

Bringing the burbot (*Lota lota*, L.) back to English rivers: Habitat, thermal and hydrological suitability at a potential English reintroduction site

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by

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I, **Reagan Pearce**, confirm that the work presented in my thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Abstract

Species reintroductions can play a major role in addressing biodiversity declines. Fish species reintroductions are, however, complex and require the investigation of multiple factors: physical habitat, water chemistry and hydrology, amongst others. The burbot *Lota lota*, L., the only freshwater member of the Cod family (Gadidae), was extirpated from English rivers due to a loss of suitable spawning and larval nursery habitat. There is potential for the burbot to be reintroduced into English rivers.

This study sought to determine the spatial and temporal extent of suitable habitat for the burbot in a potential candidate reintroduction site, the upper River Wissey, UK, to support and inform a future reintroduction. The study investigates three main areas: physical river habitat availability, thermal suitability, and local hydrology, as each could be a potential barrier to a reintroduced burbot population. The physical river habitat chapter used a bespoke walkover instream river survey to locate and quantify the availability of habitats for each burbot life stage. This was combined with an *ex situ* remote sensing study used to locate and quantify potential floodplain spawning habitat, in comparison to a burbot reintroduction site in Belgium. The temperature chapter employed data collected over three hydrological years from a sensor network with high spatial and temporal resolution to assess the Wissey's thermal suitability for each burbot life stage, and the chapter also considered climate change temperature projections. The final hydrological chapter has used observational and historical data from within the study area to characterise flood years and assess the extent and duration of floodplain inundation, and thus, spawning and larval habitat availability for reintroduced burbot. The study highlights the challenges that a burbot reintroduction attempt would face and can be directly applied to evidence-based decision making regarding the reintroduction, future river-floodplain restoration, and wider, landscape-scale habitat management and restoration.

Impact Statement

First, considering academia, the current study has contributed to the knowledge base of the Environmental Change & Biodiversity Research (ECB) Group at UCL within UCL. Further, in order to facilitate the dissemination of research findings more widely, I have presented my research at national and international conferences: *London Freshwater Group*, *Symposium for European Freshwater Sciences*, and the *International Symposium for Fish Biology*, building networks with freshwater scientists that have led to knowledge exchange and research collaboration. The methodologies applied here have also generated impact. For example, this project has developed a low-cost, open-source water depth sensor that can increase the spatial and temporal scope of data collection at a fraction of the cost of a market equivalent. Its construction and deployment is reproducible and accessible to academics through a publication in *Sensors* (Pearce et al., 2024a), but also to the general public with all resources and instruction guides hosted on GitHub (<https://github.com/rhpearce/waterdepthsensor>). The research on low-cost sensors and their applications can have far-reaching impacts. The reduced cost means increased data collection, but to ensure low-cost sensors are integrated into projects, these skills have to be taught, which I would like to organise through workshops.

Outside of academia, the impact potential of this project is varied. The clearest is the direct relation of the project's findings to the currently occurring burbot reintroduction in England, which is still in planning stages with Norfolk Rivers Trust (NRT), the Environment Agency (EA), and Natural England. These results have direct impact on the planning of the reintroduction, as I have presented at meetings with NRT and the EA. Also, the developed walkover river habitat survey is accessible to non-trained professionals and maintains the spatial relationships between the riverine features. NRT requested training in this survey methodology, which was delivered in June 2023. To ensure impact with the general public, outside of the audience of peer-reviewed journals, I have also published in *British Wildlife* magazine (Pearce et al., 2024b), to increase the visibility of a potential burbot reintroduction more generally, and to encourage wider conservation agency as well as conservation practitioner and public

support. Though a national-scale impact, this could be taken further with an article written for a more general readership in *The Guardian* for example. To encourage wider public engagement with burbot conservation and wider riverine conservation, I collaborated with two artists on The Rubbing Out Project (<https://rubbingoutproject.co.uk/The-Burbot>), which was presented in Prague, Czech Republic, reaching a more international audience. In the future, it would be effective to engage with public engagement activities, such as workshops or festivals in the UK to communicate the findings and garner public support for conservation initiatives.

There is potential for national-scale impact from this work also, beyond the subject of a burbot reintroduction. This work has added to the evidence base of catchment - based approaches to river management and conservation, as well as highlighting the importance of natural flood management to fishes and the need to research the remaining remnant floodplains in the UK.

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Abbreviations

CTSG - Conservation Translocation Specialist Group

EA - Environment Agency

EC – European Council

EEA – European Environment Agency

EU - European Union

HY – Hydrological year

INBO - Research Institute for Nature and Forest Belgium

IUCN - International Union for the Conservation of Nature

JNCC - Joint Nature Conservation Committee

LiDAR – Light detection and ranging

LWP – Large woody pieces

MBACI – Multiple Before-After-Control Impact

PVA – Population viability analysis

RRC – UK's River Restoration Centre

STW – Sewage Treatment Work

UK – United Kingdom

UKCEH – UK Centre for Ecology and Hydrology

WFD - Water Framework Directive

YBP – Years Before Present

YOY - Young of the year

Chapter 1. Introduction

1.1. The State of Our Freshwaters

Freshwater environments are some of the most threatened ecosystems globally (Dudgeon et al., 2006; Vörösmarty et al., 2010). The most recent Living Planet Report by WWF found that between 1970 – 2020 freshwater wildlife populations have declined by 85% globally (WWF, 2024). Freshwater environments currently face a myriad of adverse anthropogenic effects, which degrade the physical condition of the habitat and its interconnectivity, reduce water quality and alter flow regimes. The rate of decline of freshwater systems is due to the cumulative impact of multiple stressors that are impacting variably across the ecosystem with effects that emerge across different spatial and temporal scales (He et al., 2023). Across Eurasia, freshwater biodiversity is more intensely threatened in Europe and in more southern latitudes (Fig. 1.1). Only 40% of Europe's surface water bodies (111,000 surveyed in total) achieved good ecological status as assessed by the European Union (EU) Water Framework Directive (WFD) (2000/60/EC) (European Commission, 2000; European Environment Agency, 2018b; European Commission, 2019), with wetlands known to be widely degraded, which included 70-90% of floodplains (Fig. 1.2; European Environment Agency, 2016a, 2018c). The main reasons cited for rivers not having achieved good ecological status were hydro-morphological pressures (40%) (which includes physical habitat alteration), diffuse pollution (38%), and water abstraction (European Environment Agency, 2019). Similarly, only 38% of Europe's surface water bodies achieved good chemical status in 2018 (European Environment Agency, 2018a).

Common pressures on European surface waters include agricultural intensification, habitat modification through dam development, urbanisation, and climate change (Bagella et al., 2016). The cumulative effect of these pressures is that freshwater biodiversity is threatened, with some 50% of European freshwater species having threatened status (Gozlan et al., 2019; Van Rees et al., 2021). Habitat destruction or alteration is thought to be the main driver of biodiversity loss, with water abstraction, for example, affecting ~89% of amphibian species and ~26% of freshwater invertebrate species (Gozlan et al., 2019). Moreover, a study of Europe's threatened

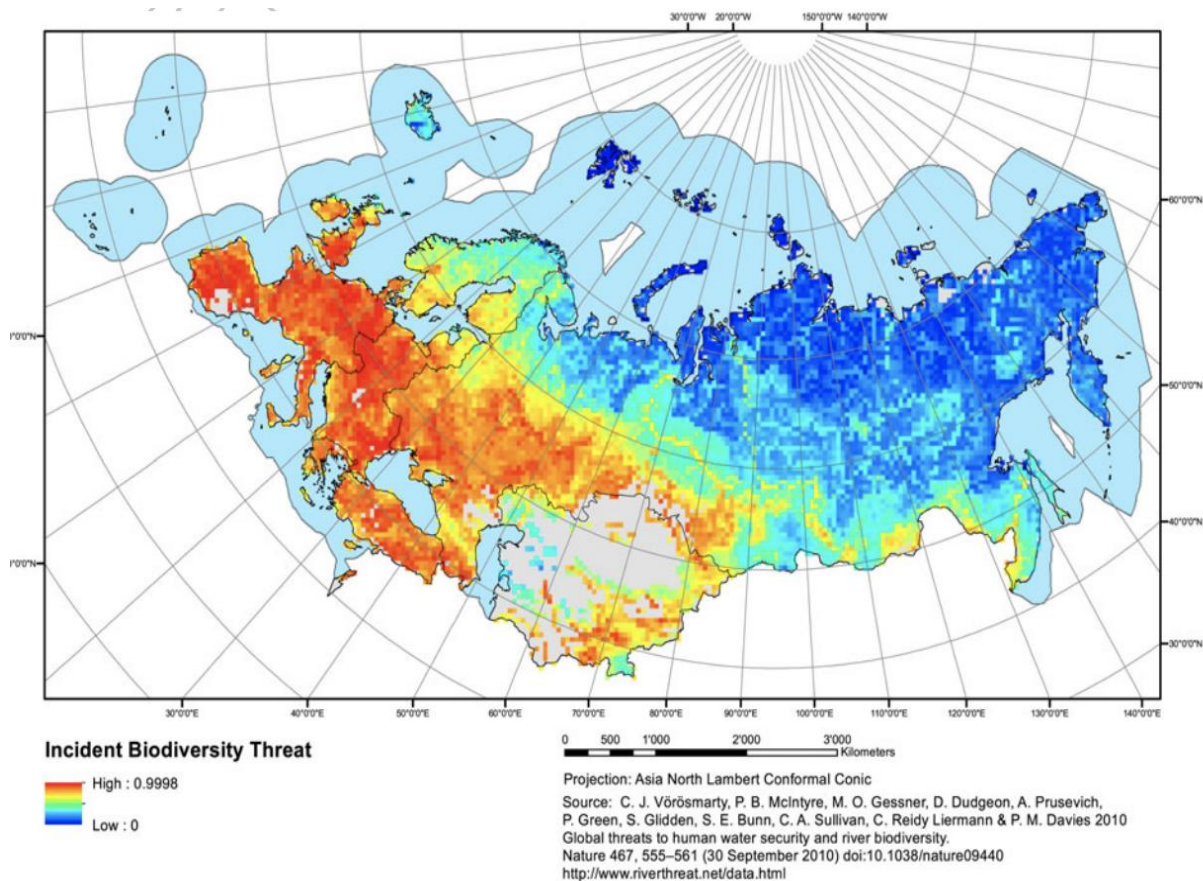


Figure 1.1. Distribution of riverine biodiversity threat. Mapping obtained from Gozlan et al. (2019) 'Status, trends, and future dynamics of freshwater ecosystems in Europe and Central Asia', *Inland Waters* © 2024 reprinted by permission of Informa UK Limited, trading as Taylor & Taylor & Francis Group, <http://www.tandfonline.com>. Original data is the property of The City University of New York hosted at www.riverthreat.net/data, published in Vörösmarty et al. (2010).

fish species found that 71.5% of threatened species are directly impacted by instream barriers and water resource management practices (Costa et al., 2021). Globally, freshwater fish are often threatened due to habitat changes, which prevent migration. WWF's Living Planet Index for migratory freshwater fish has shown a 81% decline between 1970 and 2020 (WWF, 2024). For species covered under the Habitats Directive (92/43/EEC), fish and molluscs have the highest proportion of species with a deteriorating trend (European Council, 1992; European Environment Agency, 2016b). Overall, at a European level, the population trends for most European freshwater fish species are unknown due to insufficient data (Brooks and Freyhof, 2011). Hence, there are uncertainties surrounding the actual negative extent of anthropogenic pressures, suggesting the need for more extensive and accurate monitoring. Data deficiency for freshwater biodiversity is not new, with species richness data for freshwater systems generally treated with less confidence than for

terrestrial ecosystems (Millenium Ecosystem Assessment, 2005). Further, there is not an equal trend across all water bodies. Lotic systems are regarded as having worse ecological status than lentic systems as it is recognised that river systems often have more interacting pressures impacting upon them (European Environment Agency, 2015).

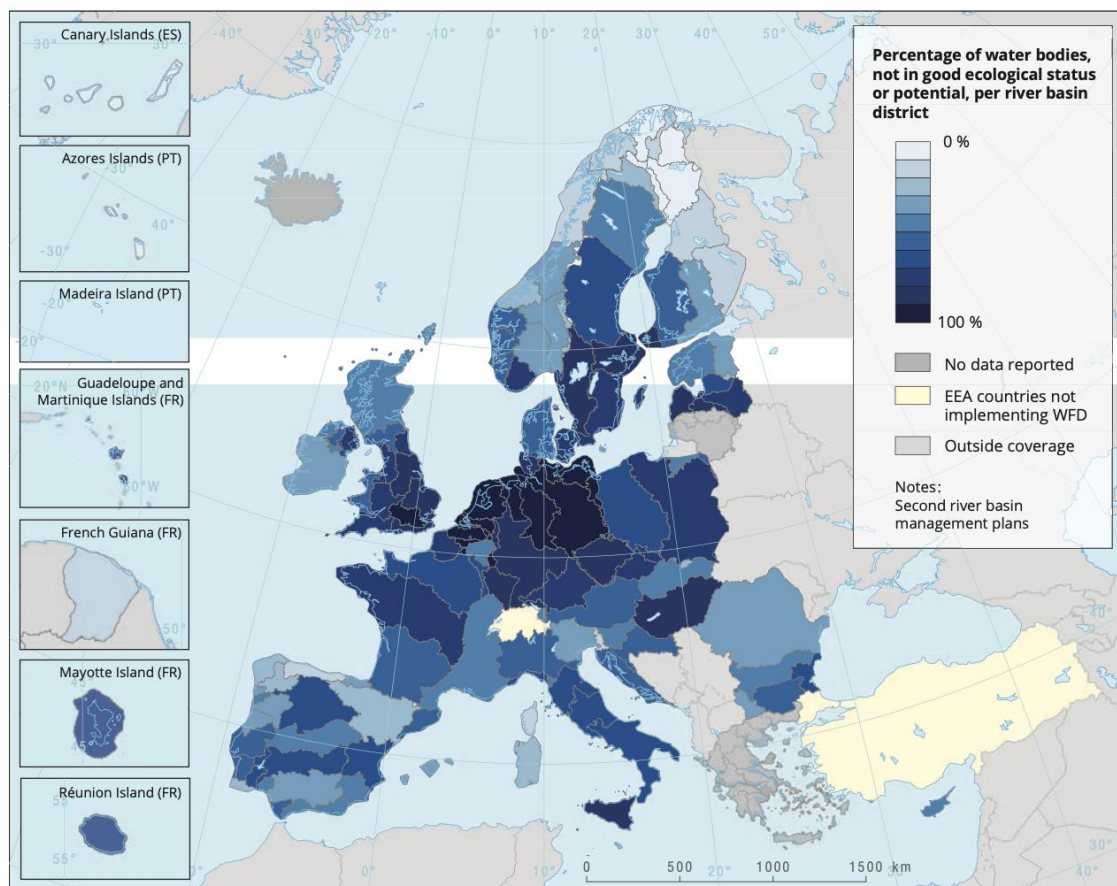


Figure 1.2. Percentage of surface water bodies not achieving good ecological status during 2018 assessment under the Water Framework Directive. Figure taken from EEA (2019) © European Environment Agency, 2019 based on data obtained from EEA (2018c).

The downward trend in European water body quality is well exemplified by the UK. Data published by the UK's Environment Agency (EA) on the ecological and chemical standards of English rivers, based on a thorough testing methodology searching for pollutants in fish and shellfish, showed that only 14% of English rivers were in good condition (Laville, 2020). Data from the UK's Joint Nature Conservation Committee (JNCC) suggest that improvements to river quality plateaued between 2009 - 2019 (Fig. 1.3) (JNCC, 2023). The International Union for the Conservation of Nature (IUCN)

identifies UK riverine habitat as being the most valuable for the region's biodiversity (Addy et al., 2016), but despite this, it is not being sufficiently protected or improved, as shown by Fig. 1.3 (JNCC, 2023). This plateau, despite efforts and apparent ecological value, can be explained partly by looking at the history of river management in the UK: the cumulative effects of river modification over centuries have influenced the ecological and chemical standard of rivers, and current conservation efforts (i.e., physical river restoration) are not returning high success rates. The main pressures on British freshwater ecosystems are habitat alteration (Brooker, 1985), agricultural runoff resulting in nutrient loading and sedimentation of water courses (Howden et al., 2013; Holden et al., 2017), land-use change, and urbanisation (Astaraié-Imani et al., 2012). It is important to understand historical trends in river and catchment modification, as related to the aforementioned factors, to understand the legacy of multiple anthropogenic influences in individual catchments and how they interact with the physical system.

In combination with changes in water resource management, such as abstraction licensing and water quality improvements, river restoration has been used to reverse historical modifications to rivers. Though studies have been published on restoring and enhancing water courses since the 1970s (Keller, 1976; Brookes, 1990), river restoration's popularity increased rapidly in the 1990s and is now incorporated into national (UK) and regional (European) policy (Smith et al., 2014). The initial focus of river restoration was on restoring in-stream habitat heterogeneity at a small spatial scale, which ultimately neglected other crucial factors, such as improving water quality or lateral connectivity (Wohl et al., 2005; Palmer et al., 2010; Friberg et al., 2016). Early work from European restoration projects emphasised the importance of planning in project success, with the emergence of several key stages in restoration execution: establishing project objectives; feasibility study; design; construction; clean-up phase; maintenance plan, and post-project appraisal (Brookes, 1987, 1990). An essential part of river restoration is not only restoring natural processes through physical alterations, such as channel modification, substrate deposition, or removal of barriers, but also to help improve habitat heterogeneity to improve aquatic biodiversity. Habitat heterogeneity is strongly emphasised in river conservation practice, as it is thought to be a key property of wilder, pre-modification rivers, which were complex, dynamic

mosaics of different habitats across the river-floodplain system (Brown et al., 2018). By restoring the physical habitat, it is thought that species will recolonise from new areas to improve the ecological quality, but this has not always been the case (Sundermann et al., 2011; Friberg et al., 2016). Another approach is to restore lost species through species reintroductions that can either engineer positive change or can be used as an umbrella species whose legal protections help to extend the spatial scope of habitat conservation (Roberge and Angelstam, 2004).

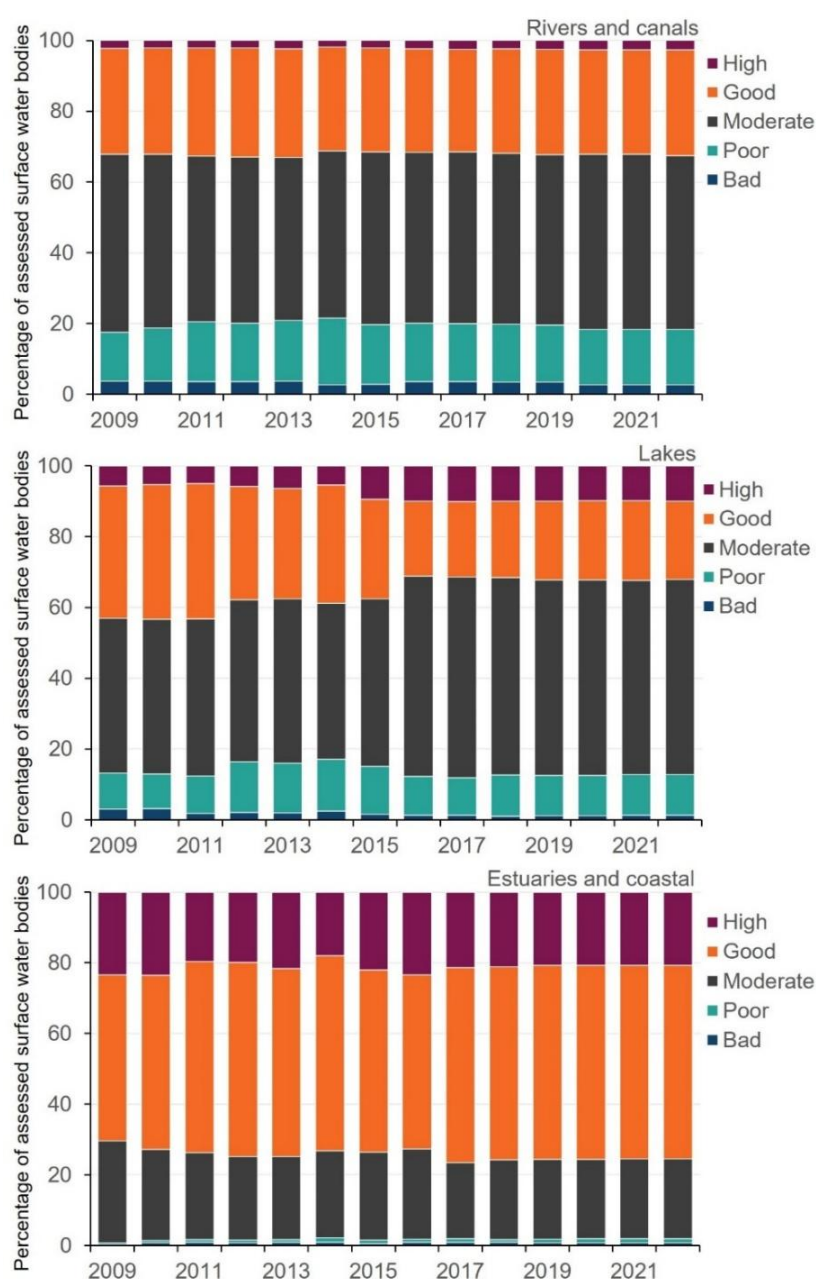


Figure 1.3. Surface water classification status of UK water bodies under WFD 2009-2022. Source: JNCC (2023). Contains public sector information licensed under the Open Government Licence v3.0.

One example of a species reintroduction that has helped to restore rivers via their own capacity as an ecosystem engineer, was the reintroduction of the Eurasian beaver *Castor fibre* to the UK in the early 2000s (Puttock et al., 2017). Beavers enhance the effect of several ecosystem services in riverine systems. At beaver sites, there is increased water storage with attenuated flow, which can help reduce flood risk downstream (Puttock et al., 2017). Moreover, there is some evidence that as dams retain sediment, they also potentially filter small amounts of nutrients (Thompson et al., 2021). Further, the disturbance created by grazing beavers on the aquatic macrophyte community increases macrophyte richness and alpha and beta diversity (Law et al., 2014). Other research has shown that the presence of beavers as “wetland managers” has increased habitat for water birds and other biota in southern Finland (Nummi and Holopainen, 2020), as well as wider benefits to wetland ecology across Europe (Brazier et al., 2021).

The present study focuses on the reintroduction of another iconic, but extirpated English species; the burbot *Lota lota* L. 1758, for which success will depend on effective, large-scale river restoration that improves lateral connectivity and water quality of a complex river-floodplain system. Restoration action with a larger spatial scope is needed in freshwater conservation to meet multiple conservation objectives while overcoming the effects of interacting pressures on freshwater ecosystems. Increasing the scale and reach of conservation activities is needed to reverse local and indeed, continental-scale declines in European freshwater habitats.

1.2. Historical, Current, and Emerging Trends in River Management

The goals of river management have evolved over time, with a distinctive shift from an anthropocentric approach, prior to the 1900s, to a more balanced, eco-centric approach today. River management requires an understanding of cumulative anthropogenic impacts throughout space, but the modification of rivers has resulted in a temporal legacy that is often neglected in current management today. River modification is well documented through historic records, archives, and journals on river development. There have been extensive reviews of the history of river

modification in the UK focusing on the anthropogenic, environmental, and legislative impacts of changes until the 1980s (Petts, 1988; Sheail, 1988; Eaton, 1989; Johnstone and Horan, 1996), as well as evidence-based reviews of the impacts of more recent river management, including river restoration (Smith et al., 2014; Friberg et al., 2016; Sayer et al., 2018; Robins et al., 2025). The literature for more emerging trends, including stage zero restoration and rewilding approaches is growing steadily (Carver et al., 2021; Flitcroft et al., 2022). The following synthesis aims to briefly review the legacy of anthropogenic river modification to understand how management approaches have changed based on river science and evidence-based decision-making.

1.2.1. Historical River Management

Across Europe, including the UK, the earliest form of river modification arguably could be forest clearance, which was as early as 3500 YBP (Godwin, 1984; Brown et al., 2018). Since this time, there have been successive changes to rivers due to human-induced modification of the landscape. Prior to deforestation, however, lowland rivers were thought to be anastomosing, anabranching, braided channels spanning at the same level across the valley floor, covered with fluvial woodlands and filled with woody pieces (Brown et al., 2018). The geological and palaeoecological record from sediment coring studies has found evidence of these kinds of systems throughout Europe (Brown et al., 2018; Hauer et al., 2021), but the impracticability of attempting to fully return rivers to these pre-deforestation states is widely recognised (Brown et al., 2018; Flitcroft et al., 2022). Gradual deforestation of the valley floors would have altered runoff characteristics, changed flow patterns, and affected water quality as a layer of nutrient storage and filtration within the system was removed (Whitehead and Robinson, 1993). Moreover, without fallen trees and woody pieces to disturb flow patterns, there would have been reduced disturbance to channel forms and flow dynamics, with the natural accumulation of sediment alongside these braided streams, forcing an element of stability for the channels (Brown et al., 2018).

The most common in-channel modification work in early history was the introduction of water mills, with the earliest being recorded in 762 (Sheail, 1988). Darby (1986) stated that by 1086 there were over 6,000 recorded water mills across England. Initially, the multi-braided systems most common to lowland Europe in the medieval period would have been appealing for the construction of watermills, utilising the natural meanders and braids as bypass channels (Brown et al., 2018). Ultimately, the increased presence of mills on these multi-channel systems, in combination with the loss of alluvial forests, would have increased channel stability further (Brown et al., 2018). From 1100 - 1300, a period of channel regulation began with the increased presence of ponds, leats, and weirs, which would have affected flow patterns, in-channel and floodplain deposition, and erosion (Eaton, 1989), stabilising the river channels further, and continuing a process of incision into the valley floor.

From 1600 onwards, an intensification of river modification began that continued to push the boundaries of current engineering, namely for land drainage and in-land navigation, the latter requiring the installation of pound locks (Skempton, 1983, 1985). The widening of channels, or the combining of multi-channel systems into single channels for the purpose of navigation was a pattern seen throughout Europe, such as the Danube, Austria (Hohensinner et al., 2004). This was also observed in England, with the Rivers Ouse, Trent, Thames, and Severn all reported to be navigable up to 100 km inland by 1700 (Petts, 1988). Concurrently, land drainage in historical wetlands expanded and intensified. The drainage of fenland expanded, for example, with the most notable works undertaken along the East Anglian Fens, to free land for agriculture and introduce basic irrigation systems such as water meadows (Sheail, 1988). The impact of land drainage, particularly in areas of wetland and unique aquatic habitat, reduced biodiversity (particularly plant species), influenced sediment transport, and decreased water quality (Sheail, 1988; Eaton, 1989).

From the 1750s, the UK entered a period of industrialisation, which used innovation to meet the growing demands of the population and industry, at the expense of riverine water quality and ecological diversity. Water abstraction, diffuse pollution, and further riverine engineering such as dams, canals, and headwater impoundment, continued

to alter the physical heterogeneity of river habitat, hydrology, and water chemistry, reducing biological diversity. Headwater impoundments would have influenced downstream flows and sediment transport, triggering changes in turbidity, which negatively influences fish and macrophyte community composition (Jones et al., 2019). The continued industrial pollution, combined with extensive headwater abstraction exacerbated lowland river pollution as the ability to dilute pollutants in the water decreased (Petts, 1988). The environmental impacts recorded were the deoxygenation of rivers, fish kills, increased odour, and ceasing of salmonid fish migrations in many rivers, especially in England (Eaton, 1989).

The “industrialisation” of rivers continued into the 1900s. As water quality became a concern for a growing population in England, legislation was slowly developed and established to regulate water pollution by industry and agriculture. From the early 1900s, a shift in river management can be observed, where river management policy was based on “flood prevention”, which at the time lacked any kind of evidential basis or understanding of potential impacts (Newson et al., 2022). To reduce flooding, between the 1930s and 1980s, the channelisation and dredging of over 8,500 km of rivers in England was undertaken (Petts, 1988; Newson et al., 2022). Not only did this approach to river management desolate any lasting riverine biodiversity by removing any remaining habitat heterogeneity, but these embanked, straightened, deepened rivers were further fixed into their singular, incised channel form that is the most common form of river observed today throughout Europe (Brookes, 1988; Brown et al., 2018). A recent study of lowland rivers in Europe, comprising 1,543 sites, with the majority from England, found that almost one-third were over-deepened (Gurnell and Downs, 2021). Moreover, the stabilisation with the embankment of the main river channel, severed the last connectivity between the river channel and floodplain, reducing the extensive network of habitat niches observed today in laterally connected wetland landscapes (Bowles et al., 2021). In combination with the dredging and channelisation, modification of the aquatic landscapes continued in the UK. Land drainage continued to increase from 1968, especially in upland peatland and in the eastern lowlands, reaching 100,000 ha yr⁻¹ in the latter (Petts, 1988). The drainage of peatland (and continued overgrazing by livestock today) had a direct impact on hydrology as water was no longer retained in upland areas by vegetation, thus

increasing floods downstream (Petts, 1988; Marshall et al., 2009). By the 1970s, there were few accessible and geologically suitable riverine sites that were still undeveloped for water retention in the uplands. The lack of suitable development sites to expand direct water supply meant that investment was undertaken in pollution control to improve water quality in the existing supply, including downstream areas (Eaton, 1989).

From the 1980s onwards, there was a distinct deviation in practice for both catchment managers as well as environmentalists. Each widened their scope to look at issues affecting the wider catchment area, which was supported by public desire to have higher quality natural landscapes, as well as changes in national (UK-level) and regional (European-level) legislation. At the same time, the expansion of environmental studies as a discipline allowed riverine processes to be recognised as parts of a more complex system whose interactions were not yet fully understood (Wood, 1981; Petts, 1988). Unfortunately, however, long before river ecology had emerged as a distinct discipline, anthropogenic change had already degraded river ecosystems extensively (Ward et al., 2001). Legislation from the 1980s onwards began to prioritise the environment when considering water supply at multiple tiers. The EU Birds Directive in 1979 (later adapted in 2009; 2009/147/EC), extended its protection to the habitat used by birds, which required river habitat of better quality for British waterbirds. Next, the Wildlife and Countryside Act of 1981 (Wildlife and Countryside Act 1981), stimulated a new direction in river management as it required water authorities to further ecological conservation and environmental enhancement (Petts, 1988).

During the 1990s, the EU continued to produce legislation that would lead to the chemical and ecological improvement of riverine habitats. The Urban Wastewater Treatment Directive of 1991 (91/271/EEC) meant the UK needed to identify sensitive areas that required monitoring for nitrate and phosphate, alongside ammonia and biological oxygen demand that already existed in UK legislation (Smith et al., 2014). Further, the Water Resources Act of 1991 was the first piece of national legislation that outlined conservation and environmental enhancement as goals in their own right

(Smith et al., 2014). In the following year, the EU Habitats Directive (92/43/EEC), was passed, which was incredibly important in shaping the goals of river management to meet biodiversity objectives by protecting ecologically valuable habitat (Smith et al., 2014). Incorporating the ecology at the centre of any conservation action is paramount, and the more recent emerging trends in river management reflect the cohesion of environmental and societal objectives to create holistic conservation action that can serve both biodiversity and people.

1.2.2. Current and Emerging River Management Practices

Since the 1990s, there has been a shift towards river management that comes with the realisation that a healthy, ecologically functioning river ecosystem is beneficial economically and socially, as well as environmentally. This shift is also reflected in research as during the 1990s, fluvial biogeomorphology, which recognised the importance of biota, such as plants, in influencing riverine processes in combination with hydrology and geomorphology emerged as a distinct discipline (Viles, 2022; Gurnell and Bertoldi, 2024). The importance of rivers for providing these benefits has emerged with increasing research on ecosystem services (Costanza et al., 1997, 2017) and now, more specifically, riverine ecosystem services (Hanna et al., 2018). While it is close to impossible to allow entire river courses to operate naturally again, due to historical modification and current demands from human populations on rivers, practices such as river restoration, stage zero restoration (Flitcroft et al., 2022), and rewilding (Sayer et al., 2024) have emerged to return natural functions to rivers where possible.

1.2.2.1. *River Restoration*

Current definitions of river restoration refer to the practice of restoring natural processes to rivers and include specific targets that can encompass hydrological, geomorphological, ecological, and societal factors. While river restoration as a practice has increased in popularity since the 1990s in the UK, there is contention over whether the practice is as successful as it could be.

In 1992, the UK River Restoration project was announced, with the aim of demonstrating how to achieve, assess the success of, and quantify the benefit of river restoration (Holmes and Janes, 2012). In 1994, a partnership between the UK and Denmark began, which undertook multiple large-scale river restoration projects (Holmes and Janes, 2012). The EU-LIFE funded demonstration project conducted river restoration projects on the rivers Brede (Denmark), Skerne (UK), and Cole (UK). The pioneering project demonstrated how to develop and conduct large, multi-disciplinary partnerships (Holmes and Nielsen, 1998), the practicalities of restoring the natural characteristics of degraded rivers (Vivash et al., 1998), and the importance of pre- and post-project monitoring of geomorphological, hydrological, water chemistry, and ecological variables both in-channel and on the floodplain (Biggs et al., 1998; Hoffmann et al., 1998; Kronvang et al., 1998). The restoration work on the River Cole was one of the earliest projects in the UK to reconnect the river and its floodplain (Biggs et al., 1998; Åberg and Tapsell, 2012). As well as being a successful demonstration of how to achieve large-scale, impactful river restoration, the project concluded that one of the greatest benefits devised from the work was the dissemination of findings (Holmes and Janes, 2012). In subsequent years, based on the conclusions of the project and shifting policies and management approaches, river restoration centres began to form.

In 1994, the UK River Restoration Centre (RRC) was formed to promote and guide river restoration activities (Smith et al., 2014). At its inception, the Centre's aims were to: establish a network of information communication; provide advice and guidance; support projects that promote the advancement of river restoration knowledge and techniques, and promote the benefits of river restoration nationally (RRC, 1997). By 2010, the core activities were knowledge exchange, advice provision, and promoting and facilitating best practice for watercourse management (Holmes and Janes, 2012). Cashman et al. (2019) report that the RRC listed over 4,894 known river restoration projects across the UK from 1960 to 2015, indicating the popularity of river restoration. With increasing research on ecosystem services and the ecosystem approach, leading to increases in catchment wide management (such as the Catchment Based Approach; see Collins et al., 2020), the term river restoration became a more commonly used and understood term (Holmes and Janes, 2012). The RRC's current

role is less focused on explaining the rationale, but advice and support. Their annual conference, Scientific Advances in River Restoration (SARR), for example, gathers and disseminates current knowledge and practice within the community. For example, SARR 2023 united 150 scientists from 26 countries, drawing perspectives on river restoration practice, during which the community identified the importance of fluvial biogeomorphology in river restoration design and practice, reflecting the shared understanding of river restoration as an inherently interdisciplinary practice (Prady et al., 2025).

The practice itself has evolved initially from being strongly focused on the physical structure and morphology of the river channel to now consider the river's margins and floodplains, toward a process-focused and holistic approach that restores hydrological regime and river functions (Friberg et al., 2016; Sayer et al., 2018; Robins et al., 2025). For example, floodplain reconnection may involve the removal of flood banks initially, but it then allows the river to return to a previous regime where winter flooding is retained on the floodplain higher in the catchment, often preventing flooding downstream (Dadson et al., 2017).

The local successes of river restoration projects, coupled often with relatively low expense, gradually resulted in river restoration being incorporated into national and international legislation. In 2000, the introduction of the Water Framework Directive (2000/60/EC) expected all EU member nations to achieve good ecological and chemical status for all water bodies by 2015. The policy supported existing trends in river restoration, returning natural processes and functioning to rivers to improve local biodiversity and habitat quality (Smith et al., 2014). By 2007, the EU's Floods Directive (2007/60/EC) was actively emphasising natural solutions to flood management, such as restoring natural river-floodplain connectivity. In 2011, DEFRA announced a £110m budget for restoration activities to improve the health of water bodies, with £92m specifically set aside for improving the physical and ecological status of rivers and wetlands (Smith et al., 2014). In 2018, the UK government introduced their 25-Year Plan for the Environment, which involved restoring 75% of water bodies in England to good condition (DEFRA, 2018). River restoration is promoted in more recent UK

legislation including in the Environment Act 2021, which aims to halt the decline of species abundance by 2030 (Wilkes et al., 2025) and the Integrated Plan for Water in England sets out actions to achieve these targets and more specifically establishes a new Water Restoration Fund (DEFRA, 2023). Despite decades of river restoration practice and implementation, freshwater ecosystems have continued to degrade, and subsequent reviews of river restoration projects have found results to vary in terms of measurable beneficial geomorphological and ecological impacts (Palmer et al., 2010; Kail et al., 2015; Friberg et al., 2016; Sayer et al., 2018; Kaiser et al., 2020).

Despite, being supported by national and regional legislation, river restoration has limitations. As the term would suggest, “river restoration” has for too long had a narrow view that focuses solely on the river. As the practice developed, it has continued to neglect the key underlying principles for ecosystem restoration, which are to use natural processes wherever possible and to aim for whole-landscape restoration, rather than focusing on only one aspect of interlinked aquatic habitats (Bradshaw, 1996; Sayer et al., 2018). Moreover, river restoration has historically neglected the link between degraded hydrogeomorphology and ecological status, with research in this area being relatively scarce. Yet degraded hydrogeomorphology is one of the most extensive impacts on river ecosystems throughout Europe (Friberg et al., 2016).

Overall, Friberg et al. (2016) succinctly summarised why river restoration has been less effective than its initial intentions, despite the number of projects increasing each year:

‘... the way in which knowledge on restoration is available and organised today provides very little concrete guidance to managers wishing to conduct cost-effective projects that deliver set targets’ (Friberg et al., 2016; p. 582).

Despite resource creation by the RRC, such as ‘The Manual of River Restoration Techniques’ and with the latest 2020 version emphasising catchment-based approaches and natural flood management (River Restoration Centre, 2020), projects

often lack a widely applicable scientific basis from which to design and implement projects (Sayer et al., 2018), as well as lack post-project monitoring (Wohl et al., 2015). The lack of understanding, post-project data, and communication of learnt pitfalls has led to projects having negative impacts in some instances. A review of 649 European river restoration projects found that re-meandering was a common technique applied in lowland rivers, which often decreased habitat micro-diversity as it decreased river velocity, increasing particulate organic matter, and resulting in unrestored sections having more microhabitats (Friberg et al., 2016). In fact, river restoration projects were found to benefit terrestrial and semi-aquatic organisms the most, with fish and macroinvertebrates benefiting the least (Haase et al., 2013). A review of 91 European restoration projects and the impact the restoration had on fish, macroinvertebrates, and aquatic macrophytes found that approximately one-third of projects had no or a negative effect on the studied taxa (Kail et al., 2015). Moreover, the impact of river restoration on ecosystem services and functioning is rarely assessed (Kaiser et al., 2020).

With river restoration, the traditional small-scale focus, the concentration on physical habitat diversity, the overlooking of biotic influences such as species interactions and dispersal limitations, and the neglect of addressing catchment-scale issues have resulted in a patchy effect on riverine ecology, with the same also true of lakes and other wetlands (Sayer et al., 2018). Moreover, the ability to determine project 'success' is challenging. Post-project appraisals can assess ecological changes compared to non-restored sites, but how ecological change compares to baseline ecology is seldom considered (England et al., 2021). Further, in the past, post-project appraisals have been hindered by a lack of funding, which reduces post-project monitoring timescales and prevents the ability to capture change over ecologically-meaningful timescales (England et al., 2021). The variability of river restoration success can be partially attributed to the fact that it is subjective. For example, a restoration project that wants to re-meander a stretch of river to enhance the area for local stakeholders may not have the benefits of improving the river for fish, invertebrates, vertebrates, or plant communities; however, if the public engages with and enjoys that space, it is considered a successful project. Cost-effectiveness, recreational and educational opportunities, aesthetics, and stakeholder satisfaction, as well as the overall

restoration criteria, must be balanced during restoration projects (Palmer et al., 2005). These multi-faceted demands can limit the success of restoration projects, as meeting the needs of all these areas is challenging. Though a more recent review of 125 river restoration studies found that economic and ecological aspects dominated river restoration studies, and thus the author's argue that there is scope to incorporate social benefits into river restoration research (Basak et al., 2021).

Previous research from riverine science, and river restoration itself, states the importance of connectivity. The most established is longitudinal connectivity, which through the River Continuum Concept (Vannote et al., 1980) emphasises how biology, hydrological dynamics, and geomorphology are intrinsically linked in riverine systems and the interactions shift down the course of the river. Later, in a discussion of the five dimensions of river restoration, Boon (1998) highlights the importance of the spatial dimension, referring specifically to longitudinal (i.e., upstream to downstream), lateral (i.e., river to riparian zone to floodplain), and vertical (i.e., hyporheic to surface water) connectivity. Boon (1998) argues these aspects are important beyond the physical connection between the river and its floodplain, but are essential in understanding processes operating at catchment scale.

Improvement to the processes used and the scale of river restoration, to move beyond in-channel physical habitat restoration towards catchment-scale projects that enhance lateral connectivity to the floodplain, as well as longitudinal connectivity must be considered. River restoration has historically focused on reaches of <1 km, but the emerging literature recognises the need to consider larger spatial scales and extend laterally into the floodplain (Sayer et al., 2018). Future river restoration must include: evidence-based decision making through assessment of pressures and impacts and the prioritisation of river restoration options based on their contribution to the alleviation of catchment-scale impacts (Robins et al., 2025). Research is beginning to show the importance of taking a wider scope in river restoration and in looking at lateral connectivity throughout the river course and catchment by reducing fragmentation by barriers (Jones et al., 2019). Research shows that enhanced lateral connectivity is beneficial to invertebrates (Castella et al., 2015), fish (Shao et al., 2019; Stoffers et

al., 2022), and plant communities (Bornette et al., 1998; Tockner et al., 1999; Keruzoré et al., 2013a), with some evidence documenting positive impact on ecosystem services (Gilvear et al., 2013; Brown et al., 2018; Shen and Liu, 2021). The European Environment Agency (EEA) notes the importance of improving the longitudinal and lateral connectivity of wetland landscapes, not only to benefit fish migration, but also to help restore the natural functioning capabilities of wetlands, which includes nutrient and sediment filtrations (European Environment Agency, 2019). Neglect of the wider aquatic landscape (i.e., mosaics of ponds, river channels, floodplain water bodies), however, and the interconnectivity between these systems has been a common pitfall in river restoration (Sayer, 2014). By moving the focus to the lateral habitat continuum, river restoration can improve habitat connectivity, as well as wider physical and ecological quality and ecosystem service provision (Kondolf et al., 2006; Mason et al., 2025).

1.2.2.2. Stage Zero Restoration

A new approach in river restoration that aims to address these key issues in recent river restoration practice is stage zero restoration. Current research demonstrates that a single channel incised in the valley floor is not how rivers have looked historically (Brown et al., 2018). A stage zero valley is described as a pre-disturbance, dynamically stable network of anastomosing and anabranching channels throughout the valley floor with patches of vegetated islands that support wet woodland or grassland (Cluer and Thorne, 2014). Stage zero restoration projects are growing in popularity in the US (Flitcroft et al., 2022), with 20 undertaken by 2018 (Bowles et al., 2021), but some projects are occurring in the UK such as the River Witham, Lincolnshire (Environment Agency, 2022), River Aller, Somerset, and River Dom, Oxfordshire (Clarke, 2025). Returning to a pre-disturbance state for rivers is regarded as close to impossible for most rivers due to historical modification (Brown et al., 2018; Bowles et al., 2021), however, where appropriate, stage zero restoration can still play a role in encouraging holistic and laterally inclusive restoration at a larger spatial scale than the average river restoration project. Thus, stage zero restoration has been defined as a valley-scale, process-based approach that re-establishes depositional environments to maximise lateral, longitudinal, and vertical connectivity at base flows, while facilitating

the development of dynamic, self-sustaining wetland-stream complexes (Flitcroft et al., 2022). By addressing hydrological, geological, and biological processes at a larger spatial scale, stage zero aims to improve aquatic biodiversity by increasing the overall habitat complexity through natural processes.

While stage zero restoration has broader ambitions than regular river restoration, in terms of extending into the lateral dimension, the practice is not without its limitations. Research has shown that in some projects, as historically incised channels are raised and the average depths across the floodplain become shallower, the surface temperature of the water can increase (Flitcroft et al., 2022). Further, it takes several years, after initial work, for vegetation to grow to an extent that would provide riparian shading, which raises concerns for fish species as temperatures increase under climate change. Moreover, not every river will be suitable for stage zero (e.g., projects can require significant lateral expansion), and as a new practice longer-term impacts of stage zero restoration projects are still unknown (Flitcroft et al., 2022). Importantly, stage zero restoration still remains a reach-scale approach and thus is not spatially extensive enough to address catchment-scale issues. In a UK context, it is important to consider the suitability of stage zero restoration, given the intensely modified and degraded rivers found across the UK, which may be incompatible with sections of stage zero restoration, due to high population densities upstream or downstream, the generation of “knick-points” where the restored stretch would re-join a modified, incised channel (Clarke, 2025), and the potential impact of polluted, low-energy streams being redirected across a valley floor.

1.2.2.3. Hydrological Rewilding

While river restoration is slowly shifting toward laterally encompassing, larger-scale projects that think holistically about restoring ecosystem functions, rewilding approaches are more boldly stimulating natural recovery in freshwater ecosystems. Rewilding approaches reintroduce missing natural processes and allow them to operate with minimal human interference (Sayer et al., 2024). Examples of rewilding approaches include the reintroduction of keystone species or ecosystem engineers,

such as beavers, or the replication of their processes, such as natural tree fall (Harvey and Bertoldi, 2015; Harvey et al., 2018).

Over the past two centuries, removal of large woody pieces (LWP) to improve navigation or for flood protection has almost completely removed evidence of how LWP jams have shaped fluvial environments in many regions (Abbe and Montgomery, 1996; Harvey et al., 2018). Recent research has shown just how important LWP are for creating physically complex riverine habitats that are beneficial to fish, invertebrates, aquatic macrophytes, and riparian species (Kreutzweiser et al., 2005; Gregory et al., 2017). For example, allowing the accumulation of natural woody jams has substantive impact on flow hydraulics and sediment characteristics, whereas the installation of flow deflectors, a common practice in river restoration, has a negligible effect (Cashman et al., 2021). Moreover, Thompson et al. (2018) identified positive causal relationships, using Multiple Before-After-Control Impact (MBACI) studies, between LWP introduction and biodiversity and food web changes, from invertebrates to an apex-predator, brown trout *Salmo trutta*. Pilotto et al. (2014) found that the introduction of LWP led to a more diverse macroinvertebrate community, both upstream and downstream. The addition of LWP, or replicating natural tree fall, is more commonly recognised as crucial to creating and maintaining physically complex and laterally connected river habitat (Gurnell et al., 2019a). Further, Parker et al. (2017) found that LWP introduction led to increases in sediment storage and reduced transport downstream at both reach and patch-scales. The accumulation of sediments by woody pieces has also been attributed to increased macrophyte diversity and abundance in streams (Gregory et al., 2017). More recently, the importance of wood being able to periodically mobilise has been shown to influence the disturbance regime in the river corridor, disperse organisms and propagules, and dissipate flow energy, amongst other influences (Wohl et al., 2024). LWP on floodplains can also have similar geomorphic and ecological effects as instream LWP, but it is relatively understudied (Wohl, 2020). Being treated as rewilding approaches (Thompson et al., 2018), trees can be categorised further as ecosystem engineers in riverine environments due to their power in influencing hydraulics, sediment dynamics, and ecological patterns and dispersal (Gurnell et al., 2013; Gurnell, 2014; Harvey and Bertoldi, 2015; Wohl et al., 2019).

Another relevant example of hydrological rewilding is the reintroduction of Eurasian beaver to areas where it has previously been made extinct. Beaver reintroductions into rivers have been shown to benefit river-floodplain systems due to their impacts on geomorphology, hydrology, and ecology (Brazier et al., 2021). New research is continuously emerging, evidencing the benefits of reintroducing beavers to riverine and wetland ecosystems. Through the manipulation of the river channel through dam and beaver canal creation, the connectivity between the main channel and floodplain increases. This connectivity can lead to flood peak attenuation and increased floodplain water storage (Puttock et al., 2017). Further, beaver dams themselves act as a filter of sediment and nutrients, improving overall water quality downstream (Thompson et al., 2021). The dams across the main channel create pools, which are beneficial for some fish (Albertson et al., 2022), macrophyte, and bird species (Nummi and Holopainen, 2020). Moreover, the beavers themselves improve the diversity of riparian and aquatic plants through grazing and disturbance mechanisms (Law et al., 2016). Beavers engineer laterally connected wetland habitat with natural functions that improve water quality and improve floodplain water storage (Brazier et al., 2021). Natural tree fall and beaver reintroductions, are forms of river rewilding and although some active human management is sometimes involved, the core purpose is the same: nature is given an initial boost to enable the restoration of rivers through natural processes and functions, which brings benefits to biodiversity and humans.

