083	NA	NA	-1.271	0.567	NA	NA
	2014 - 2021	**-3.263**	**0.009**	**3.192**	**0.011**	**-6.678**	**< 0.001**	NA	NA	**4.296**	**0.001**	NA	NA	-2.547	0.072	NA	NA
	2016 - 2020	-0.954	0.776	-0.832	0.839	2.302	0.122	NA	NA	-1.538	0.409	NA	NA	1.363	0.510	NA	NA
	2016 - 2021	-2.510	0.067	-0.228	0.996	0.213	0.997	NA	NA	0.272	0.992	NA	NA	0.000	1.000	NA	NA
	2020 - 2021	-1.556	0.410	0.604	0.930	-2.089	0.182	NA	NA	1.988	0.205	NA	NA	-1.812	0.274	NA	NA

Table C2 Results of Tukey HSD post-hoc comparison analysis for macroinvertebrate metrics following a significant effect of 'year' in main tests.

Site	Comparison	Abundance		Taxon richness		EPTA		EPTN		LIFE		PSI	
		t	p	z	p	t	p	t	p	t	p	t	p
OSTN	2013-2014	**-4.756**	**< 0.001**	**-4.982**	**< 0.001**	NA	NA	1.977	0.295	**4.458**	**< 0.001**	0.124	1.000
	2013-2016	1.876	0.347	0.152	1.000	NA	NA	**3.701**	**0.006**	**4.834**	**< 0.001**	2.454	0.122
	2013-2020	**-6.009**	**< 0.001**	**-4.831**	**< 0.001**	NA	NA	1.115	0.798	1.403	0.629	-2.377	0.142
	2013-2021	**-5.021**	**< 0.001**	**-4.932**	**< 0.001**	NA	NA	1.889	0.339	**3.049**	**0.031**	-1.212	0.745
	2014-2016	**6.632**	**< 0.001**	**5.119**	**< 0.001**	NA	NA	1.723	0.432	0.376	0.996	2.330	0.157
	2014-2020	-1.253	0.721	0.164	1.000	NA	NA	-0.862	0.909	**-3.055**	**0.031**	-2.502	0.110
	2014-2021	-0.265	0.999	0.055	1.000	NA	NA	-0.088	1.000	-1.409	0.625	-1.336	0.671
	2016-2020	**-7.885**	**< 0.001**	**-4.968**	**< 0.001**	NA	NA	-2.586	0.092	**-3.431**	**0.012**	**-4.831**	**< 0.001**
	2016-2021	**-6.896**	**< 0.001**	**-5.069**	**< 0.001**	NA	NA	-1.811	0.381	-1.785	0.396	**-3.666**	**0.006**
	2020-2021	0.988	0.859	-0.110	1.000	NA	NA	0.774	0.937	1.646	0.478	1.165	0.771
OSTW	2014-2016	1.999	0.211	2.134	0.142	-0.496	0.959	NA	NA	NA	NA	NA	NA
	2014-2020	**-3.181**	**0.017**	**-2.885**	**0.021**	2.100	0.176	NA	NA	NA	NA	NA	NA
	2014-2021	**-2.996**	**0.026**	**-5.266**	**< 0.001**	1.226	0.616	NA	NA	NA	NA	NA	NA
	2016-2020	**-5.181**	**< 0.001**	**-4.903**	**< 0.001**	2.596	0.065	NA	NA	NA	NA	NA	NA
	2016-2021	**-4.996**	**< 0.001**	**-7.118**	**< 0.001**	1.722	0.330	NA	NA	NA	NA	NA	NA
	2020-2021	0.185	0.998	-2.488	0.062	-0.874	0.818	NA	NA	NA	NA	NA	NA