1.2.3. Fish and River Management

While river restoration can be a useful tool in catchment management and is helping to undo the historical legacy of river modification, successive habitat modification and simplification of rivers throughout the centuries has had severe repercussions for native aquatic species that are hard to undo. Widespread drainage, channelisation, and introduction of longitudinal barriers have resulted in the decline of aquatic biodiversity, but more specifically fish species, in the UK. Vendace *Coregonus albula*, twaite shad *Alosa fallax*, and allis shad *Alosa alosa* are some of the rarest fish species in the UK, with the former pressured by invasive species and eutrophication (Winfield et al., 2012), and the latter two by instream barriers that prevent migratory spawning (Jolly et al., 2012). In some cases, anthropogenic pressures have resulted in the local

extinction of fish species, such as salmon *Salmo salar*, and sea lamprey *Petromyzon marinus*. Others, such as sturgeon *Acipenser sturio* have been driven to national extinction. One species that was lost nationally, primarily due to the impacts of major habitat modification that could now benefit from the emerging trend towards large scale river-floodplain restoration work is the burbot.

1.3. The Burbot: An Updated Scientific Summary

1.3.1. Physiology

The burbot is the only freshwater member of the order Gadidae, a kind of freshwater cod (Worthington et al., 2010a; Stapanian and Myrick, 2015). Burbot are thought to have transitioned from the marine environment 15 million years ago (Van Houdt et al., 2003). The burbot (Fig. 1.4) has a double dorsal fin with its pelvic fins in front of its pectoral fins and with a long anal fin (McPhail and Paragamian, 2000). The fish possess a diagnostic barbel on its chin and tube-like protrusions on each nare (nostril) (McPhail and Paragamian, 2000). It is dominantly coloured olive green to dark brown on its back and sides, with irregular, mottled blotches and a pale, yellow-white underbelly that can be occasionally speckled (Worthington, 2010). The mottling is also present on its dorsal, pectoral, tail, and anal fins (McPhail and Lindsey, 1970; Worthington, 2010). Sexual dimorphism in adults is found to be subtle and seasonal (Stapanian and Myrick, 2015). Adult burbot have been recorded to reach 120 cm length and 30 kg weight in Siberia and Alaska (Maitland and Lyle, 1991), but it is thought that adult burbot in England (prior to extirpation), and others of the western European subclade (see below) range from 30-60 cm in length (Worthington, 2010). In the River Lippe, Germany, for example, burbot rarely reach longer than 50 cm (Brackwehr et al., 2016).

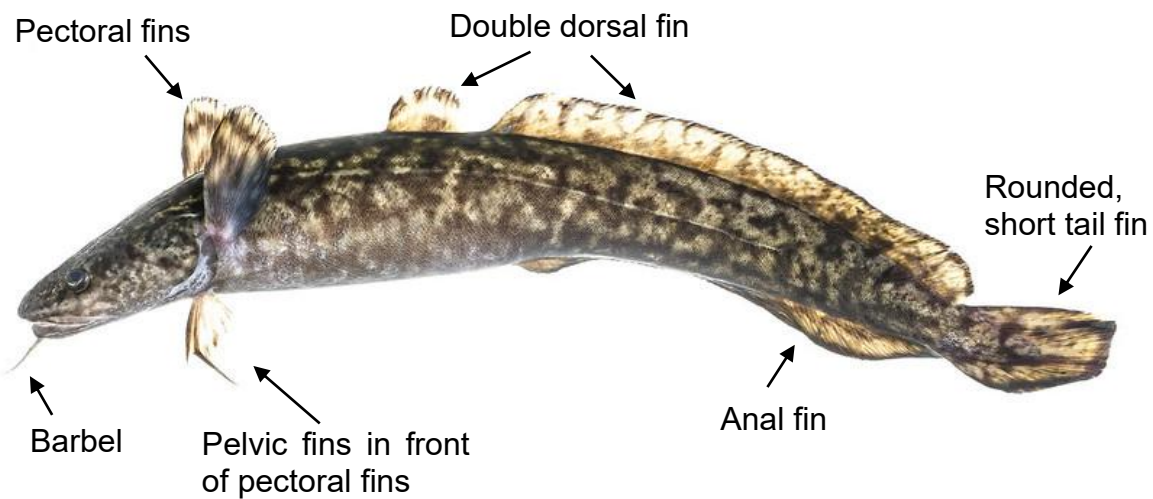


Figure 1.4. Key characteristics of burbot. Photo: Sam Stukel (USFWS).

1.3.2. Distribution and Genetics

The burbot occupies a northern circumpolar range, including all suitable freshwater and some brackish habitat of continental Europe and North America (Fig. 1.5), extending south to approximately 40°N (Scott and Crossman, 1973; Howes, 1991; Maitland and Lyle, 1991; Stapanian and Myrick, 2015). It occupies lakes, rivers, and brackish coastal areas up to 6000 mg/l salinity (Johnson, 1981) and can survive at a range of water depths. For example, in the Great Lakes of North America burbot occupy small, shallow streams as well as the 300 m deep Lake Superior (Boyer et al., 1989; Stapanian and Myrick, 2015). Population densities are variable, with the most reliable density calculations for lacustrine populations obtained from Alaska with adults (>450 mm) found at 0.24-21.9 burbot ha⁻¹ (McPhail and Paragamian, 2000). The River Lippe, Germany can support approximately 19 burbot km⁻¹ (Worthington et al., 2011a). The lower River Oder, Germany has densities of 80 – 100 burbot km⁻¹ (Wolter and Freyhof, 2004). While throughout Flanders, the Belgian Institute of Forest and Nature (INBO) researchers expect around 30 burbot per 100 m of suitable habitat (Dillen et al., 2005).

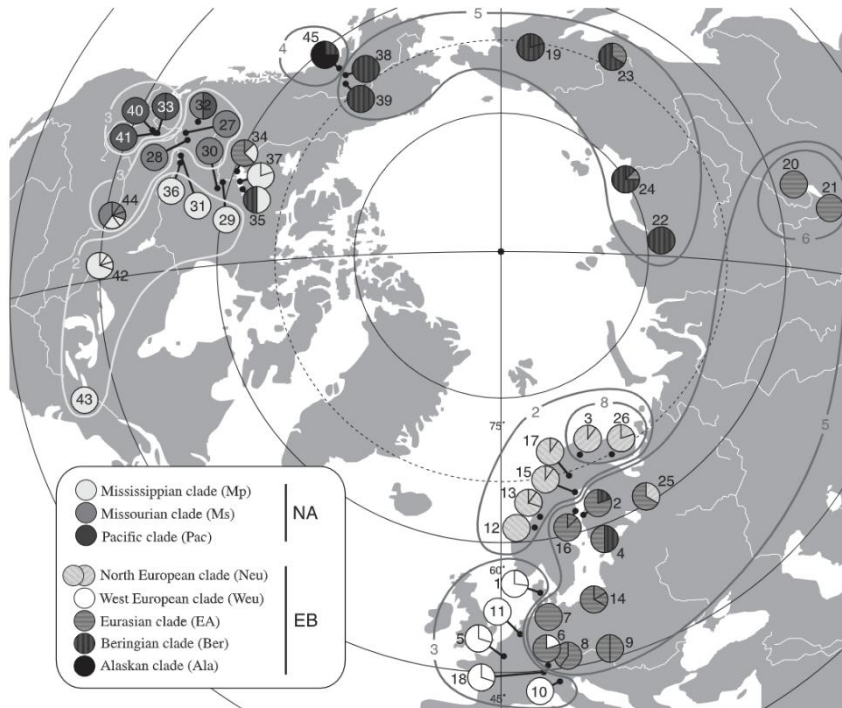


Figure 1.5. Sampling locations of burbot (*Lota lota*) across the Holarctic region and distribution of two major mitochondrial lineages, Eurasian-Beringian (EB) and North American (NA). The pies depict the distribution of the various mitochondrial clades (see source). Source: Van Houdt et al. (2005).

By the end of the 19th century, it was generally accepted that there was one Holarctic species of burbot. Scott and Crossman (1973) proposed, working on previous suggestions of three subspecies, that the morphological differences between the three were small and there were only two subspecies: *L. lota lota* and *L. lota maculosa*. Van Houdt et al. (2003) tested the designations against molecular data and confirmed the two distinct subspecies: *L. lota maculosa* is distributed across North America south of Alaska, and *L. lota lota* is spread throughout Europe and Siberia to Alaska. Within the subspecies of *L. lota lota*, there are distinct subclades, notably the north European, western European, Eurasian, Beringian, and Alaskan subclades (Fig. 1.5; Van Houdt et al., 2005).

The IUCN Species Reintroductions Guidelines states that, prior to a reintroduction, a suitable source population must be identified (IUCN, 2013). Worthington et al. (2017) concluded that the western European subclade would be the closest genetic relative to the English population, as supported by the work of Van Houdt et al. (2005).

Interestingly, sequenced DNA from preserved specimens found throughout the UK, including a specimen from the lower River Wissey, Norfolk (the focus of this PhD), found the English population to be a distinct subgroup, likely to have diverged from the European population during the last glacial maxima by surviving in thermal refugia (Worthington et al., 2017).

1.3.3. Conservation Status

Like most European freshwater fishes, the burbot is protected under a variety of legislation, including the international Convention of Biological Diversity, the regional EU Habitats Directive (92/43/EEC) in combination with the Birds Directive (79/409/EEC) (through the protection and restoration of their habitats, which includes wetland birds), as well as through continued monitoring in the IUCN's Red List assessments (Brooks and Freyhof, 2011). The burbot has the second largest distribution range of any freshwater fish (McPhail, 1997; Worthington et al., 2012), but burbot populations are declining or facing extinction throughout most of their range (Stapanian et al., 2010a). The IUCN's Red Lists suggest that the global population of *L. lota* is stable (IUCN, 2012) and the species is marked as least concern, however, the trend for the European population is unknown (Freyhof, 2010). The unknown status could be due to variation in population stability throughout the continent (Fig. 1.6; Worthington, 2010), although, there has not been a recent review of the global status of burbot in over a decade. Stapanian et al. (2010) published a conservation status update for the European range, surmising that burbot went extinct in Belgium and England, are considered vulnerable throughout Austria, Czech Republic, Hungary, Slovenia, Slovakia, France, and Poland, are declining in Estonia, Finland, and Sweden, and has uncertain population status in Germany, Bulgaria and the Netherlands.

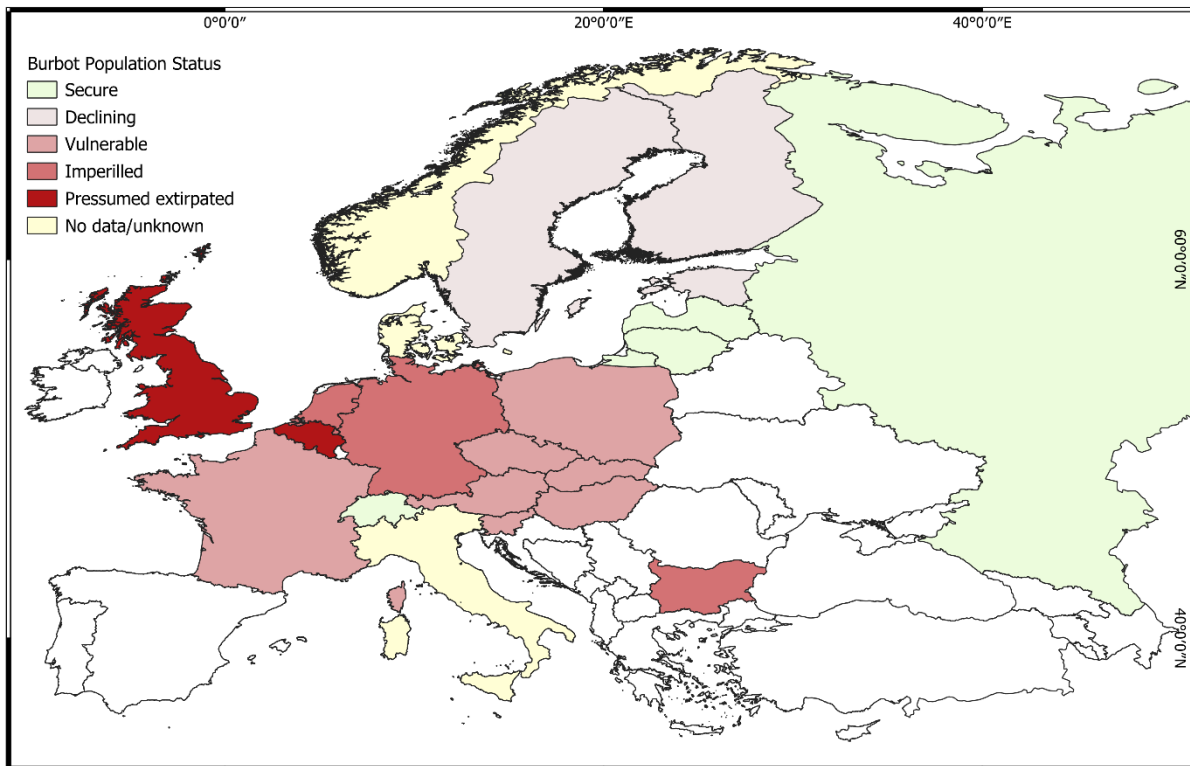


Figure 1.6. Eurasian burbot population trends based on status assessment by Stapanian et al. (2010a). Map data layers from EuroGlobalMap © EuroGeographics 2024.

Despite the burbot's widespread decline it is rarely incorporated into conservation management plans (Bosveld et al., 2015). Burbot is no longer a recreational or industrial species in most European countries, with some exceptions in Scandinavia (Stapanian et al., 2010a), and the remaining knowledge gaps in their biology and behaviour makes them a management challenge, and hence overlooked (Grabowski et al., 2020). In the Netherlands, burbot populations were relatively stable throughout the 19th century, but declined throughout the 20th century, with recent increases only attributed to stockings in the German reaches of the River Vechte in the early 2000s (Bosveld et al., 2015). In Germany, local populations faced extinction due to migration barriers and habitat pressures, but populations are now supported attributed to reintroduction programmes (Wetjen et al., 2020b). In the North Rhine-Westphalia region, burbot were classified as endangered and thought to be extinct in the North Rhine-Westphalia Highlands (Klinger et al., 1999). From the most recent assessment,

however, and with thanks to reintroduction programmes (Brackwehr et al., 2016), burbot are now classified as declining (Klinger et al., 2011). A recent study on the status of the burbot in the Lower Danube, Bulgaria, found a sharp decline in burbot populations over the last decade due to warming temperatures and fragmentation of tributaries, which suggested that it should be regarded as endangered in Bulgaria (Pandakov et al., 2020). In England, the species is accepted to have been extirpated in the 1970s (Worthington et al., 2010a). Most crucially for the prospect of a burbot reintroduction to England, is the burbot reintroduction undertaken in Belgium, as this is the western European subclade, the closest genetic relative to English burbot. Conservationists in Belgium, during the early 2000s, planned and implemented a reintroduction of the nationally extinct burbot (Dillen et al., 2005).

1.3.4. Burbot Biology

1.3.4.1. *Life History*

In terms of burbot biology, Worthington (2010) observed a distinct bias in the literature (both in terms of location and habitat type) towards lake populations in North America. Where possible, this synthesis garners evidence from European riverine burbot, but supplements with studies from North America to get a fully comprehensive understanding of burbot biology and ecology. One of the most succinct summaries of burbot life history is that of McPhail and Paragamian (2000), but later literature has filled gaps especially in migratory spawning, reproductive strategies, and behaviour. Table 1.1 provides a summary of variations in biological and ecological requirements exhibited by different subpopulations that form the foundation of burbot study today. Despite lake populations being popular subjects for burbot studies, solely riverine populations do exist, meaning burbot are not lake dependent, as observed in the North Rhine-Westphalia region in Germany (Bunzel-Drücke et al., 2004a).

Table 1.1. Summary of key burbot ecological and biological requirements and their source population locations, demonstrating the variation between subpopulations.

Parameter Studied	Finding	Lake	River	Location, Subclade*	Source
Spawning month	May/June	✓		Kooteny Lake, Canada	McPhail and Paragamian (2000)
		✓		Lake Constance, Germany	Jude et al. (2013)
	February	✓		Larcom Lake, Finland	Toivonen et al. (2020)
		✓		Lake Päijänne, Finland	Pääkkönen and Marjomäki (2000)
		✓		Lake Superior, USA	Jude et al. (2013)
		✓		Burntside Lake, USA	Cahn (1936)
	January	✓		Lake Baikal, Russia	Sorokin (1971)
		✓		Lake Michigan, USA	Jude et al. (2013)
			✓	River Lippe, Germany	Brackwehr et al. (2016)
			✓	Koontenai River, USA	Kozfkay and Paragamian (2002)
Spawning migration	March	✓		Lake Eerie, USA	Jude et al. (2013)
	Migration to river tributaries	✓		Koonteny Lake, Canada	McPhail and Paragamian (2000)
		✓		Great Lakes, North America	Jude et al. (2013)
		✓		Lake Baikal, Russia	Sorokin (1971)
			✓	Koontenai River, USA	Paragamian and Wakkinen (2008)
				Mackenzie Delta, Canada	Percy (1975)
Spawning migration direction	Estuary	✓		Larsmo Lake, Finland	Toivonen et al. (2020)
	Remain in habitat	✓		Great Lakes, North America	Jude et al. (2013)
	Upstream		✓	Tanana River, USA	Evenson (1988)
			✓	Ohře River, Czech Republic	Slavík and Bartoš (2002)
			✓	Susquehanna River, USA	Robins and Deubler (1955)
Spawning habitat	Shallows	✓		Koonteny Lake, Canada	McPhail and Paragamian (2000)
		✓		Burntside Lake, USA	Cahn (1936)
		✓		Lake Baikal, Russia	Sorokin (1971)
	Deep water		✓	River Drava, Austria	Farkas (1993)
		✓		Great Lakes, USA	Jude et al. (2013)
		✓		Burntside Lake, USA	Cahn (1936)
	Inundated floodplains		✓	North Rhine-Westphalia, Germany	Brackwehr et al. (2016)
			✓	North Rhine-Westphalia, Germany	Brackwehr, et al. (2016)
			✓	River Rhone and Danube, Europe	Aarts et al. (2004)
			✓	French and German Rivers	Worthington et al. (2012)
Spawning temperature range	2 - 9°C	✓		Lake Mondesee, Austria	Lahnsteiner et al. (2012)
	Up to 7°C			NA	Jäger et al. (1981)
	5 – 7 °C		✓	French Ardennes, France	Beelen (2009)
	< 4°C	✓		Burntside Lake, USA	Cahn (1936)

Table 1.1. Continued...

			✓	NA	Mann (1996)
			✓	Koontenai River, USA	Paragamian and Wakkinen (2008)
	0 – 6 °C	NA		Minnesota, USA	Becker (1983)
Larvae habitat	Inundated floodplain		✓	North Rhine-Westphalia, Germany	Brackwehr, et al. (2016)
			✓	River Elbe and Oder, Germany	Müller (1957)
			✓	North Rhine-Westphalia, Germany	Brackwehr, et al. (2016)
	Ditches		✓	Kleine Nete, Molenbeek, Belgium	Auwerx et al. (2019, 2022)
	Shallow, vegetated tributaries		✓	French Ardennes, France	Dillen et al. (2008a)
	Off-channel Habitat		✓	Missouri River, USA	Fisher (2000)
	< 30 cm depths		✓	Alaskan Rivers, USA	Blackman in Worthington et al. (2012)
	Aquatic macrophytes		✓	Grote Nete, Bosbeek, Maarkebeek, Belgium	Dillen et al. (2008b)
Juvenile habitat	Tree roots		✓	Grote Nete, Bosbeek, Maarkebeek, Belgium	Dillen et al. (2008b)
	Boulders/large substrate	✓		Shebanowan Lake, Canada	Ryder and Pesendorfer (1992)
		✓		Lake Constance, Germany	Fischer (2000b)
Adult habitat	Deepest water available	✓		Lake Superior	Stapanian and Myrick (2015)
		✓		Lake Baikal, Siberia	Sideleva (2003)
		✓		Lake Opeongo, Ontario	Carl (1995)
			✓	River Elbe, Germany	Eick (2013)
			✓	River Danube, Hungary	Erős et al. (2003)
			✓	French and German Rivers	Worthington et al. (2012)
	Tree roots		✓	French and German Rivers	Worthington et al. (2012)
			✓	Grote Nete, Bosbeek, Maarkebeek, Belgium	Dillen et al. (2008b)
	Large substrate	✓		Julian's Reef, Lake Michigan,	Edsall et al. (1993)
		✓		Lake Constance, Germany	Fischer (2000a)
			✓	French and German Rivers	Worthington et al. (2012)
			✓	River Elbe, Germany	Eick (2013)
			✓	Housatonic River Basin, USA	Dixon and Vokoun (2009)
	Woody pieces		✓	French and German Rivers	Worthington et al. (2012)
			✓	Grote Nete, Bosbeek, Maarkebeek, Belgium	Dillen et al. (2008b)
	Undercut banks		✓	Grote Nete, Bosbeek, Maarkebeek, Belgium	Dillen et al. (2008b)
Optimal Temperature	10 - 14°C	✓		Moosehead and Haymock Lake, USA	Cooper and Fuller (1945)
		✓		Lake Peonage, Canada	Hackney (1973)
	13.5°C		✓	River Oder, Germany	Hardewig et al. (2004)
	15.6 – 18.3 °C	NA		Canada	Scott and Crossman (1973)
Maximum Temperature	25 - 26°C		✓	River Oder, Germany	Hardewig, et al. (2004)
	27°C	✓		Lake Päijänne, Finland	Pääkkönen et al. (2003)

Table 1.1. Continued...

Dissolved Oxygen	20°C		✓	Missouri River, USA	Fisher (2000)
	21°C		✓	River Oder, Germany	Hardewig et al. (2004)
	18 - 20°C	✓		Oneida Lake, USA	Jackson et al. (2008)
	23.3 °C		✓	North Rhine-Westphalia, Germany	Brackwehr et al. (2016)
	5-7 mg l ⁻¹	NA		Canada	Scott and Crossman (1973)
	9.2-13.mg l ⁻¹		✓	United Kingdom	Maitland and Lyle (1991)
Velocity	6 mg l ⁻¹		✓	River Ohře, Czech Republic	Slavík et al. (2005)
	0.39 m s ⁻¹	✓	✓	NA	Worthington (2010)
	0.25 m s ⁻¹ .		✓	Newfoundland and Labrador, Canada	Peake (2008)
			✓	MacKenzie River, Canada	Jones et al. (1974)

1.3.4.1.1. Spawning

1.3.4.1.1.1. Spawning Migrations

While the distances, direction, and time of spawning migration vary, it has been established that burbot can migrate before spawning (Worthington, 2010). It is generally accepted that migrations of adult burbot begin in the autumn (end of August to October) for the winter spawning season (November to March) (McPhail and Paragamian, 2000) and that spawning is triggered by environmental cues, specifically, a drop in temperature and an elevation in water levels (Paragamian and Wakkinen, 2008). In Green River, Wyoming, USA, upstream and downstream spawning migrations were observed in December and January and were linked to river temperatures reaching 0°C (Brauer et al., 2020). In La Bar River, France, however, it was found that a drop in water temperature was not necessary to trigger spawning migrations, but was more strongly associated with increased water levels (Dillen et al., 2005; Pauwels et al., 2016). Slavík and Bartoš (2002) found that, in the Ohře River, Czech Republic, burbot migrations generally occurred during low discharge periods and when water temperatures decrease. Research into burbot spawning migrations in the Grote Nete, Antwerp, Belgium by INBO from November 2007 until February 2008 found three distinct upstream migrations in December and January that were all triggered by increased river discharge and water levels (Van den Neucker et al., 2009). The largest of the three migrations were in January, which coincided with a drop in water temperature, during which time the most individuals with harvestable eggs or milt were recorded (Van den Neucker et al., 2009).

Some lacustrine burbot populations have been found to be adfluvial, meaning they live in lakes, but migrate to rivers to spawn (McPhail and Paragamian, 2000). In Russian lake populations, burbot have been recorded during their autumn migration to travel 1.5 - 2.0 km per day (Sorokin, 1971). In fluvial populations of the Tanana River, Alaska, US, Evenson (1993) used telemetry to track the movements of large burbot (>650 mm) from September 1992 to July 1993 and found their migratory distances were on average 57 km with a maximum of 255 km observed within the catchment that contained burbot spawning sites. In the Green River, Wyoming USA, the maximum distance travelled by upstream adfluvial burbot populations was 5.8 km (Brauer et al.,

2020). In the fluvial population in Green River, most burbot migrated downstream and the maximum distance moved was 17.7 km (Brauer et al., 2020). In Europe, burbot have been recorded to migrate up to 204 km to suitable spawning sites (Müller, 1957). Robins and Deubler (1955) recorded a downstream migration of burbot at the south of their range in the Susquehanna River, northeast USA. Interestingly, after spawning in the tributaries of the Gulf of Bothnia, the northmost arm of the Baltic Sea, burbot migrate from Finnish and Swedish rivers to the gulf and spend six months in brackish waters along the coast (Johnson, 1981; Toivonen et al., 2020). Percy (1975) also found evidence of a freshwater to brackish migration along the Mackenzie Delta, USA following spawning.

1.3.4.1.1.2. Spawning Sites

Multiple studies in the US have shown that burbot show fidelity toward a specific spawning site, such as a tributary or estuary (Kozfkay and Paragamian, 2002; Dunnigan and Sinclair, 2007; Paragamian and Wakkinen, 2008). In the Great Lakes, Jude et al. (2013) observe that populations can remain in the lakes to spawn or can spawn in tributaries. This reflects a wider plasticity observed across the species' global distribution, with populations utilising varying spawning strategies. Burbot are thought to spawn between November to March in North America, which has advantages in reducing predation and competition for resources for adults who are active during this period (Hardewig et al., 2004). Due to climate variation across its range, however, estimates for the end of the spawning season vary with late May to early June spawning recorded for Kootenay Lake, Canada, for example (McPhail and Paragamian, 2000). In Belgium, burbot spawn between end of December and the beginning of January (Vught et al., 2015). If present, burbot will spawn under ice in the winter or early spring (Cott et al., 2014; Grabowski et al., 2020) for a relatively short (2-3 weeks) period (McPhail and Paragamian, 2000). There is agreement over the spawning period lasting between 2-3 weeks, but disagreement over whether burbot are nocturnal or day-time spawners. Some conclude that burbot spawn at night when they are most active, but other findings have suggested that burbot can spawn during the morning and evening (McPhail and Paragamian, 2000).

There is much established literature to evidence that burbot spawn in both lakes and rivers (Table 1.1). Burbot are well known litho-pelagophils, meaning that eggs are laid on gravels, sand or fine silt, which allows hatched larvae to be carried in water currents (Mann, 1996; McPhail and Paragamian, 2000; Worthington et al., 2012). In lakes, spawning usually takes place in shallow shore areas or on offshore reefs, but it has been suggested that deep water spawning is possible (McPhail and Paragamian, 2000; Jude et al., 2013). In rivers, burbot spawn in low velocity, shallow areas, in off-channel habitat, usually in fine gravel or coarse sand, while coarse gravel and cobbles are used in lakes (Sorokin, 1971; McPhail and Paragamian, 2000). In German lowland rivers, there is evidence of flooded grassland areas being important spawning and larval habitat (Müller, 1957; Brackwehr et al., 2016). In the River Lippe, Germany, high burbot recruitment was strongly correlated with good flood years at the Klostermersch floodplain (Bunzel-Drüke et al., 2004b). In this area, the best recruitment year observed was in 2000, when the floodplain was inundated continuously for 35 days between the end of February and March (Bunzel-Drüke et al., 2004b). More generally, riverine populations make use of a variety of habitats for spawning and larval rearing, including backwaters and small tributaries (Dillen et al., 2005; Worthington et al., 2012; Jude et al., 2013; Brackwehr et al., 2016). In Sweden burbot population size has also been positively influenced in areas where rivers connect to lakes or floodplain water bodies (Degerman and Sers, 1994).

In both lake and riverine systems from American studies, burbot spawn at approximately 1 m (McPhail and Paragamian, 2000), but this could be due to the burbot themselves being of larger average size than their European counterparts. More precise measurements have been recorded: 33 - 132 cm in Burntside Lake, USA (Cahn, 1936); 50 - 80 cm in Lake Baikal, Russia (Sorokin, 1971); and 18 - 20 cm for the Drava River, Austria (Farkas, 1993). The shallow depths of the spawning grounds are crucial as once hatched, larvae must reach the surface to fill the swim bladder (Brackwehr et al., 2016). Slow flow conditions are also required for spawning, which are common in tributaries and shallow habitats, but this is spatially variable. During their studies, Farkas (1993) determined spawning flow rate to be 0.15 m s^{-1} in the shallow spawning habitat. In two tributaries of Lake Baikal, Sorokin (1971) found a current of 0.03 m s^{-1} distributed the spawned eggs, but did not wash them away. Slow

flows of 0.08 m s^{-1} are crucial as it lifts the eggs to clean them from silt, but ensures eggs are not washed out of nursery areas (Sorokin, 1971; Beelen, 2009). Another limiting factor for suitability of spawning and larval rearing habitat is predator pressure on the eggs and hatch larvae (Brackwehr et al., 2016).

1.3.4.1.1.3. Spawning Temperatures

The generally accepted temperature range for burbot spawning is between $0.5 - 4^{\circ}\text{C}$ (Mann, 1996). Paragamian and Wakkinen (2008) state that, under optimal conditions, temperatures should reach below 5°C by the first week of November, with temperatures maintained between $1 - 4^{\circ}\text{C}$ throughout December and February for burbot spawning along the Kootenai River, USA. The spawning temperature range for burbot is sensitive as a change of 2.5°C can delay spawning by up to 14 days (Kouřil et al., 1985). Lahnsteiner et al., (2012) found that, at a constant temperature (2°C in this case), a high percentage of eggs hatched and were often normal-shaped. However, they found that the percentage of normal-shaped hatchlings decreased as temperature increased, suggesting that temperature is a key factor in population viability, with no larvae hatched beyond 9°C . Worthington (2010) argues that an anomalous finding by Jäger et al. (1981), which suggested critical temperature for spawning could be up to 7°C , is key to ascertaining whether the burbot could survive following a reintroduction to English rivers under climate change. Based on their own lab experiments, INBO have shown that at 8°C , 18% of burbot eggs were able to remain viable and hatch (Pauwels et al., 2016). The known variation in burbot spawning temperatures once more illustrates the plasticity of this species. For example, the Euro-Beringian subclades exhibit slightly different temperature ranges for spawning, with the north European group needing $1 - 2^{\circ}\text{C}$ and the western European $5 - 6^{\circ}\text{C}$ (J. Auwerx, pers. comms., 2021). For burbot in the French Ardennes, part of the western European subclade (Fig. 1.5), a spawning temperature range of $5 - 7^{\circ}\text{C}$ has been suggested (Beelen, 2009). Based on their observations, INBO suggest egg incubation temperatures are strongly associated with spawning temperatures, and thus it could be suggested that with burbot that produce eggs that can incubate at 8°C , it is likely that these fish could spawn at 8°C also, though these would be suboptimal conditions (Pauwels et al., 2016). Climate predictions for the UK suggest that, under a high emission scenario, winter air temperature could increase between $0.7 - 4.2^{\circ}\text{C}$

by 2040 (Met Office, 2019a). Johnson et al. (2014) have shown that air temperature can explain 84 - 94% of variability in water temperature, and this increase in air temperature is likely to facilitate an increase in water temperature and it should be considered whether under current climate change projections, English rivers will be able to provide suitable spawning conditions for burbot in their utilised spawning habitats in the future. Though, drivers of water temperatures in rivers are complex and vary spatially and temporally (Wilby and Johnson, 2020).

1.3.4.1.1.4. Sexual Maturity and Reproduction

The age of burbot sexual maturity varies depending on location. The overall pattern is that burbot mature slower at higher latitudes. Age of sexual maturity in burbot ranges from 3 - 7 years from lower to higher latitudes, with most fish reaching maturity at age 3 - 4 (Worthington, 2010). Spawning activity is undertaken by a ball of fish, usually 10 – 12 individuals, with a few females at the centre of a number of males and gametes released directly into the water column directly above the substrate (McPhail and Paragamian, 2000). Burbot also use acoustic vocalisations during spawning between sundown and sunrise to indicate reproductive readiness and to assist with pre-spawning aggregating (Grabowski et al., 2020; Putland et al., 2022). As for other cod species, the batch fecundity of the burbot is extensive, ranging from 6,300 (Miller, 1970) to 3.4 million eggs (Roach and Evenson, 1993). Fecundity varies with location and habitat, with average fecundity shown to vary between 24 lake-dwelling populations across Canada (Cott et al., 2013). There is a positive relationship between body length and fecundity with larger burbot individuals producing more eggs, but this effect is not as pronounced as for other fish (Roach and Evenson, 1993). The time for eggs to hatch is dependent on temperature, with high temperatures resulting in shorter times to hatching. Some studies have suggested that hatch time is between 120 to 140 degree days, which is approximately 32 days at 4°C (Müller, 1957; Kainz and Gollmann, 1996; Woher, 2010; Donner and Eckmann, 2011). The eggs can hatch after 30 days at 6°C or 41 days at 2°C (Nagel et al., 2011).

Not all adults spawn every year. Evenson (1991) estimates that only 15% of female and 17% of male burbot aged 7 or older spawn per year in the Tanana River, Alaska.

A lab experiment on maternal age impacts on egg development showed that 100% of age-5 females spawned during the experiment compared to older and younger age groups, suggesting these are the most consistent spawners in a population (Ashton et al., 2019). Another experimental study showed that, under hatchery conditions in Belgium, all female burbot spawn (Vught et al., 2008). In Finland, it was found that ~30% of sexually mature adults in a burbot population do not spawn annually (Pulliainen and Korhonen, 1993). A population viability analysis (PVA) for burbot population persistence modelled for an example reintroduction site, the River Wissey, Norfolk, UK, showed that population persistence was dependent on the percentage of females successfully producing offspring (Worthington et al., 2011a). Those scenarios run with high numbers of females producing offspring (100% and 50%) showed >99% population persistence over 100 years, but the 50% females scenario resulted in an overall smaller population size (Worthington et al., 2011a). While the exact biological reason for this is not determined, more research is beginning to show that environmental factors influence the amount of adult burbot spawning per year, including river discharge (Paragamian and Hansen, 2009), increased water temperatures (Paragamian and Wakkinen, 2008), and chemical pollution (Pulliainen et al., 1992). This would support an argument by Worthington (2010) that burbot spawning behaviour is less defined than for other fish species with the evidence suggesting that spawning is driven by a combination of habitat availability and environmental factors.

1.3.4.1.2. Larvae

While research on larvae morphology and development is limited for the burbot, especially in riverine environments, it is key to determining long-term population viability (Worthington, 2010; Ritz et al., 2020). Burbot hatch at 3-4 mm length and have been observed to passively drift in the water column until swimming improves (McPhail and Paragamian, 2000). Larval stages are characterised first by allometric growth, which is an unequal development of body parts that will assist survival, such as swimming or feeding, then to an isometric or proportional growth period as critical structures have already developed (Fuiman, 1983). A study from Lake Constance, Germany found that burbot larvae disappeared from the sampled limnetic zone, which was assumed to be through drift or swimming development (Wang and Appenzeller,

1998). Little is known about the critical period after hatching where survival rates are known to be low (Marr, 1956). For other cod species, the time between hatching to first feeding to established feeding is thought to significantly influence survival rate (Voss et al., 2001). The larvae feed endogenously in the littoral zone prior to migrating to the surface 11 - 23 days post-hatch where they begin to feed exogenously (Clady, 1976; Fischer, 1999). From observations in Lake Shebandowan, Canada, burbot larvae are described as being phototactic and vulnerable to wind and current conditions with a shift towards becoming solitary and benthic in habit once they attain >30 mm length (Ryder and Pesendorfer, 1992; Hochleithner, 2020).

Overall, the larval stage lasts approximately 60 days (Freyhof and Kottelat, 2007). In Lake Oneida, USA, throughout early burbot life stages prey consumption was shown to be limited by the diameter of its prey (Ghan and Sprules, 1993). Ryder and Pesendorfer (1992) assessed diet and size, stating that burbot of 11 - 20 mm feed mostly on zooplankton, with a shift to insects and amphipods from 21 - 30 mm, followed by an amphipod dominant diet from 31 - 40 mm, signalling a transition from an open water to a benthic feeding lifestyle. In the Kootenai River, USA, larval burbot (~40 days) were found to feed primarily on zooplankton, mainly Cyclopoida (Klein et al., 2016a).

Larvae are most commonly found in depths between 0.5 to 1.5 m (Hojtink, 1998). Other studies have suggested, however, that larvae must have habitats <0.2 m depth as they do not possess a swim bladder to float to the surface (Harsányi and Aschenbrenner, 1992; Vught et al., 2015). Refuge from elevated flow is needed as hatched larvae could be flushed entirely out of a riverine system (Worthington et al., 2012). Brackwehr et al. (2016) estimate that with a development time of at least three weeks and a river current of 0.5 m s^{-1} , larvae could travel up to 900 km, emphasising the importance of refuge areas in riverine systems if the slow flows of floodplain inundation for 2-3 months cannot be achieved. A study by Müller (1957) in Germany found burbot larvae in inundated floodplain vegetation from the end of March to mid-April, demonstrating the importance of low velocity, sheltered areas for larval life stages. In years without spring floods larvae were found in shallow areas close to the

banks (Müller, 1957). Burbot larvae have been found in lateral ponds of a Grote Nete side channel, Asbeek, in Belgium from 2014 – 2017, and in the Heiloo side channel of the Grote Nete from 2019 – 2021 (Vught et al., 2015; Pauwels et al., 2016; Vandamme et al., 2017, 2020, 2024; Van Wichelen et al., 2018). These densities have been as high as 13 ind m⁻² which is close to the common 15 ind m⁻² density of larvae found just after hatching in stable populations (Ryder and Pesendorfer, 1992; Ghan and Sprules, 1993). Along the River Lippe, Germany, inundated meadows are crucial habitat for larvae as the meadows provided slow flow conditions, and by spring, the shallow well-warmed waters provided an abundant food source (i.e. zooplankton) for development (Brackwehr et al., 2016). Dillen et al. (2008a) found that both fingerlings and larvae in northern France were found in small tributaries (<2 m width), with low flows (0.05 - 0.15 m s⁻¹) and high densities of vegetation (>25%). Even if a site possesses suitable habitat for larvae, overall larval survival is low, thought to be 1% of hatched eggs (Carl, 1992), which reflects their reproductive strategy of producing large numbers of eggs to balance the vulnerability of eggs and larvae to predation or unsuitable environmental conditions (i.e., temperature or hydrology).

1.3.4.1.3. Fry and Juveniles

The persistence of juvenile fish or fry in shallow areas of riverine environments indicate the importance of low velocity areas for spawning and rearing habitat for burbot. In the Missouri River, USA, Fisher (2000) found that off-channel habitat was important for the survival of burbot aged 0 to 1. In Alaskan rivers, fry were found in shallow (<30 cm) and low flow (<0.3 m s⁻¹) areas (Blackman, 1997 in Worthington et al., 2012). In northern France, juveniles were often present in river tributaries with low to moderate flow velocities of 0.05 – 0.15 m s⁻¹ (Beelen, 2009). In France, burbot between 20 - 40 mm were captured in areas of high macrophyte cover and abundant bankside tree root exposure (Dillen et al., 2008a). In the Shebandowan Lake, Canada, it was rare to find juveniles unconcealed, often discovered under a structure such as a boulder, sunken tree, or bark (Ryder and Pesendorfer, 1992). Other studies have shown that juvenile burbot will choose the largest substrate available for shelter, regardless of current diet and predation (Fischer, 2000b).

In Lake Oneida, USA, burbot length was found to increase exponentially from hatching in April to their disappearance from the limnetic zone in May (Ghan and Sprules, 1993). It was found that, as length increased, so did the number and size of prey in their stomachs, which was thought to be controlled by prey width and not prey length (Ghan and Sprules, 1993). In Lake Constance, Germany, juvenile burbot were found to exhibit high predation pressure on invertebrates, actively predating larger species (Baumgärtner and Rothhaupt, 2005). Fisher (2000) looked at larval and juvenile diet in two rivers in Missouri, USA and found similar patterns to lake-based burbot in North America. Stomachs of larval burbot contained copepoda nauplii and *Keratella* sp., while the juvenile burbot mainly consumed macroinvertebrates (Odonata, Amphipoda, and Plecoptera) and some Catostomidae larvae, where available. Copepods are thought to be the main source of food for young (3 – 10 mm) larvae (Ryder and Pesendorfer, 1992). In Lake Constance, a shift of juveniles from the littoral zone to cold profundal waters was recorded from spring through to early summer under reduced growth rates (Hofmann and Fischer, 2001). Interestingly, it is not temperature demand that drives this shift, but availability of shelter in deeper water as burbot grow (Hofmann and Fischer, 2003).

1.3.4.1.4. Adults

The burbot is a physoclistous fish, meaning it has a gas gland with a swim bladder to regulate its buoyancy allowing it to transition across various depths (Cott et al., 2015). There have been multiple observations, in both lake and riverine habitats, of adult burbot inhabiting the deeper water available to them, which Worthington (2010) argues is due to cooler temperatures and increased availability of suitable shelter. In Lake Superior, burbot have been recorded at 300 m water depth (Boyer et al., 1989) and in Lake Baikal, Siberia, burbot at depths of 200 m (Sideleva, 2003). Thus, burbot can inhabit deeper lake zones, despite the availability of prey increasing near the surface where the habitat is most productive. A study of burbot in Alexie Lake, Canada during the ice-free season found a pattern of diel bank migration that occurs along the bottom of the lake instead of through the freestanding water column, suggesting that burbot movements are in response to light and temperature, but also foraging opportunities and predator avoidance (Cott et al., 2015). The study observed that adult burbot occupied deeper water during daylight ascending from rocky bottom to shallower water

habitats at night. During early summer, with nearly 24 hours of daylight, diel bank movement (i.e., where vertical migration occurs along the lake bottom rather than the water column) was low, but began to increase by mid-summer when there was a more prominent night-cycle, evidencing that burbot are a light-responsive species (Cott et al., 2015). Though Cott et al. (2015) were only able to use telemetry on four adult burbot, the high-resolution methodology gives an increased level of detail to the supporting literature indicating a preference for occupying deeper waters. Though less understood, research has shown that adult burbot use the deepest areas available in riverine environments, such as pools (Carl, 1995; Erős et al., 2003; Eick, 2013). It is thought that, as in lakes, a need for daylight cover is a limiting factor for burbot survival in riverine environments (Worthington, 2010). In this respect, in an examination of burbot habitat preferences in German and French rivers, Worthington et al. (2012) found that adults prefer areas of cover including larger substrate, tree roots, and deep waters during daylight hours.

Growth rates in burbot are varied across life stages, latitude, and habitat type, but predictable in one aspect: growth rate is fastest in years 1-2 (Živkov et al., 1999). In the south of their range, burbot are known to grow faster than those at higher latitudes (Jobling, 2002). Moreover, there is variation in growth rates between the sexes, with females exhibiting faster growth than males (Madenjian et al., 2013). Different factors can cause changes in growth rate. For example, a shift in diet was found to be the main driver of juvenile growth rates in Lake Shebandowan, Canada (Ryder and Pesendorfer, 1992), but in Finland, at Lake Kuohijärvi, age-0 burbot growth were influenced by temperature, which was not found to influence older fish as much (Kjellman and Eloranta, 2002). In a laboratory experiment Hofmann and Fischer (2003) found that juvenile burbot growth was influenced by temperature, with increasing temperatures increasing rates of food uptake, thus contributing to growth.

1.3.5. Adult Ecology and Behaviour

1.3.5.1. Feeding

The feeding habitats of adult burbot have been well studied in the literature, for both riverine and lake environments. Burbot are a benthic, top-level predator (Hardewig et al., 2004; Paragamian and Wakkinen, 2008; Cott et al., 2015; Stapanian and Myrick, 2015; Worthington et al., 2017). A study of US, small stream dwelling burbot found that their diet was varied, but largely dependent on mayflies (Ephemeroptera) and a variety of invertebrates, such as water beetles (Coleoptera), caddisflies (Trichoptera) and flies (Diptera) (Dixon and Vokoun, 2010). For this study, 80% of the burbot sample was aged between 2-3 years and averaged a length of 191 mm, suggesting that burbot do not often grow very large in small streams, only switching to a piscivorous diet here at 330-480 mm in length. Another portion of diet was found to be obtained from Decapoda, which includes crayfish, crabs, lobsters and prawns. A study of 734 burbot from Lake Biel, Switzerland showed that, although dietary composition varied throughout the year, choronomids (Chironomida) comprised the largest portion of burbot diet (Guthruf et al., 1990). Other groups included Amphipoda, Decapoda and Isopoda, Ephemeroptera, stoneflies (Plecoptera) and Trichoptera (Guthruf et al., 1990). A study of burbot food sources on floodplains and floodplain water bodies laterally connected to the Grote Nete, Belgium found that the most common invertebrate group in the diet was Copepods while other food sources included snails (Gastropoda), cnidaria (Cnidarians), Trichoptera, arachnids (Arachnida), roundworms (Nemotoda), crustaceans (Ostracoda), dragonflies (Odonata), Coleoptera, Ephemeroptera, and worms (Oligochaeta) (Vandamme et al., 2020).

Burbot can also be described as opportunistic piscivores with their indiscriminate feeding strategy evidenced by consumption of non-native and invasive species, such as round gobies *Neogobius melanostomus* in the Great Lakes of North America (Hensler et al., 2008; Hares et al., 2015). The literature evidences that burbot diet shifts from invertebrates to fish with increasing body size (Beeton, 1956; Ryder and Pesendorfer, 1992; Ghan and Sprules, 1993; McPhail and Paragamian, 2000; Baumgärtner and Rothhaupt, 2005; Klein et al., 2016a). The shift from an invertebrate to a fish-based diet is determined by gape size (Worthington, 2010; Klein et al., 2016a).

Beeton (1956) found that burbot of <17.8 mm length from the White River, USA, predominately fed on crustaceans, aquatic insect larvae, and mayfly nymphs. By contrast burbot of 178 - 253 mm predominantly fed on crayfish, and those >253 mm consumed fish (Beeton, 1956). There are exceptional cases, however, with burbot of 90 mm from Lake Eerie reported to predominantly predate on fish (Clemens, 1951a).

Studies have shown that burbot will change their feeding habitats dependent on prey abundance, a key characteristic of opportunistic feeders. Therefore, their feeding habits will change depending on season (Wagner, 1972) and environmental factors. An experiment in which adult burbot from Finland were fed daily under different temperatures showed that food intake increased with temperatures up to 23.4°C at which point consumption then decreased (Pääkkönen and Marjomäki, 2000). Similarly, Hardewig et al. (2004) suggested that higher summer temperatures induced burbot to reduce their food intake along with their energy expenditure to cope with the thermal extreme, and instead rely on their winter reserves. Adult burbot have been estimated to consume 9.7 and 24.3 kg ha⁻¹ annually when burbot biomass was 2.0 and 5.0 kg ha⁻¹, respectively, based on experiments of Finnish burbot daily food intake (Pääkkönen and Marjomäki, 2000). Further, a study from Lake Muddusjärvi in northern Finland showed that, as burbot length increased, maximum prey size increased, but minimum prey size increased less quickly comparatively, suggesting that larger burbot still target smaller prey (Kahilainen and Lehtonen, 2003). An earlier study by Fratt et al. (1997) found a relationship between presence of prey at certain depths and burbot predation rate. There is also clear evidence of cannibalism of younger burbot by adults (Nelichek, 1973; Guthruf et al., 1990; Gallagher and Dick, 2015).

In the context of a future burbot reintroduction to England, identifying a river with sufficient sources of zooplankton (Ryder and Pesendorfer, 1992; Klein et al., 2016a), a variety of invertebrates including mayflies (Ephemeroptera), water beetles (Coleoptera), caddisflies (Trichoptera) and flies (Diptera) (Dixon and Vokoun, 2009), and smaller fish classes (Vught et al., 2008) is crucial to a reintroduced population's survival. Before any reintroduction is attempted, the Environment Agency's Water

Framework Directive monitoring data of water quality and macroinvertebrates could be used to evidence the suitability of candidate reintroduction sites.

1.3.5.2. Competition, Predation and Ecological Interactions

An understanding of interspecific interactions for the burbot, such as predation and competition, has been furthered by several *in situ* and *ex situ* studies. Burbot can co-exist with other large predatory fish. In five of the Great Lakes, the burbot is considered an important keystone species due to its role as a consumer and co-predator (Hensler et al., 2008; Jude et al., 2013). Similarly in sub-arctic boreal lakes burbot have been found to occupy an apex predator position, playing an important role in ecosystem function, alongside lake trout *Salvelinus namaycush* and northern pike *Esox lucius* (Cott et al., 2011). In Lake Michigan, North America, burbot have been shown to prevent the rehabilitation of Lake Trout due to predation pressure (Jacobs et al., 2010); however younger burbot especially, are still prey to a variety of other fish, including walleye *Sander vitreus* (Ryder and Pesendorfer, 1992) and lake herring *Coregonus sardinella* (Carl and McGuinness, 2006). A study in Finnish boreal forest streams with a history of dredging that had been linked to diminished brown trout populations found that burbot had a negative impact on brown trout recruitment (Luhta et al., 2012). The presence of burbot has also been found to influence the behaviour of other fish, such as the arctic char *Salvelinus alpinus* in lakes in Norway, with high densities of burbot forcing char to use the limnetic zone whereas in low density circumstances it occupies littoral zones (Knudsen et al., 2010). High burbot densities can also exert predation pressure on macroinvertebrate communities (Baumgärtner and Rothhaupt, 2005).

Research by Filipsson et al. (2019) used a stream experiment to investigate the response of juvenile (one-summer old) brown trout to the presence and absence of adult burbot under different temperature and light conditions. The presence of adult burbot can induce increased shelter use by brown trout during bright light and cause displacement behaviour during dawn and night conditions (i.e., lingering further downstream than when the burbot was absent). Ultimately, the findings suggested that juvenile brown trout were pressured by burbot during night conditions as it ultimately triggered avoidance behaviour and altered diel movements. However, this relationship

between adult fish and juvenile fish is common and juvenile burbot have also exhibited avoidance behaviour due to the presence of older burbot and other predatory fish (Donner and Eckmann, 2011). Predation pressure can induce a change in behaviour in burbot, with juvenile fish shown to suspend foraging at night (Fischer, 2004). Aside from predation by other fish species, burbot are also prey for birds, such as great cormorant *Phalacrocorax carbo* (Cowx, 2003) and mammals, such as Eurasian otter *Lutra lutra* (Brzezinski et al., 2006).

Prior to a reintroduction, a study on how burbot would fit into local ecology is crucial and it is important that any reintroduction strategy considers stocking densities and includes post-release monitoring of local ecology (fish and macroinvertebrates) as well as the reintroduced burbot population itself.

1.3.5.3. *Habitat*

Shelter structures are crucial for burbot survival, and each life stage utilises a different type of habitat (Table 1.1). Both Belgium and the Netherlands have undertaken reintroductions or translocations of burbot and have assessed reintroduction site suitability based on thorough literature reviews of burbot habitat requirements (Dillen et al., 2005; Verdonshot and Verdonshot, 2012). Table 1.2 summarises the key burbot features recorded in their habitat suitability assessments. It should be noted that the habitat suitability assessment for the Netherlands was created for identifying other instream fish species, as well as burbot. Key features which appear in both assessments are undercut banks, water depth, dissolved oxygen, flow, as well as the presence of different aquatic vegetation types.

A lack of adequate shelter has been found to affect the metabolism and somatic growth rates of burbot (Fischer, 2000a). There are varying findings with regards to substrate preference, with some indicating burbot preference for stony substrate (>110 mm) (Fischer, 2000a; Fischer et al., 2001) and cobble substrates (Eick, 2013) and others for bedrock and rubble (65 – 256 mm) (Julian's Reef, Lake Michigan, Edsall et al., 1993).

Table 1.2. Key features recorded in habitat suitability assessments designed for burbot in Belgium and the Netherlands. The Belgium assessment is adult and juvenile habitat suitability features combined.

Belgium	Netherlands
Dissolved oxygen	Dissolved oxygen
Ammonia	Channel width
Channel position	Depth
Undercut bank presence	Clarity
Depth	Surface flow rate
Flow velocity	Temperature
% overhanging vegetation	% non-floating algae
% emergent vegetation	% aquatic plants
% submerged vegetation	% dead wood
	% tree roots
	% fine detritus/sludge
	% coarse detritus
	% sand
	% fine gravel
	% coarse gravel/pebbles
	% stones/debris
	% shading
	% undercut banks
	Peak discharge frequency
	Crayfish presence
	Fish stocking presence
	Longitudinal connectivity upstream and downstream

Due to their nocturnal behaviour and hunting technique, in which they ambush their prey, burbot require shelter during the day, in which they utilise natural structures, such as larger substrates (Dixon and Vokoun, 2009), undercut banks (Dillen et al., 2008a), woody pieces and tree roots (Worthington et al., 2012), and even anthropogenic debris, such as tyres and bricks (Ryder and Pesendorfer, 1992). Adult burbot have also been observed to defend their shelters from smaller species (Fischer and Öhl, 2005). It is thought that the only limiting factor for adult burbot in river systems is the availability of habitat for concealment (e.g., large wood pieces, aquatic plants, undercut banks, boulders, tree roots) (Worthington et al., 2011a). In their study of burbot in northern French rivers, Dillen et al. (2005) found that rivers were not suitable for burbot adults when the density of undercut bank microhabitat was too low.

Burbot preference for shelter and habitat shifts ontogenetically. Larvae will drift in off-channel habitat (inundated floodplain vegetation, back channels, wetlands), juveniles are found in low velocity areas with abundant macrophytes (Dillen et al., 2008a), and adults prefer deeper waters with larger substrates, or structures, such as tree roots and fallen trees (Worthington et al., 2012). A river habitat that is connected to these

meso-habitats both longitudinally and laterally would be a complex and highly heterogeneous river habitat, beneficial to multiple taxa due to the connectivity of numerous niches - a potential goal of wider river conservation and restoration (Sayer et al., 2018, 2024).

1.3.5.4. Temperature

Temperature is regarded as one of critical factors determining burbot distribution and survival (Table 1.1; Worthington, 2010; Ch.4). Adult burbot are thought to have an optimal temperature range of 10 - 14°C (Stapanian et al., 2010a). Hardewig et al. (2004) determined optimum temperature for burbot to be 13.5°C under experimental conditions and further estimated critical maximum temperature for adults to be above 20°C (Hardewig et al., 2004). Some burbot populations in European rivers are known to have survived summer temperatures of 25 - 26°C (Hardewig et al., 2004). For burbot taken from Lake Päijänne, 27°C was identified as the upper thermal limit for burbot acclimated at 12°C (Pääkkönen et al., 2003). A different experiment acclimated fish at 19.6°C, and still determined the upper thermal limit to be 27°C (Fisher, 2000). Jackson et al. (2008) argues that, for North American burbot, 30 - 40 days above 21°C could represent the threshold at which populations begin to decline. Even within the same region, there is variation in thermal optimum for adult burbot between neighbouring populations, which shows localised adaptations (Vught et al., 2015). For example, burbot toward the south of their global range are thought to be better adapted to higher water temperatures (Vught et al., 2015).

As fully developed burbot have strategies to withstand extremes in temperature, and based on the literature offer plasticity across their range in terms of maximum critical temperature, winter spawning temperatures are arguably the more crucial aspect for burbot survival as spawning has a much narrower thermal range for success. Considering the evidence that climate change is already influencing burbot populations globally, the persistence of a suitable spawning range into the future is a key concern. In Curonian Lagoon, Lithuania, declines in burbot catches have been attributed to warmer winter climate negatively influencing reproduction (Švagždys, 2002). In Lake Onedia, USA, summer temperatures have also led to declines in burbot

abundance with higher temperatures thought to have inhibited feeding (Jackson et al., 2008).

1.3.5.5. Water Chemistry

Burbot could be an asset to environmental managers as they are a good indicator species for water quality and studies of freshwater contaminants (Stapanian and Myrick, 2015). Temperature and dissolved oxygen are the water chemistry properties that are most impactful to burbot and are well studied, but with other chemical properties (e.g., ammonia, nitrates, phosphates) the exact tolerances are poorly understood. More specific boundaries have been calculated for aquaculture conditions. For example, a recent study by Vaage and Myrick (2021) found that, under aquaculture rearing conditions, un-ionised ammonia concentrations should not exceed $\leq 0.03 \text{ mg l}^{-1}$, as above this limit, growth is significantly affected. For these water quality parameters, however, wild populations of burbot will be more indirectly impacted by increases in these parameters through eutrophication, for example. Due to strict national and international legislation (such as the EU's WFD), ammonia, nitrates, and phosphates may not attain concentrations sufficient to result in direct fish kills, but in the UK there are reports of algal blooms linked to land use change and nutrient inputs in rivers (Bowes et al., 2012; Kelly and Hassall, 2018). The increase in algae reduces oxygen content for fish and, if extreme enough, can result in fish kills (Henderson et al., 2008).

The literature varies over pH thresholds for burbot, but for there to be no interference with spawning, reproduction, or embryo development the boundaries are thought to be pH 6.0 - 8.0 (Worthington, 2010). Burbot prefer high dissolved oxygen content in the deeper waters of lakes (Stapanian et al., 2010a) and have an intolerance for low oxygen (Holzer, 2008 in Lecaudey et al., 2019). Maitland and Lyle (1991) reported that burbot require an oxygen range of 5 - 7 mg l^{-1} . In the River Ohře, Czech Republic, a burbot population had a dissolved oxygen preference of between 9.2 - 13 mg l^{-1} for the period of study (3 months) (Slavík et al., 2005). A study of rivers in northern Alberta, Canada, found that a low dissolved oxygen concentration ($\sim 5 \text{ mg l}^{-1}$) caused the spawning period of burbot to be extended (Chambers et al., 2000). In a mass rearing

experiment of burbot, dissolved oxygen was maintained above 6 mg l⁻¹ (Kwiatkowski and Targońska, 2009). In a substantial review of published burbot studies on dissolved oxygen preferences, Worthington (2010) concluded that the critical survival dissolved oxygen threshold is 2 mg l⁻¹ and the long-term survival boundary is 6 mg l⁻¹.

1.3.5.6. Hydrology

Burbot are known to have low swimming endurance, which can limit their movements (Stapanian et al., 2010a). Burbot have been found to switch to sprint swimming, a periodic propulsion swimming that may only be maintained for a temporary period (Webb, 1984), when velocity is increased in controlled experiments, as well as abandoning attempts to ascend fish passes at lower nominal velocities than other fish species (Vokoun and Watrous, 2009). A Canadian study found that the mean critical swimming speed was 0.39 m s⁻¹ for a 370 mm burbot (Peake, 2008). Jones et al. (1974) found that large fish could not maintain their swimming velocity for more than 10 minutes when velocities were increased beyond 0.25 m s⁻¹. In Lar Bar River, France, most burbot were found in areas with stream velocities of <0.25 m s⁻¹, with no burbot found at velocities greater than 0.5 m s⁻¹ (Dillen et al., 2005). Therefore, with a slow swimming endurance, any river habitat needs areas of shelter and refuge for each life stage to support a burbot population.

Disparities observed between studies of burbot chemical tolerance, temperature, and swimming velocities could be due to the experimental design of these studies, or natural variation between source fish populations for experiments. More research is needed at larger scales, particularly for European burbot populations, to more precisely determine threshold responses to key environmental variables to better aid burbot population management and conservation. Overall, however, for burbot of the western European subclade, the presence of low velocity or static floodplain habitat is key for the larval development stage (Worthington et al., 2010a; Van Wichelen et al., 2019). Any burbot reintroduction must ensure that these hydrological features are present at a reintroduction site to ensure burbot can complete their life cycle.

1.3.6. Human Influence and Burbot Decline

Anthropogenic pressures including pollution, habitat modification, and introduction of invasive species have been the main causes of burbot population decline throughout their natural range. An understanding of these causes and persisting human influences can help to identify issues for reintroduction programmes, which is invaluable in early project planning stages.

1.3.6.1. Pollution and Water Chemistry

Water pollution and chemical contaminants have been found to affect burbot in several ways. Stapanian and Myrick (2015) argue that chemical contaminants affect the exhibited sexual differences between males and females. In Norway, around Lake Mjøsa, direct urban runoff and industrial pollution, especially large quantities of persistent organic pollutants, have been discharged into the lake over the last century, in which concentrations of these pollutants inside burbot have exceeded concentrations in a reference lake by a factor of 113 in some cases (Olsvik et al., 2013). Further, burbot in Lake Mjøsa were found to have higher densities of *Mycobacterium salmoniphilum*, suggesting that contaminants in the lake were affecting the overall health of wild fish (Berg et al., 2013). While no definitive link could be proven, in the Swedish-Finnish Gulf of Bothnia, high numbers of sterile burbot were found in areas heavily influenced by industrial runoff. The sterile fish had a higher rate of irregular growth and bone resorption, while several toxic chemicals (i.e., PCBs, PCDD, Al, Hg) were found in their muscles and liver (Pulliainen et al., 1992). In Poland, burbot abundance was found to decrease as pollution increased across the Warta River, with lowest abundances found in the area characterised by low dissolved oxygen and high nitrate concentrations (Kruk, 2007). A study of Finnish lakes found that agricultural runoff influenced the eutrophication of lakes, which was a direct cause in reducing burbot abundance (Tammi et al., 1999). Thus, it is important to consider any reintroduction site in the context of its surrounding land use, as well as pollution sources throughout the entire catchment due to the interconnectivity of aquatic landscapes and the importance of burbot dispersal after an initial reintroduction.

While burbot are regarded as a sensitive indicator species, they also demonstrate a level of resistance to some pollutants. An experiment to study the effect of inorganic (cadmium, copper, mercury, lead, zinc, and nitrite) and organic (cyclohexane and 2,4-dichlorophenol) pollutants on sperm mobility of some freshwater fish species, found that burbot sperm mobility showed medium resistance to the pollutants, which was greater than for other fish, such as brown trout (Lahnsteiner et al., 2004). Interestingly, a study in boreal Canadian lakes found that mining effluent did not affect the ability of burbot to accumulate energy reserves and survive the winter period (Bennett and Janz, 2007). Therefore, due to a general tolerance of burbot to most pollutants in moderate doses, if diverse fish communities are persisting naturally in a system, it is likely that burbot will be able to survive in that system, provided that there is appropriate and sufficient habitat.

1.3.6.2. Habitat Alteration

Stapanian et al. (2010a) argued that habitat modification, especially dam development in North America, was the main cause of declining riverine burbot populations. Dams change river discharge and thermal regimes across temporal and spatial scales, and reduce habitat complexity (Stanford et al., 1996). For example, the Kootenai River in the USA, burbot population collapse was largely attributed to the Libby Dam, built in 1972, which altered flow and increased winter water temperature above the spawning threshold (Paragamian et al., 2000; Beard et al., 2017).

Aside from the influence of in-channel barriers and the decline of longitudinal connectivity, the effect of a loss of lateral connectivity and a reduction of complex river habitat on burbot populations is poorly studied, though it is implied (Stapanian and Myrick, 2015). Burbot migrate between shallow and deep water habitat daily (Cott et al., 2015), annually, and across their lifespans (McPhail and Paragamian, 2000) during different life stages (Harrison et al., 2013), so the connectivity of these different habitats is incredibly important as the loss of one of these habitats (i.e., floodplain spawning habitat, low velocity back channels, and deeper main channel habitat with larger substrate or tree roots) could jeopardise a whole population over time. Globally, the decline of burbot populations in lowland systems, like other fish species, has been

linked to a loss of off-channel habitats (i.e., wetlands and backwaters) (Aarts et al., 2004; Olivier et al., 2009). In the Kootenai River, the process of channelisation, of removing meanders to straighten the river, as well as the appearance of dams and dykes, is thought to have reduced shallow off-channel habitat leading to zooplankton decline and hence a reduced food source for the burbot at early life stages (Hardy and Paragamian, 2013; Frazier et al., 2020). Brackwehr et al. (2016) argue that the limiting factor on burbot survival in Germany is the suitability of current riverine habitat for larvae. This is due to the need for inundated floodplains or shallow water habitats with near slack water conditions for 2 - 3 months, as well as low temperatures ($< 6^{\circ}\text{C}$ initially, slowly rising to 9°C), abundant zooplankton, low predation, and minimal competition (Brackwehr and Kühlmann, 2016; Brackwehr et al., 2016). Due to extensive modification of the river-floodplain ecosystem, there are very few areas that exhibit a winter-spring flood regime that the burbot can rely on to complete its life cycle. In the Netherlands, burbot population declines are thought to have been mainly driven by agricultural intensification and habitat modification, as most Dutch rivers have lost their natural characteristics and floodplain spawning habitat due to development and drainage activities (Bosveld et al., 2015).

Climate change is accepted to be one of the most influential pressures on burbot in the south of its range (Stapanian et al., 2010a). Interestingly, in a study of over 400 freshwater European fish, the burbot was not found to be of high risk of extinction from climate change (Jarić et al., 2019). Logez et al. (2012) modelled habitat requirements for European riverine fish and found that upstream drainage area had more of an influence on burbot distribution than temperature, which is supportive of their preferences for low energy streams. Thus, more testing of these models may be needed, with the burbot being a good potential candidate. Beyond the direct warming influence of water temperature, Carrie et al. (2010) found that contamination of mercury and PCBs was increasing in Arctic burbot populations due to warming temperatures and reduced ice cover leading to higher exposure to these atmospheric contaminants. Their study found a relationship between increasing primary productivity and concentrations of contaminants, suggesting that they are moving through the system faster and accumulating in larger concentrations at higher trophic levels. Similarly, in Finland, warming temperatures have caused increased snowmelt

since the 1960s, thus increasing surface runoff over acid sulphate soils (Saarinen and Kløve, 2012). The direct run-off into watercourses and the Gulf of Bothnia are periodically, heavily acidifying the areas with waters of pH <5.5, which also liberate heavy metals, especially aluminium from the soils (Toivonen et al., 2020). The study found that periodic winter runoff was influencing burbot larval abundance as the runoff coincided with spawning, thus reducing the survival rate of larvae.

1.3.6.3. Invasive Species

As well as pollution, introduction of invasive species has been a key cause of lacustrine burbot population decline (Stapanian et al., 2010a). In Lake Eerie, invasive sea lamprey led to the decline of burbot populations due to predation pressure and the eventual control of sea lamprey populations allowed the burbot population to increase between 1987 and 2003 (Stapanian et al., 2006). Further, invasive alewives *Alosa pseudoharengus* were found to be limiting burbot abundance in Lakes Michigan and Ontario, as Alewives compete with fry and young-of-the-year (YOY) burbot for food (Bunnell et al., 2006). With specimens from the European Lake Constance, interactions with spiny-cheek crayfish *Orconectes limosus* have also been studied, showing that YOY burbot change their behaviour and avoid shelter opportunities if occupied by spiny-cheek crayfish, although this effect declines after one year (Hirsch and Fischer, 2008). Similar avoidance behaviour has been induced by signal crayfish *Pacifastacus leniusculus* in Swedish Lakes (Josefsson and Andersson, 2001). It is unknown, however, whether this extends to other crayfish species, and the extent to which this would affect the survival of younger burbot. Aside from its vulnerability to invasive fish species that can out-compete and predate it, the burbot may have potential to control invasive species due to its opportunistic feeding strategy; however, more research on this is needed. For example, in Lake Eerie, North America, there is evidence that burbot consume 61% of the invasive round goby standing stock, suggesting that a higher burbot abundance has the potential to exert predatory control on some invasives (Madenjian et al., 2011).

1.3.7. A Reintroduction to England: Burbot History

Lota lota has gone by many names in England - burbolt, eelpout, lawyer fish, lingcod - but most commonly, burbot. The last recorded catch of the burbot in England was in 1969 at the Old West River at Aldreth, Cambridgeshire (Marlborough, 1970), meaning it is possible that a few local people alive today can still remember catching a burbot. Thus, there is not only an environmental legacy, but also a cultural legacy to explore, one of angling and domestic use, that can justify the burbot's reintroduction to English rivers (Pearce et al., 2024b). Comparatively, the burbot is not as popular as it was historically as a recreational and game fish in North America (Stapanian et al., 2010a), but it continues to engage anglers. For example, it remains a common angling fish in Scandinavia (Maitland and Lyle, 1991; Everard, 2021; Marjomäki et al., 2022). The historical data, however, from angling and catch records demonstrate its previous use in fishing in England (Marlborough, 1970; Worthington et al., 2010a). In England, they were once so plentiful that they were sold in markets and even fed to pigs (Maitland and Lyle, 1991).

1.3.7.1. Distribution

Worthington et al. (2010) analysed historical, anecdotal literature, found ~194 records of burbot catches, and created a historical distribution of the burbot throughout England. It was found that archaeological records of burbot corresponded closely with the historical literature. 42 rivers were identified in which the burbot was likely to have existed as indicated by the historical records (Worthington et al., 2011b). There were four areas with overwhelming evidence of burbot presence: the Yorkshire rivers, the Trent catchment, Norfolk and Suffolk rivers, and the Fenland rivers (Fig. 1.7). The abundance of burbot records along eastern flowing rivers is consistent with the idea that burbot entered England from rivers flowing over the land bridge from Europe. The genetic divergence of the English genetic subclade occurs prior to the last glacial maximum, suggesting burbot survived in thermal refugia (Worthington et al., 2017).

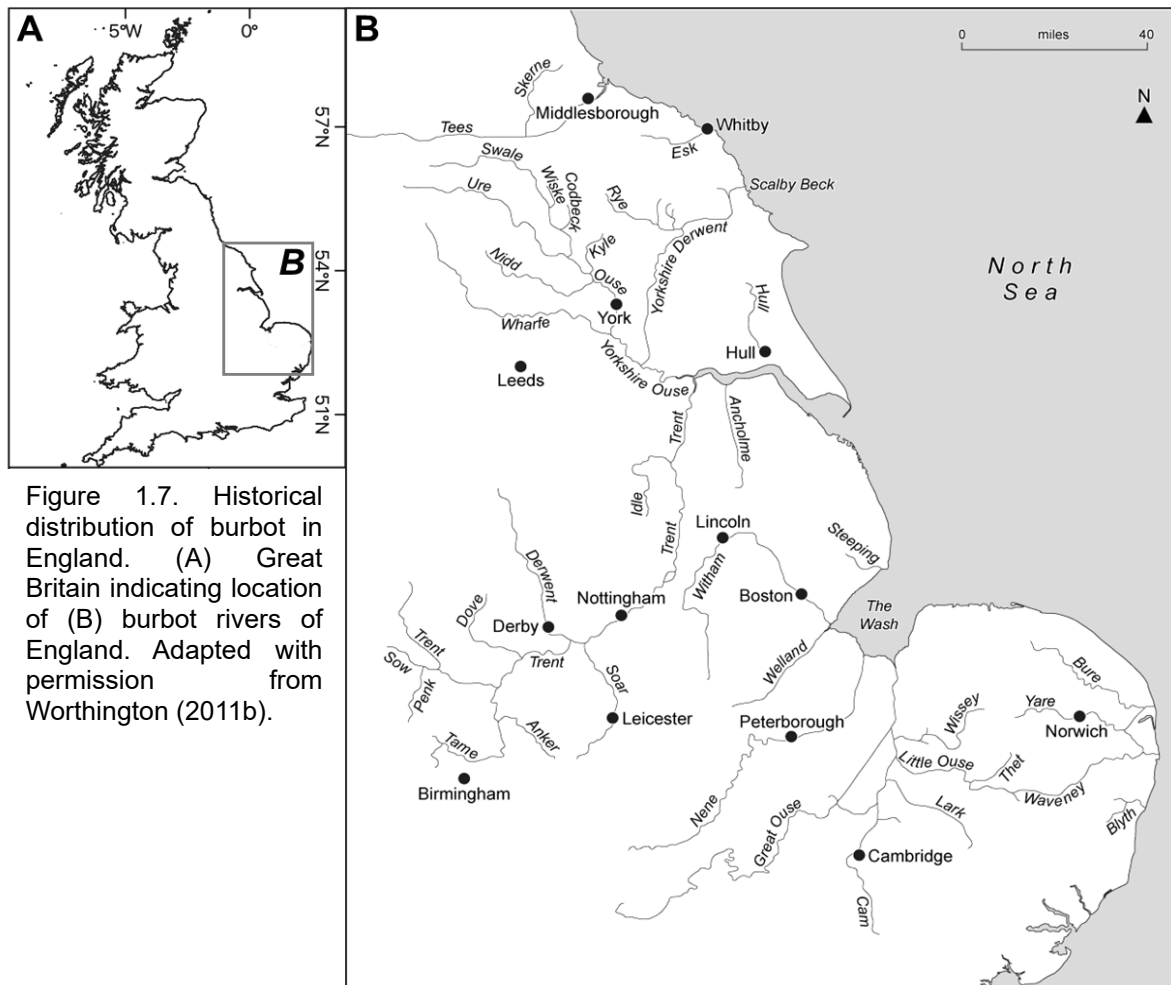


Figure 1.7. Historical distribution of burbot in England. (A) Great Britain indicating location of (B) burbot rivers of England. Adapted with permission from Worthington (2011b).

1.3.7.2. Drivers of Decline

Worthington et al. (2010) were able to establish that the decline in English burbot populations was not spatially even, suggesting that no one single cause is likely to have led to the extirpation of the burbot, but a combination of factors. The main factors identified were river modification, or habitat alteration, and some influence by anthropogenic pollution (Worthington et al., 2010a). Some other papers suggest that river temperature, and local fishing pressure also played a role (Marlborough, 1970). Overall, the English population of burbot transitioned to a negative population phase in the early 1900s, but this varies in England with the Trent catchment exhibiting the earliest decline (1894) and with the Yorkshire rivers last to go into decline in around the 1920s. Worthington (2010) details the extent of river modification of the three regions (Trent, Yorkshire rivers, Fenland rivers) with historical catches of burbot, detailing the extensive damming and widening of channels for navigation and

agriculture in the lower reaches of rivers, a pattern seen across the UK, that led to the isolation of burbot habitats and its ultimate decline.

Worthington (2010) used historical maps to identify habitat alteration (i.e. stretches of straightened river by comparing different map editions), combined with archival water quality data, and air and water temperature relationships to assess whether any factor (habitat alteration, water quality, water temperature) correlated with burbot population decline throughout its historical range, where records existed. The results showed that, when compared to changes in historical burbot population size, habitat alteration and water quality decline coincided with burbot population decline. Across England, lowland rivers have been found to be overdeepened due to historical modification, which would preclude any overtopping to create lateral connectivity (Gurnell and Downs, 2021). Habitat alteration, especially the channelisation of rivers and the construction of embankments, prevented connection between the main channel and the floodplain, reducing burbot access to necessary spawning habitats (Worthington et al., 2012). For example, there was a trend in the burbot decline linked to increases in river modification from the 1880s in the River Trent (Worthington, 2010). Overall, there are slight variations across the historical range as to when the burbot decline began and the exact driver of decline, but it is clear that habitat alteration has coincided with burbot decline throughout its historical range in England.

1.3.7.3. Towards A Burbot Reintroduction

In England, the burbot is still protected under Schedule 5 of the Wildlife and Countryside Act of 1981 and is a Biodiversity Action Plan (BAP) species, which means the British government is obliged to investigate population status and improvement opportunities (Worthington et al., 2010a). The reintroduction of the burbot would therefore, from a legal and policy perspective, be open to advancement. A reintroduction project would be foremost concerned with habitat restoration and ensuring sufficient suitable habitat for all life stages of the burbot. In turn, this will require improved longitudinal and lateral connectivity to floodplain spawning habitat. Further, a scheme with sufficient monitoring could not only fill in gaps in the species' biology and ecological niche, but research could be conducted on the potential

benefits it would bring to other species and local biodiversity. The burbot's requirements for cooler temperatures, a mixture of off-channel, shallow, lateral habitats, and in-channel, deep-water habitat, fallen-tree and woody structures and good water quality could ensure that any burbot-focused habitat restoration work would benefit many other river-floodplain species. Essentially, habitat restoration for the burbot would improve habitat heterogeneity within rivers, likely increasing aquatic biodiversity, as well as affording high quality natural flood management (Pearce et al., 2024b).

1.4. Species Reintroductions: Part of The Conservation Toolkit

Species reintroductions are increasingly applied as conservation tools. Despite the acknowledged difficulties in planning and executing these projects, species reintroductions have the potential to protect and improve biodiversity, reverse extinctions, and restore ecosystem functioning (Hale and Koprowski, 2018). Similar to river restoration, species reintroductions as a conservation tool and practice have also suffered from a series of pitfalls that can hinder the effectiveness of a project and can even result in its failure. To avoid this going forward, it is important to understand the nuance of species reintroductions, identify common causes of failure and adapt a project accordingly, being strategic when selecting a species for reintroduction. The outcome will be to maximise the benefits brought by the reintroduced species, spanning both local biodiversity and ecosystem health.

1.4.1. Defining Species Reintroductions

Species reintroductions are a form of translocation, which is simply the movement of a species from one area to another (Jachowski et al., 2016). There have been many reasons for species reintroductions: hunting; pest control; aesthetic value; wildlife rehabilitation; and for conservation objectives (Carter et al., 2017). Jachowski et al. (2016) argue that species reintroductions push beyond the traditional boundaries of conservation, which is holding the line against negative anthropogenic impacts, to returning species that were lost and restoring the ecological conditions and complexities of ecosystems in the past.

It is hard to define the success and failure of a reintroduction programme as their planning, methods, monitoring, and budget all vary so there is no standardised approach. The international framework set out by the IUCN is highly useful and regarded in this respect, however (IUCN, 2013). The most crucial aspects highlighted by the IUCN are: deciding when translocation is appropriate; release strategy including planning, site selection, and assessment; designing the post-release monitoring programme; feasibility and design to incorporate social and biological factors; risk assessments; and finally dissemination of information (IUCN, 2013). Based on unpublished data from the IUCN's Conservation Translocation Specialist Group (CTSG) only 5% of 250 recent reintroductions were classified as complete failures (Seddon and Armstrong, 2016). The CTSG state that over 1,500 species have been translocated globally (Conservation Translocation Specialist Group, 2021).

1.4.1.1. Definitions: Invasives, Exotics, Umbrellas

Species translocations or reintroductions cannot be discussed without giving insight into the many varied terms that are associated with the intentional and unintentional movement of species. The labels of “naturalised”, “non-native”, “exotic”, “alien” and “invasive” species are all linked to the movement of plants or animals by humans. As a species' population establishes, it may find a local niche and thrive while doing no harm to other species (non-native, exotic, or alien) or they may out-compete or detrimentally predate another species in the local ecosystem, causing harm (invasive) (Shine et al., 2000). Many of the species in the UK that are considered invasive were introduced in the 19th century during a period of importation of exotic species. *Rhododendron ponticum*, introduced in 1763 (Elton et al., 2020), is a popular plant in the UK due to its flowers, but it is extremely competitive and has greatly damaged native woodland habitats where it produces dense shade and where it has allelopathic effects that prevent the successful germination of native seedlings (Rotherham and Read, 1988). Muntjac deer *Muntiacus reevesi*, first imported in 1838, were brought over from Asia to be kept in private collections, but escapes have allowed a population to become widespread across England and Wales, which puts immense pressure on woodland understories (Chapman, 2021). American mink *Neovison vison* were

introduced in 1929 for the fur industry, but are now widespread, leading to a rapid decline of the water vole *Avricola amphibius*, estimated across Britain to be an 88% loss in the 1990s alone (Fraser et al., 2017). The issues that these introduced species caused were not known when they were introduced.

The interesting aspect of the aforementioned definitions related to species invasions is that the time it has taken for a species to be classified as invasive vs. non-native or exotic is variable, ultimately being driven by the emergence of harm on wildlife. An element of subjectivity can always be found around the discussion of these terms too. For example, in Brooks and Freyhof (2011), a status review of European freshwater fishes only considers fish to be native or naturalised if their presence was documented in Europe before 1500 AD. The justification for this cut-off date is not determined, but the question of time is important when considering the reintroduction of a species, even for conservation objectives. For example, can a reintroduced burbot population from a European source be classified as native despite evidence showing that the English population was a distinctive and now extinct genetic subclade of the wider European population (Worthington et al., 2017)? If so, could there ever be a point in time when the burbot could be classified as invasive in England? The last burbot catch was 55 years ago (at the time of writing) and what if, after a potential future reintroduction, it emerged that reintroduced burbot from a different clade have an unforeseen negative impact on native river biology? Could the burbot then be regarded as an invasive species, despite its native origins?

These nuanced classifications, which are also based on subjective or moveable boundaries, illustrate the importance of a thorough reintroduction scheme. Every aspect, including genetics, ecosystem interactions, disease, habitat, ecosystem services, and public perceptions must be considered and analysed. Thoroughness is particularly important when considering a fish reintroduction as Europe is vulnerable to invasive species due to the intricate network of waterways that allows invasives to spread (Nunes et al., 2015). To mitigate against risk with a reintroduction programme, the first crucial step is selecting the species to be reintroduced. With heavy investment into these programmes, it is important that maximum benefits are reaped. For

example, choosing a lost umbrella or keystone species might be crucial to restoring ecological processes, improving biodiversity, or increasing ecosystem services (Johnson et al., 2017). An umbrella species is one that, if reintroduced would benefit other multiple taxa and wider biodiversity. A keystone species would restore a lost function of the ecosystem or support ecosystem functioning throughout the trophic pathways. By selecting a species that has a crucial function or benefit to the wider ecosystem, the species reintroduction can be considered as a wider conservation tool as it takes a holistic, almost landscape-scale approach to conservation that brings maximum benefits to the environment, ecology, and people.

1.4.2. A Brief History of Species Reintroductions

While species reintroductions for conservation purposes are increasing in frequency in recent years, they have a long history. Australasia has been a hotspot for species reintroductions and has the first recorded translocations for conservation purposes: in the 1880s, large numbers of kakapo *Strigops habroptilus* and kiwi *Apteryx australis*, were moved to an offshore island marking the first attempt to protect New Zealand's native species from the impacts of exotic mammalian predators (Seddon et al., 2005). Seddon and Armstrong (2016) record a detailed history of species reintroductions, with releases of species aimed at restoring wild populations being recorded as early as the 1910s. Despite the practice's early origins, it was not until the 1960s and 70s that some successful attempts began to raise the profile of species translocations as a conservation tool. For example, in the USA, the peregrine falcon *Falco peregrinus* was subject to a captive breeding and release programme in the 1970s and this, in combination with the ban of DDT, an organochlorine pesticide, helped raise breeding pairs from ~40 in 1975 to over 1,600 pairs by 1999 (Heinrich, 2009). Another reintroduction motivated by conservation objectives was the Arabian oryx *Oryx leucoryx* in the Middle East, where the wild population was rendered extinct by the mid-1970s, except for a few individuals caught near Oman by Phoenix Zoo, Arizona. This capture, and later the reintroduction of a few individuals at Jiddat al-Harasis, Oman in 1982 (Price, 1989), has been a success in increasing the wild population to 1,100 individuals with 6,000-7,000 estimated to be in captivity (Al Rawahi et al., 2022).

Species reintroductions as a conservation methodology have had mixed results, which, as for the field of river restoration, without proper documentation of the pitfalls, has not benefitted subsequent reintroduction programmes. It was not until the 1970s that legal and scientific frameworks for reintroductions began to be implemented, with conferences being organised to discuss correct handling procedures occurring in 1977 (Temple, 1978). Eventually, in 1987, the IUCN gave a statement on species translocations (IUCN, 1987). Within a year, the IUCN's specialist group on species reintroductions had established itself (Price and Soorae, 2003), but it was not until 1995 that the IUCN's guidelines on species reintroductions became official policy (IUCN, 1998), with these updated again in 2013 (IUCN, 2013). Research and collaboration within the scientific community on species reintroductions have become more common in recent decades, and it is perhaps the slow pace of legal frameworks compared to the rate of species translocations that have hindered the effectiveness of this conservation tool, which has been learning from its own pitfalls and failures (Berger-Tal et al., 2020).

There is no doubt that, despite questionable success and limitations along the way, the popularity of species reintroductions has increased rapidly over the decades (see Fig. 2.1 in Seddon and Armstrong, 2016). While it is hard to determine whether there is a spatial bias in reintroductions (i.e., are species reintroductions higher in areas that have lost more of their native species?), there is an overwhelming taxonomic bias that may warrant further investigation into whether some regions have a trend towards certain taxa and specific motivations. In their study of 699 recent, ongoing, or planned species reintroductions from IUCN data, Seddon et al. (2005) found vertebrates to be overrepresented compared to their prevalence in nature. Specifically, mammals and birds were overrepresented, and fish were underrepresented. Interestingly, over half of the birds being reintroduced were classified as 'Least Concern' by the IUCN, suggesting that species reintroductions are driven more by national than international agendas and priorities (Seddon et al., 2005). This is due to a country only being able to operate within its legal jurisdiction, despite species distributions extending beyond borders. The selection of a species for reintroduction is crucial, which is especially the case in England, where, depending on the species in question, reintroductions have received a mixed reception from the public.

1.4.2.1. UK Species Reintroductions

One of the earliest, though unsuccessful, UK reintroduction projects was the release of large coppers butterfly *Lycaena dispar* in 1927 (Carter et al., 2017). A review of species reintroductions in the UK between the 1970s and 2016 found that there had been nine species reintroductions: five birds; one mammal; one amphibian; and two invertebrates (Carter et al., 2017).

For the birds, there were reintroductions for white-tailed eagle *Haliaeetus albicilla* (1975 – ongoing), red kite *Milvus milvus* (1989 – 2013), osprey *Pandion haliaetus* (1996 – 2005), corncrake *Crex crex* (2002 – ongoing), and great bustard *Otis tarda* (2004 – 2015) (Carter et al., 2017). The reintroduction for the white-tailed eagle was the first programme with the intent of restoring an extinct species for conservation purposes in 1975. One of the mammals to be successfully released is the Eurasian beaver, first in Devon, but now amongst many other locations reintroduction trials are being held in Norfolk, Nottinghamshire, and Scotland (Puttock et al., 2017). Attempts have been made to reintroduce the Eurasian lynx *Lynx lynx* (Hawkins et al., 2020), grey wolf *Canis lupus lupus* (Nilsen et al., 2007), and the brown bear *Ursus arctos arctos* (Wilson, 2004), but all have been denied or prevented so far.

Since the study of Carter et al. (2017), pine marten *Martes martes* have been released in the Forest of Dean (O'Hara, 2018) and wild boar *Sus scrofa* have begun to establish themselves after escapes or illegal releases by private groups (Bearman-Brown et al., 2018). The pool frog *Pelophylax lessonae* is the only amphibian to be reintroduced to the UK from 2005-2008 (Carter et al., 2017). Two of the recent invertebrates to be reintroduced are the large blue butterfly *Phengaris arion* from 1983-ongoing and the short-haired bumblebee *Bombus subterraneus* from 2012-on-going (Carter et al., 2017). In Britain, species reintroductions are decisively increasing in popularity, stemming from the progression of conservation work from intense management and single species focus, to an increasingly landscape-scale, rewilding-based approach (Pettorelli et al., 2018). Additionally, in 2023, Natural England published a UK species reintroduction case studies report, which included projects for the red skipper *Carterocephalus palaemon* butterfly, netted carpet moth *Eustroma reticulatum*,

freshwater mussel *Margaritifera margaritifera*, tansy beetle *Chrysolina graminis*, water vole *Arvicola amphibius*, and lesser bladderwort *Utricularia minor* (Wells and Heydon, 2022).

1.4.3. Benefits of Species Reintroductions

While species reintroductions should not be driven by aesthetics, more popular species with the public have the benefit of increasing public engagement with conservation work, which could be a potential source of funding (Carter et al., 2017). When species are reintroduced, their legal status can give them protections that extend to other species. For example, after the red kite was reintroduced across England and Scotland as part of a reintroduction programme beginning in 1989 it was negatively affected by lead ammunition and illegal poisoning, and as a result, policy was developed to change ammunition types and better deter illegal poison baiting (Pain et al., 2007). This not only protected the red kite population, but benefited other scavenging and predatory species also susceptible to poisoning (Smart et al., 2010).

Prior to reintroduction, a programme may require the restoration of habitat to a better quality in preparation for the new species, which not only improves habitat integrity and quality, but extends benefits to other species in that habitat. For example, the reintroduction of the short-haired bumblebee to south-east England required improved management of 850 ha, which also benefited the rare shrill carder bee *Bombus sylvarum* (Brown et al., 2017). In the UK, where habitats are extremely fragmented (Jones et al., 2019; Razzaque and Lester, 2021), species reintroductions can help a sensitive species re-colonise and establish a self-sufficient population. To achieve this, the habitat must be researched in exceptional detail encompassing geology, geomorphology, existing ecological interactions and niches, chemical aspects, and local hydrology and climate, to identify suitable areas and those to be improved. This approach is often large in scale, encompassing multiple habitats and biotopes, which extends scientific understanding and eventual protections to multiple species beyond the reintroduction species.

1.4.4. The Challenges and Limitations of Species Reintroductions

Species translocations are often expensive, require extensive planning, and are complex, as each species has its own requirements for survival, making it a hard procedure to standardise (Carter et al., 2017). The complexity of species reintroductions means that there are obstacles that can seem insurmountable when there are budgetary and time restraints. Nevertheless, common pitfalls have emerged, which can help to improve the chances of success of future projects if better disseminated. During an analysis of the IUCN's *Global Reintroduction Perspective Series*, Berger-Tal et al. (2020) analysed 293 species translocation studies for common difficulties faced by project implementers. They identified over 1,200 difficulties, reflecting how each species' reintroduction faces its own unique challenges as a product of individual species' requirements, project design, and available resources. It was concluded that the key pillars of reintroduction success are having good quality release habitat, understanding the species' biology and behaviour, and having an efficient monitoring programme for post-release observations. The study also further illustrates the taxonomic bias in species reintroductions, as across the six volumes of the *Global Reintroduction Perspective Series*, of the 293 animal translocations, 28 were invertebrates, 35 fish, 20 amphibians, 37 reptiles, 66 birds, and 106 were mammal translocations, emphasising the taxonomic bias toward birds and mammals once more. While the most common pitfalls are evidenced, the severity of each issue and how much its occurrence can impact a project was still not understood (Berger-Tal et al., 2020).

Another concern presented by species reintroductions is disease risk. This is not only concerned with reintroduced species introducing or helping to spread new diseases in the environment, but also whether there are any pathogens or parasites that will prevent it from surviving in its new environment (Carter et al., 2017). Overall, conservation-based species translocations are regarded as a minimal threat in the spread of disease compared to invasive species, but it is still important to contemplate this risk when planning species reintroductions (IUCN, 2013). Further, other challenges species reintroductions must overcome are public attitudes towards the candidate species. For example, the first attempts to reintroduce the Eurasian Lynx to

the UK were a failure and have been hindered ever since because not enough time was invested in researching public attitudes (Hawkins et al., 2020). The main pitfalls large predator reintroductions must overcome are perceived worries about public safety and the larger obstacle of conflict with agriculture as farmers often fear that larger predators will impact their livestock (Wilson, 2004).

An increasingly prevalent challenge in managing species reintroductions is climate change (Pearce-Higgins et al., 2015). Carter et al. (2017) argue that, in combination with extensive habitat fragmentation and anthropogenic pressures, an increasing number of species will require human assistance as the climate changes. This need is reflected in the development of a new sub-section in the IUCN guidelines (2013), including 'assisted colonisation' and 'ecological replacements', suggesting species will have to be moved to ensure their long-term survival and to find a replacement species for those that are likely to be lost as the climate changes (Seddon and Armstrong, 2016). With air temperature set to increase across the UK and precipitation patterns less certain, these methods might become increasingly popular in UK conservation in the future (Carter et al., 2017).

The fragmented UK landscape, combined with an extensive agricultural influence, and growing urban areas, make the UK a challenging landscape for any sensitive species to survive. It has been estimated that the UK has only 50.3% of its former biodiversity left (Hudson et al., 2017). These obstacles mean that reintroduction programmes must take a landscape-scale approach, which, while being extremely beneficial, is more complex to implement and manage as there are many factors that could have a negative effect on a population as the ecosystem is intrinsically linked with the surrounding environment, especially in hydrological ecosystems. Landscape fragmentation also hinders the mobility of mammals, reptiles, and amphibians (Kolozsary and Swihart, 1999; Fischer and Lindenmayer, 2007; Edgar et al., 2010). Importantly, fragmentation also extends to aquatic environments as a recent study found that rivers in Great Britain have on average one barrier (e.g., weir, dam, lock, etc.) per 1.5 km, suggesting that only 1% of rivers in England, Scotland, and Wales are free from artificial barriers (Jones et al., 2019).

Ultimately, a species reintroduction project is complex due to its many moving parts. The planning stages involve research into the species itself and must produce a thorough understanding of its life history and genetics (IUCN, 2013; Cochran-Biederman et al., 2015). Investigations into candidate reintroduction areas must also be thorough considering all aspects of current established life history and potential future change (IUCN, 2013). Moreover, this must be repeated beyond the initial reintroduction site throughout its natural range to meet the reintroduction goals of a self-sustaining population. Planning stages must also consider social and economic factors including public perceptions, community engagement, funding, and post-release monitoring (Worthington et al., 2010b; IUCN, 2013). Implementation requires the investment of rearing and breeding facilities before individuals can be released (Vught et al., 2008). Releases must continue for multiple years to produce mixed-age population dynamics, increasing genetic heterogeneity within the population, and to supplement the population until natural recruitment and self-sustainment is achieved. Prior to and following releases, monitoring must be undertaken every year to understand how the reintroduced population is impacting the local ecology as well as its own population health and dynamics (emigration, immigration, death, birth) (Robert, 2009). Due to the many steps involved, reintroductions can quite often fail. Thus, it is important to build the knowledge and evidence base prior to any releases to increase the chance of success.

1.4.5. Fish Reintroductions

Freshwater ecosystems support 43% of described fish species (Grosberg et al., 2012), with freshwater fish having higher extinction rates than many terrestrial taxa (Ricciardi and Rasmussen, 1999), yet freshwater habitats are persistently stressed by anthropogenic pressures and climate change (Cochran-Biederman et al., 2015). From published studies, Cochran-Biederman et al. (2015) identified 260 fish reintroductions, distinguished by species, location, or method, from 1989 to 2013. They found that North America had 75% (194) of the cases identified and that most cases were for riverine fish (60%). Table 1.3 summarises a further 65 fish reintroductions, some previously unidentified by Cochran-Biederman et al. (2015) and other studies published from 2014 to 2024. Common fish conservation strategies are habitat

Table 1.3. Additional fish translocations unmentioned by Cochran-Biederman et al. (2015) and those from 2014 - 2024.