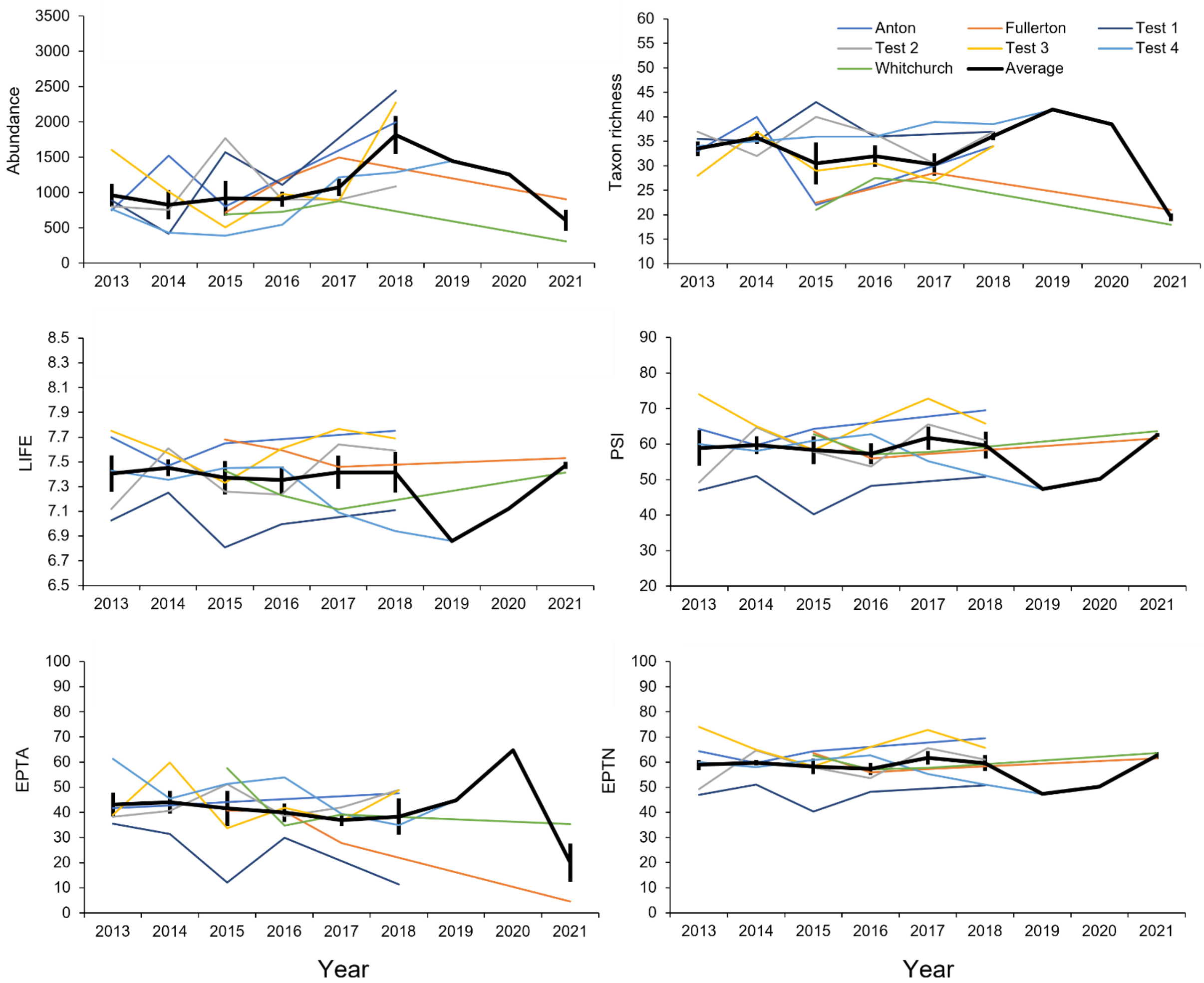

Figure C1 Macroinvertebrate metrics at seven control sites collected from Environment Agency (nd) and SmartRivers (nd) across the River Test and its tributaries and the average of these (mean ± SD). National grid references: Anton = SU3787039460, Fullerton = SU3822139000, Test 1 = SU3443032520, Test 2 = SU3316025230, Test 3 = SU3547917847, Test 4 = SU3535015300, Whitchurch = SU4776448086.

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