Species Name	Common Name	Location	Year	Source
<i>North America</i>				
<i>Oncorhynchus tshawytscha</i>	Chinook salmon	McKenzie River, USA	Since 1996	Banks et al. (2014)
		Lookingglass Creek, USA	Since 2001	Nuetzel et al. (2023)
<i>Oncorhynchus nerka</i>	Okanagan sockeye salmon	Skaha Lake, USA-Canada Border	Since 2015	Blanchet et al. (2022)
<i>Empetrichthys latos</i>	Pahrump poolfish	Springs Preserve, USA	2018	Saumure et al. (2021)
<i>Moapa coriacea</i>	Moapa dace	Muddy River, USA	Since 2008	Syzdek et al. (2021)
<i>Gasterosteus aculeatus</i>	Three-spined stickleback	Mountain Lake, USA		Young (2018)
<i>Cottus cognatus</i>	Slimy sculpin	Driftless Region streams, USA	Since 2003	Huff (2013)
<i>Oncorhynchus mykiss aquilarum</i>	Eagle Lake rainbow trout	Eagle Lake, USA	Long-term	Carmona-Catot and Moyle (2013)
<i>Oncorhynchus clarkii lewisi</i>	Westslope cutthroat trout	Cherry Creek, USA	Since 1997	Kruse et al. (2013)
<i>Oncorhynchus virginalis</i>	Rio Grande cutthroat trout	Rio Grande River, USA	Since 1998	Kruse et al. (2013)
<i>Noturus baileyi</i>	Smoky madtom	Little Tennessee River, USA	Since 1986	Shute et al. (2005)
<i>Noturus flavipinnis</i>	Yellowfin madtom	Upper Tennessee River, USA	Since 2003	Shute et al. (2005)
<i>Salvelinus confluentus</i>	Bull trout	Yakima River, USA	Since 2018	Hayes and Banish (2017)
		Glacial Lake National Park, USA	Since 2014	Downs and Fredenberg (2016)
		Clackamas Basin, USA	Since 2013	Barrows et al. (2016)
		Wallowa River, USA	1997	Whitesel et al. (2022)
<i>Fundulus sciadicus</i>	Plains topminnow	Great Plains, USA	2014 - 2016	Schumann et al. (2017)
<i>Atractosteus spatula</i>	Alligator gar	Western Kentucky, USA	2009 – 2014	Richardson (2015)
<i>Scaphirhynchus platyrhynchus</i>	Shovelnose sturgeon	Bighorn River, USA	1996 – 2020	Hogberg et al. (2021)
<i>Xyrauchen texanus</i>	Razorback sucker	San Juan River, USA	Since 2000	Diver et al. (2021)
<i>Meda fulgida</i>	Spikedace	Blue River, USA	2012 - 2016	Hickerson et al. (2021)
<i>Rhinichthys cobitis</i>	Loach minnow	Blue River, USA	2012 - 2016	Hickerson et al. (2021)
<i>Gila robusta</i>	Roundtail chub	Blue River, USA	2012 - 2016	Hickerson et al. (2021)
<i>Coregonus hoyi</i>	Bloater	Lake Ontario, Canada	2012 - 2020	Weidel et al. (2022)
<i>Salmo salar</i>	Atlantic salmon	Inner Bay of Fundy, Canada	Since 2015	Bryson et al. (2022)
<i>Coregonus huntsman</i>	Atlantic whitefish	Anderson Lake, Canada	2005 - 2012	Bradford et al. (2015)
<i>Moxostoma hubbsi</i>	Copper redhorse	Rivière Richelieu, Canada	2004 - 2018	Lamothe et al. (2019)
<i>Acipenser transmontanus</i>	White sturgeon	Upper Fraser River, Canada	Since 1990	Lamothe et al. (2019)
<i>Oceania</i>				
<i>Galaxias fuscus</i>	Barred galaxias	Victoria, Australia	2010	Ayres et al. (2009)
<i>Galaxias pedderensis</i>	Pedder galaxias	Tasmania, Australia	1991 - 2007	Chilcott et al. (2013)
<i>Paragalaxias mesotes</i>	Arthurs paragalaxias	Tasmania, Australia	2004 - 2013	Lintermans et al. (2015)
<i>Galaxias auratus</i>	Golden galaxias	Tasmania, Australia	1996 - 1998	Hardie (2003)
<i>Gadopsis bispinosus</i>	Two-spined blackfish	Australian Capital territory, Australia	2004 - 2006	Lintermans et al. (2015)
<i>Gadopsis marmoratus</i>	River blackfish	South Australia	2011	Hammer et al. (2013)
<i>Macquaria australisica</i>	Macquarie perch	New South Wales, Australia	1987 - 2014	Lintermans et al. (2015)

Table 1.3. Continued...

		Australian Capital territory, Australia	Since 2006	Lintermans et al. (2015)
		Victoria, Australia	Since 1990	Lintermans et al. (2015)
<i>Tandanus tandanus</i>	Freshwater catfish	Victoria, Australia	1998 - 2008	Lintermans et al. (2015)
<i>Maccullochella ikei</i>	Eastern freshwater cod	New South Wales, Australia	1989 - 2003	Nock et al. (2011)
<i>Maccullochella mariensis</i>	Mary River cod	Queensland, Australia	1983 - 2011	Lintermans et al. (2015)
<i>Ambassis agassizi</i>	Olive perchlet	New South Wales, Australia	2010 - 2014	Lintermans et al. (2015)
<i>Melanotaenia eachamensis</i>	Lake Eacham rainbowfish	Queensland, Australia	1989	Lintermans et al. (2015)
<i>Melanotaenia sp.</i>	Running River rainbowfish	Running River, Australia	Since 2015	Moy et al. (2018)
<i>Melanotaenia sp.</i>	Malanda rainbowfish	North Johnstone River, Australia	2016	Moy et al. (2021)
<i>Nannoperca obscura</i>	Yarra pygmy perch	Murray-Darling Basin, Australia	2011 – 2018	Beheregaray et al. (2021)
		South Australia	2011 - 2012	Hammer et al. (2013)
<i>Nannoperca australis</i>	Southern pygmy perch	Murray-Darling Basin, Australia	2008, 2011–2018	Beheregaray et al. (2021)
		South Australia	2008, 2011 - 2012	Hammer et al. (2013)
<i>Craterocephalus fluviatilis</i>	Murray hardyhead	Lodden River system Victoria, Australia	2012 – 2014	Stoessel (2012)
<i>Mogurnda adspersa</i>	Southern purple-spotted gudgeon	New South Wales, Australia	2003 - 2008, 2011	Lintermans et al. (2015)
<i>Galaxias fasciatus</i>	Banded Kokopu	Kaiwharawhara stream, New Zealand	Prior to 2015	Pham et al. (2016)
<i>Galaxias argenteus</i>	Giant Kokopu	Nukumea stream, New Zealand	Since 2009	Franklin and Baker (2016)
<i>Europe</i>				
<i>Umbra kramera</i>	European mudminnow	Szada, Hungary	Since 2008	Bajomi et al. (2013)
<i>Alosa alosa</i>	Allis shad	Rhine system, Netherlands, Germany, France	Since 2003	Beeck et al. (2008)
<i>Aphanius iberus</i>	Spanish toothcarp	Valencia, Spain	Since 1992	López and Mata (2008)
<i>Misgurnus fossilis sp.</i>	European weatherfish	Rhineland-Palantinate and Hesse, Germany	2014 - 2016	Schreiber et al. (2018)
<i>Cottus rhenanus</i>	Rhine sculpin	North Rhine-Westphalia, Germany	2015 - 2020	Hempel et al. (2020)
<i>Chondrostoma nasus</i>	Nase	River Lahn, Germany	2014 - 2015	Wetjen et al. (2020a)
<i>Acipenser oxyrinchus</i>	Sturgeon	Gulf of Riga, Latvia	2013 - 2015	Purvina and Medne (2018)
<i>South America</i>				
<i>Zoogoneticus tequila</i>	Tequila splitfin	Teuchitlán River, Mexico	Since 2012	Domínguez et al. (2018)
<i>Notropis boucardi</i>	Morelos minnow	Barranca de Chapultepec streams, Mexico		Contreras-MacBeath et al. (2016)
<i>Asia</i>				
<i>Oncorhynchus masou formosanus</i>	Formosan landlocked salmon	Shei-Pa National Park, Taiwan	Since 1992	Wu et al. (2008)
<i>Puntius bandula</i>	Bandula barb	Kegalle district, Sri Lanka	2001	Soorae (2003)
<i>Pseudopungtungia nigra</i>	Black shinner	Gapcheon, Ungcheoncheon Streams, Korea	Since 2000	Kim et al. (2023)

restoration, removal of invasive species, and stocking (Cochran-Biederman et al., 2015); however, reintroductions are becoming an increasingly popular tool for freshwater fish conservation. Due to the complexity of aquatic systems, additional guidelines beyond the IUCN's have been developed (George et al., 2009). Despite an underrepresentation in reintroduction programmes on a global scale, fish reintroductions have been extensive enough to allow for a review of best practice and of pitfalls.

In North America, fish reintroductions are common practice for conservation and recreational objectives. The south-east United States has undertaken several successful freshwater fish reintroductions, such as lake sturgeon *Acipenser fulvescens* in the 1990s and barrens topminnow *Fundulus julisia* in the 2000s, both in Tennessee, with continuing success attributed to the importance of providing education opportunities to the public where possible (George et al., 2013). They state that treating species reintroductions as a long-term investment or programme instead of a temporary project, will allow the public to become invested, which builds trust for subsequent species reintroductions. This is a lesson that the UK can learn from, as some reintroduction programmes have either neglected the public or focused on local area only.

Across Europe, 37% of freshwater fish are threatened and translocations have become an increasingly popular tool (Tatár et al., 2017). While there is no current review of fish reintroduction projects in Europe specifically, there are several success stories to learn from, as summarised in Table 1.3. A reintroduction programme in Rhineland-Palatinate and Hesse, Germany for the European weatherfish *Misgurnus fossilis* reported short-term reintroduction success, which reflected the appropriateness of their considerations of stocking strategy and habitat assessments (Schreiber et al., 2018). A reintroduction project for bleak *Alburnoides bipunctatus* in central Germany used eDNA monitoring and successfully detected the species at all reintroduction sites, reflecting its potential usefulness as an inexpensive monitoring tool in the future (Riaz et al., 2020). In the Carpathian Basin, Hungary, a combination of translocation, captive breeding, restocking, and reintroduction was used to help the

endemic European mudminnow *Umbra kramera* under pressure from habitat loss and invasive species (Tatár et al., 2017).

Under the Fish Recovery Programmes run by the Belgian government, several fish species have been successfully reintroduced using a combination of captive breeding and restocking, including the burbot (Dillen and Vlietinck, 2008). INBO implemented the reintroduction which required several distinct stages: brood stock selection, rearing burbot under hatchery conditions, habitat suitability and site selection, release strategy over time, and post-release monitoring. The reintroduction programme was nationally funded, allowing for the application of extensive fieldwork and computational modelling. Based on their research the Bosbeek and Grote Nete were selected as candidate reintroduction sites for burbot (Dillen et al., 2008b). The main field work was conducted by a team between 2002 – 2004 (Dillen et al., 2005) with 200,000 larvae reintroduced into the rivers in 2005 (Dillen et al., 2008b).

After almost 10 years, reintroduction efforts were concentrated on the Grote Nete as evidence of natural recruitment had only been found there. Electrofishing data from INBO's Fish Information System (<https://vis.inbo.be>), which compiles all fish surveying data show burbot have been observed in the Grote Nete and throughout Antwerp since 2006 (Table 1.4). Fig. 1.8. shows catch data from INBO's burbot-targeted adult, juvenile, and larvae surveys in the Grote Nete from 2007 to 2023. The reintroduction in the Grote Nete recorded its first evidence of natural recruitment in 2010 with the capture of one juvenile fish (Van den Neucker et al., 2010a). In the following years the presence of larvae in the Asbeek (and later Heiloo) side channel also evidenced natural recruitment in 2014, 2015 and 2016 (Vught et al., 2015; Pauwels et al., 2016; Vandamme et al., 2017). Stocking continues in the lower areas of the Grote Nete, but stocking ceased from 2017 above Hoolstmolen. The mill at Hoolstmolen prevented any upward migration and above the mill was the site (Asbeek) where larvae had previously been found. In August 2020, 38 adult burbot were found, with 20 estimated to be three years or younger, providing the strongest evidence that burbot can reproduce naturally in the Grote Nete, albeit in small numbers (Vandamme et al., 2020).

Table 1.4. Electrofishing data for burbot catches throughout Antwerp from VIS. The Antwerp data includes the Grote Nete data. # Surveys is indicative of surveys in which burbot were caught and not total surveys in the year. Length data were not recorded for all individuals.

Year	Antwerp				Grote Nete			
	# Surveys	# Individuals	Min. Length(cm)	Max. Length(cm)	# Surveys	# Individuals	Min. Length(cm)	Max. Length(cm)
2006	1	2	9.8	42.2	2	2	9.8	17.3
2007	3	11	13	39.5	-	-	-	-
2008	-	-	-	-	4	4	30	37.5
2009	6	26	9.3	41.8	2	4	9.3	41.8
2010	2	5	13.5	36.8	-	-	-	-
2011	3	16	14.3	27.8	-	-	-	-
2012	10	172	13	35.9	2	16	16	30.2
2013	17	223	12.9	40.2	4	46	15.7	40.6
2014	8	57	12	12	5	40	12	24.4
2015	24	306	6.4	46	12	190	6.4	46
2016	5	19	NA	NA	1	8	NA	NA
2017	3	12	NA	NA	-	-	-	-
2018	4	21	11.2	22.9	-	-	-	-
2019	3	4	25.5	42.4	2	2	NA	NA
2020	5	22	5.6	33.6	5	22	5.6	33.6
2021	2	2	18.7	38.8	-	-	-	-
2022	1	9	20.4	39.5	-	-	-	-
2023	2	9	7.3	29	2	9	7.3	29

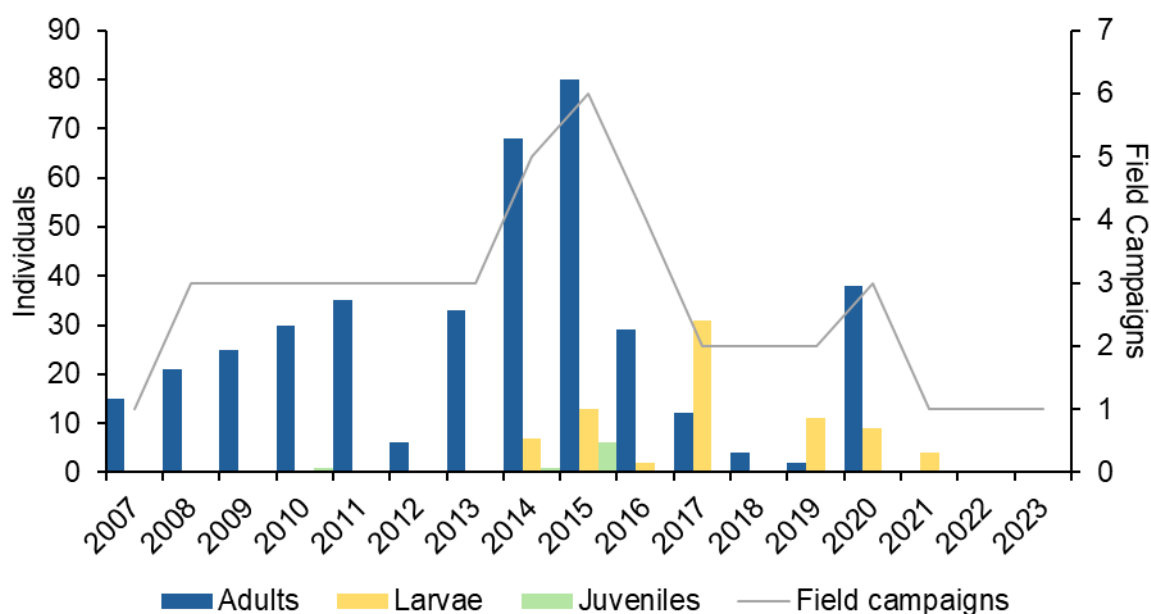


Figure 1.8. Catch data for adult, juvenile, and larval burbot from 2007 - 2023 from INBO's targeted fish research in the Grote Nete, Belgium. The number of field campaigns per year are also shown to give an indication of sampling effort.

The burbot reintroduction is not yet considered successful, however, as the low recruitment numbers suggest the population is not yet self-sustaining. The evidence of natural recruitment, however, suggests suitable habitat to allow life stage completion

is present in that area and thus would be beneficial to classify. Burbot releases have occurred in 15 rivers since 2005 (Van den Neucker et al., 2013) with the Grote Nete having the most consistent annual releases. Over this period burbot have been found in an additional 10 rivers as shown in the available VIS data, though it is uncertain if this is through their own migration.

Burbot translocations and reintroduction efforts have occurred elsewhere in Europe. Work such as floodplain restoration, artificial breeding, and stocking since the 1990s has allowed a self-sustaining population of burbot to thrive in the River Lippe, Germany (Bosveld et al., 2015). In the Netherlands, local translocations of burbot to the River Beerze occurred from 2009 to 2013 with first evidence of natural recruitment found in 2019 (Beelen et al., 2019). In general, burbot population doubling time is thought to be between 4.1 to 14 years (Beelen, 2009; Vught et al., 2015). The slow recovery time and approximate 10-year period to evidence natural recruitment observed in both Belgium and the Netherlands suggests any burbot reintroduction programme in England will require long-term investment and monitoring. Prior research, focused on the availability of suitable instream river habitats for adults, as well as wetland habitats for spawning sites, identified 20 potential areas as suitable for species reintroduction for the burbot in England, the majority being concentrated in the eastern flowing east Anglian rivers in the Great Ouse catchment (Worthington et al., 2012).

1.4.6. Considering a UK Fish Species Reintroduction

The UK has 55 species of freshwater fish, 13 of which have been introduced by humans (Maitland and Lyle, 1991). Many of the species are confined to the south and the east of the country, suggesting there is conservation importance in the southeast (Maitland and Lyle, 1991). There have been known extinctions of burbot and sturgeon across the UK, with some extinctions of whitefish populations (i.e., vendace) in Scottish lakes (Winfield et al., 2004), and currently, salmon and European eel *Anguilla anguilla* populations are declining (Butler et al., 2009; Harwood et al., 2022), thus it can be concluded that freshwater fish populations are pressured in the UK. Considering the trend in conservation and the popularity of species reintroductions for

other taxa, as well as the increasing number of river restoration projects restoring natural reaches of rivers in the UK, it is likely that fish reintroductions could become a common conservation tool in the future (Carter et al., 2017).

Before undertaking a fish reintroduction, it is crucial to understand the risks and pitfalls. When analysing the common difficulties of fish reintroductions around the globe, it was found that post-reintroduction monitoring problems were prevalent often due to a lack of funding (Berger-Tal et al., 2020). Out of a study of 260 published fish reintroductions by Cochran-Biederman et al., (2015), inadequate consideration of the cause of initial decline was found to be the common cause of reintroduction failure. This study also found that solving issues associated with habitat quality (i.e., water quality, prey abundance), followed by stocking (i.e., genetic diversity of stocking source, duration of stocking event) were the best indicators of reintroduction outcomes (Cochran-Biederman et al., 2015). A review of fish reintroduction projects in Canada for species under the Species at Risk Act (2002) found that reintroduction success relies heavily on having a comprehensive understanding of species ecology and life history, with consideration of genomics being crucial (Lamothe et al., 2019). In preparing more detailed guidelines for fish reintroductions George et al. (2009) stated that scientifically based protocols for propagation, translocation, reintroduction, and augmentation are the most important aspect of species reintroductions, which often require diverse skill sets and long-term investment from all parties involved, including collaboration and funding. Despite these requirements being the most appropriate methods to achieve successful reintroductions, they are often unattainable as reintroduction projects in the UK are spearheaded by NGOs, meaning some areas of the project are often lacking, such as scientifically robust post-release monitoring due to lack of long-term funding. Moreover, the appropriateness of applying a species reintroduction as a conservation methodology, must be considered.

IUCN (2013) guidelines state that the causes of the candidate species' historical decline must be addressed before a reintroduction can be attempted, and in the case of local extinction, this can prove sufficient in allowing a locally extinct population to re-establish itself. For example, Castañeda et al. (2020) found the eradication of an

invasive species, smallmouth bass *Micropterus dolomieu* in the Rondegat River in South Africa, allowed for the recolonisation and recovery of several endemic native fish species, such as Clanwilliam redbfin *Sedercypris calidus* over a 10-year period. This example emphasises the importance of addressing the initial cause of decline for any species reintroduction, as otherwise without the initial cause of decline addressed, the conservation objectives of the reintroduction project would not have been achieved. Therefore, in any situation, before undertaking the steps of the translocation guidelines, the appropriateness of a species reintroduction to achieve conservation goals must be evaluated because it is not the panacea of all biodiversity declines.

Thus, when considering an English burbot reintroduction, there are potential benefits and risks to consider. The burbot is a top-level predator, which can co-exist with other predatory species (Stapanian et al., 2010a), but has a ecological role in English rivers. While no ecosystem engineer, the burbot's requirements for different habitat niches across its life stage, combined with its legislative protections, would mean the active conservation of lateral and longitudinal river habitat. Considering current trends towards catchment-scale river restoration, the conservation actions for burbot are highly compatible. The risks associated with a burbot reintroduction to England are similar to other species reintroductions: economic loss if the reintroduction fails; decrease of public trust in species reintroductions generally if the reintroduction fails; and potential parasite/disease risk dependent on how the reintroduction is plan (e.g., importing adult fish could bring disease or parasites, but this could be avoided by importing eggs; J. Auwerx, pers. comms. 2023).

Overall, when analysing the literature, fish reintroductions have had varied success globally. There are, however, lessons to be learnt when considering an English fish species reintroduction: causes of original decline must be addressed and there must be adequate release habitat. Further, understanding the biology and ecology of the species to be reintroduced is paramount, as these will dictate the requirements of the habitat, shaping any pre-reintroduction work to prepare the habitat for release.

1.5. Bringing Back The Burbot

It is possible, given the success of reintroductions elsewhere, that the burbot would be a suitable candidate for a species reintroduction to England and would bring benefits to the local ecosystem and wider society. Reflecting on the fish biology and ecology, its requirements for slow-flowing water, a mixture of floodplain, backwater, shallow and deep-water habitat, various substrate and shelter opportunities, and good water quality, would provide an agenda to any river restoration project that would increase habitat heterogeneity, which would improve local biodiversity for the wider benefit of ecosystem function (Schulze and Mooney, 1994). Further, the benefits of this type of habitat restoration extend to people through improved water quality, more recreation and tourism opportunities, and at a local scale, there may be benefits to the angling community.

The burbot has a clear historical legacy in England, as indicated by the literature and archival records (Marlborough, 1970; Worthington et al., 2010a, 2017). In investigating the feasibility of reintroducing the burbot to English rivers, Worthington (2010) used the IUCN reintroduction guidelines (IUCN, 1998) as a framework. Worthington (2010) found that the key factor that caused burbot population declines was the loss of lateral connectivity to marginal spawning habitat (i.e., backwater, wetland, floodplain) due to river-floodplain habitat modification. A Population Viability Analysis showed that the key to long-term survival is persisting suitable spawning habitat (Worthington et al., 2011a). It was found, based on a genetic study of 6 preserved specimens from throughout the English historical range compared to the sequenced haplotypes of Alaskan, Beringian, Eurasian, north European, and western European burbot specimens (Worthington et al., 2017), that the western European subclade is the closest population genetically. The western European subclade is defined as those populations found from northern France, Germany, Belgium, Netherlands, up to mainland Denmark (Van Houdt et al., 2005). Moreover, considering the societal and cultural impacts of species reintroduction, which has been shown to hinder reintroduction efforts in the UK (Wilson, 2004; Nilsen et al., 2007; Hawkins et al., 2020), Worthington et al. (2010b) found ~90% of anglers, conservationists, and members of the public supported a potential burbot reintroduction. These findings, and

overall trends in societal acceptance, suggest that a reintroduction will not be met by significant public opposition and that the burbot would generally be well received by anglers.

Reversing habitat modification that has reduced lateral connectivity to ensure suitable spawning habitat is available is the most important factor in avoiding a reintroduction failure for the burbot (Cochran-Biederman et al., 2015; Berger-Tal et al., 2020). Further, considering climate change, the question of whether river temperature in England is still suitable for burbot spawning requirements is also a crucial question (McPhail and Paragamian, 2000).

Building on the work of Worthington (2010), this project will analyse the suitability of the currently most promising reintroduction site identified in the burbot's former range, the upper River Wissey, Norfolk. Thus, when considering the local habitat along the River Wissey, a number of questions remain: is there suitable and sufficient habitat for all life stages of the burbot, from floodplain spawning habitat, backwater for juveniles, and deeper, cooler water for adult burbots and where is it located? Contextually, have all causes of its initial decline, especially habitat modification and pollution as identified by Worthington (2010), been ameliorated? How does temperature vary spatially and temporally across the habitat and is it within the critical spawning temperature range for the burbot? The burbot shows resilience to pollution and thermal extremes, but with uncertainty surrounding climate change, is there any habitat with a suitable thermal regime, both diurnally and annually? Considering these results, does the burbot have a long-term future in England given potential climate change trends? Baseline data covering all aspects of the ecosystem must be established to achieve an understanding of the upper River Wissey habitat, ensuring that a future reintroduction project would not fail due to the well-known pitfalls of species reintroductions. If any barriers to reintroduction remain, there might well be potential to address these through river restoration and rewilding methodologies, hence the importance of identifying them.

1.6. Study Focus

This study focuses on assessing habitat suitability for burbot, which is evaluated from the species' biological and ecological requirements as established by the existing literature. Here, ecological requirements refer to the interactions of the species with its environment (i.e., shelter, food sources, predation pressures, swimming capacity), biological requirements relate to its internal functioning and survival needs (i.e., lethal temperature thresholds, dissolved oxygen) and habitat refers to physical qualities of the environment that relate to the needs of each burbot life, which can overlap with both biology and ecology (i.e., burbot eggs require slow flow conditions and temperatures <9°C). This study recognises that survival requirements can be both biological and ecological and by specifically stating both biological and ecological requirements it is to emphasise that this thesis is trying to ascertain beyond whether a single reintroduced burbot could theoretically survive, but whether an entire reintroduced population has potential to eventually reach a self-sustaining population, which requires the consideration of biological and ecological factors.

The burbot is threatened throughout much of its natural range, particularly in Europe (Stapanian et al., 2010a), where habitat modification has resulted in extirpation in some countries such as Belgium (at least prior to its recent reintroduction) and England (Marlborough, 1970; Maitland and Lyle, 1991; Dillen et al., 2008; Worthington et al., 2011a). In the last 20 years, conservation action has been taken across Europe to improve burbot population status.

The present research builds on prior UK and European-based research that adheres to the reintroduction guidelines (Van Houdt et al., 2005; Worthington et al., 2010a; b, 2011a; b, 2012, 2017) and the literature on reintroduction success and pitfalls (Berger-Tal et al., 2020), particularly for fish reintroductions (Cochran-Biederman et al., 2015). Further, this research applies the published literature on burbot biological and ecological requirements to assess the suitability of the currently identified, most suitable potential candidate reintroduction site, the River Wissey, Norfolk, UK. Based on prior literature, the key concerns surrounding a reintroduced population's survival

and eventual long-term persistence are the presence of sufficient habitat for each life stage, which relates to river-floodplain geomorphology and hydrology as well as water temperature. These key elements are the prime focus of this thesis.

1.7. Research Objectives

The overall aim of this research is to determine the spatial and temporal extent of suitable habitat for the burbot in the upper River Wissey system, Norfolk, UK, to support and inform a future, perhaps imminent reintroduction. To pursue this primary aim, the following research objectives were identified:

- 1) Assess the extent of suitable habitat for each life stage present within the candidate reintroduction site and contextualise habitat availability against Belgian reintroduction sites.
- 2) Determine the current and future thermal suitability of the study site considering the temperature requirements of each burbot life stage and under climate change scenarios.
- 3) Identify and assess the extent and location of suitable burbot spawning and larval habitat in terms of hydrological characteristics.
- 4) Compare hydrological, thermal, and geomorphological characteristics of the River Wissey to the survival and reproductive requirements of the burbot as established by existing literature and by comparison with extant European burbot sites.

1.8. Rationale

This thesis is organised into six chapters. Following the introduction (Ch. 1), a methodology chapter includes information on the study and study areas (Ch. 2). The methodology is followed by three data chapters, which focus on physical habitat (Ch. 3), temperature (Ch. 4), and hydrology (Ch.5). These chapters are intrinsically linked and it is the combination of all factors (i.e., physical habitat, thermal conditions, and hydrological conditions), which determine overall suitability. Though divided into individual chapters, the structure is intended to build on the findings of the last to determine suitability of the candidate reintroduction area as the thesis progresses. By

identifying the location of suitable habitat by life stage initially (Ch. 3), then applying thermal thresholds for each life stage (Ch. 4), and finally examining hydrological conditions, which are most pertinent for spawning, eggs, and larvae, (i.e., life cycle completion and thus future population stability) the thesis can conclude whether or not the candidate reintroduction site is suitable for a potential reintroduction (Ch. 6).

1.9. Thesis Structure

This study encompasses the geomorphological, hydrological, and temperature requirements of the burbot, which are explicitly linked to the species' unique biology and ecology, to present an evidence-based conclusion on the suitability of the candidate reintroduction site for a reintroduced burbot population, including consideration of its long-term persistence in the area. The thesis also recommends required river restoration actions, to increase the likelihood of reintroduction success.

The components of the thesis are interconnected, focusing on habitat, hydrology, and temperature requirements of the burbot within the upper River Wissey system (Fig. 1.9). Chapter 1 has provided a review of river modification and conservation practice, of research on the burbot with a specific focus on the western European and other European subclades, as well as a review of how species reintroductions are applied as conservation tools and the common challenges they face. Chapter 2 focuses on the study area for the PhD.

Chapter 3 uses a custom walkover river habitat survey centred on the burbot's habitat preferences across each life stage, as determined by a literature review, in combination with an *ex situ* remote sensing study of floodplain habitat. Floodplain habitat availability for burbot spawning at the River Wissey was compared to that of three burbot reintroduction sites in Belgium to contextualise the results and hence gauge the suitability of the English candidate reintroduction site (Objective 1).

Chapter 4 focuses on burbot temperature requirements across different life stages. Burbot are winter spawners that require low water temperatures for egg development and hatching success. Additionally, burbot require warmer nursery habitat during larval growth, and as adults, they have a maximum critical temperature threshold during summer (Objective 2). A network of temperature sensors was installed across the candidate reintroduction site. Sensors were placed in a variety of meso-habitats, reflective of burbot habitat preference across different life stages, to accurately assess the study site's ability to provide suitable thermal conditions. Climate projections for the region were used to contextualise the long-term suitability of the reintroduction site (Objective 2).

Chapter 5 focuses on hydrogeomorphology as related to the burbot's ecology. Burbot commonly use inundated floodplains as spawning habitat, so the location, extent, and duration of suitable floodplain spawning habitat was determined for the study area (Objective 3). A network of water depth sensors, in conjunction with a flow meter, were deployed to collect information on floodplain inundation and instream flow characteristics that lead to sufficient floodplain inundation for potential burbot spawning as well as nursery conditions for larval rearing. Ground data were used to determine minimum flow requirements that will support burbot spawning based on biological and ecological requirements established in the literature. Once minimum flow requirements were determined, a comparison with historical hydrological data from the area were used to determine the current frequency of successful spawning events.

The final chapter (Chapter 6) critically reflects on the overall aim of the study and, based on the findings of the data chapters, discusses the suitability of the study site for a reintroduced burbot population both today and in the future (Objective 4). The chapter suggests conservation actions to support the reintroduction and to strengthen the scientific basis to support evidence-based decision-making. Finally, the chapter reflects on the limitations of the study before suggesting further research to address gaps in knowledge.

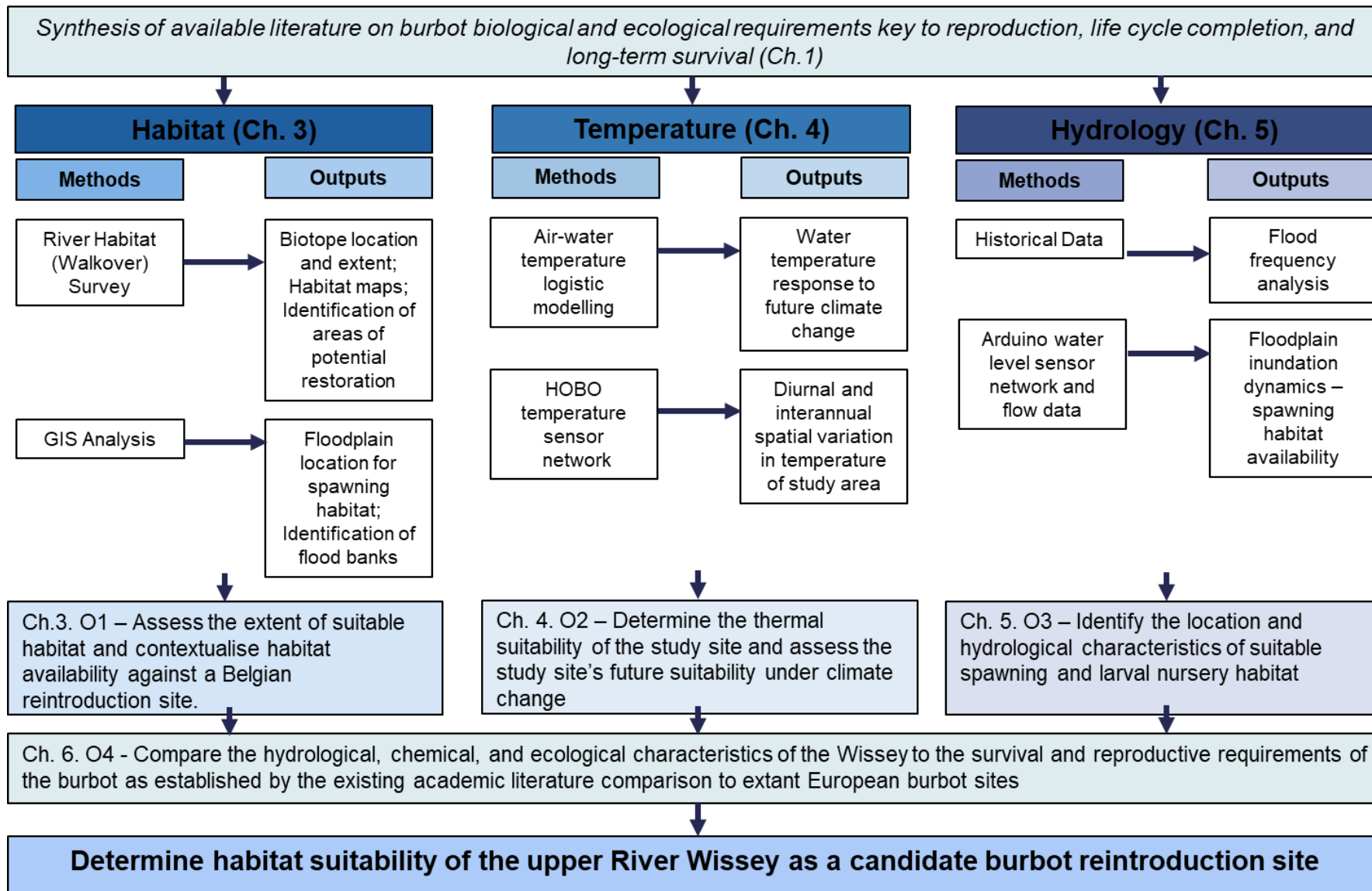


Figure 1.9. Research overview demonstrating three key data chapters and summarised methodologies applied. Ch.X refers to chapter number and OX refers to objective number.

Chapter 2. Methodology

2.1. Methodological Approaches

For Chapters 3-5, individual methodologies are listed within the chapters. The following chapter details the justification for selection of the candidate reintroduction site and uses secondary data to investigate biological and ecological requirements (i.e., water quality, food sources, existing fish community) that could not be included in the current thesis. To investigate this, Environment Agency monitoring data (water quality, invertebrates, fish) are used both within the study area itself (see below) and immediately upstream and downstream of the study area to consider the future of the reintroduction beyond the initial, assessed release site. Throughout the thesis, (explicitly in Ch. 3 and 4) this study draws comparisons with the Belgian burbot reintroduction that has been ongoing since 2005 to contextualise potential responses of a reintroduced burbot population. These comparative study areas and the rationale for selection are discussed here.

2.2. River Wissey - Study River Selection Rationale

The River Wissey (hereafter, Wissey) was chosen as the study area for this thesis due to published evidence for its suitability, and the ongoing activity for the burbot reintroduction at the time of this study being conducted. In the existing literature, historical evidence has shown that burbot were present in the Wissey. In particular a dried specimen from along the Wissey (exact location unknown) which dates to 1936, kept in Norwich Castle Museum (Worthington, et al., 2017) and a single specimen spotted near Northwold in 1968 during April or May (Marlborough, 1970), shows that the River Wissey is within the historical range of the burbot (Worthington, 2010). Moreover, fishing records indicate that burbot were present in the Great Ouse (the river the Wissey is a tributary of), as well as the Great Ouse's other tributaries: the Little Ouse and Cam (Worthington et al., 2010a) and in the Thet, Welney, and Old West River (Worthington et al., 2017). Hence the Wissey, as a tributary of the Ouse, is centrally located within the burbot's former eastern English range making it of high potential importance as a reintroduction site. In a previous study by Worthington et al. (2012), which investigated habitat suitability for a burbot reintroduction at catchment-

scale, they identified the Great Ouse and its tributaries as most likely to contain the most suitable habitat to support a reintroduced burbot population. A PVA was undertaken for a reintroduced burbot population into the Wissey and the only limiting factor identified was the availability of spawning habitat (Worthington et al., 2011a). A similar conclusion was reached by Worthington et al. (2012) at catchment-scale. Thus, from historical evidence and recent research, the Wissey is within the historical range of the burbot and is likely to contain the most suitable habitat for all life stages, but the availability of spawning habitat should be thoroughly assessed.

2.3. River Wissey – Study Area Selection Rationale

This project focuses on a section of the upper River Wissey, Norfolk, UK (Fig. 2.1). When discussing physical characteristics, human influences and ecological characteristics within the Wissey and throughout the catchment, any locations mentioned in the text are indicated in Figures 2.2 and 2.3 (whole catchment and study area specific locations, respectively), with grid references and site descriptions given in Appendix 1.

The Wissey is 50 km long and has a catchment area of 460 km². Elevation ranges from 60 mAOD at its source near Shipdham, meeting the Great Ouse at 3 mAOD (Petts and Bickerton, 1994). The Wissey derives its name from the town Wisbech through which it flowed before its course was altered (Blair, 2006). The Wissey is a chalk stream of high conservation importance (Petts and Bickerton, 1994), as reflected by several conservation designations in its valley including, a Valley Fen Special Area of Conservation (SAC) and a Breckland Special Protected Area (SPA), as well as a number of sites of special scientific interest (SSSIs), including the mixed interest Stanford Training Area (STANTA) SSSI, which is favourable for wet woodland, a Breckland Farmland SSSI, which is of biological interest for stone curlew *Burhinus oedicnemus*, and Hooks Well Meadow SSSI, a biological interest site due to rich fen meadow with acid fen vegetation.

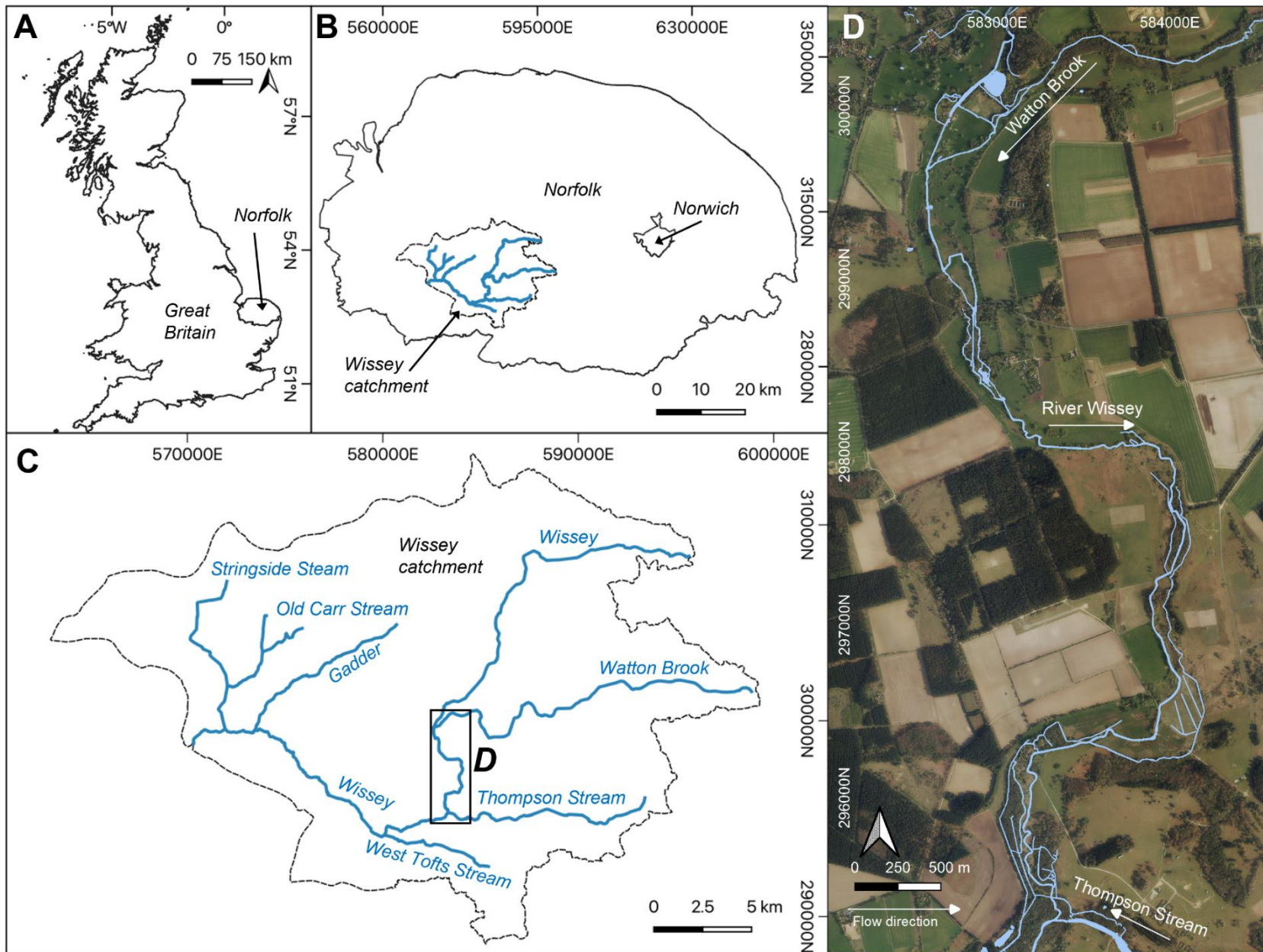


Figure 2.1. Location of Norfolk highlighting location of (B) the Wissey operational catchment from Northwold in Norfolk, highlighting (C) the River Wissey operational catchment from Northwold highlighting (D) the Wissey study area.

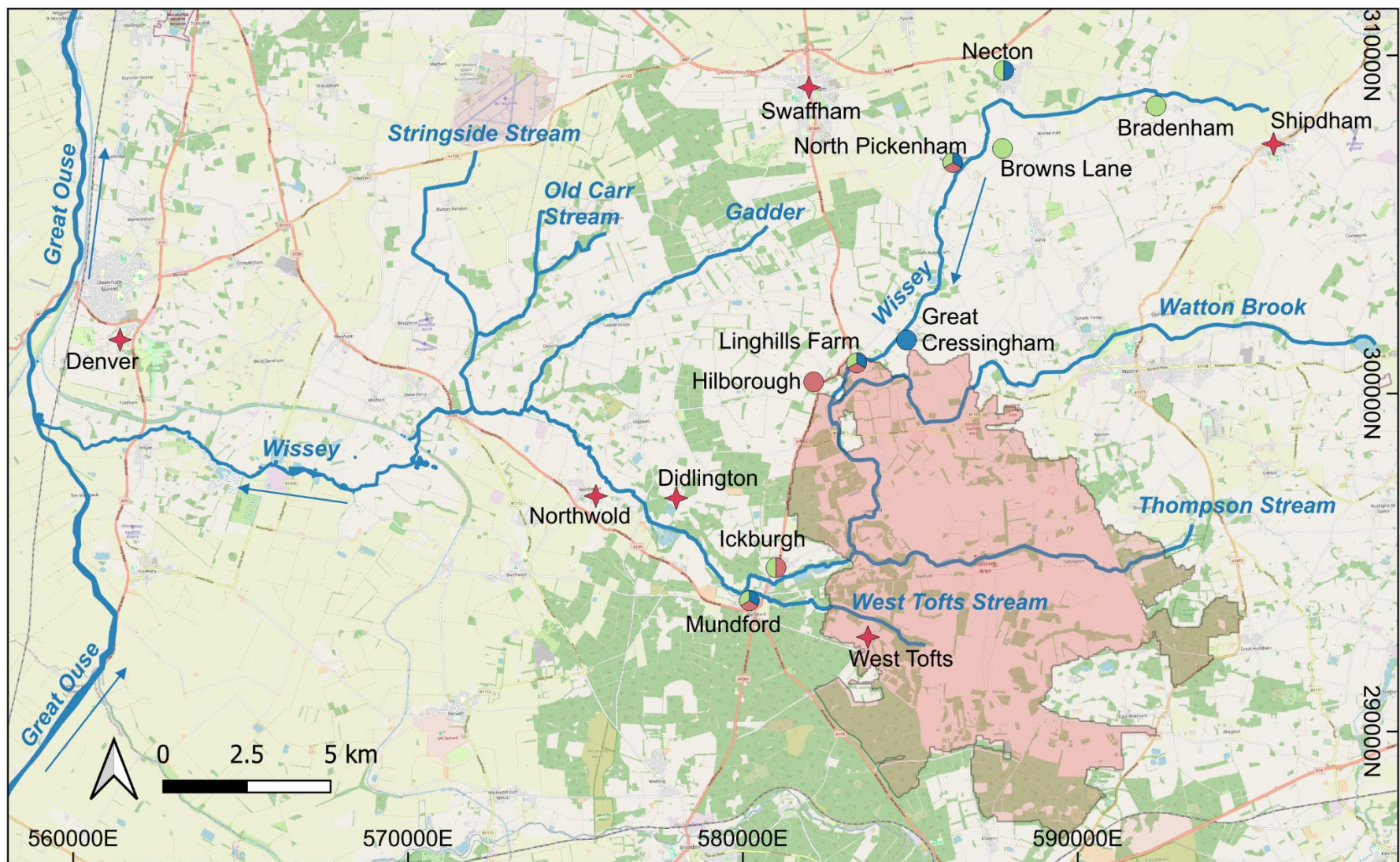
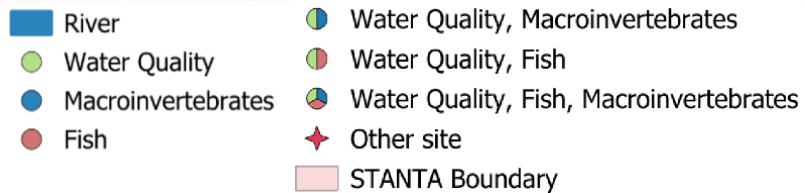


Figure. 2.2. Sites mentioned in text across the Wissey catchment. Some sites are monitoring locations for either water quality, macroinvertebrates, fish surveys, or multiple. Arrows indicate direction of river flow.



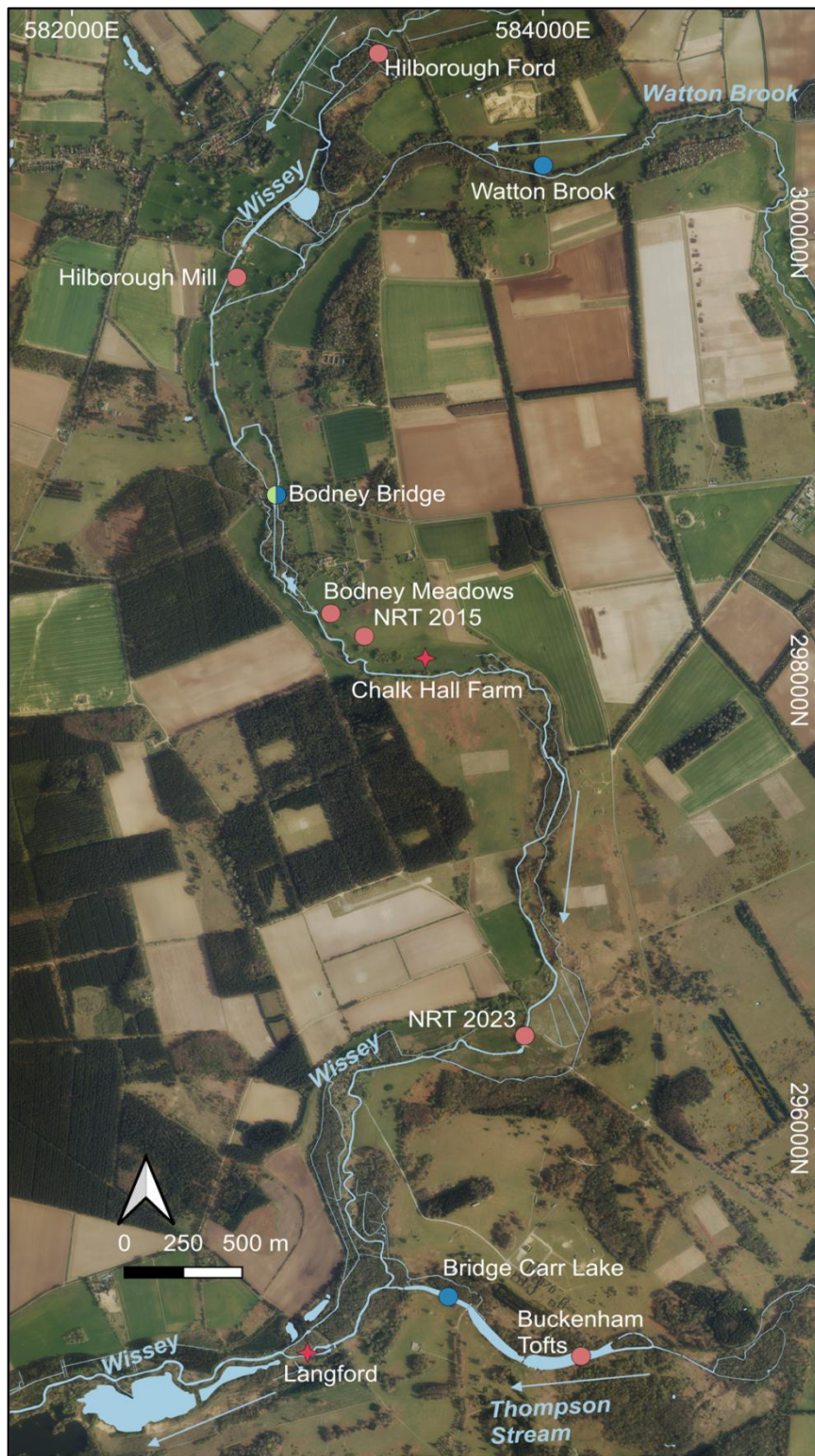


Figure 2.3. Sites mentioned with text within the Wissey study area. Some sites are monitoring locations for either water quality, macroinvertebrates, fish surveys, or multiple. Arrows indicate direction of river flow.



A review of burbot catches by Marlborough (1970) identified 28 burbot rivers. Of these, which includes the Wissey, only nine can be identified as chalk streams by the Chalk Stream Restoration Group (Rangley-Wilson and Sykes, 2021). A more recent overview of anecdotal evidence on burbot presence by Worthington et al. (2011a), identified 42 English rivers in which burbot were caught. Though burbot are clearly not dependent on chalk stream environments, the high habitat heterogeneity inherent to high quality lowland chalk streams could be advantageous to burbot due to their requirements for multiple mesohabitats across their life cycles (Worthington et al., 2012; Brackwehr et al., 2016). Part of the upper Wissey flows within the Ministry of Defence STANTA, which has protected it from excessive and major river habitat modifications (e.g., major channelisation, embankment, widening, or drainage work) as seen in other former English burbot rivers. STANTA covers 120 km², incorporating over 7 km of the Wissey (14% of the total river length) and two tributary streams: Watton Brook and Thompson Stream (Fig. 2.1). This study focuses on the STANTA area due a relative lack of human modification in this area since the 1940s. Much of the river is bordered by semi-natural grassland and woodland and a reduction in flood management has driven “rewilding” processes without intention, providing evidence for a more “hands-off” approach to conservation. Petts and Bickerton (1994: p.26) describe this sector of the Wissey [Watton confluence to Buckenham Tofts] as *“the most natural sections of the River Wissey, notably the Breckland- and woodland-bordered section through the army training area”*.

The Wissey catchment has been subject to several past studies. A query search for “River Wissey” in Google Scholar provided 159 results, including 36 studies that had specifically collected data as part of a larger study or based the entire study within the Wissey catchment. Table 2.1 categorises the field of research, the broad topic, and the author of the studies. The disciplines varied from river ecology (i.e., otters, crayfish, aquatic macrophytes) to biogeography and landscape modelling. The most substantial research is from Petts and Bickerton (1994), which investigated eco-hydraulics across the entire catchment. While this work gives an overall characterisation of how riverine habitat changes from source to mouth, habitat at fine spatial scales (i.e., < 100 m) is not quantified. Given that it is 30 years old, the Petts and Bickerton (1994) study provides a good baseline with which to compare data collected in this study.

Table 2.1. Published studies partially or fully conducted in the River Wissey, Norfolk, UK as well as their broad disciplines, topics, and sources.

Discipline	Topic	Source
<i>Biogeography</i>	Grass-heath management	Sheail (1979)
<i>Climatology</i>	Climate change impacts on rural areas	Dockerty et al. (2005)
<i>Ecology/Hydrology/Geomorphology</i>	River Wissey	Petts and Bickerton (1994)
<i>Environmental Planning</i>	Agricultural intensive areas	Lovett et al. (2003)
<i>Geology</i>	Climate change impacts on groundwater	Yusoff et al. (2002)
	Peatlands	Dawson et al. (2010)
<i>Geomorphology</i>	River habitat classification	Maddock (1994)
<i>Hydrology</i>	Chalk stream flow	Acreman and Dunbar (2010)
	Environmental flows through rivers	Neachell (2015)
	Soil erosion and runoff	Evans (2017); Boardman et al. (2019)
	Sustainable water projects	Crawford-Brown et al. (2015)
	Wetlands	Acreman et al. (2011); Herrera-Pantoja et al. (2012)
<i>Paleoecology</i>	Vertebrate assemblages	Schreve (2006)
<i>Parasitology</i>	Trematodes of <i>Talpa europaea</i>	Frankland (1959)
<i>Riverine ecology</i>	Biotopes and invertebrates	Demars et al. (2012)
	Burbot	Worthington et al. (2011a; b)
	Abstraction impacts on ecology	Bickerton et al. (1993)
	Otter	Wayre (1979); Mason and Macdonald (1993, 2004)
	Macrophytes	Demars and Gornall (2003); Demars and Harper (2005)
	Reed warbler	Batey (2018)
	Salmon spawning grounds	Milan (1994)
	Water moulds	Hunter (1975)
	White-claw crayfish	Brand (2007)
<i>Soil Chemistry</i>	Peat	Kechavarzi et al. (2010a; b)
<i>Water Chemistry</i>	Biocide impacts	Lambert et al. (2006)
	Diffuse pollution	Evans (2012)
	Phosphorous	Evans (1999)
	Thermal profiles in riverbeds	Evans et al. (1995)

For the present study, the main study area (Fig. 2.1) begins near the confluence with the Watton Brook, flowing south through STANTA to meet at a confluence with Thompson Stream (between TL 82502 99600 and TL 83326 95289). Part of the study area also extends into the Watton Brook to TF 83374 00319 (~1 km). The study area possesses river-associated habitat in the Priority Habitat Inventory (Natural England, 2020), which includes floodplain grazing marsh, calcareous grassland, lowland meadow, Calaminarian grassland, lowland heathland, lowland fen, and reedbed. Land use surrounding the study area is a combination of arable agriculture, grazed grassland (mostly unimproved), and woodland (UKCEH, 2023).

The previous in-depth hydrogeomorphological, ecological study by Petts and Bickerton (1994) provided a thorough documentation of semi-natural riverine habitat and indicated the presence of suitable burbot habitat. From the published literature on burbot habitat preference, key meso-habitat utilised across different life stages include: a geomorphological mixture of run-riffle-pool sequences, marginal and emergent macrophytes (Dillen et al., 2008a), presence of tree roots (Worthington et al., 2012), large substrate (Dixon and Vokoun, 2010), undercut banks (Dillen et al., 2008b), and “natural” river sections, unmodified by humans (Bosveld et al., 2015) that allow connection with spawning and rearing habitat such as backwaters, wet woodlands, side channels, marshes, and floodplain meadow (Worthington, 2010; Brackwehr et al., 2016). More recently, the Wissey has also undergone river restoration to improve habitat quality. Below Bodney, 4.8 km of the Wissey was renaturalised via large woody piece addition and increasing lateral connectivity (Norfolk Rivers Trust, 2015). While around Great Cressingham, approximately 5.7 km of river had been reprofiled (Norfolk Rivers Trust, 2018). Both actions are likely to have been beneficial in improving conditions for fish, including burbot, though no post-project appraisals are available so this cannot be confirmed.

In summary, the study area for this thesis was selected for study and as a potential burbot reintroduction site due to its previously evidenced and currently suspected high environmental and ecological quality and its location within the natural historical range of the burbot.

2.4. The River Wissey Catchment: Physical Characteristics

2.4.1. Climate

The closest, open-source weather station in the Met Office MIDAS Open: UK Land Surface Stations Data is at Denver (TF 59162 00899) (Met Office, 2023), which is 1.88 km from where the Wissey joins the River Great Ouse, approximately 23 km from the uppermost part of the study site. Overall, from the dataset on daily maximum and minimum air temperature for Denver, averaged monthly maximum and minimum air temperatures (1979 – 2022) show a slight warming trend (Fig. 2.4). The data show that the month with the highest average maximum air temperature is August (22.27°C), with the maximum daily air temperature recorded (during the timeframe of this study) being 37.4°C on 20th July 2022. The month with the lowest average minimum temperature is January (1.08°C). The lowest daily minimum temperature recorded was -15.5°C on 11th February 2012. Average daily minimum and maximum temperatures for the Denver data (1979 – 2022) for the accepted burbot spawning period determined by the literature (i.e., November to March) (McPhail and Paragamian, 2000) are given in Fig. 2.6. This shows a large diurnal temperature range during the winter period (average difference of 5.9°C in January) with average daily maximum temperatures between 8 to 10°C during the coldest months.

2.4.2. Precipitation

Daily total rainfall (mm) data obtained from the National River Flow Archive (UKCEH, 2023) from the closest monitoring station to the study site at Northwold (TL 771 965, Station ID: 3306), approximately 6.59 km downstream from the bottom of the study area. Data from this gauge, spanning 1956 - 2017 showed average annual rainfall to be 685 mm. Maximum average monthly rainfall was in November (66 mm), and minimum average monthly rainfall was in February (43 mm).

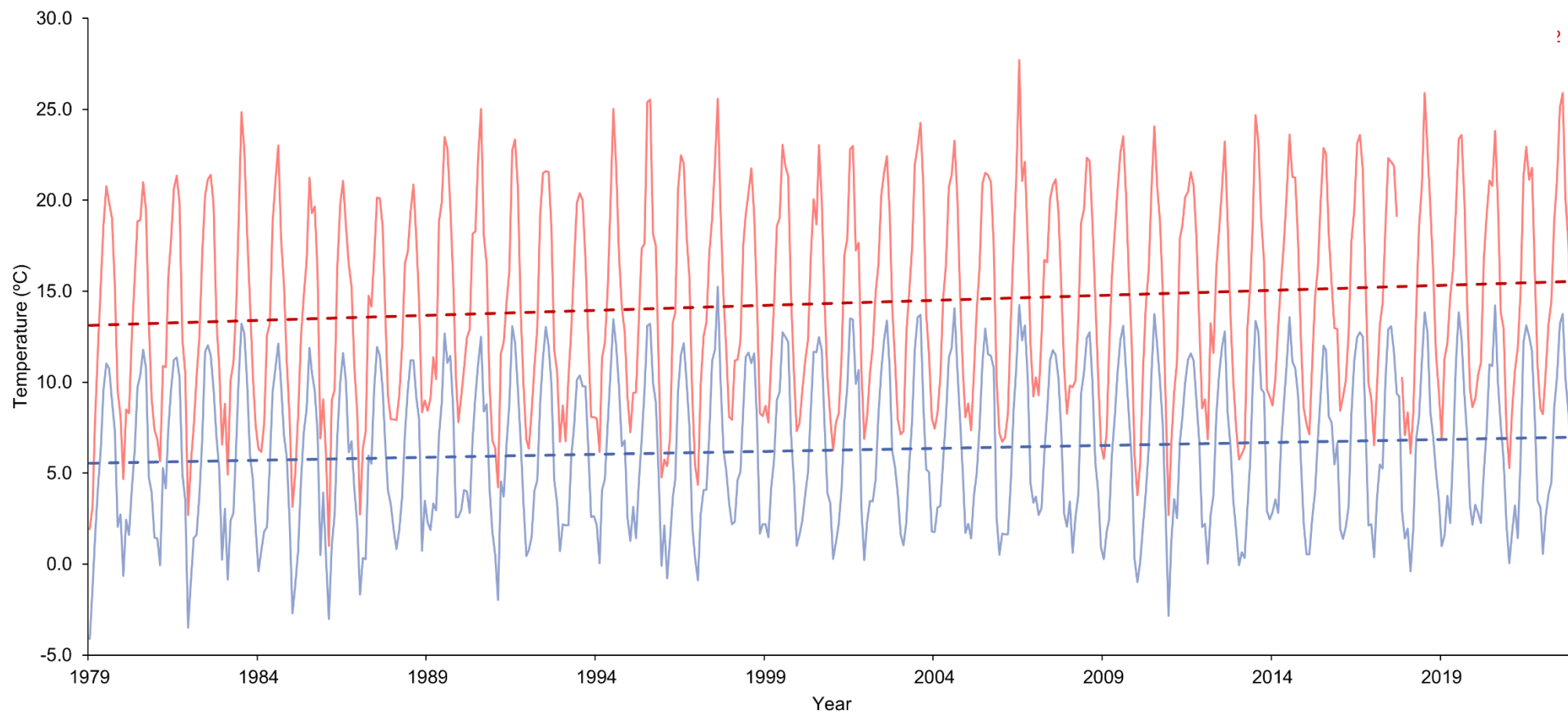


Figure 2.4. Monthly maximum (red) and minimum (blue) air temperature from Denver (TF 59162 00899) 1979 – 2022 with linear trendlines.

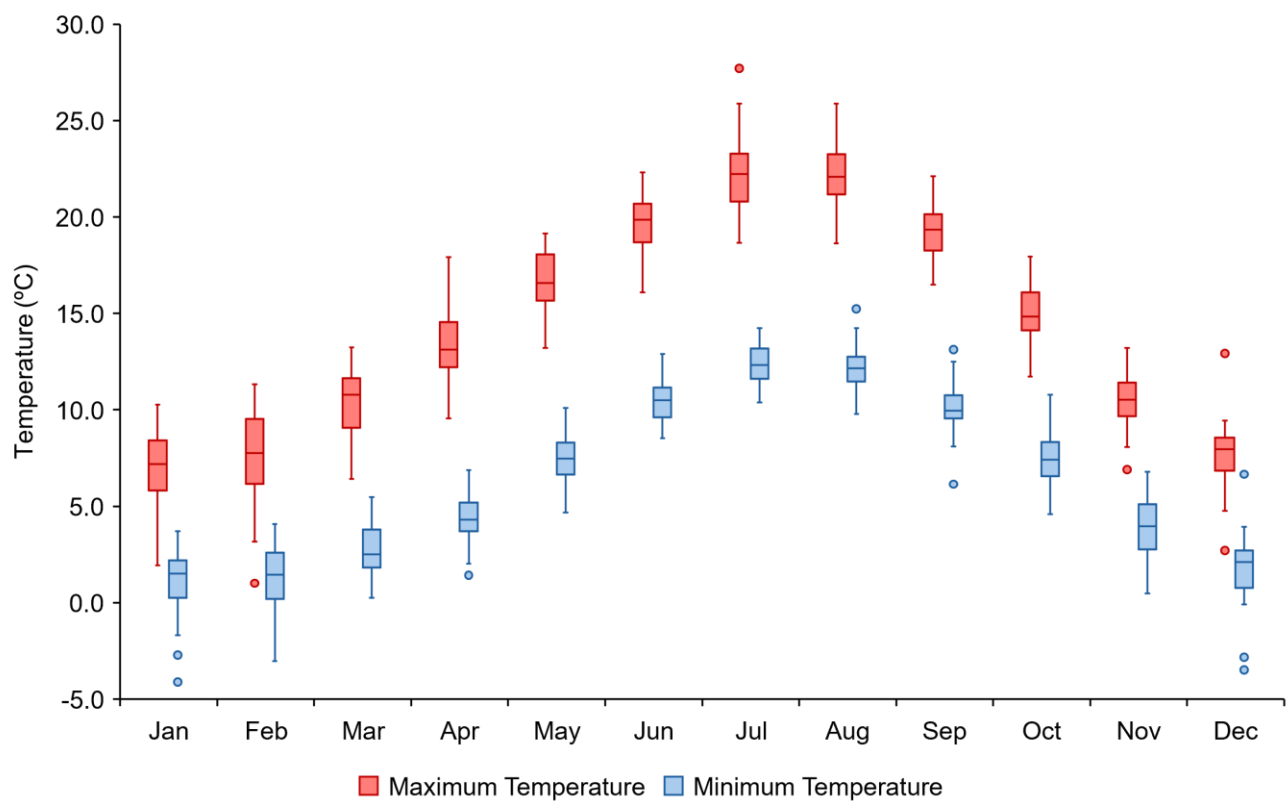


Figure 2.5. Monthly averages of daily maximum and minimum air temperature at Denver (TF 59162 00899) 1979 – 2022.

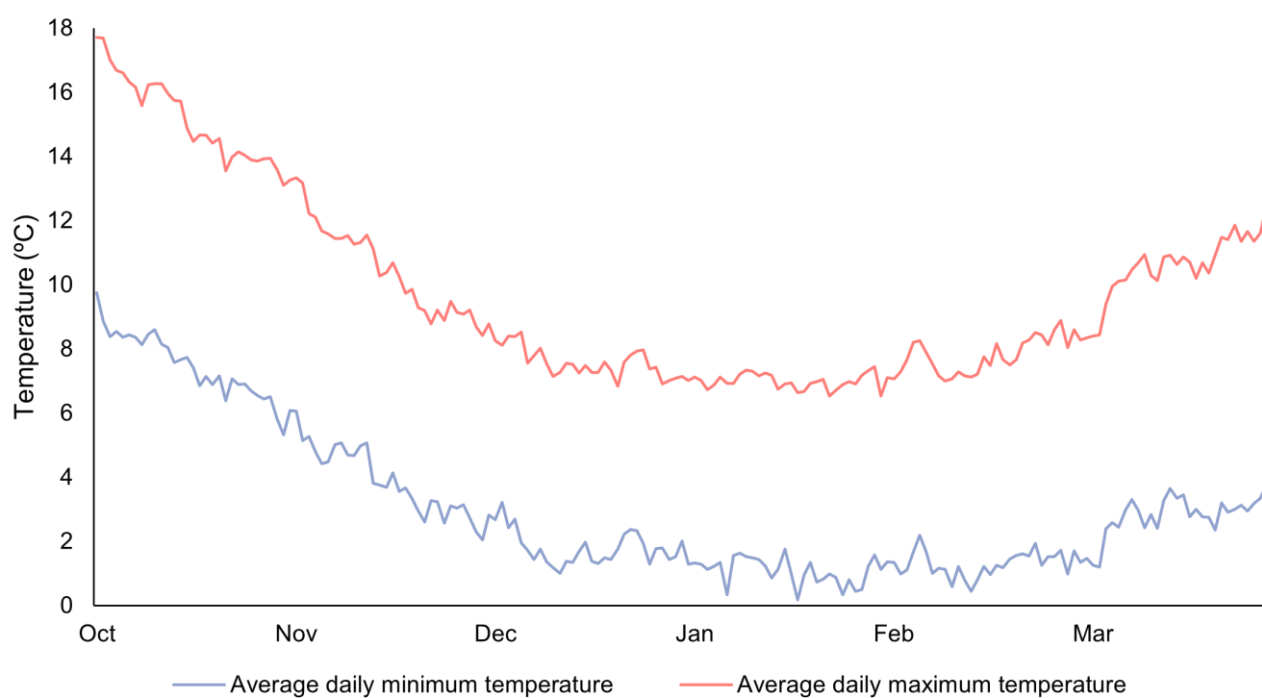


Figure 2.6. Average daily maximum and minimum air temperature from Denver record (TF 59162 00899) 1979 - 2022.

Comparatively, daily summed rainfall data from 1974 – 2022 from Denver, recorded average annual rainfall as 600 mm, with maximum and minimum monthly rainfalls of 59 mm (October) and 38 mm (April), respectively. From the rainfall and temperature record at Denver, in corroboration with climatological data from the region, there are 15 drought periods in the record, varying from seasonal dry spells (e.g., summer 2018) to extreme drought years (e.g., 1976 and 1995 – 1998). Table 2.2 provides a summary of temperature and rainfall data for drought years compared to an average wet year for Denver. For the period 1956 – 2017 daily rainfall data from Northwold (UKCEH, 2023), show low monthly variability. Monthly rainfall data could be obfuscating more short-term temperature and rainfall patterns (i.e., heatwaves) (Finney et al., 2022) and reflects the importance of high temporal resolution monitoring data for this study. Based on data collected in the EU-funded Agricultural Measures for Water Management (AMEWAM) project on the upper Wissey and Watton Brook, Evans (2012) identified that, between October 2003 and June 2006, there were only 171 days of rainfall >5 mm, with 13 days where rainfall was over 20 mm. Evans (2012) suggests that, even 5 mm of rainfall, can cause soil runoff from roads (deposited from tractor tyres and surface field runoff) within the Wissey catchment. From the record at Denver (1979 – 2022), both 2003 and 2006 were classed as drought years with 520 mm and 697.7 mm of annual rainfall respectively. Despite total annual rainfall reaching above the long-term annual average in 2006, it is still classified as a drought year due to the continuation of drought conditions throughout the year, which was only mitigated by October – December being extremely wet (Marsh et al., 2008).

2.4.3. Geology and Geomorphology

The entire upper Wissey catchment is chalk overlain by mostly permeable Boulder Clay (UKCEH, 2023). Thus soils, tend to be calcareous (National Soils Research Institute, 2005). Fig. 2.7 displays the parent material lithology of the Wissey study site derived from the British Geological Society (2019) dataset.

Table 2.2. Rainfall and temperature data for drought-containing years captured at Denver (TF 59162 00899) monitoring station (1979 - 2022). Individual drought containing years are averaged to give a typical drought year and the data of non-drought-containing years in the record are averaged to give a typical wet year to compare the variation between drought years. Figures in bold highlight extremes.

	Drought-containing Years															Av. drought year	Av. wet year
	1988	1989	1990	1991	1992	1995	1996	1997	1998	2003	2006	2011	2018	2020	2022		
Max. temp. (°C)	27.6	31	34.6	28.9	29.3	33.5	31.5	31.5	29.1	34.7	33.2	30.9	33.2	34.5	37.4	31.7	30.1
Min. temp. (°C)	-5.5	-3.4	-4.8	-12.2	-5.2	-8	-5.5	-6.6	-6.6	-5	-7.7	-3.9	-6.6	-4	-8.8	-6.8	-7.1
Max. daily rainfall (mm)	38	24.1	18.4	17.7	27	14.2	22.3	19.2	53.2	23.9	37.1	23	30.1	91.3	45.5	32.5	35.4
Min. monthly total (mm)	20.3	23.2	16	11.7	17.4	2.7	4.3	9.5	7.3	8.1	16.3	3.7	1.8	6.7	5.3	11	15.2
Max. monthly total (mm)	111.4	92.4	65.8	97.3	81.1	85.1	83.8	111.5	159.1	92.1	165.7	71.3	70.6	141.5	75.5	99.7	99.9
Total annual rainfall (mm)	606.2	539	444.3	444.3	637.1	463.3	440.6	547.7	707.2	519.8	697.7	427.6	524.3	705.8	496.3	572	628
Max. period no rainfall (days)	12	10	22	21	12	27	14	14	11	20	11	30	46	15	29	19	15
Total days with 0 mm	171	195	228	211	186	213	217	193	173	212	178	203	208	193	227	197	180

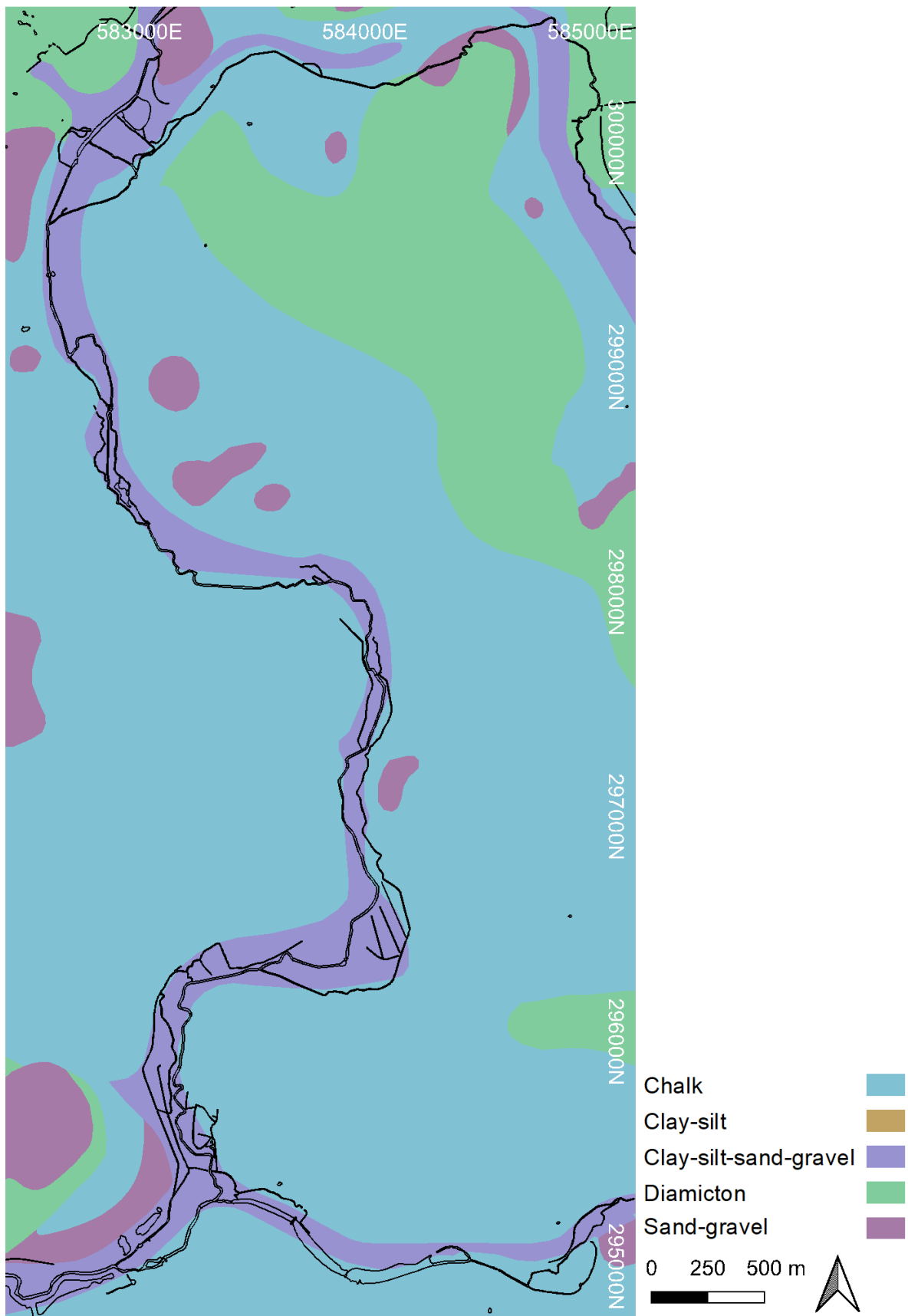


Figure 2.7. Soil parent lithology within Wissey study area. Data obtained from British Geological Society 2019.

The River Wissey has six tributaries along its course with the uppermost (Watton Brook) joining at Hilborough. The Wissey's channel width varies between 2 m in the headwaters to 18 m downstream at its confluence with the Great Ouse (Petts and Bickerton, 1993). Between Hilborough and West Tofts, the present study recorded bank full channel width as between 1.5 m and 18 m. Petts and Bickerton (1994) found that sites at Bodney Bridge (TL 828 988), Chalk Hall Farm (TL 835 981), and Langford Hall (TL 830 950) in the upper Wissey catchment and further downstream at Didlington (TL 785 957) were dominated by cobble gravel and sand. All sites in the survey were found to have deeper substrates composed of sand or gravel-sand (Petts and Bickerton, 1994). The gravel-bed sites contain finer gravel (5-28 mm) and a larger component of materials in the sand size range (0.125-1.0 mm). Only Chalk Hall Farm had gravels that contained more than 40% of material >28 mm (Petts and Bickerton, 1994).

The study area (Fig. 2.1) has some distinct geomorphological features that are ecologically important. The river is connected to multiple back and side channels. Some of these floodplain waterbodies are permanently connected to the river and others only during flood events. Some of the back channels are spring fed, providing thermal refugia in the summer due to cooler temperatures. Some sections of the main channel retain meanders, but others are straightened and embanked resulting in reduced river-floodplain connectivity. The straightened sections tend to be concentrated in the upper parts of the study area, above Bodney Bridge. An interesting feature within the study area is Bridge Carr Lake, a small, predominantly shallow (<3 m) lake formed by damming the Thompson Stream. The weir at the lake outfall provides a major barrier for fish passage. It is currently unclear whether there is any active fish passage between the river and Bridge Carr lake though LiDAR imagery and OS mapping show small streams that may connect the Wissey channel and lake, such as at TL 83435 95299. Within the study area, the most common land use type on the left-hand bank is mixed reed swamp, which occupies 30.92% of river length. On the right-hand bank the most common land use is open unimproved grassland, occupying 29.9% of river length, some of which is used for grazing. Wet woodland occupies 27.9% of the right-hand bank and 23.02% of the left-hand bank. Wet woodland and mixed reed swamp are concentrated below Bodney Bridge, providing a mixture of

open and shaded riverine habitats. The wet woodland is dominated by alder (*Alnus glutinosa*) carr woodland.

There is no river habitat survey data from the Wissey catchment from the Modular River Physical Habitat Survey (Shuker et al., 2017; Gurnell and Shuker, 2022), but there are 63 River Habitat Surveys (Environment Agency, 1997, 2003; Raven et al., 1998) from 1994 – 2022. Though within the specific study area of this thesis, there have only been six surveys. The latest occurred in 2013, but the others were conducted between 1994 - 1995. Thus, there is clear need for a new physical river habitat assessment of the Wissey study area.

2.4.4. River Hydrology

The nearest river gauging station is downstream of the study area at Northwold (TL 771 965). Northwold covers a catchment area of 274.5 km² and here the Wissey has a mean daily discharge of 1.95 m³s⁻¹, averaged over 1956-2022 (UKCEH, 2023). Flow at Q₅ (5% exceedance) is 4.68 m³s⁻¹ and Q₉₅ (95% exceedance) is 0.486 m³s⁻¹, as shown in the flow duration curve given in Fig 2.8. An annual average hydrograph for Northwold (1956 to 2017) is shown in Fig 2.9. Overall, the hydrograph for the catchment area is relatively flat. Periods of high discharge are typically found between December - March, with highest average monthly discharge occurring in February at 3.06 m³s⁻¹ (Fig. 2.8); the highest discharge on record occurred on 26th June 2016 (13.3 m³s⁻¹). The month with the lowest average discharge is September with 0.97 m³s⁻¹. The lowest discharge on record occurred on 19th September 1991 (0.181 m³s⁻¹). The Baseflow Index is 0.82, which reflects the large proportion of the river runoff, which is derived from stored sources, reflective of more permeable chalk geology (UKCEH, 2023). Petts and Bickerton (1994) recorded discharge monthly at 16 sites along the Wissey from 1991 – 1992. Average discharge recorded at Bodney Bridge was 0.27 m³s⁻¹ and maximum discharge was 0.64 m³s⁻¹. Their findings correlated well with the data for Northwold ($r^2 = 0.85$), suggesting a good relationship between Bodney Bridge and Northwold. Despite the correlation between Northwold and Bodney Bridge, there is a need to collect study area-specific flow data for this study, as West Tofts and

Thompson Stream also contribute to the flow at Northwold, potentially not being reflective of the hydrology within the study area.

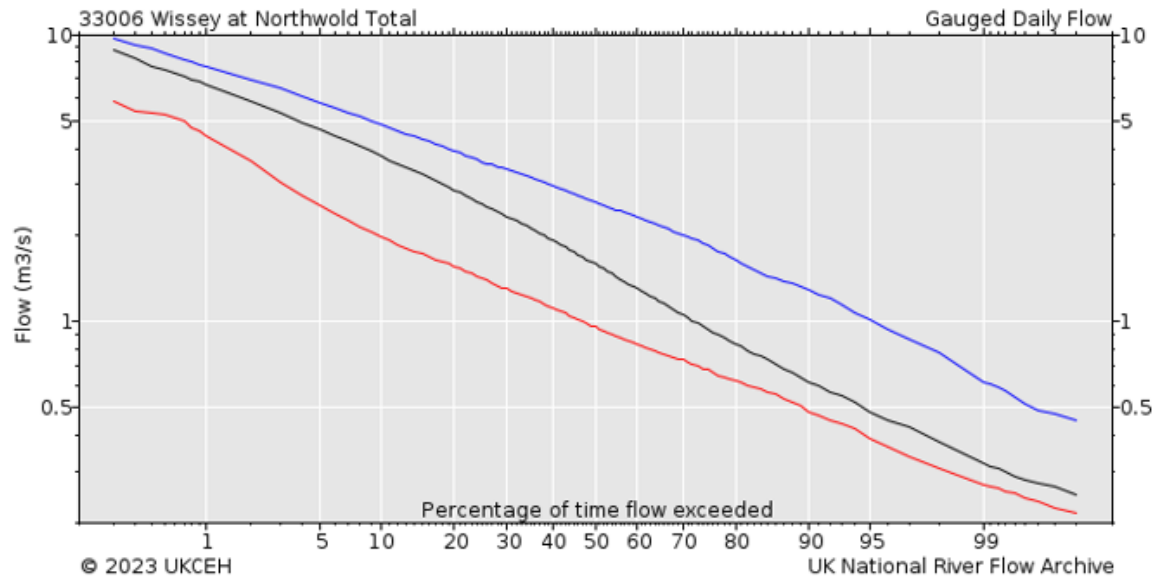


Figure 2.8. Flow duration curve for discharge at Northwold for 1956 – 2022 record. Black line refers to annual average data, blue line December to March, and red line June to September. Source: UKCEH (2023) Acknowledgement: Data from the UK National River Flow Archive.

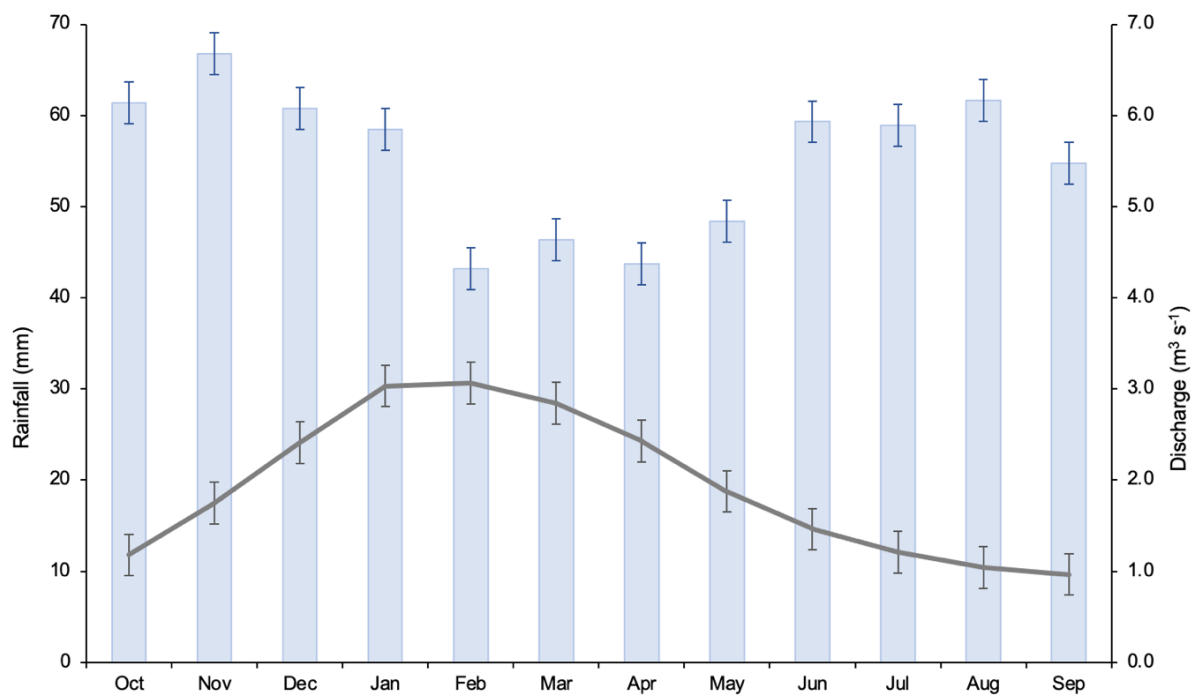


Figure 2.9. Average monthly discharge compared with average monthly rainfall for the period 1956 – 2017 at Northwold monitoring station. Acknowledgement: Data from the UK National River Flow Archive.

Flow velocity can be a direct determinant of fish habitat suitability as each fish species has its own swimming endurance and swimming physiology (Copp, 1997a; Bolland et al., 2015; Klein et al., 2016b; Walton et al., 2017). Due to its low swimming endurance (Jones et al., 1974), ensuring velocity is within a suitable range is crucial for burbot survival. During their study, Petts and Bickerton (1994) conducted monthly transects from 1991 to 1992 at seven sites along the Wissey, with 20 point measurements for depth (m) and velocity (m s^{-1}). They found that mean velocity between Bodney Bridge and Northwold (TL 771 965) varied minimally, ranging from 0.14 ms^{-1} at Langford Hall and 0.28 m s^{-1} at Chalk Hall Farm (TL 834 980).

Little information is available on instream water depth variation along the River Wissey. The present study recorded a range of water depths between 0.05 and 2 m between Hilborough and West Tofts. From their study, Petts and Bickerton (1994) record a depth range of 0.1 to 1.0 m. Data from Wissey Sluice at Northwold from 2012 to 2023 show an average water depth of 1.75 m and a maximum depth of 3.91 m. During the Petts and Bickerton (1994) study from 1991 to 1993, the Wissey experienced over 3 years of low flow conditions. Despite, this, however, a diverse range of instream habitats were maintained during low flows due to the upper Wissey's diverse channel form and associated high macrophyte cover (Petts and Bickerton, 1994).

2.4.5. Surface-Groundwater Exchanges

The south and east of England are underlain by productive aquifers, with groundwater being the source of 70% of local water supplies (Folland et al., 2015). Baseflows of the River Wissey are predominantly groundwater derived, and overall, the upper Wissey has a positive hydraulic gradient between groundwater and channel. From stream gauging at 16 sites, Petts and Bickerton (1994) found that 10 sites extending along the Wissey between West Bradenham and Northwold, showed no evidence that water was lost through the channel bed, and while flow was intermittent at West Bradenham, there was considerable gain in flow along a 2.5 km stretch between Great Cressingham and Hilborough, reflecting a high groundwater gradient through this

reach. This influx of groundwater plays a key dilution and flow regulation role within the main Wissey catchment.

2.5. The River Wissey Catchment: Human Influences

2.5.1. Historical Pressures and Modifications

Historical modifications of rivers within and surrounding the Wissey catchment follow the pattern of other rivers across Great Britain. The lowland rivers of the East Anglian Fens (including the Rivers Cam, Great and Little Ouse, Wissey, and Lark) are some of the most pressured by land drainage in the UK due to their proximity to the heavily drained farmland of the East Anglian Fens (Darby, 1983; Butlin, 1990). Today, the Wissey transitions into a fenland drain-type river at Methwold Fen, approximately 7.15 km west of Northworld (Dawson et al., 2010). The following will discuss records of river channel modification for these rivers. There is not extensive documentation of modification in the Wissey, so the pressures experienced by neighbouring catchments are also discussed inferring potential pressures experienced within the Wissey catchment.

Land drainage in the East Anglia Fens extends back to Roman times, and it incrementally increased after this time, until the late 16th and 17th centuries when more organised and intense efforts were made to drain land for farming (Darby, 1956; Dawson et al., 2010). Before this period, the Rivers Nene, Ouse, Cam, Lark, Little Ouse and Wissey meandered freely to the Wash, frequently connecting with the floodplain to form a mosaic of shallow lakes and floodplain water bodies across the Fenlands making the area a truly extensive wetland landscape (Huisman et al., 2017). Godwin (1978) revealed that historic maps of the Fens often show lakes and meres scattered across the landscape. Such a myriad of aquatic systems, including tidal channels that penetrated a great distance in-land (Smith et al., 2012) is thought to have contained diverse wetland fish, mammal, bird, plant and macroinvertebrate communities (Martay et al., 2012; Smith et al., 2012; Irvine, 2017), as well as being home to the burbot (Worthington et al., 2011a).

By the 17th century, however, the Fens and the Norfolk rivers, including the Wissey, were deteriorating severely. In 1649, specific policy to drain the Fenland, 'Drayning the Great Level of the Fens' Act, resulted in the construction of Denver Sluice, preventing tidal flow coming up the river (Butlin, 1990). The extensive modification of the Great Ouse catchment, including the construction of multiple parallel, straightened channels has majorly reduced aquatic biodiversity through the drainage of wetland habitat and simplification of channel geomorphology (Pinder, 1997). For the River Cam during the 1600s, the installation of four locks, removal of trees, deepening of the river, and widening of the channels was conducted further altering the natural hydrology and ecology of the local river systems (Preston et al., 2003). From the 1700s, drainage of wetland areas continued throughout Norfolk.

During the 19th and early 20th century, lowland rivers were more directly affected by instream barriers and pollution. The sluice at Langford on the Wissey appeared as early as 1880 in historical maps (EDINA, 2023). In the Norfolk Broads (eastern Norfolk) in the 19th century, increased rural-to-urban migration increased pressure on sewage disposal systems, and in turn, increasing quantities of effluent in broads-feeding rivers (Moss, 1983). These discharges ultimately led to the eutrophication of the Broads shallow lakes and considerable species loss (Moss, 1983). Less information is available on historical pollution of the Fenland rivers.

In combination with continued land drainage, pollution pressures, and shifting agricultural practices, physical river modification continued throughout the 20th century. In terms of physical river modification, one of the most detrimental periods for English rivers occurred from 1930 to 1980. During this period, the use of dredging to protect land and manage flooding was applied and rivers were deepened and embanked with the bed material dug out of the rivers (Eaton, 1989). Nationally, approximately 8,504 km of rivers were straightened during this period (Brookes et al., 1983).

Interestingly, despite the Wissey being influenced by fenland drainage and channel modification in the late 16th and 17th centuries, in its upper reaches (i.e., above the

confluence with Thompson Stream) it has remained one of the most unmodified rivers in Great Britain, particularly in comparison to its neighbour, the Little Ouse. Petts and Bickerton (1994) state that below the confluence of Gadder Stream, the Wissey becomes canalised and embanked frequently on both sides to its confluence with the Great Ouse, which is supported by examination of aerial and LiDAR imagery.

A key threat to the East Anglian Fenland rivers, including the Wissey, is water abstraction. Wilby (1993) showed that the 17 chalk streams in Norfolk, including the Wissey, have low recharge rates, making them vulnerable to abstraction. Groundwater abstraction, due to boreholes, can reduce flows in chalk streams, which can reduce macrophyte cover and negatively influence macroinvertebrate communities (Bickerton et al., 1993). The Wissey is part of the Cam-Ouse catchment from which 341 million m³ of water are extracted annually (Environment Agency, 2020). From Petts and Bickerton (1994), there are four boreholes above the study area stated in this research. For the Wissey, however, the effects of bore hole abstraction are mitigated downstream due to groundwater inputs (Bickerton et al., 1993). Petts and Bickerton (1994) investigated the link between groundwater abstraction and river flora and fauna throughout the Wissey and identified a declining trend in average fish biomass from 1983 -1993. This was attributed to both pollution events and low flows.

2.5.2. Current Pressures

2.5.2.1. *Temperature*

Water temperature is a key factor determining the distribution of aquatic communities, due to its influence on growth, embryonic development, reproductive behaviour and physiology (Olden and Naiman, 2010; Woodward et al., 2010; Golovanov, 2013; Harrison et al., 2016). Historically, Worthington (2010), by using air temperature as a proxy for water temperature (Webb et al., 2003; Johnson et al., 2014), found that for Fenland and Norfolk rivers, the number of days per year that river temperature was below 4°C decreased between 1800 and 2000 (Fig. 2.10). More recent data collected by the Environment Agency (EA) Water Quality Archive (Environment Agency, 2023a) (site locations shown in Fig. 2.2 and 2.3) for the upper Wissey shows that average

winter water temperature (2000 - 2023) is 6.24°C, with the minimum recorded being 1°C. Average summer water temperature (2000 - 2023) is 15.77°C, with the maximum recorded temperature being 21.5°C. The EA data do show a slight warming trend over 2000 - 2023, but there are some issues with the data (Fig. 2.11). First, the datasets for each site do not have a regular recording pattern, meaning some sites have extensive gaps or shorter records and even the sites with more established records have a lower temporal resolution with a reading taken, on average, every 3 months. This means that often only one reading is taken per season, so these data cannot be used to draw strong conclusions on temporal patterns in temperature. In the context of a burbot reintroduction, these shortfalls highlight the need to establish a robust spatial and temporal river water dataset for the Wissey.

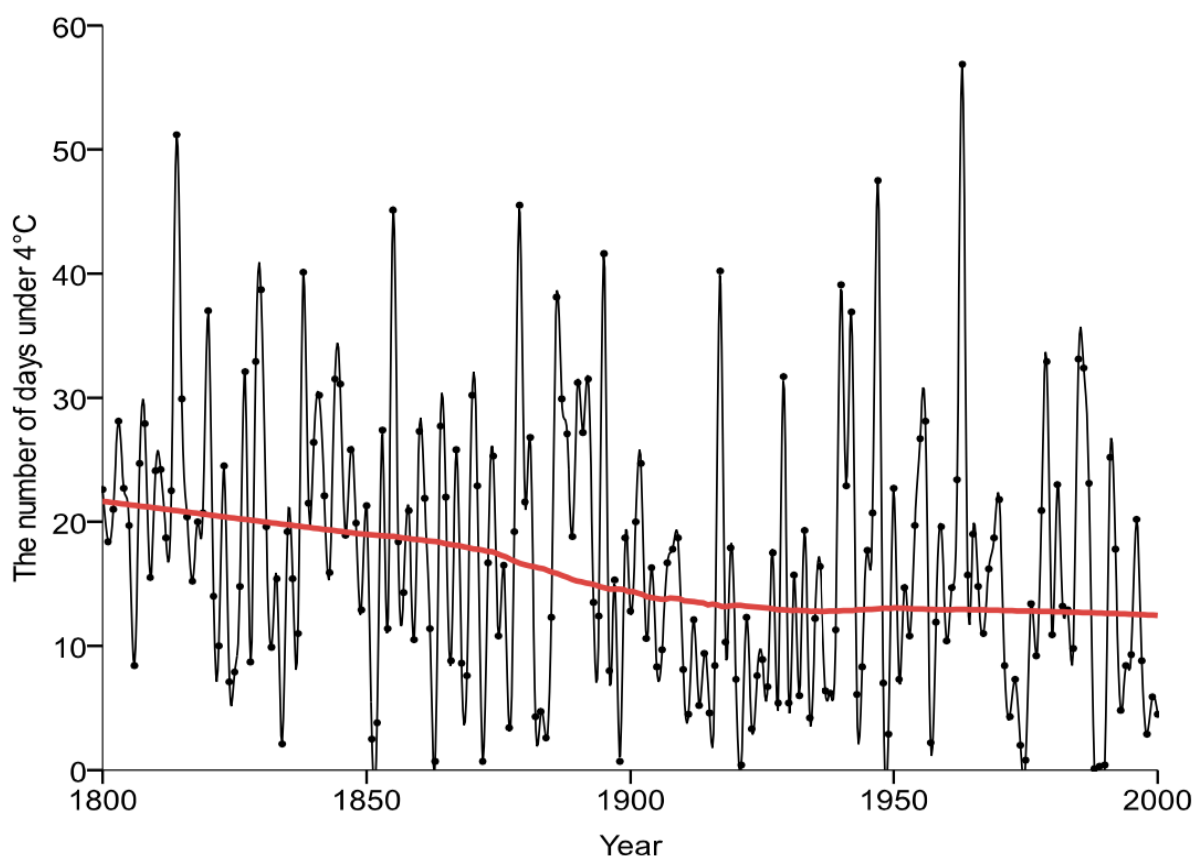


Figure 2.10. Long-term trend in mean number of days below 4°C for 10 sites on rivers in the Fens and Norfolk, trend fitted with a LOWESS smooth line. Used with permission from Worthington (2010).

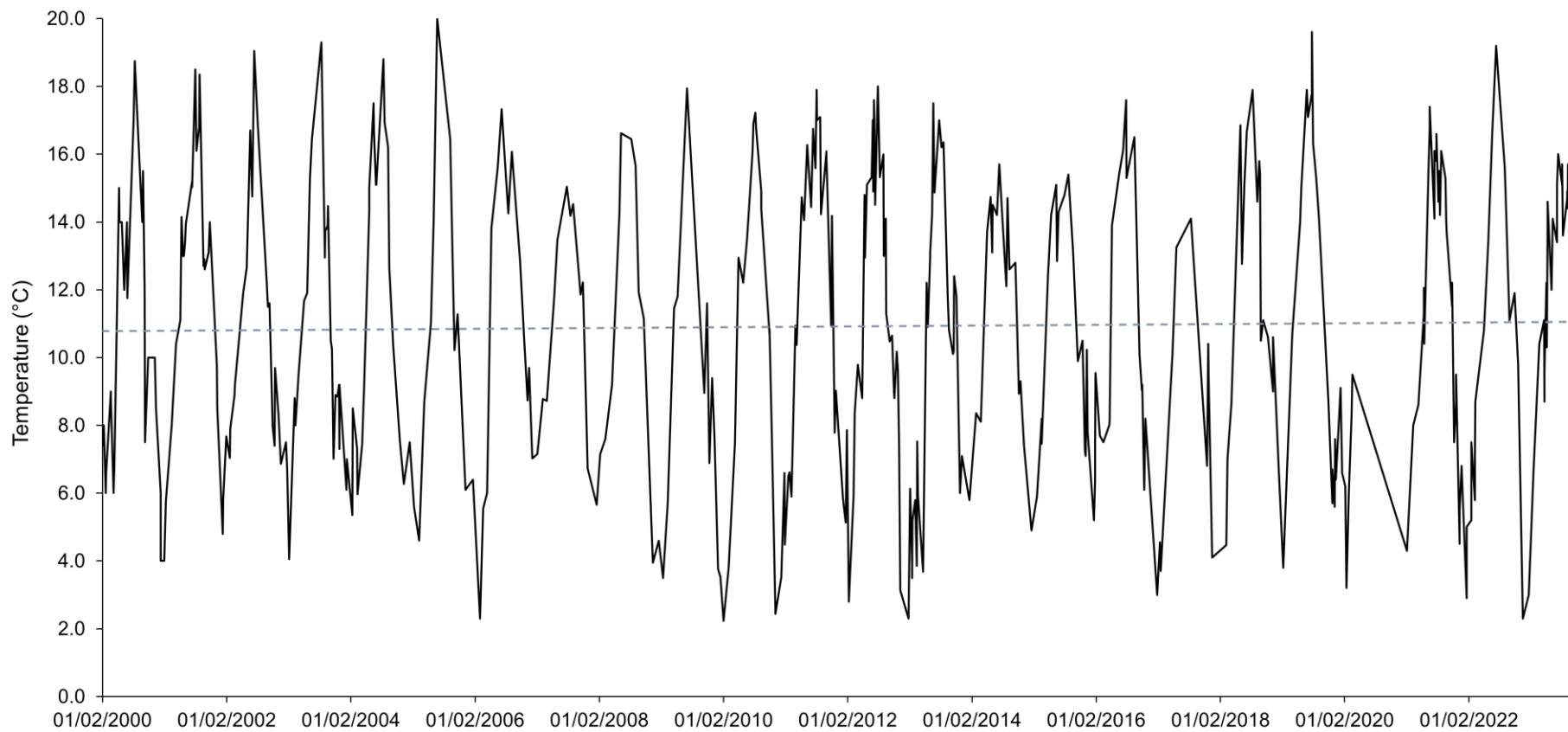


Figure 2.11. Water temperature during the period 2000 to 2023, averaged from Environment Agency water quality sites as shown in Fig 2.3 and 2.3.

2.5.2.2. Dissolved Oxygen

Compared to temperature records, data on dissolved oxygen is even more scarce for the upper Wissey catchment. Historically, the health of the Wissey system can be inferred from the state of the surrounding Norfolk and Fenland rivers. Worthington (2010) found that, since the 1920s, the dissolved oxygen concentration for the River Cam did not fall below 2 mg l^{-1} , which has been regarded as the lower critical survival threshold for burbot (Black et al., 1954). Compared to the Wissey, the Cam is a more heavily modified and pressured river, so it can probably be assumed that the Wissey was at least no worse than this in terms of dissolved oxygen. However, in the absence of robust long-term data for the Wissey, it is impossible to determine its historical patterns, and in turn, how this might have affected the burbot.

Recent data (2000 - 2023) collected by the EA show that, overall, dissolved oxygen is above the critical survival threshold (2 mg l^{-1}) for burbot (Fig. 2.12). However, these data are patchy and fragmentary, and it cannot be concluded how long dissolved oxygen persists at lower concentrations in some areas. This is important as Worthington (2010) suggests that long-term dissolved oxygen for burbot should not persist below 6 mg l^{-1} . From the EA data (Environment Agency, 2023a) for the Wissey (2000 – 2023), the average dissolved oxygen across the monitoring sites is 10.15 mg l^{-1} . The minimum dissolved oxygen observed in the record is 0.046 mg l^{-1} at Bradenham, observed on 10th January 2013. Though low, no other readings were taken at the site on the same date, nor within a 7-day period either side of the event to corroborate the low reading. The maximum dissolved oxygen observed in the record is 16.9 mg l^{-1} as observed at Necton Common on 11th May 2000. The month with the lowest average dissolved oxygen is August with 8.28 mg l^{-1} , and the highest average dissolved oxygen is March with 11.99 mg l^{-1} .

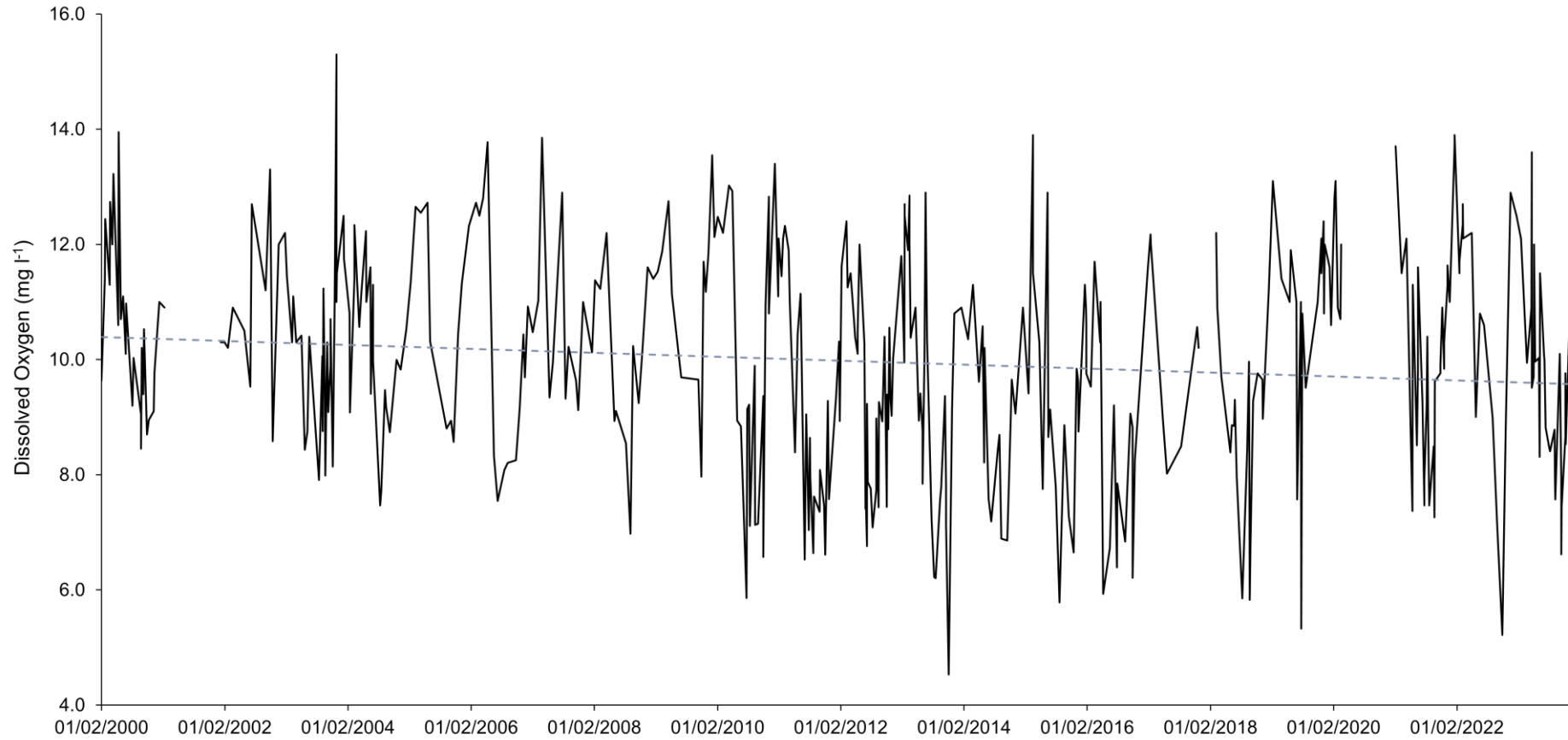


Figure 2.12. Dissolved oxygen (mg l⁻¹) levels for the period 2000-2023, averaged from all EA water quality monitoring sites as mapped in Fig. 2.2 and 2.3.

2.5.2.3. Sediment Loading and Agriculture

Agriculture comprises approximately 53.38% of catchment land cover in the Wissey catchment above Northwold, with grassland following at 26.82%, and then woodland (16.03%) and urban (3.66%) land uses (UKCEH, 2023). It is clear that agriculture exerts pressures on the river through sediment and nutrient pollution. A 10-year study of erosion rates in the upper reaches of the Wissey found the volumes of surface wash from a mixture of agricultural sites (e.g. cereal crops, outdoor pig farming), were responsible for loading fine-grained sediments, nutrients, and pesticides into local water courses (Evans, 2017). The study found that autumn-sown crops (i.e., beans and cereals) yielded six erosion events on average per year and following rainfall, water turbidity was found to increase, due to sediment runoff from surrounding fields. The Sediment Issues Priority list for England, however, does not list the Wissey as a priority area (Environment Agency, 2015a). Evans (2012) found that mean concentrations of suspended sediment, as measured by turbidity (FTU), were 3.0 - 4.4 times lower in the mostly non-agricultural Thompson Stream basin than in the main Wissey and Watton Brook (Fig. 2.1 and 2.2).

2.5.2.4. Pollution Pressures and Water Quality

Similar to most rivers in England, the Wissey receives outputs from sewage treatment works (STWs). On the upper Wissey, there are five STWs, at Necton, Bradenham, Swaffham, Great Cressingham and Hilborough, with the latter two confirmed to not remove phosphorous (Rangle-Wilson and Sykes, 2021). On the lower Wissey, there are two STWs at Mundford and Foulden, and the Watton Brook has three STWs at Carbrooke Church Road, Ovington and Watton (Rangle-Wilson and Sykes, 2021). Thompson Stream has one STW (Rangle-Wilson and Sykes, 2021). While there are no recent studies on the effect of sewage effluent on water quality in the Wissey, earlier work by Petts and Bickerton (1994) suggested a high correlation between levels of total oxidised nitrogen and Swaffham (TF 858 047) sewage fallout that caused poorer water quality downstream at Great Cressingham (TF 848 015).

The EA data for electrical conductivity is temporally sporadic for the Wissey. The most consistent long-term records exist for Bradenham, Necton Common, North

Pickenham, Linghills Farm, Bodney Bridge, and Ickburgh, from approximately 2000 - 2023. Fig 2.13 shows the average conductivity for these sites for the length of the record. There is a slight decreasing trend amongst high variability. Maximum conductivity reached $1400 \mu\text{S cm}^{-1}$ at the Mundford monitoring site in July 2010 and minimum conductivity was also at Mundford, at $236 \mu\text{S cm}^{-1}$ in October 2013.

There are indicators from nutrient data for the Wissey that suggests a nutrient-enrichment problem. Though sporadic, EA data (2000 – 2023) (Environment Agency, 2023a) show that total oxidised nitrogen (TON) fluctuates around 10 mg l^{-1} , with the most reliable records coming from Linghills Farm, Bodney Road, Browns Lane, and North Pickenham. Fig 2.14 shows the average TON over time based on these four sites, with the former two being within or near the study area. Other EA nutrient data, for ammonia and nitrites, show that concentrations are generally low, with 0.09 mg l^{-1} and 0.04 mg l^{-1} on average for ammonia and nitrites respectively. The data also suggest, however, that there could be discharge or pollution events that cause spikes in ammonia and for nitrites. For example, the maximum nitrite level recorded (2000 – 2023) was 0.24 mg l^{-1} on 29th May 2008, while maximum ammonia concentration was 1.7 mg l^{-1} recorded on 13th November 2002. Both maxima were recorded at Northern Pickenham. Vaage and Myrick (2021) state that, for juvenile burbot, the acute (96-hour) un-ionised ammonia concentrations is 0.58 mg l^{-1} and chronic exposure (60-days) is 0.03 mg l^{-1} . Beyond these levels they showed there is impact on burbot food consumption and growth.

Though sporadic, the records for orthophosphate evidences how nutrients move through the river following pollution inputs. Fig 2.15 shows spikes of pollution with diminishing strength with distance downstream. The data show that orthophosphate can spike over 2.5 mg l^{-1} at Northern Pickenham. The Watton Brook has a WFD ‘moderate’ rating overall and a ‘poor’ rating for orthophosphate (2016 classification) (Simpson et al., 2021). Evans (2012) states that levels of orthophosphate have diminished over those reaches where STWs have been updated or closed, which likely explains much of the spatial variation in orthophosphate. The England Phosphate Issue Priority areas lists the whole of the Wissey as a high priority area for phosphate

(Environment Agency, 2015b). A study by Simpson et al., (2021) found that agriculture contributes 32% to total phosphorus found in the Watton Brook, with STWs being a source of 52% of in-river loads. Another source of TP in the Watton Brook identified by Simpson et al. (2021) was septic tanks. Septic tanks have been found to contribute around 1% of TP found in the river, contributing to an estimated TP loss from the catchment of 1094 kg yr⁻¹ (Simpson et al., 2021).

Compared to the Watton Brook, the nutrient spikes observed along the Wissey are suspected to link to STWs, and possibly septic tanks, rather than agricultural inputs. In 1996, the upper Wissey was designated as a Nitrate Vulnerable Zone which forced farmers to comply with new regulations relating to the use of nitrogen fertilisers, the storage of organic manure, and the prevention of water pollution; however, in areas where STWs have not been uprated, closed, or had their sewage diverted to other STWs, there has been no effect on the levels of total oxidised nitrogen or orthophosphate (Evans, 2012). Overall, this suggests that runoff of sediments and nutrients from surrounding agriculturally dominated basins are not exclusively causing the variation in nutrient concentrations, as STWs are significant contributors. Further, Evans (2012) identifies that sediment washing from fields is highest in winter, but there are no peaks in orthophosphate or total oxidised nitrogen during the winter in the Environment Agency (2023a) data, suggesting that orthophosphate spikes later in the year are due to sewage. Septic tanks within the Wissey catchment can also cause point source pollution. Evans (2012) estimates that the presence of septic tanks in the upper reaches of the Watton Brook could explain the difference in orthophosphate between Watton Brook and the Thompson Stream. Similarly, algal blooms have been observed along a tributary to the Wissey in the summer below the location of known septic tanks (Petts and Bickerton, 1994).

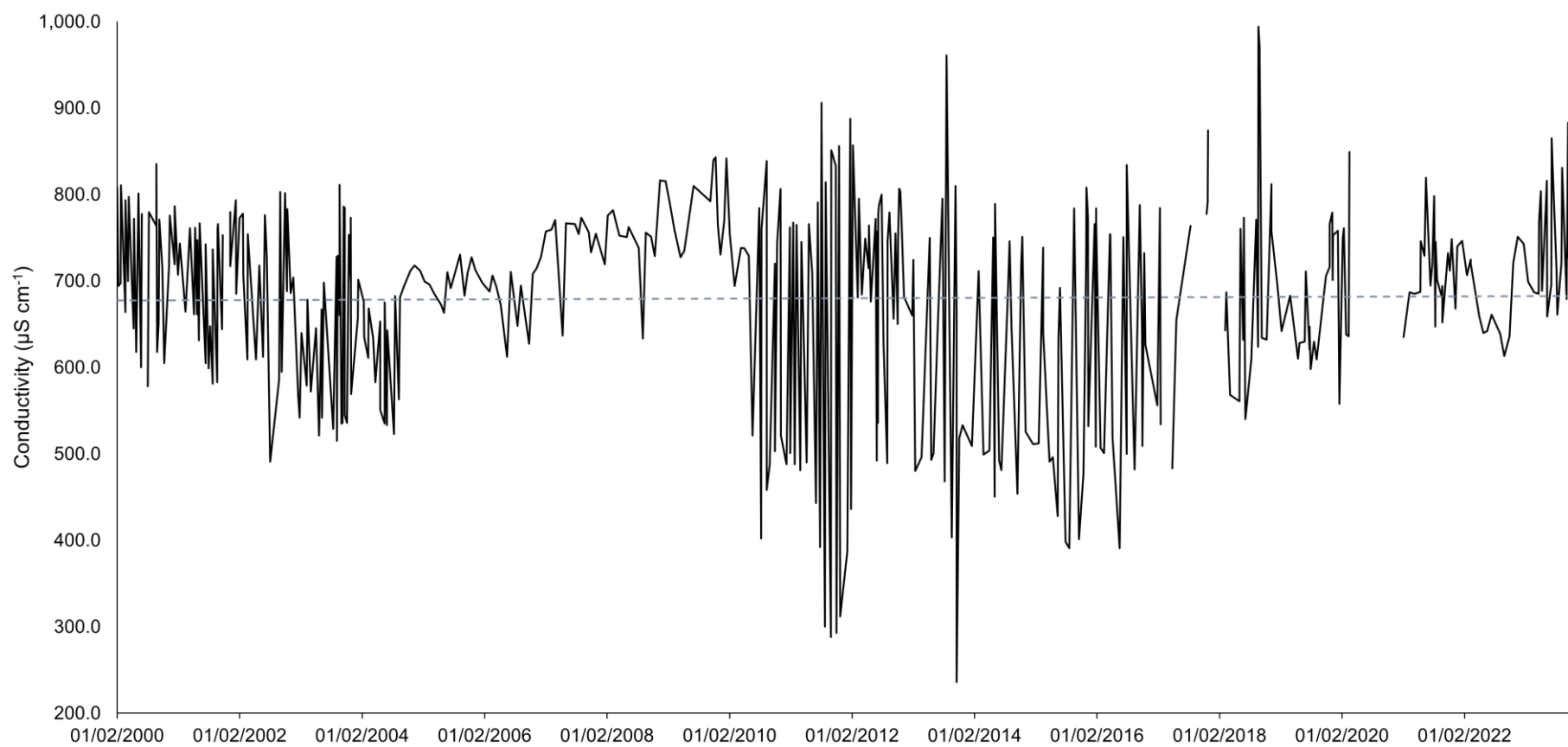


Figure 2.13. Average conductivity ($\mu\text{S cm}^{-1}$) for upper Wissey (EA record, 2000 – 2023) as mapped in Fig. 2.2 and 2.3.

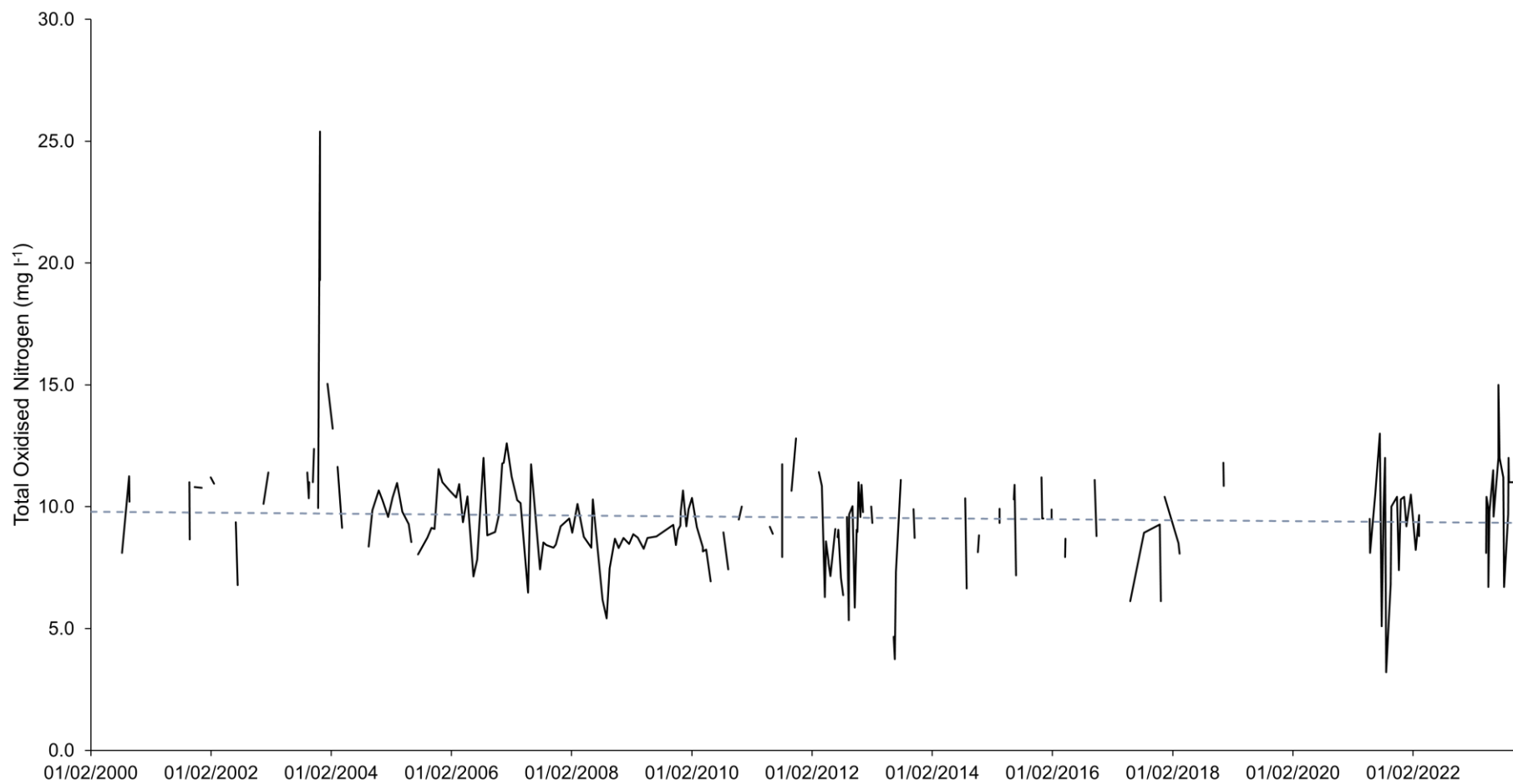


Figure 2.14. Average total oxidised nitrogen (mg l⁻¹) trends for the period 2000-2023 extracted from Environment Agency water quality stations: Bodney, Browns Lane, Linghills Farm, and Northern Pickenham.

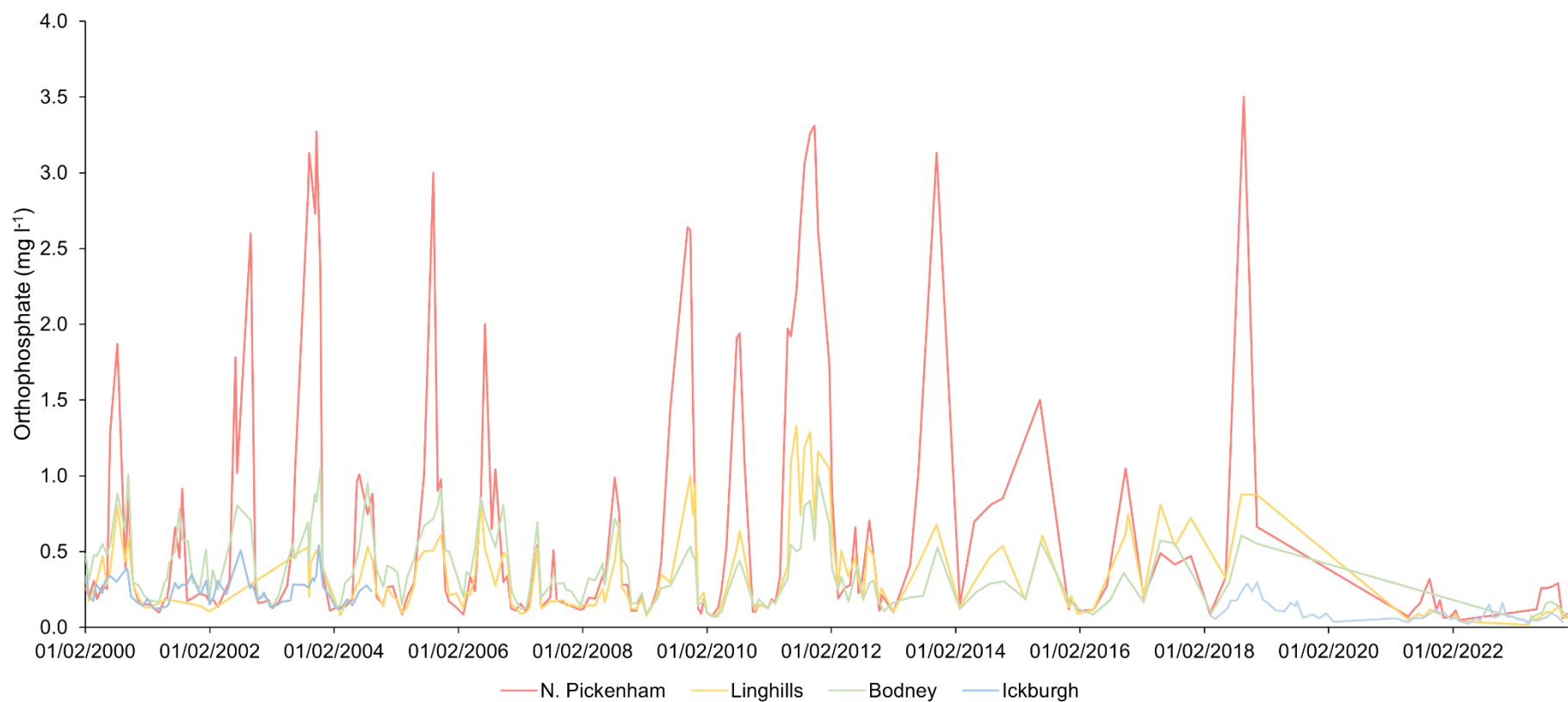


Figure 2.15 Concentrations of orthophosphate (mg l⁻¹) as a measure of reactive phosphorus for the period 2000-2023 from EA water quality monitoring stations with the most consistent records. The labels are arranged moving downstream along the Wissey, starting with Northern Pickenham down to Ickburgh. Data are sporadic so gaps between data points are interpolated with a line.

Overall, the EA Water Quality Archive (Environment Agency, 2023), despite limitations in temporal coverage, shows that there are some concerns over nutrient concentrations linked to the discharge and overflow of sewage treatment works (Evans, 2012), private septic tanks (Petts and Bickerton, 1994), combined with diffuse agricultural nutrient sources (Simpson et al., 2021). Notwithstanding these pressures, the Wissey is fed by groundwater and the presence of STANTA has allowed its semi-natural riverine ecology and geomorphology to drive a filtration and dilution effect for sediment and nutrients.

2.6. The River Wissey Catchment: Ecological Characteristics

The upper Wissey is a unique and important chalk stream site that has received multiple designations because of its ecology, including a national designation as an Important Bird Area (BirdLife International, 2021) and an Important Area for Plant Life (PlantLife International, 2007).

2.6.1. Macrophytes

Chalk streams typically have a higher species richness of instream and riparian plants than other river types in England and the UK. Petts and Bickerton (1994) described the Wissey as having one of the most characteristic examples of a rich wetland plant flora associated with a calcareous river. During their survey, the upper Wissey was found to have the greatest macrophyte growth, with the dominant species being *Ranunculus penicillatus* subsp. *pseudofluitans*, with *Nasturtium officinale* and an array of emergent species, such as *Sparganium erectum* found across the site. All three species can be described as ecosystem engineers. They influence river hydrology through flow resistance creating lower stream bed velocities within the dense plant stands and hence higher velocities in the water that flows around them, as well as the same dense stands increasing sediment accumulation (Gregg and Rose, 1982; Cotton et al., 2006; Wharton et al., 2006; O'Hare et al., 2012; Gurnell et al., 2013; Gurnell, 2014; Cornacchia et al., 2018). Within the stands, these low flow conditions generate ideal refuge habitat for juvenile fish (Copp, 1997b; Copp et al., 1998), including burbot (Auwerx et al., 2019).

2.6.2. Macroinvertebrates

Complex and abundant chalk stream macrophyte stands, in turn, provide abundant habitat niches for macroinvertebrates. The Environment Agency Ecology and Fish Data (Environment Agency, 2023b) for macroinvertebrates along the upper Wissey (Mundford, Thompson Stream, Bodney, Linghill, Great Cressingham, North Pickenham, and Necton Common) starts from 1986, and overall, all show a positive trend for the Biological Monitoring Working Party (BMWP) index, and by inference, albeit against a backdrop of changes to the sampling regime, an improvement in water quality since the 1980s (Fig. 2.2 and 2.3). However, when comparing the BMWP scores to Average Score Per Taxon (ASPT), the data show less of an improvement. This suggests that, while more invertebrate families are being supported by the river system, these are still families that indicate moderate water quality, reflected by the slow improvement of ASPT scores (Fig. 2.16). In 2020, Mundford had the highest scores for both ASPT and BMWP, while N. Pickenham had the lowest. This longitudinal improvement downstream could be due to Mundford being below STANTA, which filters pollution compared to N. Pickenham, which is situated higher in the catchment with increased agriculture and population pressure.

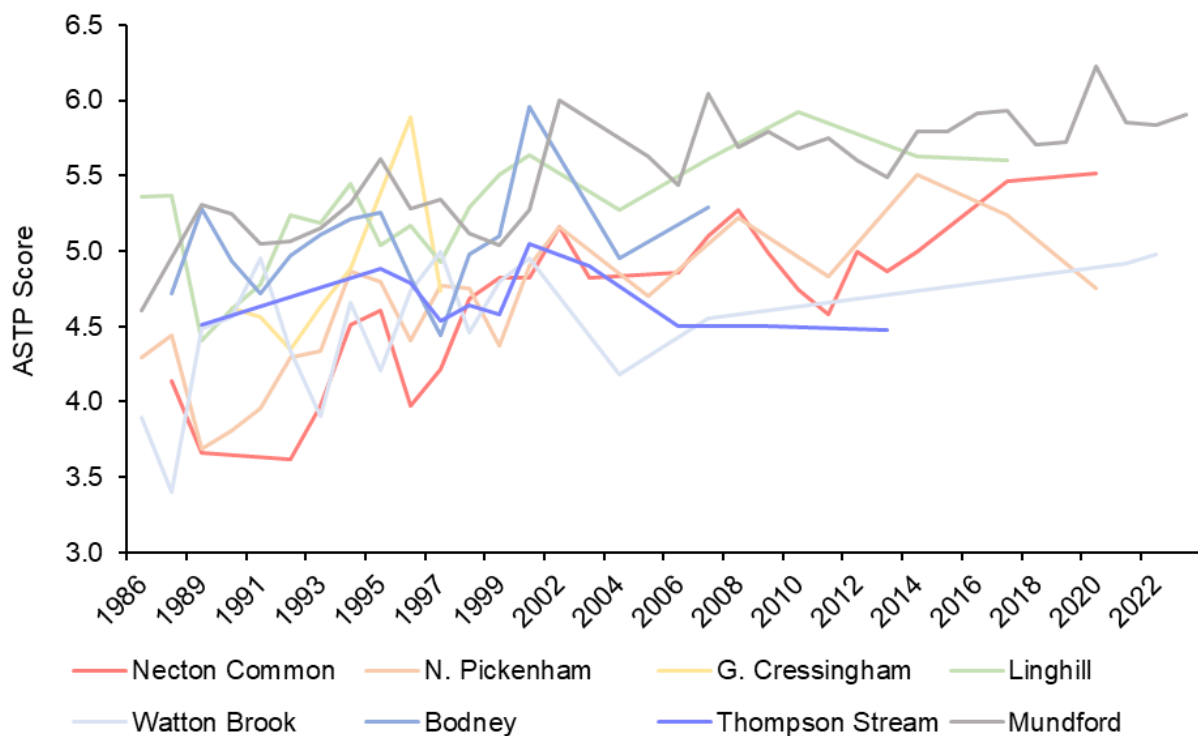


Figure 2.16. ASPT score for the period 1986 - 2023 from Environment Agency sampling sites illustrated in Fig. 2.3 and 2.4.

2.6.3. Fish

There have been distinctive shifts in fish community composition throughout space and time in the Wissey study area. The EA fish data (Environment Agency, 2023b) from 1990 to 2018 for the upper Wissey area has recorded a variety of fish species (Appendix 2). The available survey data records 17 species across time, with one occurrence of a roach-rudd hybrid *Rutilus rutilus* x *Scardinius erythrophthalmus*, but not all 17 species were recorded at each site.

From the EA data it is possible to see variations in fish community over time. Findings from the earlier surveys by the EA (Environment Agency, 2023b), such as in 1990, show European eel to be dominant, or most common, throughout the upper reaches of the Wissey, with brown trout and dace *Leuciscus leuciscus* second most common. Fig. 2.17 shows that the three sites in the upper Wissey catchment that have the most consistent fish community records from 1990 to 2015: Hilborough Mill, Hilborough Ford, and Linghills Farm. Despite their close proximity, in 1990 each had a relatively distinct fish community, with different common species. By 2015, however, Fig. 2.17 shows that, for all sites, brown trout is the most common species surveyed, comprising between 25-95% of all individual fish recorded by electrofishing. This is likely due to the stocking of large-bodied triploid brown trout by the STANTA Fishing Association, but could also be due to changes in fish survey methodologies and priorities by the EA. Similar trends are observed within the STANTA area itself from 1990 – 2023, Fig. 2.18 shows electric fish surveying data from Bodney Meadows (TL 83100 98300) from 1990 and 1993 and more recent data from Norfolk River's Trust (NRT) from 2015 at TL 83171 98078 (0.23 km from Bodney Meadows) and 2023 at TL 83922 96415 (2.05 km from Bodney Meadows). The data suggest a shift in fish community composition within the study area itself, from eel to brown trout and an overall increase in fish abundance. The NRT 2023 survey caught 62 brown trout, compared to 31 three-spined stickleback *Gasterosteus aculeatus*, which were the next most common catch. For the brown trout the survey showed that mean total length for brown trout was 125.1 ± 53.17 mm, with maximum length of 215 mm and minimum length of 60 mm.

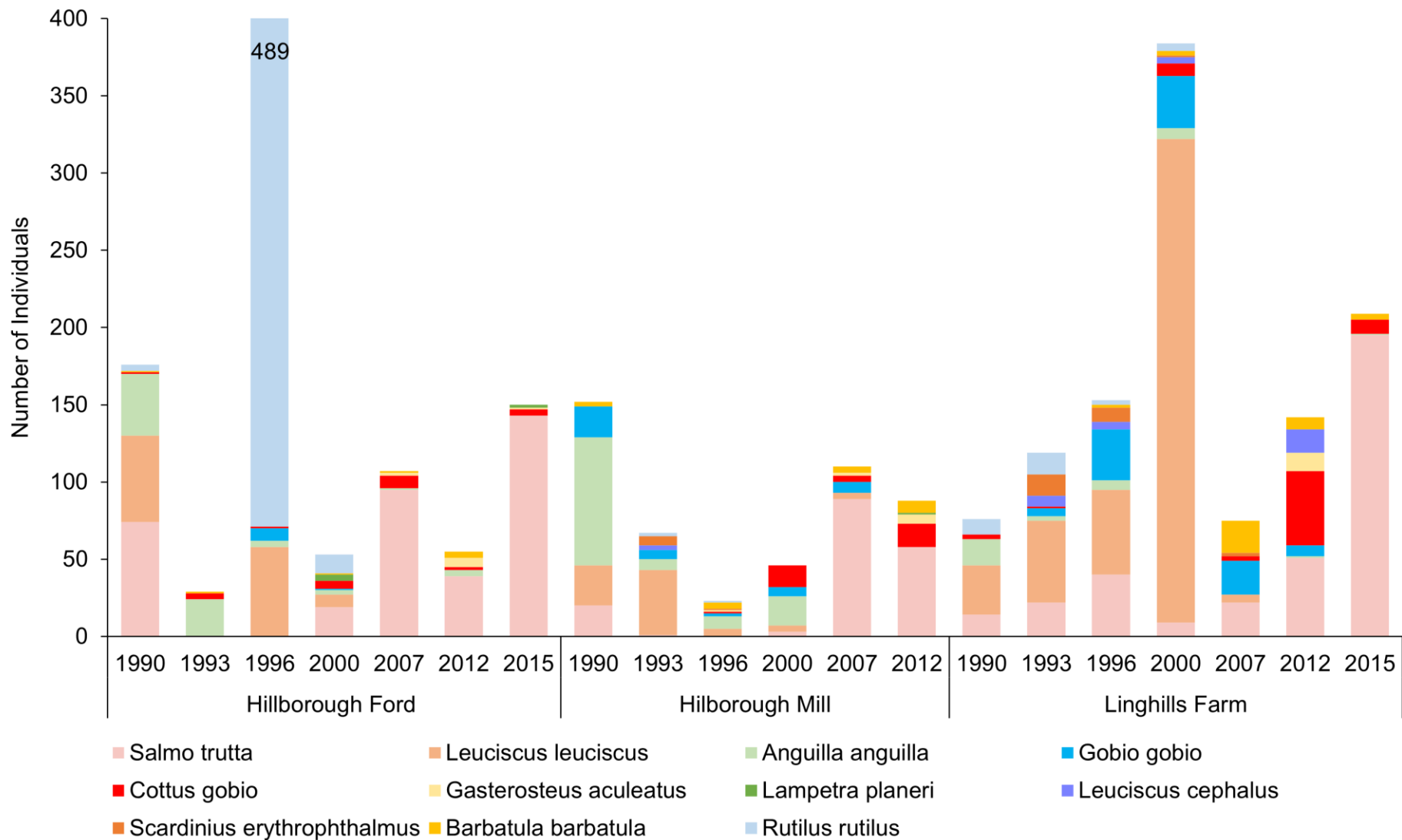


Figure 2.17. Fish survey records for 1990 - 2015 obtained from the Environment Agency from Hilborough Ford, Hilborough Mill, and Linghills Farm. To streamline data visualisation, those species with less than 10 individuals caught during the survey record were excluded.

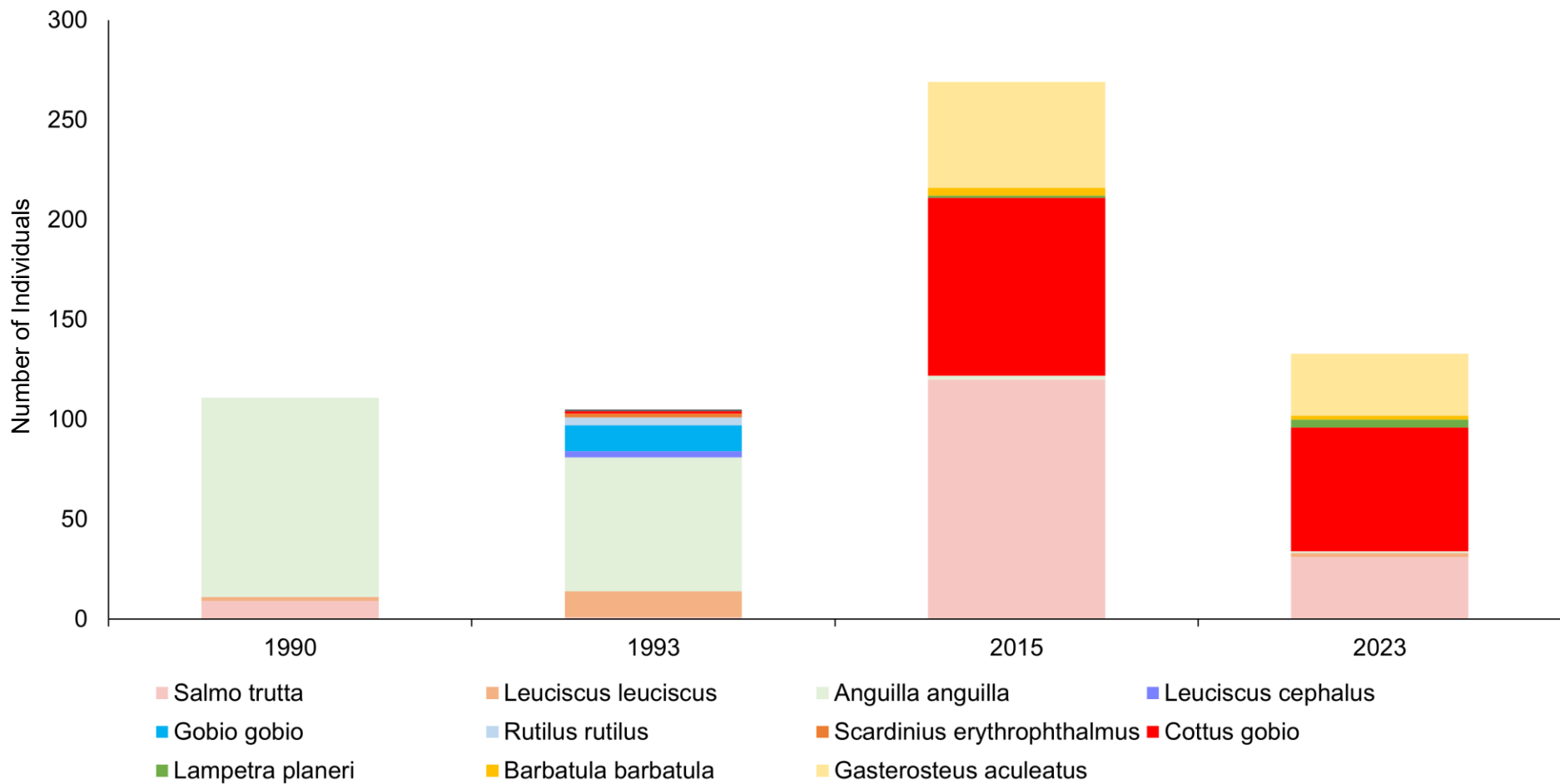


Figure 2.18. Fish community composition change from 1990 to 2023 compiled from data within the STANTA study area at Bodney Meadows (1990 and 1993) and two Norfolk Rivers Trust fish surveys (2015 and 2023).

It is important to evaluate the known ecological relationship between the burbot and the Wissey's fish community. As brown trout are routinely stocked into the Wissey it is unlikely that burbot will affect brown trout recruitment, but these stocked fish could exert predation pressure on newly introduced burbot. Thus, it is important to the success of the reintroduction and the health of the ecosystem that the impact of fish stocking in the Wissey be considered and it would be beneficial to begin regular monitoring of all fish populations.

2.7. Future Pressures: Chalk Streams and Climate Change

It is important to consider future pressures when assessing the survival and longevity of a reintroduced species (IUCN, 2013). Warming of river temperature due to climate changes will have a direct impact on fish biology and ecology, with cold-adapted fish species being most vulnerable (Worthington, 2010). Therefore, the subject of climate change must be addressed.

It is estimated that, in southeast England, over the last 20-30 years, river temperatures have increased by $\sim 1^{\circ}\text{C}$ (Hammond and Pryce, 2007). Regional climate projections based on different emissions scenarios suggest that East Anglia is projected to become warmer with wetter winters and drier summers, which could decrease average summer flows and groundwater levels depending on the intensity of summer heat (Met Office, 2019b). According to Taylor (2014), the Wissey falls under a climate change vulnerability zone. Based on a model run by Natural England, which uses metrics based on sensitivity to climate change, adaptive capacity, and conservation value, the low-medium ranking suggests that the Wissey does not have sufficient climate change adaptations to protect the priority habitat it contains (Taylor, 2014). The Environment Agency modelled monthly mean daytime water temperature for chalk streams, based on observed relationships between air and water temperature, under the Met Office's UKCP18 datasets air temperature projections for 12 km grids for the years 1981 to 2080 for the high emission RCP8.5 scenario (Finney et al., 2022). Based on their models for chalk stream catchments, summer maxima water temperatures are projected to increase by 0.58°C per decade from reference levels (1981 to 2005) to

2080 (Finney et al., 2022). Projections were not even regionally across the UK , with slower rates of warming in the northeast, including Yorkshire, and higher rates of warming amongst the southern chalk streams, particularly those rivers close to London (Finney et al., 2022). Due to the coarseness of the data, conclusions based on daytime maximum projections or catchment specific analysis were difficult to make, with concerns that the projections underestimate daily maximum temperatures and minimise the short-term climatic impact of heat wave events (Finney et al., 2022). Their model also neglects the complex future scenarios generated by incorporating changes in rainfall frequency and intensity, groundwater/surface water balance, and evapotranspiration (Finney et al., 2022).

Aside from temperature, it is difficult to predict other meteorological impacts of climate change in the UK due to interacting climatological factors and modelling capabilities. Historical data and some climate change projections suggest an increasing trend in the intensity of winter rainfall, which, coupled with changes in evapotranspiration, could change flow regimes in rivers (Watts et al., 2015; Garner et al., 2017a). Common predictions are that summer flows may decrease on average, but that floods may become larger and more frequent, though some argue that human modification of rivers (i.e., dams, instream barriers) prevents an accurate assessment of how hydrological factors are and will alter under climate change (Hannaford, 2015). Impacts of climate change can be compounded by other anthropogenic pressures. For example, potentially decreasing summer flows under climate change combined with continued discharge of effluents by STWs, could increase habitat unsuitability for fish species (Whitehead et al., 2009; van Vliet et al., 2013). For groundwaters, research on the impact of climate change is more uncertain. Some studies suggest that groundwater temperatures will increase, but it is still thought that upwelling groundwater in chalk streams will still create patches of relatively cool water compared to the surrounding river temperature in summer or during hot periods (Mondon et al., 2021).

In terms of ecology, projections of chalk stream water temperature increase under high emission scenario RCP8.5 predict that the critical temperature range for Atlantic

salmon *Salmo salar*, which is between 6 and 22.5 °C (see Solomon and Lightfoot, 2008), could start being exceeded as early as 2050 (Finney et al., 2022). Water temperature directly influences egg development and eventual mortality and projections suggest that, for Atlantic salmon and brown trout, a crucial boundary of 12 °C could be exceeded at 85% of all spawning sites by 2080 (Finney et al., 2022). Due to the cold water adaptation of most British fish, climate change will result in a contraction of suitable ranges for some fish species, particularly salmonids, while also facilitating range expansions of invasive species (Wrona et al., 2006; Hellmann et al., 2008; McDowell et al., 2014), such as the zebra mussel *Dreissena polymorpha*, which could have a range expansion of up to 20% by 2050 (Gallardo and Aldridge, 2015). This discounts, however, the potential for thermal adaption by resident populations (Comte and Olden, 2017).

An increasing trend in low flow summer conditions further exacerbates stressed environments such as chalk streams that are more commonly experiencing drought conditions (Visser et al., 2019). For chalk streams, the mosaic of habitats throughout the catchment, from winterbournes to permanent wetted channels, produces a variety of habitat niches that supports high macroinvertebrate and macrophyte diversity (Ladle and Westlake, 2006). Higher temperatures are expected to increase the length of the plant growing season, causing temporal changes in the occurrence of individual species and community composition (House et al., 2017). If plant community structure changes, this will have knock-on effects on macroinvertebrate community composition. Ultimately, climate change influences on river hydrology and water chemistry will favour some species of macrophytes and macroinvertebrates, and will affect others negatively (Domisch et al., 2011; Rosset and Oertli, 2011). For the burbot, a fish species that has a large global distribution and varied thermal requirements between genetic subclades, its future under climate change is uncertain, but the potential for reduced summer flows and warming summer water temperatures, as well as increases in episodic extreme conditions (i.e., heatwaves), could reduce physically and thermally suitable habitat. It is important, therefore, to discuss any burbot reintroduction in the context of climate change (Chapter 4).

2.8. Belgian Burbot Reintroduction – Comparison Study Sites

The ongoing burbot reintroduction in Belgium has recorded some evidence of reintroduction success, and thus, its candidate reintroduction sites present a good opportunity for comparison with the Wissey. The reintroduction occurred in 2005, and prior to this, habitat suitability assessments were undertaken from 2003 - 2004. A burbot habitat suitability survey was designed and implemented based on burbot habitat use by French burbot populations in the French Ardennes (the closest genetic relatives to the Belgian population and part of the western European subclade, see section 1.3.2), to understand the macro- and micro-habitats they used during adulthood, spawning, and juvenile stages (Dillen et al., 2005). In combination with the physical river habitat, they assessed chemical suitability (dissolved oxygen, ammonia, and biological oxygen demand) using secondary data. Using this information, they applied habitat suitability models to calculate the number of individuals per 100 m these river sections could support (Dillen et al., 2005). The whole survey was based on published literature and field observations on burbot habitat preference and ecological and biological requirements. The habitat surveys were conducted on 8 rivers and the Grote Nete and Bosbeek were selected as candidate reintroduction sites (Dillen et al., 2008b). The instream habitat data from the habitat suitability assessments in Belgium is not available.

Unfortunately, due to differences in applied methodologies, it is not possible to apply a direct comparison, but the Belgian burbot reintroduction allows an inference for how a potential reintroduced burbot population might respond in England dependent on habitat availability in the Wissey. This comparison is possible as the Belgian burbot population are part of the same genetic subclade as the extirpated English population (Van Houdt et al., 2005; Worthington et al., 2017) and burbot within the same genetic subclade have similar environmental requirements.

The main reintroduction site for the Belgian reintroduction was the river Grote Nete, but more recent efforts in the reintroduction have also focused on the rivers Klein Beek and Molenbeek, within the Viersels Gebroekt nature area, which is managed as an

active wetland (J. Auwerx, pers. comms. 2022). The Grote Nete is the main comparison site within the thesis. In Chapter 3, two sections of the Grote Nete (Straalmolen and Schepps) are part of the floodplain habitat analysis along with the Viersels Gebroekt nature area, which aims to compare floodplain habitat availability (a proxy for spawning habitat availability). Later, in Chapter 4, daily maximum water temperature data from the main channel of the Grote Nete just downstream from Straalmolen is compared to daily maximum water temperature from the main channel of the Wissey to contextualise whether thermal conditions in the Wissey are similar to an area that can facilitate suspected natural reproduction. An overall comparison of sites is given in Table 2.3.

Table 2.3. Geomorphological, hydrological, and climate comparisons between the River Wissey, Grote Nete, and Viersels Gebroekt.

	Wissey	Straalmolen	Schepps	Viersels Gebroekt	Sources
Catchment size (km ²)	460	561	561	573	Dillen et al. (2005); Baeyens et al. (2010); UKCEH (2023)
Study area size (km ²)	1.74	0.89	1.41	1.29	
Land use	Mixed woodland and rough grassland	Mixed woodland and rough grassland	Mixed woodland and rough grassland	Rough grassland	Agentschap Digitaal Vlaanderen (2021); UKCEH (2023)
Geology	Lime-rich soil over chalk	Sand	Sand	Peat and wet clay	National Soils Research Institute (2005); Ondersteunend Centrum Databank Ondergrond Vlaanderen (2017)
River type	Alluvial	Alluvial	Alluvial	Alluvial	
Average maximum air temperature (°C)	21	23	23	23	WeatherSpark (2023a; b; c)
Average minimum air temperature (°C)	1	1	1	1	WeatherSpark (2023a; b; c)
Average annual rainfall (mm)	685	546.9	546.9	547.1	WeatherSpark (2023a; b; c)
Average annual discharge (m ³ s ⁻¹)	1.937	NA	NA	NA	(UKCEH, 2023)
Velocity range (m/s)	0 – 1.09	0.1 - 0.5	0.1 - 0.5	0.1 – 0.3	Dillen et al. (2005); Baeyens et al. (2010)
Depth range (cm)	5 - 200	NA	NA	30 - 87	Baeyens et al. (2010)
Width range (m)	2 - 10	7 – 11	7 – 11	NA	Dillen et al. (2005)

Chapter 3. Assessing instream and floodplain burbot-associated habitat availability using *in situ* and remote sensing approaches

3.1. Introduction

Freshwater ecosystems comprise just 0.8% of the Earth's surface (Dawson, 2012), yet contain over 9.5% of known animal species and over 30% of vertebrate species globally (Dudgeon, 2010). Combinations of anthropogenic pressures, known as multiple stressors (He et al., 2023) such as pollution and habitat modification, greatly threaten freshwater biodiversity across multiple species groups with extinction rates estimated to be four times higher than for terrestrial systems (Moorhouse and Macdonald, 2015). Freshwater fish populations are severely affected by pollution and habitat modification with some 37% of European freshwater species classified as 'threatened' (Brooks and Freyhof, 2011). Habitat fragmentation due to structural river modifications including instream migration barriers (e.g., dams, weirs, and sluices) and disconnection of rivers from their floodplains are major drivers of freshwater fish species declines (Gozlan et al., 2019). In Europe, an estimated 1.2 million instream barriers are present across 36 countries (Belletti et al., 2020), but these are patchily distributed. Some remote parts of Europe still have sections of free running 'wild' rivers, most notably the Vjosa River, Albania (Schiemer et al., 2020; Hauer et al., 2021; Pessenlehner et al., 2022), but most areas are greatly impacted, including in Great Britain where only 1% of rivers are known to be free from artificial barriers (Jones et al., 2019).

Longitudinal connectivity is not the only form of connectivity that is important to riverine biodiversity. Lateral connectivity across the river-riparian- floodplain gradient, vertical connectivity from the hyporheic zone through the water column to the surface (Vannote et al., 1980; Boon, 1998), as well as temporal connectivity, all influence heterogeneity in rivers (Wohl, 2017; Grill et al., 2019; Harvey et al., 2019; Shao et al., 2019). The importance of connectivity is not just evidenced in research, but also in international policy. As part of the EU's Biodiversity Strategy under the EU Green Deal, there is a

target to restore 25,000 km of European rivers to free-flowing rivers by 2030, removing obsolete barriers and restoring floodplains (European Commission., 2024), reflecting growing international understanding of the importance of spatial and temporal connectivity.

Recolonisation of locally lost fishes from other populations is often prevented by instream barriers in freshwater systems, such that the resilience of declining fish populations is extremely low (Catalano et al., 2007; Kiffney et al., 2009). Species reintroductions are a popular conservation tool (IUCN, 2013) that can provide solutions to declining or extirpated fish populations (Hodder and Bullock, 1997; Cochran-Biederman et al., 2015; Lamothe et al., 2019). Species reintroductions are supported by international guidance from the IUCN on planning, feasibility, risk, and monitoring (IUCN, 2013). Species reintroductions are often expensive and are susceptible to a series of pitfalls: they often lack baseline data, funding, post-release monitoring, and sometimes even a fundamental understanding of species' behaviour and ecology, and thus, require extensive planning (Berger-Tal et al., 2020). The key pillars of reintroduction success identified across diverse animal groups (including fish) include good quality release habitat, an extensive understanding of species' biology and behaviour, and an effective post-release monitoring programme (Berger-Tal et al., 2020). Focusing on fish specifically, Cochran-Biederman et al. (2015) found the most common indicator for translocation failure was not adequately addressing the original cause of species decline, while habitat quantity and quality also had a strong influence on success. There are many examples of fish reintroductions (Cochran-Biederman et al., 2015). For example, in Belgium, the regionally extinct chub *Leuciscus cephalus*, dace, brown trout (Boets et al., 2018), and (in 2005) the nationally extirpated burbot have been reintroduced (Dillen and Vlietinck, 2008).

3.1.1. Burbot Habitat Associations

A reintroduction for any species must be grounded in biology and ecology of the species, and thus, availability of suitable habitat must be assessed. Here, habitat refers to physical qualities of the environment that are utilised based on the needs of

each burbot life stage. For fish species it is hard to determine preferred habitat requirements (i.e., those that offer a validated fitness advantage), and it is more common to observe habitat selection by species, without knowing if those specific habitats offer a survival advantage (Rosenfeld, 2003). For burbot, most literature is observational and thus infers habitat use or selection over a definitive habitat requirement. Habitats often selected by riverine burbot populations and those habitats they are frequently associated with comprise the basis of this study.

Connectivity of habitat niches associated with each life stage is critical for any chance of considering a burbot reintroduction successful in the long-term. Widespread channelisation and dredging of rivers, which disconnects river channels from their floodplains, is thought to have been the main cause of the burbot's decline in England, and, more generally, the western subclade of this species has been shown to be associated with inundated floodplain and/or off-channel habitat for winter spawning (Worthington, 2010; Worthington et al., 2011a, 2012; Brackwehr et al., 2016; Auwerx et al., 2019; Beelen et al., 2019). Indeed, spawning habitat loss is also thought to have been the main driver of burbot population decline in the Netherlands (Bosveld et al., 2015), Germany (Wetjen et al., 2020b), and Belgium (Vught et al., 2015). Inundated floodplains are thought to be crucial to burbot spawning in many areas, although they are also known to spawn in main channel and tributary habitat on gravel and sand substrates (Sorokin, 1971; Jude et al., 2013). Some adult burbot undertake spawning migrations of 1.5 - 2.0 km per day (Sorokin, 1971) to find suitable habitat. Other specific habitat spawning-related associations, including water temperatures and water depth, can vary between different subclades (Van Houdt et al., 2005). For the western European subclade, $<7^{\circ}\text{C}$ for at least a two-week period to facilitate spawning (Vught et al., 2008) is crucial.

Importantly, it is the slow flow conditions of inundated floodplains and back-channel systems that provide ideal nursery habitat for newly hatched larvae, preventing them being flushed out of the system before their swimming physiology develops (Klein et al., 2016a). Independent larvae or fry are dependent on floodplains for around a further 6 - 10 weeks (Brackwehr et al., 2016).

Juvenile burbot are known to occupy areas of slow flow conditions, such as slack water or secondary channel systems (Fisher, 2000; Worthington et al., 2012). They can often be found in areas of high macrophyte cover (Dillen et al., 2008a; Auwerx et al., 2019), which act as flow refugia (Koporikov and Bogdanov, 2011).

As adults, burbot are ambush-oriented top-level predators, mostly nocturnally active and associated with deeper water (Nieminen et al., 2003; Eick, 2013). The burbot's low swimming endurance (Jones et al., 1974), relative to other species such as European grayling *Thymallus thymallus* or Northern pike, has strong association with high instream habitat complexity (woody pieces, undercut banks, boulders) to offer shelter or ambushing opportunities (Dillen et al., 2008a; Worthington et al., 2012; Eick, 2013; Brackwehr et al., 2016). The use of a different habitat for each life stage (Fig. 3.1), especially its floodplain phase, represents a major challenge for any potential future reintroduction. The connectivity and proximity of the different habitat niches occupied for each life stage, as well as their areal cover, is hence critical to the reintroduced burbot survival and long-term persistence. Therefore, reintroductions for burbot require a holistic view of river-floodplain ecosystems.

The reintroduction programme by INBO and the Flemish Environment Agency identified the importance of grounding burbot ecology within habitat suitability assessments, as well as the need for a multi-year release strategy and monitoring programme. Reviewing annual fish reports by INBO, covering the progress of the burbot reintroduction (2007 onwards), during the initial habitat surveys and during later re-surveying (Dillen et al., 2005; Van den Neucker et al., 2010a), the results show that there were sections of the Grote Nete that were shown to be unsuitable for larvae and adults, yet burbot of all life stages continue to be caught (Fig. 1.8). The studied unsuitable sections of the Grote Nete might be the cause of the slow recovery of the reintroduced Belgium population, but it could also be linked to other factors. For example, La Bar River in the French Ardennes was used as the standard of habitat suitability for all burbot life stages for the Belgium reintroduction (Dillen et al., 2005), but conclusions from the work have changed. The habitat assessments were conducted under the assumption that larvae can survive and develop in flowing water,

which has now been disproven by INBO as larvae are carried out of the system by currents (J. Auwerx, pers. comms., 2024). Thus, the experiences from Belgium emphasise that floodplain and lateral habitats cannot be neglected from habitat suitability assessments.

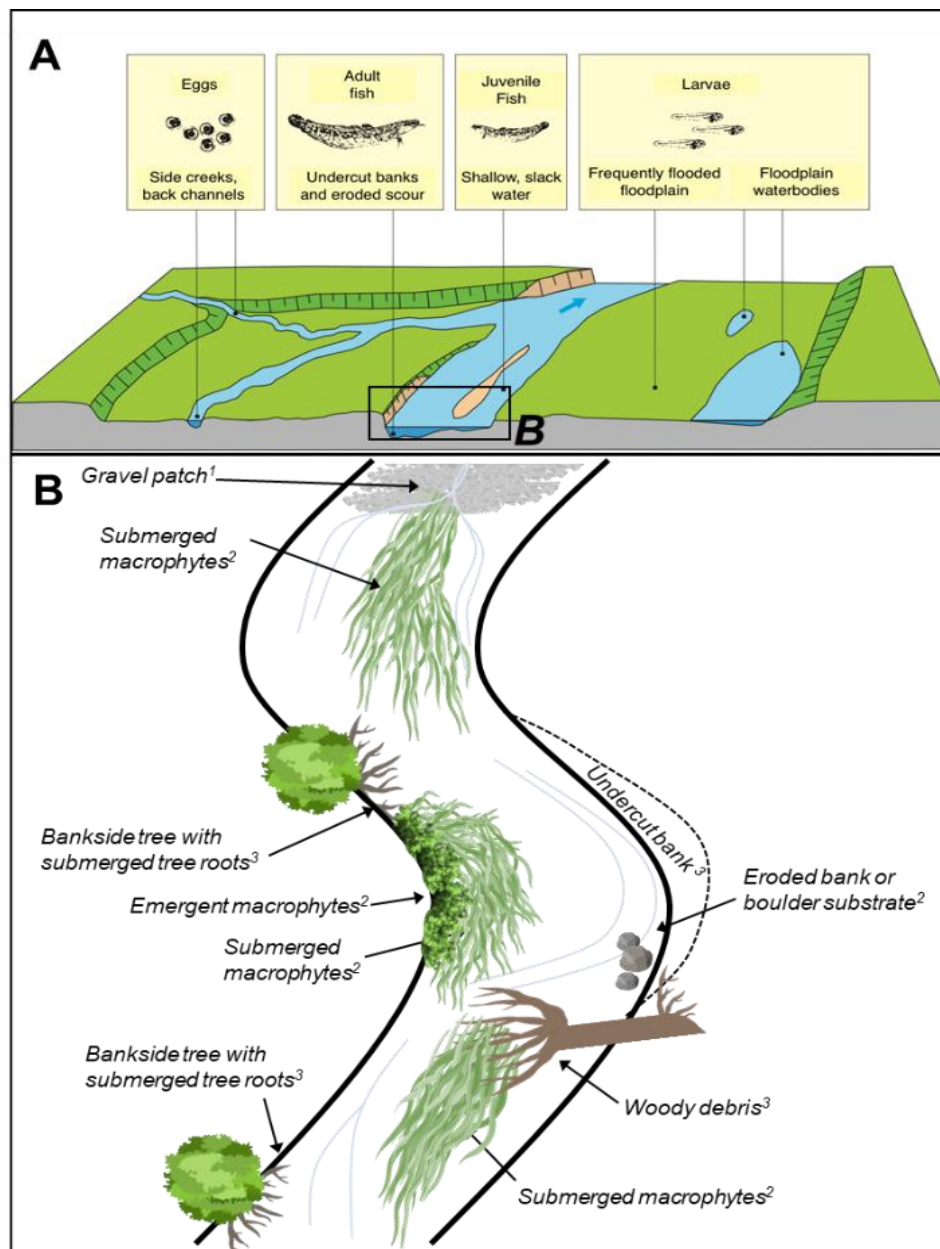


Figure 3.1. (A) Lateral habitat use by different burbot life stages (adapted from Bunzel-Drücke et al., 2004a) and (B) Example of burbot instream habitat use. ¹Instream spawning habitat, ²Juvenile habitats, ³Adult habitats.

Overall, the burbot reintroduction in Belgium cannot yet be considered a “successful” reintroduction as the low recruitment numbers suggest the population is not yet self-sustaining. The majority of burbot populations remaining in Europe, particularly the western European subclade (Van Houdt et al., 2005), are facing severe anthropogenic pressures, particularly habitat modification. Thus, it is likely that no ideal reference population or habitat can be used to assess burbot habitat use for each life stage and as a comparison to existing English river habitat. Belgium, however, represents a realistic comparison due to environmental similarities between lowland England and the rivers supporting reintroduced burbot in Belgium. Hence, the Belgium reintroduction acts as a potential framework to set relative expectations for how a reintroduced population to England could respond to the existing habitat.

3.1.2. River-Floodplain Habitat Assessments

The Belgian reintroduction programme identified the importance of grounding burbot ecology and biology within the habitat suitability assessment, and subsequent research identified the importance of lateral floodplain habitats and thus it is crucial that any habitat suitability assessment includes these aspects. A comparison of common river habitat surveys is given in Table 3.1.

While several methods for biophysical river habitat assessment are available for UK rivers, the River Habitat Survey (RHS) (Environment Agency, 1997; Raven et al., 1998) and the Modular Physical River Habitat Survey (MoRPh) (England et al., 2017) are most common and recommended by the EA. The RHS is a standardised river survey that allows for replicability and tracked change over time (but not ideally suited for regular monitoring) (Maddock, 1999; Naura et al., 2016), with data collected on physical biotopes, channel modification, geomorphology, and the riparian corridor (Harvey and Wallerstein, 2009). Moreover, a citizen River Habitat Survey was developed in 2021 to increase the scope of data collection. A large amount of data is collected for the small amount of time spent in the field and the RHS database provides extensive data across a large spatial and temporal scale to follow various research avenues including exploring river restoration impacts (Moore et al., 2021). Previously,

Table 3.1. Comparison of river survey methods that concern physical river habitat. 'Custom Walkover Survey' refers to the survey presented in this chapter

Survey	Type	Format	Standard Length	Conductors	Features Recorded	Time	Additional outputs	Advantages	Disadvantages	Sources
Custom Walkover Survey (This thesis)	Field and remote	Mapping	Various	Non-experts	23 (adaptable)	20 min per 100 m		+ Open source + Adaptable + Accessible + Spatial relationships preserved + Qualitative and quantitative + Species specific	- Snapshot in time - Inter-surveyor variability	
River Corridor Survey	Field	Mapping	500 m	NA	>51	NA	Feature analysis Floodplain habitat analysis	+Spatial relationships preserved + Qualitative and quantitative +Scalable	- Snapshot in time - Degree of spatial error	National Rivers Authority (1992) Angold et al. (1995) Gurnell et al. (1996)
River Habitat Survey (RHS)	Field	Tabular	500 m	Experts	> 200	57 min	>8 broad indices of habitat assessment that cover fluvial biogeomorphology	+ Extensive data collection + Quantitative + Database access	- Neglects floodplain - Expertise required, increases expense - Non-continuous - Snapshot in time	Fox et al. (1998) Harvey and Wallerstein (2009)
Modular River Physical Habitat Survey (MoRPh)	Field	Tabular	400 m	Non-experts	NA	NA	14 indices of habitat assessment	+ Accessible + Scalable + Open-source data sharing + Quantitative + Easily repeated	- Reduced data quality	England et al. (2017) Shuker et al. (2017)
System for Evaluating Rivers for Conservation (SERCON)	Field or remote	Tabular	500 m (up to 4 – 5 km per surveyor per day)	Experts	NA	NA		+ Extensive data collection + Wide spatial scope + Specifically designed for management	- Inaccessible for non-experts - Expensive	Boon et al. (1998)
PHABSIM	Field and remote	Computational	NA	Experts	NA		Daily suitable habitat sequence Habitat duration curve	+ Can use secondary data + Species specific + Quantitative	- Expensive - Time consuming - Expertise required - Simplistic	Spence and Hickley (2000)

RHS data have been used to identify specific species habitat availability for upland river birds (Buckton and Ormerod, 1997) and white clawed crayfish *Austropotamobius pallipes* (Naura and Robinson, 1998). When considering a burbot species reintroduction, however, the RHS does not collect sufficient data on floodplain habitat. Identifying spawning habitat availability on the floodplain as well as in-channel is crucial to a burbot reintroduction (Worthington et al., 2011a).

MoRPh follows a similar methodology to the RHS, conducting a tabular, bankside survey. It is sensitive to differences in hydraulic, sediment, geomorphological, and vegetation habitat characteristics (Shuker et al., 2017), and each 400 m survey module can be combined into a reach assessment, comprised of 10 modules, allowing for analysis through space and time (MoRPh10). The survey has the benefit of being simplified and open source compared to the RHS, allowing members of the public to undertake brief training to improve surveyor accuracy (Shuker et al., 2017). Though MoRPh can be scaled and takes into account floodplain features to an extent, lateral habitat is crucial to burbot life cycle completion and thus any riverine habitat assessment undertaken at the Wissey should examine lateral habitat in detail.

River Corridor Surveys (RCS) were designed by the National Rivers Authority and precedes RHS and MoRPh. The RCS produces 500 m standardised maps of vegetation structure and physical habitats within a water course (National Rivers Authority, 1992). The mapping approach preserves spatial relationships between features, but can be subjective, reducing spatial accuracy. This reduction in accuracy also influences the quality of quantitative data that can be extracted from the qualitative data (Gurnell et al., 1996). Considering the required application in this study, the RCS also maps up to 50 m of floodplain habitat either side of the river channel, which would allow potential spawning and larval nursery habitat to be captured.

Computer-based methods, such as Physical Habitat Simulation (PHABSIM) (Bovee, 1982), or other habitat suitability models (HSMs) offer certain advantages when

assessing physical river habitat. PHABSIM, though an environmental flow methodology, was created out of the need to better understand how changes in flow dynamics affect fish populations and aquatic communities (Spence and Hickley, 2000). It is a predictive model that uses hydraulic variables to determine habitat availability for a certain species (Gostner et al., 2013). While PHABSIM was originally praised for its ease-of-use, as other ecological modelling approaches have evolved, the base assumptions of the model and its operations have been shown to fall below current standards for ecological modelling (Armstrong and Nislow, 2012; Railsback, 2016). Other important criticisms are the small spatial area and short timescales it is able to consider (Shenton et al., 2012), and it has been considered expensive and time-consuming (Spence and Hickley, 2000). In terms of being suitable for assessing burbot habitat ahead of a reintroduction, there are clear shortcomings of the aforementioned modelling approaches. Any habitat suitability assessment needs to comprehensively assess habitat for different life stages across an area that is representative of where all life stages could occupy, which outstrips the limits of the PHABSIM model both temporally and spatially (Shenton et al., 2012). Alternatively, individual-based models, which are inclusive of demographic processes such as survival, reproduction, and dispersal (Bradter et al., 2021) focus on incorporating species biology and ecology at the core of the model and have been specifically designed to overcome the limitations of HSMs, including PHABSIM (Gore and Hamilton, 1996; Railsback, 2016). Though individual-based models require immense amounts of data on demographics that are often only available for well-studied species (Bradter et al., 2021), and they have not often been applied to fish species.

While existing field-based methods, such as MoRPh and RHS, have the advantage of collecting extensive geomorphological, hydrological, and ecological data, they could overlook the biological or ecological requirements that are required for a species-specific habitat assessment. These requirements and associations should be central when assessing habitat availability for the purpose of a fish species reintroduction. Conversely, computational models have the benefit of focusing directly on a species' habitat preferences and can even be directly guided by a species' ecology and biology, but offer their own limitations. Some are static and offer only a snapshot in time, while others are limited by spatial resolution. A direct barrier to modelling compared to field

surveys like MoRPh is the required technological expertise and associated resource costs (e.g., time) in producing HSMs. PHABSIM, for example, would not adequately address a large enough spatial area (i.e., multiple kilometres) that is required to assess a candidate reintroduction site. One method that stands out as potentially compatible with the aims of the assessment is the RCS due to its specific extension of the survey into the floodplain, which could gather qualitative information on potential spawning and larval nursery habitats (up to 50 m). The RCS captures over 50 features, so may also lack some of the biological and ecological requirements needed for a species-specific assessment to support a reintroduction. Though, the RCS method does have some limitations when it comes to data quality: the spatial inaccuracies that can be obtained through mapping can influence the accuracy of the quantitative data when extracted from the qualitative.

It is clear that when considering existing methods, there are benefits and limitations to all existing methodologies for the current context: assessing the habitat availability of a candidate reintroduction site for a fish species reintroduction. All have drawbacks, but the commonality between all is the neglect of the wider floodplain, which is an essential habitat component in burbot life history, except for the RCS. Though, in order to ensure the expansion of habitat suitability assessments beyond the candidate reintroduction site, an accessible, quick, species-centred protocol that can support fish species reintroductions is needed. Such protocols must explicitly capture the candidate species' ecology and biology, consider habitat associations across the life cycle, and align with available budget and expertise, since species reintroductions are often led by NGOs, particularly in the UK. In the case of the burbot, a species that uses both longitudinal and lateral habitats, then both instream and floodplain habitat must be considered.

The present study develops and applies a protocol for assessing instream and floodplain habitat for a candidate burbot reintroduction site to assess the extent of suitable habitat present for each life stage and contextualise habitat availability against Belgian reintroduction sites. The protocol draws on (i) published literature; and (ii) floodplain habitat assessments at three burbot reintroduction sites in Belgium. The

protocol is designed to evidence the suitability of the proposed reintroduction site to help support a potential future English burbot reintroduction programme.

3.2. Materials & Methods

3.2.1. Approach to Burbot Habitat Assessment Protocol

The candidate burbot reintroduction site is the River Wissey, Norfolk, UK. To ensure suitable habitat exists for burbot in the Wissey study site, river and river-floodplain habitat assessment protocols were developed. Field-based survey was combined with decision tree modelling to classify instream habitat based on published habitat preferences of the western European burbot subclade, the closest genetic relative to English burbot (Worthington et al., 2017). The comparison to a population of the same genetic subclade is crucial due to the different habitat uses and environmental requirements exhibited by each subclade. Analysis of remotely sensed data was used to identify and classify floodplain habitat suitability at a greater spatial scope than current existing survey methodologies (i.e., RCS, MoRPh) for the Wissey, in comparison to three burbot (western European subclade) reintroduction sites in Belgium (Van Houdt et al., 2005; Auwerx et al., 2019).

3.2.2. Field Site and Comparative Sites

The study was conducted across the entire Wissey study area (see Ch. 2; 7.34 km reach; 1.74 km² study area, 52°34'09"N, 000°42'48"E to 52°31'28"N, 000°42'00"E). The burbot reintroduction sites used for comparison with the Wissey (Table 2.3) are located along the Grote Nete (0.89 km², 51°8'37"N, 5°7'34"E to 51°9'7"N, 5°8'46"E; 1.41 km², 51°8'43"N, 5°9'5"E to 51°9'3"N, 5°10'29"E) and the rivers in the Viersels Gebroekt nature area, Klein Beek and Molenbeek (1.29 km², 51°11'19"N, 4°39'21"E to 51°10'32"N, 4°38'9"E), in Antwerp, Belgium. The Kleine Nete (where the Viersels Gebroekt rivers are tributaries) and Grote Nete are 50 km and 76 km, respectively. Here, three sections are compared to the proposed Wissey reintroduction site, referred to hereafter as Viersels Gebroekt, Straamolen and Scheps (Fig. 3.2).

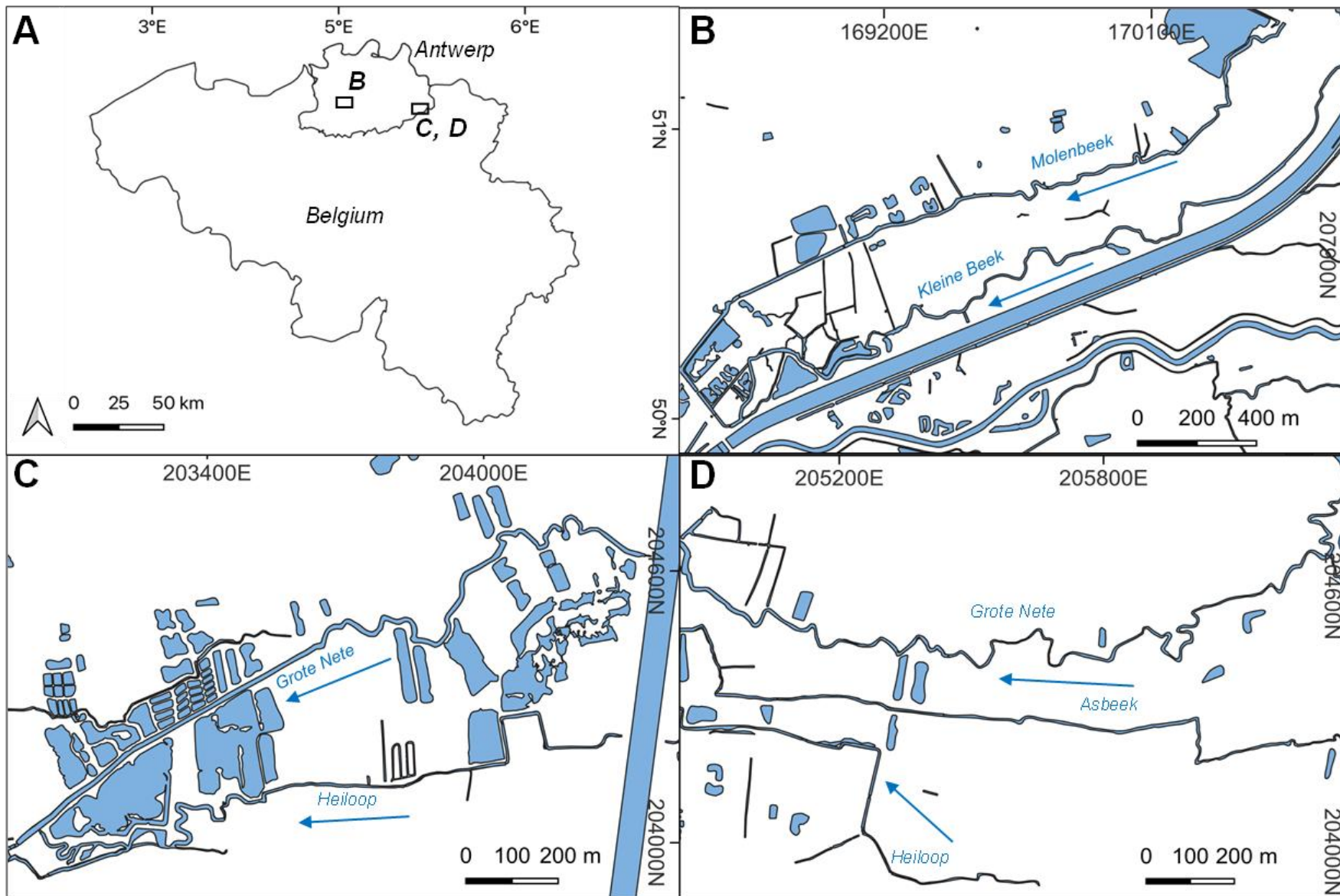


Figure 3.2. (A) Antwerp Province in Belgium highlighting (B) Viersels Gebroekt, (C) Straalmolen and (D) Scheps study area.

The Schepps site has the strongest evidence for natural recruitment (Vandamme et al., 2021) as well as multiple sightings of larvae in 2011, 2015, 2016 and 2017 at densities up to 13 individuals/m² (Vught et al., 2015; Pauwels et al., 2016; Vandamme et al., 2017). This is comparable to larval densities (c. 15 individuals/m²) just after hatching in presumed stable burbot populations (Ryder and Pesendorfer, 1992; Ghan and Sprules, 1993). INBO assessed the side channel within the site, Asbeek, as having suitable habitat for 0+ year burbot using their instream habitat methodology in 2011 (Van den Neucker et al., 2012). Juveniles were found in the Asbeek in 2010, 2014, and 2015 (Van den Neucker et al., 2010a; Vught et al., 2015; Pauwels et al., 2016). Moreover, after stocking above the instream mill, Hoolstmolen, within the Schepps site stopped in 2017, and in 2020, 20 burbot estimated to be <3 years old were found, providing the strongest evidence of natural recruitment, albeit in small numbers (Vandamme et al., 2020). Hence, this site represents an example of suitable habitat for all burbot life stages.

Straalmolen has lower instream habitat quality for adults and 0+ burbot (Van den Neucker et al., 2012), yet has recorded adults consistently and two juveniles were found in 2015 (Pauwels et al., 2016). In 2019, 2020, and 2021, 11, 9, and 4 larvae were found, respectively in the Heiloo side channel (Vandamme et al., 2020, 2021). The site represents an example of suspected suboptimal instream and floodplain habitat but supports burbot although natural recruitment cannot be definitively proven.

The final site, Viersels Gebroekt was chosen based on ~20 years of burbot reintroduction research at INBO as an anticipated site with high spawning and larval habitat suitability (Auwerx et al., 2019; J. Auwerx, pers. comms., 2023). Since 2011, Viersels Gebroekt has undergone restoration and the floodplains are suspected to be suitable for spawning and larvae as they are managed as an active wetland, providing ideal static waters for burbot larvae (J. Auwerx, pers. comms., 2023). Burbot larvae with yolksacs were released into this site from 2018 to 2021. Natural recruitment has not yet been observed, but 10 adults were found in this site between 2021-2022 (between 21 – 39.5 cm lengths).

3.2.3. Instream Habitat Classification

Habitat associations of the western European subclade were determined from a detailed literature review (Table 3.2). This revealed the distinct, frequent habitat associations for each burbot life stage, enabling a compilation of burbot-relevant features. Based on the review of river habitat assessment literature, a mapping approach similar to RCS was chosen to preserve spatial relationships between features to allow subsequent analysis of habitat connectivity. The RCS methodology, however, was streamlined to focus on burbot relevant features and conducted continuously across the whole study area.

3.2.3.1. *Survey design*

The survey was designed to achieve continuous coverage along river sections of varying length. Habitats were mapped to preserve detailed spatial relationships among habitat features (c.f. River Corridor Surveys; National Rivers Authority, 1992; Gurnell et al., 1996) rather than recorded via a tick-sheet (c.f. RHS and MoRPh). All known burbot relevant habitat features were cross-referenced with features captured in existing surveys (RHS and MoRPh) and any other established biophysical habitat categories (e.g. substrate categories; Wentworth, 1922; and flow biotopes; Newson and Newson, 2000) to ground the protocol in established methodologies, ensure rapid assessment, and maximise data compatibility (Padmore, 1998; Raven et al., 1998; Newson and Newson, 2000; Environment Agency, 2003; England et al., 2017). In total, 23 habitat features directly related to burbot ecology and biology were included (Table 3.2, Appendix 3).

3.2.3.2. *Survey Implementation at The Wissey*

The survey was applied to ~6 km of the River Wissey and ~1 km of its Watton Brook tributary (Fig. 2.1d). The river was divided into 100 m survey sections and habitats were mapped along sequential 10 m channel units using 5 m resolution basemaps (OS MasterMap® Topography 1: 1250 shapefile; Ordnance Survey (2021)). Each channel unit was photographed, instream habitat features mapped, average water depth (cm) measured or estimated, and channel width at bankfull (m) recorded using

Table 3.2. Burbot-relevant features identified from literature review and classified during instream habitat analysis, their definitions and sources, and RHS equivalent name. Recorded name in River Habitat Survey source: Environment Agency (2003).

Feature	Definition source(s)	Relation to burbot ecology/biology	Source(s) for burbot	Recorded name in River Habitat Survey
Channel spanning barriers/ Anthropogenic structures	Environment Agency (2003)	Low swimming endurance, any barrier could impact the migration of migratory burbot	Koporikov and Bogdanov (2011)	Artificial Structures
Wooded adjacent land use within 10 m	Environment Agency (2003)	Known spawning habitat during inundation; riparian shading.	Worthington et al. (2012); Pusey and Arthington (2003)	Broadleaf/mixed woodland (semi-natural); Broadleaf/mixed plantation; Coniferous woodland (semi-natural); Coniferous plantation
Grassland/meadow adjacent land use within 10 m	Environment Agency (2003)	Known spawning habitat during inundation	Müller (1957), Worthington et al. (2012)	Improved/semi-improved grassland
Floodplain ponds	Gurnell et al. (2019)	Larvae refuge when winter flooding recedes	Brackwehr et al. (2016)	Natural open water
Side channels	Environment Agency (2003)	Back/side channels shelter juveniles and acts as spawning habitat.	Aarts et al. (2004), Worthington et al. (2012), Jude et al. (2013)	Side channels
Flood banks (with height estimation)	Environment Agency (2003)	Identification of barriers preventing access to lateral spawning habitat	Bosveld et al. (2015), Wetjen et al. (2020)	Combined with artificial/modified bank profiles and channel dimensions
Trees close to riverbank (within 10 m)		Riparian shading; potential sources of instream wood.	Pusey and Arthington (2003); Worthington et al. (2012)	Extent of trees and associated features
River shading by trees	Environment Agency (2003)	Riparian shading	Pusey and Arthington (2003)	Shading of channel
Overhanging branches trailing water	Environment Agency (2003)	Cover and shelter for juveniles	Worthington et al. (2012)	Shading of boughs
Underwater tree roots	Environment Agency (2003)	Shelter habitat for adults	Dillen et al. (2008)	Underwater tree roots
Pools	Newson & Newson (2000)	Adult habitat	Eick (2013)	Pool
Run	Newson & Newson (2000)	Proxy indicator of velocity, determines habitat suitability	Müller (1957), Sorokin (1971)	Rippled flow
Glides	Newson & Newson (2000)	Proxy for slow-flowing habitat, suitable for juveniles	Dillen et al. (2008)	Smooth flow
Riffles	Newson & Newson (2000)	Proxy indicator for shallow water habitat	Müller (1957), Sorokin (1971)	Unbroken standing waves
Slack water	Newson & Newson (2000)	Juvenile habitat	Dillen et al. (2008); Worthington et al. (2012)	Marginal dead water; no perceptible flow
Undercut banks	Gurnell & Shuker (2022)	Shelter habitat for adults	Dillen et al. (2008)	Undercut bank profile
Boulders	Wentworth (1922)	Shelter habitat for adults	Fischer (2000b)	Boulder
Gravel/cobble	Wentworth (1922)	Instream spawning substrate	Jude et al. (2013)	Cobble; gravel/pebble
Fine sediments	Wentworth (1922)	Instream spawning substrate	Sorokin (1971)	Sand; silt; clay
Fallen trees	Environment Agency (2003)	Shelter habitat for adults and juveniles	Worthington et al. (2012)	Fallen trees
Instream wood	Thevenet et al. (1998)	Shelter habitat for adults and juveniles	Dillen et al. (2008), Worthington et al. (2012)	Large woody debris
Submerged vegetation	macrophyte Gurnell & Shuker (2022)	Shelter habitat for juveniles	Dillen et al. (2008)	Submerged broad leaved; submerged linear leaved; submerged fine leaved
Emergent vegetation	macrophyte Gurnell & Shuker (2022)	Shelter habitat for juveniles	Müller (1957); Dillen et al. (2008)	Emergent broad-leaved herbs; Emergent reeds/ sedges/ rushes/ grasses/ horsetails

a Nikon LASER 30 rangefinder (± 0.5 m). Key habitat features were geolocated using a handheld GPS ($\pm 3 - 20$ m). Visual estimates were made for submerged macrophyte cover (%), dominant substrate type, flow type, canopy shading (%), flood bank height (m), floodplain land use, and presence of instream wood, tree roots, and undercut banks. Evidence of river restoration (e.g., berms or pinned wood pieces) or anthropogenic modification (e.g., bridges or bank reinforcements) were recorded. The survey was completed in eight days over two-weeks in August/September 2021, a period ideal for assessing habitat availability for YOY and adult burbot, due to high water clarity and macrophyte cover (Dillen et al., 2005). Survey maps were scanned, georeferenced using nine, equally spaced ground control points that were identified from the OS map grids, and digitised. Digitisation into geospatial software enabled the quantification of frequency and areal cover of habitat features in each 10 m channel unit ($n = 734$) using the buffer tool and zonal statistics in QGIS (v.3.18.3). Water clarity and hence visibility was high on all survey days but one, resulting in minimal missing data ($n = 97$, 13%). From the extracted quantitative data, analysis of the relationship between variables (i.e., depth, macrophyte percentage cover, slack water patches, shelter structures) and space (i.e., distance downstream) were analysed using Pearsons's correlation coefficients (r).

3.2.3.3. *Decision Tree Classification, Construction and Calibration*

A decision tree classifier was used to classify each channel unit as suitable habitat for either adult, juvenile or instream burbot spawning, or as unsuitable, using the Gini index (Equation 1; Breiman, 2017). A decision tree was chosen as the aim was to produce an accurate classifier system rather than investigating the predictive structure of the variables (Breiman, 2017). The Gini index is given as:

$$Gini = 1 - \sum_{i=1}^n (p_i)^2 \quad (1)$$

Where p_i is the probability of a channel unit being classified as a particular class and n is the number of units in the class. Variables were selected for the systematic construction of the decision tree based on the known burbot habitat preferences given

in Table 3.3. The categorical variables used to determine habitat suitability classification were water depth, dominant substrate, macrophyte percentage cover, dominant flow type and presence of shelter opportunities (i.e., instream wood, tree roots, or undercut banks), and presence of flow refugia (i.e., slack water patches). Categorical data can streamline model structure by reducing possible associations between variables. Channel units containing missing data were excluded from the analysis prior to decision tree construction.

To build the decision tree, a 20% ($n = 125$) subsample of channel units was obtained through random sampling and manually classified into adult, juvenile, and spawning burbot habitat using Table 3.3. The Gini index was then manually calculated for each variable to determine which variable had the greatest probability of dividing the data into a specific group (Breiman, 2017). This process selected water depth as the root node variable, followed by macrophyte cover and substrate type, with shelter presence used as the final level (Table 3.4). The manual classification was checked computationally using the 'rpart' package (v.4.1.19) (Therneau et al., 2022) in R (v2022.7.2). The rules from the computational decision tree followed those calculated during the manual classification, and thus, the structure of the decision tree (Table 3.4), was subsequently employed to predict the outcome of the remaining dataset (i.e., the 80% subsample) using the 'rpart.predict' function. If a channel unit did not contain any of the features of adult, juvenile, or instream spawning habitat, it was labelled unsuitable. The constructed tree classification model predicted the remaining 80% successfully. After classification, a nearest neighbour analysis was used to identify trends in the spatial distribution of adult, juvenile, spawning, and unsuitable habitat classifications, to understand connectivity between the same classifications across the Wissey site.

Table 3.3. Variables included in the classification for instream habitat and relevance to burbot ecology and biology derived from the literature on burbot habitat preference across life stage and amalgamation of variables for decision tree analysis based on data observed during field survey

Variable	Burbot Relevance	Source(s)	Data Type	Min.	Max.	New Categorisations
Depth (cm)	Indicator of adult habitat, known to occupy the deepest habitat available; known to spawn in shallow areas	Eick (2013); Jude et al. (2013)	Scale	5cm	200cm	"Shallow": ≤ 50 cm "Mid": $51 \leq x \leq 99$ cm "Deep": ≥ 100 cm
Macrophyte Cover (%)	High macrophyte cover provides juvenile habitat	Dillen et al. (2008)	Scale	0%	100%	"Low": ≤ 30 % "Medium": $31 \leq x \leq 59$ % "High": ≥ 60 %
Dominant substrate type	Gravel patches are an instream spawning strategy	Jude et al. (2013)	Categorical			"Fine": silt, sand, silt and sand "Coarse": gravel, cobble, gravel and cobble "Mixed": mixed substrates "NV": not visible
Dominant flow type	Pools are occupied by adults; slack water and glide flow type indicate slow flow conditions suitable for juveniles	Eick (2013)	Binary	0	1	
Slack water patches	Occupied by juveniles	Worthington et al. (2012)	Binary	0	1	
Submerged tree roots*	Shelter for adults	Dillen et al. (2008), Worthington et al. (2012)	Binary	0	1	
Undercut banks*	Shelter for adults	Dillen et al. (2008)	Binary	0	1	
Instream wood*	Shelter for adults	Worthington et al. (2012)	Binary	0	1	

* = All aggregated into:
"Shelter Present": one or more of any categories present
"Shelter Absent": no category present

Table 3.4. Gini Indices used to construct decision tree from a manual sort of the 20% subsample. Bold text highlights lowest Gini index and thus the variable chosen for the leaf node to divide the data group

Decision Tree Level	Depth	Macrophyte Cover	Substrate	Shelter	Slack	Flow Type
Root Node	0.335	0.617	0.585	0.683	0.685	0.621
Level 1, left branch		0.143	0.574	0.47	0.53	0.487
Level 1, right branch		0.29	0	0.326	0.327	0.281
Level 2				0.114	0.408	0.396
Level 3					0.267	0

3.2.4. Floodplain Habitat Classification and Comparison

A remote sensing approach was used to classify floodplain habitats (Fig. 3.3), enabling more extensive spatial coverage at lower spatial resolution than required for instream

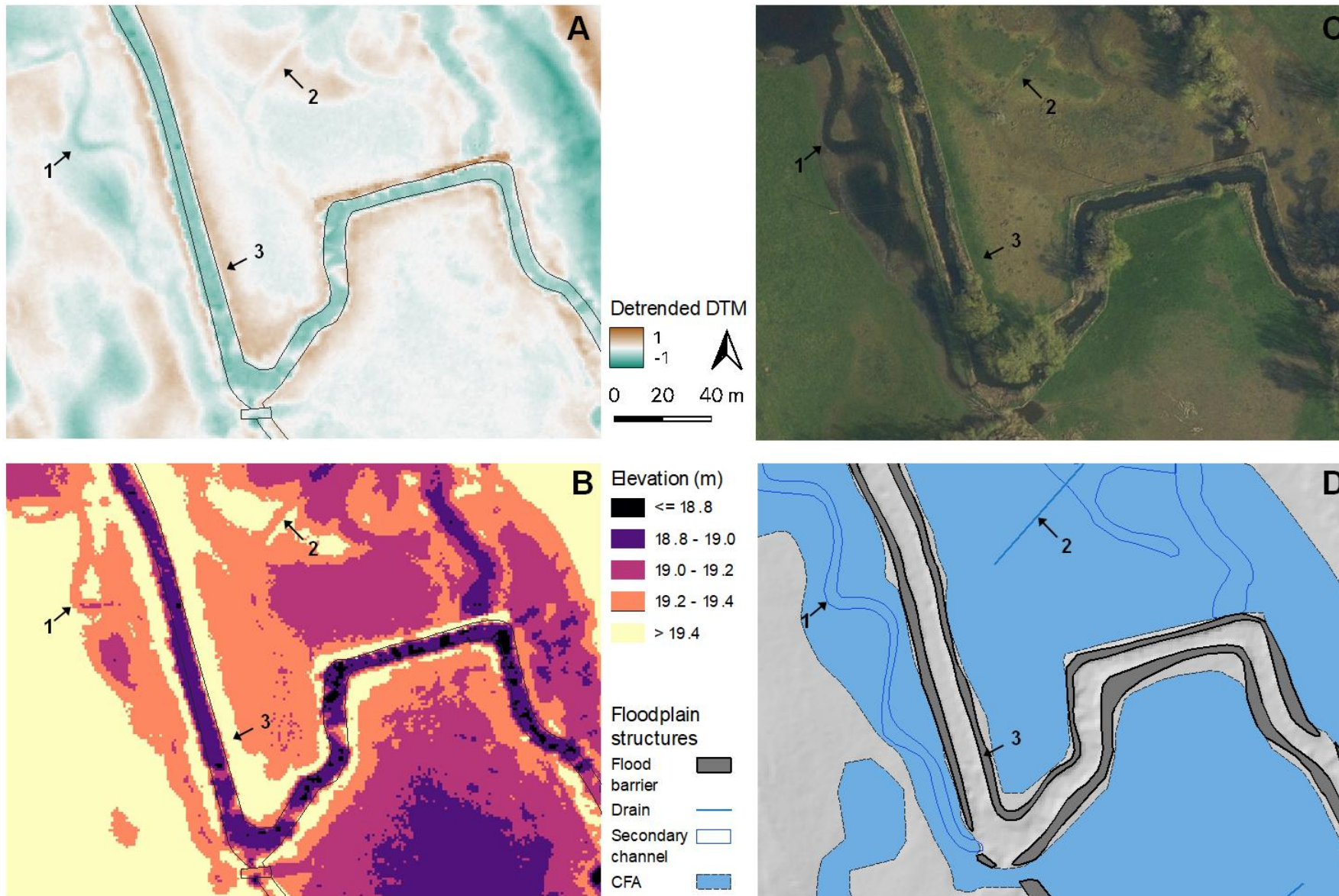


Figure 3.3. Example of lateral habitat classification from 52°33'31"N, 000°41'30"E to 52°33'37"N, 000°41'44"E of River Wissey. The classification compares (A) a detrended 1 m resolution LiDAR DTM layer from 2018, (B) 1 m resolution LiDAR DTM showing a range of 1.5 m elevation changes, and (C) aerial imagery from winter 2020 at 25 cm resolution to corroborate older LiDAR sources, to produce (D) a digitised classification of lateral habitats on top of a hill shade layer. Comparing the images, the example identification of (1) a secondary channel, (2) a drain, and (3) a flood barrier.

habitat features (Shuker et al., 2017; Roni et al., 2019). Compared to instream riverine habitat research, few studies attempt to classify floodplain habitat (Varga et al., 2013; Campana et al., 2014; Rinaldi et al., 2017), but often employ LiDAR and aerial imagery to identify floodplain features (e.g., secondary channels). This approach was applied to indicate presence of burbot spawning habitat. The Wissey floodplain was classified using 25 cm resolution aerial imagery from winter 2020 (EDINA Aerial Digimap Service, 2021) and 1 m resolution Digital Terrain Model (DTM) imagery from 2018 (EDINA Aerial Digimap Service, 2020). This imagery was the latest available with high spatial resolution. For the Grote Nete and Viersels Gebroekt sites the latest available LiDAR imagery was used: Digitaal Hoogtemodel Vlaanderen II from 2013 with 1 m resolution (Digitaal Vlaanderen, 2014), in combination with aerial imagery from winter 2021 at 25 cm resolution (Digitaal Vlaanderen, 2021). Detrended DTMs were created for each site to smooth elevation differences and assist feature identification (Steenvoorden et al., 2023). DTM-identified features were verified using aerial imagery across all sites and only verified features were retained for analysis. Raster calculator and zonal statistics tools in QGIS were used to calculate coverage of floodplain features across the sites.

The resolution of the remotely sensed data enabled identification of five floodplain features: floodplain extent, secondary channels, connected floodable areas (CFAs), drains, and flood barriers. Floodplain extent was determined through manual inspection of the LiDAR data and delineated by sudden elevation difference in the DTM (Nardi et al., 2006). Secondary channels were defined as channels that existed in the floodplain (wetted or dry), which may or may not be connected to the main channel (David et al., 2017). Drains were identified as narrow and linear channels in the floodplain (Bailly et al., 2008). CFAs were determined as areas of similar elevation (within 40 cm) which might have potential to connect during a hypothetical flood event, similar to the use of elevation to identify flood risk areas (Coveney and Roberts, 2017). To verify the flood magnitude needed to achieve delineated CFAs, hydraulic modelling would be necessary at a later stage. The CFAs presently are used to identify priority areas of potential spawning habitat that can be investigated hydrologically in further research. Based on data collected during this study (see Ch. 5), average 40 cm depth on floodplains would correlate with main channels flows of $\sim 0.6 \text{ m s}^{-1}$ (i.e.,

<Q₅). This indicates that the CFAs map high flood scenarios, close to maximum floodplain inundation extent, which should be considered when interpreting results.

Flood barriers were classified as structures of higher elevation, such as walls, irrigation canals, raised footpaths, or flood banks that represent a physical barrier within the floodplain (Environment Agency, 2003). Floodplain features were manually digitised using polygon features in QGIS. The average height of flood barriers (m) relative to local floodplain elevation was calculated using zonal statistics. To compare differences between sites for recorded features, Kruskal-Wallis tests were conducted on the non-parametric data in R (v2022.7.2).

3.3. Results

3.3.1. Instream Burbot Habitat Suitability at the Wissey

The decision tree classification showed suitable burbot habitat for adults and juveniles, and instream spawning present at the Wissey site (Fig. 3.4, 3.5). The spatial distribution of habitat types revealed that all habitat classifications for each life stage are clustered within the lower part of the site, providing an array of connected mesohabitats: instream wood, macrophyte cover, deep pools, and gravel beds. Fig. 3.6 demonstrates some of the complex, burbot-relevant meso-habitats observed in the Wissey study area. In contrast, unsuitable habitat patches showed the least strong spatial trend or clustering (Table 3.5).

Table 3.5. Nearest neighbour analysis demonstrating the average proximity between specific channel unit classifications to demonstrate the connectivity of the same classified channel units across the study area, with life stage classifications representative of a specific combination of habitat features suitable to each life stage.

Classification	Count	Observed Mean Distance	Expected Mean Distance	ANNI	Z-Score
Adult	146	22.77	102.46	0.22	-17.98
Juvenile	127	28.56	110.29	0.26	-15.98
Spawning	74	36.53	142.89	0.26	-12.25
Unsuitable	291	15.4	80.25	0.19	-26.37

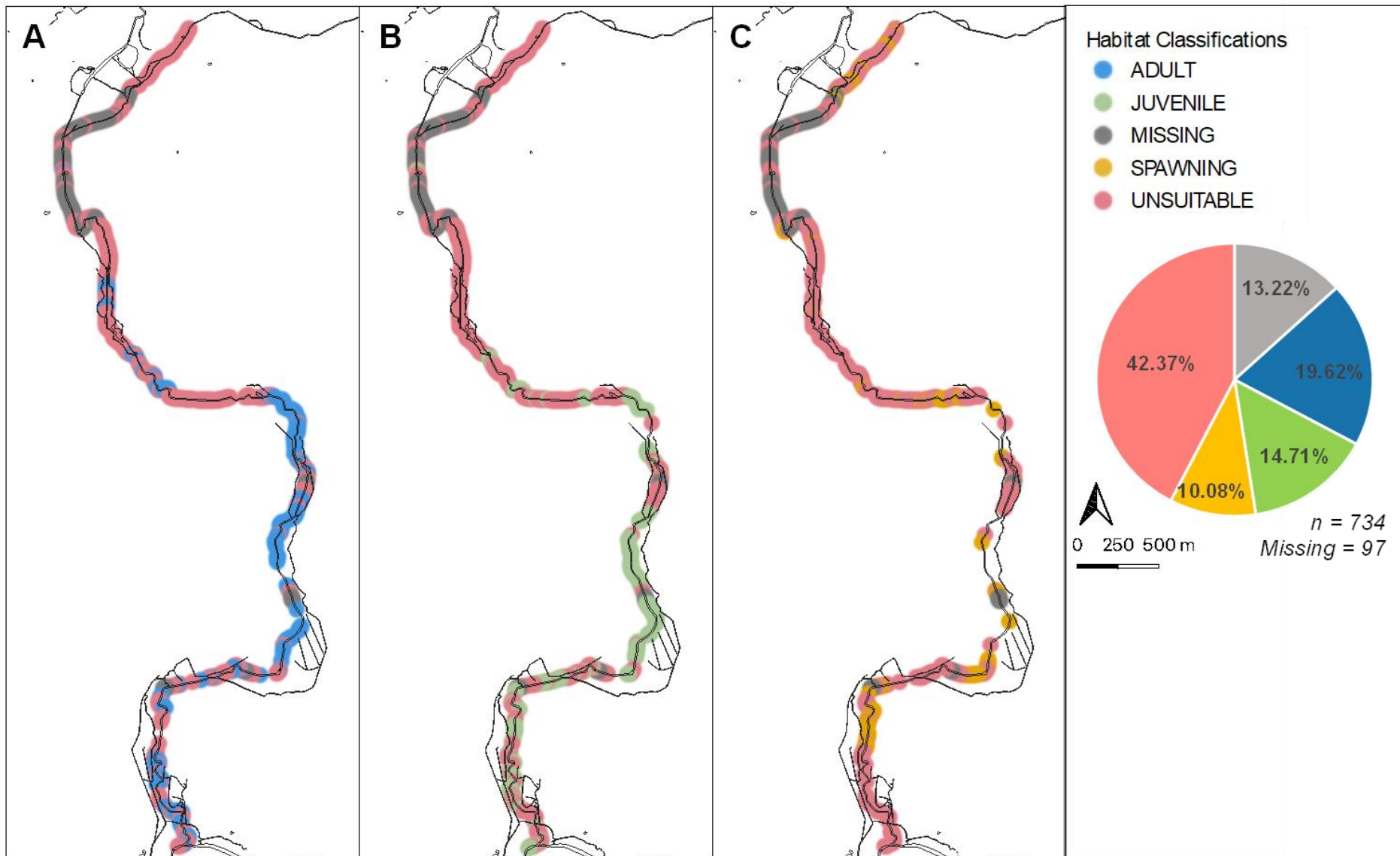


Figure 3.4. Habitat suitability for each burbot life stage with missing data (grey) and unsuitable (pink) spots included for location of (A) adult suitable habitat, (B) juvenile suitable habitat, and (C) instream spawning suitable habitat. Each circle represents a 10 m unit that has been scaled to 100 m diameter for visibility in the figure.

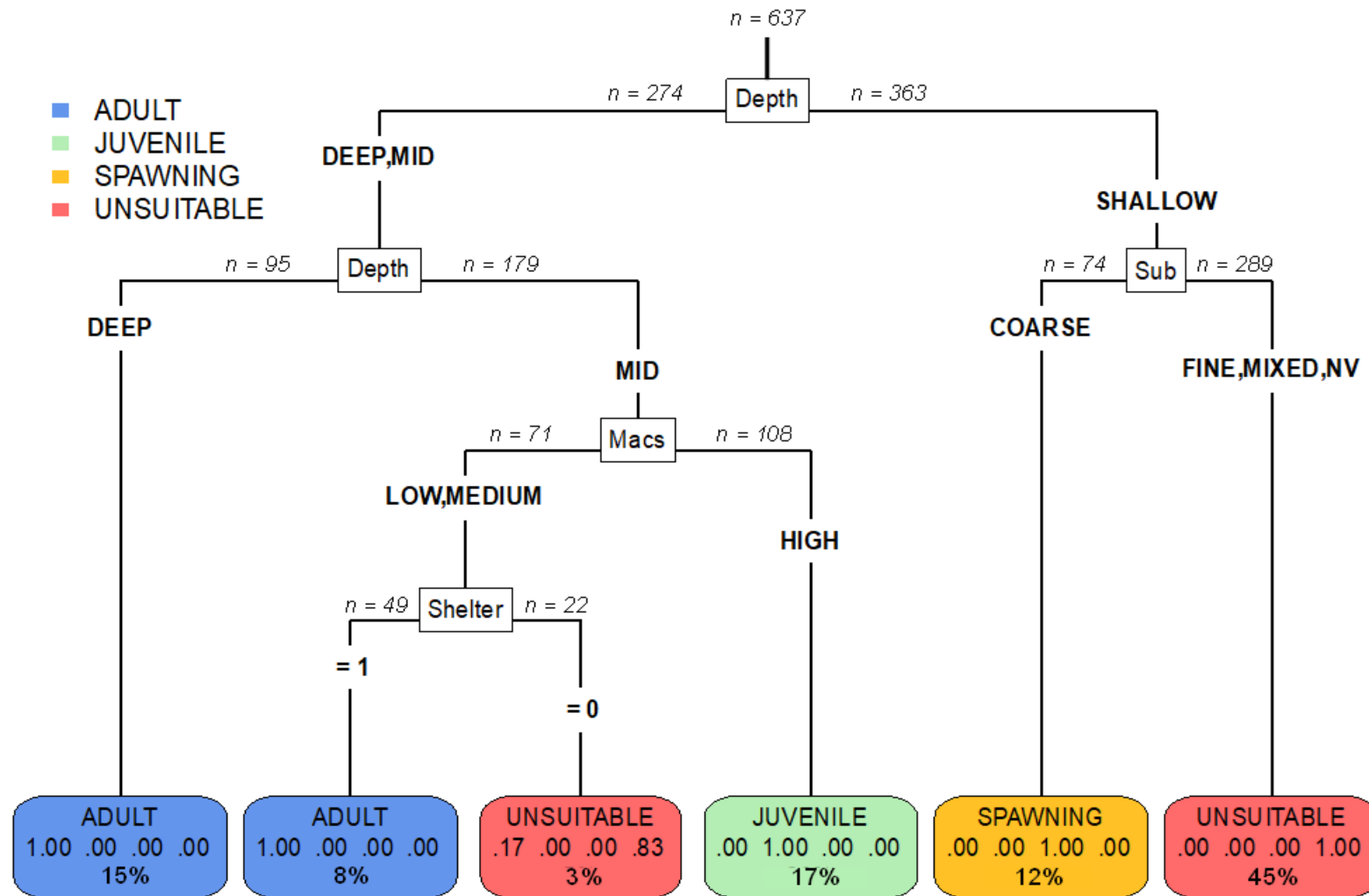


Figure 3.5. Final decision tree classifier generated by RStudio showing splits and group sizes. Terminal nodes show percentage of total units classified into that node and probability of classification for each group in decimals (adult, juvenile, spawning, and unsuitable from left to right). Groups are proportionally larger than those displayed in Fig. 3.4 as missing data were excluded.



Figure 3.6. Mesohabitats recorded during the habitat surveying of summer 2021, showing identifiable habitats that burbot have been evidenced in other rivers and have preference for based on the literature. (A) Fallen trees alter flow dynamics to form pools, utilised by adults; (B) a wetted back channel with dense macrophytes, potential habitat for juveniles; (C) Dense midstream emergent and floating macrophytes, potential shelter habitat for juveniles; (D) Complex tree root structures extending into the main channel with plenty of submerged macrophytes, potential shelter habitat for adults and juveniles; (E) A fallen tree has created lateral slack water patches that could shelter larvae or YOY fish, while the macrophytes could be utilised by juveniles, and the woody pieces by adults for shelter; (F) A shallow gravel run, potential instream spawning habitat.

Key features that determine habitat suitability for adult burbot include water depth and flow type, such as pools, and presence of shelter structures. Average water depth was 54.03 ± 34.7 cm, and depth increased with distance downstream ($r = 0.48$, $p = <0.001$) with a concentration of deep-water patches (≥ 100 cm) in the downstream half of the study reach. The most common flow type was glide, indicative of slow flow conditions (84% of channel units), followed by run and pool (8% and 3%, respectively). Over half of the channel units (56%) had shelter opportunities present as instream wood (32%), submerged tree roots (25%), and undercut banks (30%). Over 859 bankside trees were recorded in total, averaging 117 km^{-1} and instream wood averaged 51 pieces km^{-1} . The most common type was large wood, which occurred in 14% of all units. Fallen trees occurred in 80 units (11%), but more complex wood structures, such as jams, occurred in only 11 channel units (2%). Smaller pieces of wood were present in 37 units (5%). The occurrence of instream wood and tree roots decreased slightly with distance downstream ($r = -0.14$, $p = <0.001$ and -0.17 , $p = <0.001$ respectively), while presence of undercut banks had no statistically significant change with distance downstream ($r = 0.015$, $p = 0.6752$). The nearest neighbour analysis shows a distinct clustering of adult habitat ($z = -17.97$) with a low mean observed distance (22.76 m). The longest stretch of adult habitat was 150 m, with this the only occurrence of continuous habitat exceeding 100 m, and adult suitable habitat was absent from the upper 2 km of the study reach. An important observation from the instream habitat survey was the lack of definitive barriers that would limit longitudinal connectivity, and thus influence seasonal burbot migrations, but a sluice was found at $52^\circ 33' 32.418''\text{N}$, $0^\circ 41' 44.00923''\text{E}$. The sluice is 1.8 m wide and approximately 0.5 m in height (estimated from LiDAR data).

Juvenile habitat suitability was associated with high macrophyte cover and slow flow conditions. Average macrophyte percentage cover was $56 \pm 28\%$ and 49% of the study length had high macrophyte cover ($\geq 60\%$ cover). In total, 11 species of floating and submerged plants were identified during the survey, with a maximum of five species recorded in a channel unit. *Helosciadium nodiflorum* was the most common plant and was recorded in 395 (54%) habitat units. *Ranunculus penicillatus* subsp. *pseudofluitans* occurred in 221 (30%) habitat units. Around 2% of the study length had

slack water as the dominant flow type and over one third (38%) had an identifiable lateral or marginal slack water patch. Occurrence of macrophytes and slack water patches increased slightly with distance downstream ($r = 0.25$, $p = <0.001$; $r = 0.32$, $p = <0.001$, respectively) and juvenile habitat was also clustered with a low average nearest neighbour index (ANNI) score of 0.26, but a higher observed mean distance (28.56 m) compared to adult habitat (Table 3.5). There was a concentration of juvenile habitat in the downstream sections of the reach. Continuous suitable juvenile habitat stretches reached a maximum of 130 m.

Instream spawning habitat includes shallow waters and coarse substrates. In total, 363 (49%) channel units were classified as shallow water habitat (≤ 50 cm). Fine sediment (silt or sand) was the dominant substrate type (48%), and only 17% of the study length contained ideal instream spawning habitat (coarse gravel/cobble). The longest continuous stretch of gravel or cobble substrate was 120 m. The spatial distribution of suitable instream spawning habitat was uneven and non-random according to nearest neighbour analysis, but there was no clear spatial trend with the low z score ($z = -12.25$) and high mean distance (36.53 m) suggesting a lack of spatial connectivity. The longest continuous stretch of spawning habitat was 70 m.

In total, 43% of the instream habitat was classified as unsuitable burbot habitat (Fig. 3.4, 3.5), most commonly due to fine substrate-dominance when channel units had shallow depths (289 units; 39%). Unsuitable habitat was concentrated in the upper part of the site (maximum stretch 280 m; Fig. 3.4). Spatial clustering of unsuitable channel units is supported by the nearest neighbour analysis, which showed the unsuitable classification to have the lowest ANNI score (0.19), the lowest z -score ($z = -26.37$), and lowest observed mean distance (15.4 m), suggesting a more even spatial distribution, due to the high frequency of occurrence throughout the study area.

3.3.2. Wissey and Belgian Floodplain Habitat Analyses

For the Wissey, Viersels Gebroekt, Straalmolen, and Scheps, the floodplain analysis classified 61%, 49%, 49% and 20% of total floodplain extent, respectively. Maximum

floodplain width was 1.02 km for the Scheps study area, 0.68 km for both Viersels Gebroekt and Straalmolen and 0.84 km for the Wissey. Comparatively, the Wissey had the smallest minimum width of 0.07 km, while Viersels Gebroekt had 0.3 km, Straalmolen 0.5, and Scheps 0.7 km. Table 3.6 compares summary statistics for all four sites. The Kruskal-Wallis test showed that the differences between all sites were statistically significant ($p = <0.05$) for all floodplain features identified, except for flood barrier height ($p = 0.26$).

Table 3.6. Summary statistics for the floodplain habitats classified during this study. Count refers to the total number of individual floodplain features under each category and thus unit for each category does not apply. *Indicates values for flood barriers adjacent to main channel of the Grote Nete only.

Variables	Wissey	Viersels Gebroekt	Straalmolen	Scheps
Total Floodplain Extent (km²)	1.74	1.29	0.89	1.41
Connected Floodable Area (km²)				
Count	86	19	66	44
Total	0.885	0.515	0.36	0.212
Mean	0.01	0.028	0.054	0.0048
Median	0.0005	0.0009	0.001	0.0035
Minimum	0.000001	0.0002	0.00008	0.0004
Maximum	0.28	0.25	0.11	0.026
Drains (km)				
Count	29	92	58	202
Total	4.7	10.66	8.6	21.16
Mean	0.16	0.16	0.15	0.1
Median	0.14	0.1	0.13	0.08
Minimum	0.05	0.02	0.02	0.01
Maximum	0.67	0.29	0.51	0.47
Secondary Channels (km)				
Count	37	8	6	8
Total	16.04	1.37	3.6	3.87
Mean	0.23	0.17	0.6	0.48
Median	0.12	0.08	0.15	0.13
Minimum	0.03	0.04	0.09	0.02
Maximum	2.36	0.52	2.23	2.03
Flood barriers (km)				
Count	69	32	24	82
Total	7.4	5.6	3.21*	3.86
Mean	0.14	0.17	0.27*	0.05
Median	0.1	0.1	0.1*	0.04
Minimum	0.01	0.004	0.02*	0.004
Maximum	0.56	0.85	1.4*	0.26

3.3.2.1. Proposed Reintroduction Site – River Wissey

Connected floodable areas (CFAs) comprised 51% of Wissey floodplain. Mean CFA was 0.01 km², and the range of individual CFAs was large (0.000001 - 0.28 km²) (Fig.

3.7a). CFA size distribution was positively skewed with most CFAs typically smaller. The Wissey had 37 secondary channels, comprising 5% of the floodplain. The total secondary channel length was 16.04 km, over 2.23x river length in the study reach. In total, 29 individual drains were identified, totalling 4.7 km. Five drains led directly into the main channel, 17 into secondary channels with seven appearing to be hydrologically isolated from the river network. Floodplain storage capacity (i.e., combined area of CFAs, secondary channels, drains) was 0.98 km², so ~56% of the floodplain could provide spawning and larval habitat, although this may be further limited by hydrological (dis)connectivity not directly captured here, as connectivity was assessed only in relation to flood barriers. The Wissey had 69 flood barriers, average flood barrier height was 0.44 m and the maximum flood barrier height at a single point was 2.48 m (Fig. 3.7b). In total, 2.57 km (29%) of main river channel was free from barriers on both sides. The total river length with embankments on both banks was 2.33 km, comprising 26% of the main channel, and the maximum length of river with double embankment was 0.29 km (3%). A stretch of 0.56 km (6% of total river length) was the longest single flood barrier.

3.3.2.2. Exemplar Reintroduction Site – Viersels Gebroekt

For Viersels Gebroekt, 42% of the floodplain was classified as CFA, but individual CFA size was on average larger in size compared to the Wissey (Table 3.6). Viersels Gebroekt had eight secondary channels, with five connected directly to Kleine Beek and three connected to the drain network. The secondary channels were overall smaller in terms of total floodplain area (0.4%) compared to the Wissey. Total secondary channel length was also lower than the Wissey at 1.4 km (4.2x smaller than the Viersels Gebroekt reaches combined). Compared to the Wissey, there were triple the number of drains at Viersels Gebroekt (92), with 10.7 km total length being 1.5x longer than the Viersels Gebroekt total river lengths combined (Fig. 3.7c). Of the 91 drains, 67 led directly into the main rivers, with 24 appearing to be hydrologically isolated from the river network. Floodplain storage capacity was 0.55 km² (42% total floodplain extent), smaller relatively and absolutely compared to the Wissey.. Viersels Gebroekt had 32 flood barriers (~7% floodplain extent). Average flood barrier height was 0.42 m, and maximum height at a single point was 2.49 m, similar to the Wissey

(Fig. 3.7b). For the Molenbeek, 0.045 km (2%) was free from barriers on both sides, compared to 0.182 km (6%) for the Kleine Beek, both being more embanked than the Wissey. Compared to the Wissey, the Molenbeek and Kleine Beek had less occurrences of double embankments: 0.18 km (7%) and 0.47 km (15%), respectively. The Molenbeek and Kleine Beek also had shorter maximum stretches of double embankment compared to the Wissey at 0.098 km (4%) and 0.182 km (6%), respectively. The Molenbeek had a longer continuous stretch of flood bank on one side compared to the Wissey at 0.85 km (32%), while the Kleine Beek's was shorter at 0.4 km (12%).

3.3.2.3. Exemplar Reintroduction Site – Straalmolen

For Straalmolen, 41% of floodplain was classified as CFA. Similar to the Wissey, Straalmolen had many smaller CFAs (Fig. 3.7a), but these were larger on average (Table 3.6). Straalmolen had 6 secondary channels, comprising a lower proportion (2%) of floodplain comparatively. Total secondary channel length was 3.63 km, less than the total secondary channel length for the Wissey, and just under 1.75x the length of the Straalmolen reach. The site had 58 distinct drains, 20 directly linked to the main channel, and 27 appearing to be hydrologically isolated from the river network. Total drain length was 8.6 km, 3.34x longer than Straalmolen and 2x that of the total Wissey drains. The narrower range of drain lengths (Table 3.6), yet greater total drain length compared to the Wissey suggests Straalmolen had more short-length drains (Fig. 3.7c). Floodplain storage capacity was 0.38 km² (43% of floodplain extent). Straalmolen had 24 individual flood barriers (6% of floodplain). Average flood barrier height was 0.53, and maximum height at a single point was 2.72 m (Fig. 3.7b). Just 0.067 km (3%) of the Straalmolen stretch was free from embankments on either side. In total, 1.6 km (82%) of the study reach had double embankments, markedly more than the Wissey. The longest continuous flood barrier was 1.37 km (70%), also longer than the Wissey. Overall, Straalmolen was characterised by fewer, yet longer flood barriers (Fig. 3.7d).

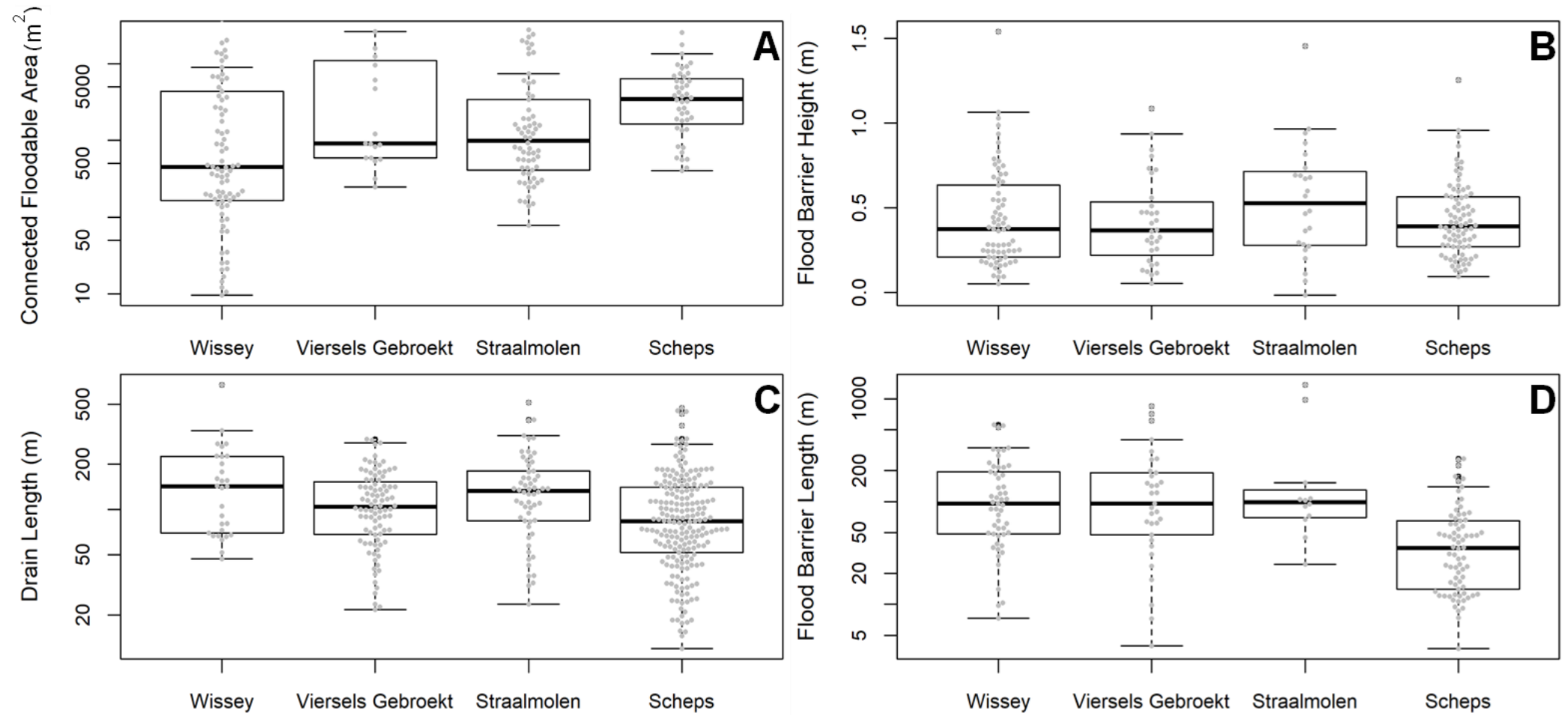


Figure 3.7. Distribution of (A) connected floodable area (m^2), (B) flood barrier height (m), (C) drain length (m), and (D) flood barrier length (m) across the four study areas. Plotted using Tukey whisker extent where the top and bottom of the box represent 75th and 25th percentiles, respectively, with the median line in between. Bars extend less than x1.5 the interquartile range from the first and third quartile. Outliers are excluded from A for better visualisation. A, C, and D are plotted on a logarithmic scale due to the non-parametric distribution of the data to provide better data visualisation.

3.3.2.4. Exemplar Reintroduction Site - Scheps

CFAs comprised 15% of the floodplain at Scheps. Scheps had smaller CFAs on average compared to the Wissey (Fig. 3.7a; Table 3.6). Scheps had 8 secondary channels, comprising a lower proportion (1.2%) of the floodplain comparatively. Total secondary channel length was 3.87 km, less than the Wissey and 1.5x longer than Straalmolen. There were 202 drains: 30 connected to the main channel, 154 connected to side channels, and 18 appearing hydrologically isolated from the river network. Total drain length was 21.16 km some 4.5x greater than the Wissey. Compared to the Wissey, Scheps had more, yet shorter drains (Fig. 3.7c; Table 3.6). Floodplain storage capacity was 0.23 km² (17% of floodplain extent). Scheps had 82 flood barriers (4% of floodplain). Average flood barrier height was 0.43 m, and maximum height at a single point was 1.25 m, both smaller than the Wissey (Fig. 3.7b). Here, 0.14 km (6%) of the river reach was free from embankments on either side. In total, 0.9 km (35%) had double embankments, proportionally more than the Wissey. The longest continuous stretch of flood barrier was 0.26 km (10%), greater proportionally than the Wissey. Overall, Scheps had more flood barriers, that are shorter in average length compared to the Wissey (Fig. 3.7d; Table 3.6).

This study developed and applied a burbot ecology-informed survey of instream and floodplain habitat and compared this with exemplar Belgian reintroduction sites to assess an English candidate burbot reintroduction site. The approach enabled an assessment of the amount, type, spatial distribution and connectivity of available habitat for different burbot life stages including a comparison with ongoing reintroduction sites of varying habitat quality and evidence for success.

3.4. Discussion

3.4.1. Wissey Riverine Characteristics

In terms of the amount and type of instream habitat, the Wissey candidate site exhibited high structural complexity with abundant riparian trees and associated features, including protruding tree roots and instream wood, that provide refuge for both adult and juvenile life stages (Fig. 3.6; Dillen et al., 2008; Worthington et al., 2012). Macrophyte cover and species richness were also high, comprising a mix of emergent, submerged, and floating species, including known ecosystem engineering

species such as *S. erectum* (O'Hare et al., 2012; Gurnell et al., 2013; Gurnell, 2014) and *R. pencillatus* subsp. *pseudofluitans*, which both provide refuge habitat for burbot fry (Auwerx et al., 2019). Undercut banks used by adults for ambush opportunities (Dillen et al., 2008a; Worthington et al., 2012; Eick, 2013; Brackwehr et al., 2016) were also common together with slow-flow conditions associated with the dominant glide flow type and frequent lateral slacks. Overall, consistent with IUCN (2013) reintroduction criteria, the study found suitable instream habitat for each burbot life stage, and the river is also connected longitudinally to a network of other suitable habitats throughout the Great Ouse and its tributaries (Worthington et al., 2012). These two characteristics greatly strengthen the case for the Wissey as a burbot reintroduction site. The main cause for concern in relation to instream habitat, was a lack of instream spawning habitat, which has been identified by previous studies as a potential limiting factor for a burbot reintroduction (Worthington et al., 2011a, 2012). The low estimated availability of instream spawning habitat in the Wissey site is conservative, and potentially an underestimate however, as it assumes spawning on gravel only, while some burbot populations, including the Eurasian and North American subclades, can also spawn on silt and coarse sand (Sorokin, 1971; Mann, 1996; Van Houdt et al., 2005; Jude et al., 2013). If the fine sediment spawning strategy is included in the Wissey classification, then instream spawning habitat increases to 35% of the surveyed section (excluding missing units). This once more reflects the knowledge gaps in the burbot's biology and ecology, specifically the importance of sediment in burbot spawning. Without further research on riverine western European populations, it is hard to conclude the availability of instream spawning habitat in the Wissey. Fortunately, western European populations are more strongly associated with floodplain habitats for spawning.

Some studies describe burbot as sedentary (Larsson, 1985; Koporikov and Bogdanov, 2021), while others show rapid spawning migrations (1.5 – 2.0 km/day; Sorokin, 1971). Following IUCN criteria (IUCN, 2013) and given burbot move between different habitats, it is crucial to consider not only existing habitat, but inter-habitat connectivity. At the Wissey, habitats associated with different life stages were not evenly distributed, suggesting burbot would need to move to find suitable habitat as they grow. In favour of the Wissey, the site is unobstructed by instream barriers for ~6 km, compared to

the English average, 0.75 barriers/km (Jones et al., 2019). The fine sediment-dominated upper reaches contained the largest proportion of unsuitable habitat. Total juvenile and adult habitat increased with distance downstream, and instream spawning habitat was generally spatially isolated. Hence, it is concluded that restoration work centred on increasing instream complexity in the upper study area is needed to create evenly distributed adult, juvenile, and greater instream spawning habitat. The introduction of large wood pieces aimed at increasing refuge habitat, as well as riverbed scour and the exposure of gravels (Abbe and Montgomery, 1996; Parker et al., 2017; Harvey et al., 2018; Cashman et al., 2019, 2021) would also be beneficial.

The only potential physical barrier to fish movement is the sluice located at 52°32'03"N, 000°42'37"E. During this survey, it was not observed as a barrier, but it could, nonetheless, be a barrier at high flows, as there are known critical velocities for burbot swimming capacity. Recorded critical velocities include, $<0.25 \text{ m s}^{-1}$ for a riverine fish of less than 500 mm (Jones et al., 1974), 0.39 m s^{-1} for a 370 mm adult burbot from a Canadian population (Peake, 2008), and 1.00 m s^{-1} have been observed for a 300 mm burbot from a Colorado river population by Gardunio (2014) in which barrier length (m) and flow velocities were tested against burbot swimming capacity to determine appropriate barrier design. The sluice at high flows could potentially limit access to spawning habitat during the winter spawning season. If spawning migrations begin in autumn (Sorokin, 1971; Slavík and Bartoš, 2002), then most adults should pass this barrier before peak flow months, typically December to March (UKCEH, 2023). Any individuals that could not pass the barrier could use the extensive back channels to access the floodplain (Aarts et al., 2004; Worthington et al., 2012; Jude et al., 2013).

3.4.2. Wissey and Belgian Floodplain Characteristics

Considering floodplain habitat, the Wissey has diverse floodplain features that contribute to floodplain water storage. This includes secondary channel systems (2.23x main river length) associated with juvenile habitat, and potential areas of floodplain inundation for spawning and larvae. Compared to Belgian exemplar reintroduction sites, the Wissey has a greater absolute quantity and areal proportion

of potential floodplain spawning and larval habitat, and a higher absolute length of secondary channels. In terms of potential connectivity, the Wissey is intermediate between the exemplar sites. While there are fewer CFAs in the Viersels Gebroekt site, they are individually larger, meaning greater burbot access to potential spawning habitat, and reduced risk of individual entrapment post-spawning as flood waters recede (Glińska-Lewczuk et al., 2016). Further, Viersels Gebroekt has an extensive drain network, leading directly to the rivers there, which is actively managed to ensure connectivity to the floodplain during high flows (J. Auwerx, 2022, pers. comms.). In all Belgian sites, drains have a deliberate function of promoting connectivity between main river and floodplain, and the drainage networks offer additional habitat, greater than the length of the actual river.

The Wissey has proportionally fewer artificial drains but an extensive secondary channel network. These secondary channels provide a similar connectivity function to the floodplain as the drain systems in Belgium, and additional habitat (1.5 times main channel length). Importantly, some of the Wissey's secondary channels were observed to be permanently wetted and spring fed (Fig. 3.6b), offering potential for floodplain spawning habitat regardless of floodplain inundation. The secondary channels along the Wissey could provide an access route to the floodplain and a return to the main channel for adults, and subsequently after 2-3 months, the newly hatched larvae, allowing life cycle completion. These cold and spring-fed channels also offer some mitigation (via provision of thermal refugia) against the effects of climate change, an important consideration of reintroduction guidelines (IUCN, 2013, p.13). Climate change is predicted to increase water temperatures in chalk streams (Finney et al., 2022), but it is harder to predict the effect of climate change on rainfall, with some predictions stating increased rainfall in winter, resulting in increased flooding, with decreased rainfall over summer, and others predicting the opposite (Kay et al., 2021). Any future burbot reintroduction will have to consider future climatic changes in river water temperature and rainfall.

There was a wide range of flood barrier type throughout the Wissey site. Despite this, flood barriers make up proportionally less of the Wissey floodplain than the exemplar reintroduction sites, Viersels Gebroekt and Straalmolen. Though Scheps had the

greatest number of individual flood barriers, main channel embankments were most extensive along the Straalmolen stretch of the Grote Nete, although their impact may be mitigated by extensive drains and secondary channel networks that will provide burbot access to floodplain habitat. The Wissey possesses an extensive secondary channel network but fewer drains. Hence, removal of flood barriers may be more important to ensure flooding at early stages in the hydrograph and more prolonged connectivity with the floodplain to increase burbot spawning habitat availability. Thus, to maximise the long-term success of a burbot reintroduction, river restoration at the Wissey site needs to be sharply focused on increasing the connectivity between the main channel and floodplain through removal or modification of embankments. This approach would align naturally with prevailing emphasis on giving space to rivers to facilitate natural morphodynamics and river-floodplain hydrological connectivity (Brown et al., 2018; Sayer et al., 2018). Removal of flood banks is key to restoring floodplain habitats including inundated floodplains, annual and perennial floodplain waterbodies, secondary channels, and marshes, which are rare in heavily modified lowland catchments yet are beneficial to multiple species beyond the burbot (Copp, 1989; Bolland et al., 2015; Castella et al., 2015; Friberg et al., 2016; Brown et al., 2018). This can be seen as a form of hydrological rewilding, whereby natural hydrological and linked biological processes regenerate lost river-floodplain habitats and their associated biological communities, including fish communities.

Potential outcome indicators for any burbot reintroduction at the Wissey come from observational data from the Belgian reintroductions. Considering burbot larvae have been found within the Scheps study area from 2014 – 2017 in off-channel habitat, and in the Heiloo side channel of the Straalmolen study area from 2019 – 2021 (Vught et al., 2015; Pauwels et al., 2016; Vandamme et al., 2017, 2020, 2024; Van Wichelen et al., 2018; Fig. 1.8), there is some indication of the sites being suitable for burbot spawning and as larval nursery habitat. It should be noted, in 2017, ‘hundreds’ of larvae were found in an off-channel pond on the Asbeek (Van Wichelen et al., 2018). Further, it emphasises the importance of lateral, floodplain habitat for burbot spawning as larvae were no longer found in Scheps after 2017 due to the siltation and later filling in of a connected floodplain pond on the Asbeek side channel (Van Wichelen et al., 2019). Combined, these findings emphasise the overriding, critical importance of

lateral, floodplain habitat that possess annual and perennial floodplain water bodies, providing mixed flow and oxygenation dynamics for burbot spawning, egg development, and larval rearing.

As evidence of a self-sustaining population is lacking and the number of larvae found remains low, the Belgian reintroduction cannot be considered a success. However, it is an ongoing reintroduction and is a beneficial example of burbot response to habitat change and varying quality of in-channel habitat. Thus, the Belgian reintroduction represents the most detailed framework available for the English reintroduction to follow, despite the outcome of the reintroduction still being unknown.

3.4.3. Caveats and Applicability to Future Reintroductions

The methodologies presented here are adaptable and quick to complete, draw on open-source software and datasets, and require minimal equipment, technical expertise, or formal habitat assessment training, though any assessor would benefit from an understanding of riverine ecology and geomorphology. As a result, the approach is also relatively low-cost, an important consideration given that reintroductions are often undertaken by NGOs with tight budgets. The overall approach is also transferable beyond the burbot to other species reintroductions and conservation projects, especially where time and resources are restricted, to help ensure reintroductions are biology-centred (Berger-Tal et al., 2020). Moreover, while the methodology currently only focuses on physical habitat, it presents a first step for NGOs to inexpensively assess potential candidate reintroduction sites before further investigations. For example, now that physical river habitat is mapped, data could be collected on hydraulic variables to implement environmental flow models and further assess suitability. Further research could analyse other biotic factors to look at food sources and predator density that is directly related to existing physical river habitat.

Limitations of the habitat assessment methods presented here are similar to other rapid surveys: they provide only a snapshot in time, rely on discrete categories to characterise complex biophysical features leading to between-surveyor variability (Naura et al., 2016) and do not explicitly incorporate analysis of seasonal and episodic

environmental variations that contribute to reintroduction success or failure (IUCN, 2013). Moreover, the mapping approach comparative to tabular surveys also pose issues. The walkover survey presented here has accuracy issues when recording the spatial extent of features, such as wood pieces, undercut banks, or tree roots, which is similar to the critiques of Surface Flow Type mapping (Woodget et al., 2016) and RCS (Gurnell et al., 1996). To reduce the effect of inaccuracy on spatial recording during analysis, these features were reduced to 'present' or 'absent' in a 10 m area, but if this analysis was reduced to smaller spatial scales (1 x 1 m grids sometimes applied in macrophyte surveying (Wright et al., 1981), recording accuracy could reduce the reliability of the method. Moreover, the quantitative data extracted from the digitised qualitative data lacked validation, which is also a common error to mapping approaches that extract quantitative information from the qualitative data collected (Woodget et al., 2016). This could be mitigated by introducing spot measurements, such as one transect per survey sheet, similar to RCS (National Rivers Authority, 1992) or spot checks in the RHS (Environment Agency, 2003). Accuracy and spatial resolution of remotely sensed data were also an issue for floodplain habitat assessment, although higher resolution datasets are increasingly available subject to varying cost. Accuracy could also be improved by using UAV-Based structure-from-motion photogrammetry (Fleming, 2025).

There are a few important caveats to the present study. The work represents a reasonable estimate of potential burbot habitat use based on current existing knowledge, which has clear knowledge gaps that still exist for certain areas of the species' biology and ecology, including spawning habitat use and population dynamics, which reduces the certainty of the results presented. Physical habitat models provide an accessible medium to implement assessment criteria for species reintroductions with ease of measurement (Maddock, 2001). Conclusions, however, drawn from models based solely on physical habitat downscale the complexities of habitat use, preference, and suitability, which are similar, yet distinguishable concepts, that are driven by interconnected factors of hydrology, water chemistry, sediment characteristics, biotic factors, and geomorphology (Maddock et al., 2001; Parasiewicz and Dunbar, 2001; Conallin et al., 2010). Particularly for freshwater fishes, habitat requirements are often inferred from habitat associations from observational data in

the wild (Rosenfeld, 2003). This assumes that the associated habitats selected by individuals provide adequate fitness gains (i.e., shelter, growth, survival, reproductive success) and without technical and extensive experiments that manipulate habitat to measure these variables, it remains an assumption (Rosenfeld, 2003). The burbot literature is mostly observational, so habitat associations in observational studies are assumptions of beneficial habitat use. More confidence is given to the recurrence of mesohabitats in multiple studies. Thus, the basis of this present study is on habitat associations, but unlike other physical habitat studies, which use the parameters to predict species presence/absence or carrying capacity of the study reach (Rosenfeld, 2003), this study aims to document the presence of habitats associated with burbot, of which there are adult, juvenile, instream, and floodplain spawning associated habitats. Post-release monitoring would be able to focus further on determining whether habitat suggested in this study is utilised by the different life stages.

Moreover, physical habitat is not the only remaining uncertainty within the potential reintroduction site that could be a barrier to the burbot's short-term and long-term survival. For this cold water stenotherm, temperature is a key variable that needs to be investigated, as well as hydrology. While an element of connectivity has been assessed in the work presented here, hydrological connectivity needs to be further investigated to determine the location, extent, and duration of floodplain inundation to definitively determine spawning and nursery habitat availability.

It is important to reflect on Belgium as a country with comparison sites. Table 1.4 shows fish survey data since 2006 from across Antwerp and shows some years recording high numbers of individuals. Stocking of the Grote Nete is still ongoing, but has ceased since 2017 above the instream migration barrier at Scheps, which has provided evidence of natural recruitment there, albeit in low numbers (Vandamme et al., 2021). It is difficult to determine whether the low number of individuals recorded after 2015 is due to dispersal of individuals or death. At Straalmolen, natural recruitment has been recorded since 2018, but each year the surveying has found small numbers of individuals. Similarly, local translocations within the Netherlands reported similar time periods before natural recruitment was recorded (Beelen et al., 2019). INBO, similar to organisations in Germany (Brackwehr et al., 2016) and the

Netherlands, found the detection of larvae as well as the monitoring of adult burbot to be extremely challenging (Beelen, 2014; Auwerx et al., 2022). The selection of the Viersels Gebroekt area, managed as an active wetland, represents the application of our current understanding of burbot habitat use by Belgium as a potential area that may support burbot. Under current monitoring efforts, the detection of small numbers of burbot, and no natural recruitment at Viersels Gebroekt, it is still too early to definitively determine the Belgium sites as reintroduction “successes”.

With 2014 being the first year larvae were found in Belgium, it can take ~10 years for evidence of natural recruitment to be found, which is a similar period to the local reintroductions in the Beerze river undertaken in the Netherlands from 2009 to 2013 (Beelen et al., 2019). These reintroductions evidence the slow population recovery for burbot as they persist in modified environments. The most common way to define reintroduction success is through a self-sustaining population, which requires long-term data on natural recruitment, population size, dispersal, turnover, and health (Robert, 2009), which is not currently available for Belgium. Thus, without data on immigration, emigration, death, and birth, it is hard to determine the health of the Belgian burbot population. The subjectivity of determining species reintroduction success is similar to that of river restoration objectives, which can be considered successful on multiple aspects (i.e., aesthetic, physical habitat), but not improve local ecology (Palmer et al., 2007). Even the IUCN’s *Global Reintroduction Perspective Series* that aims to share reintroduction successes and failures to facilitate learning and avoid common pitfalls has a subjective set of criteria that can define reintroduction success (Berger-Tal et al., 2020). A review of fish reintroduction studies states that determination of project’s success or failure is challenging due to the varying goals between projects (Cocharan-Biederman et al., 2014). Interestingly, in this review, the determinants for classifying success comprised evidence of natural recruitment with at least 6 months of post-release monitoring (Cocharan-Biederman et al., 2014). Under those criteria, the reintroduction of burbot to the Grote Nete could be considered successful.

In the context of an English burbot reintroduction, Belgium represented the best comparison as an ongoing reintroduction of the same genetic subclade because it sets out a realistic and detailed framework to follow, one that applied to an environment similar to lowland England. Despite small population numbers, there is arguably no “healthy” population of burbot to compare to within the western European subclade. Even in France, where INBO based their initial habitat assessment for their own reintroduction, burbot are considered vulnerable (Stapanian et al., 2010a). Thus, it is crucial to remember that burbot are persisting in heavily modified habitats, which could be why population growth is slow in Belgium and in decline in countries with no specific conservation interventions for the species. The most important lesson to be learned from Belgium that can be applied to an English reintroduction is the establishment of a post-release monitoring framework that can be used to monitor fish recruitment as well as immigration and emigration into the release area. If any burbot are detected after release, it is likely that population recovery will be slow, like Belgium, and long-term monitoring will be crucial to determining the efficacy of the reintroduction programme. The monitoring is also useful for understanding the impact of burbot on the existing aquatic community, as an established burbot population that negatively affects native species could also be considered a reintroduction failure, despite recruitment, population health, and dispersal.

3.5. Conclusions

Species reintroductions are becoming an increasingly popular conservation tool, particularly in freshwater systems. The key to any long-term reintroduction success is to thoroughly understand the candidate species’ biology and ecology and make sure its known habitat associations are provided extensively in the release habitat. The burbot was extirpated in England due to habitat modification and now habitat availability remains a potential key barrier to reintroduced burbot survival. The species-specific habitat assessment and classification approach presented here reveals that there is suitable habitat available for every life stage of the burbot in a candidate reintroduction site (River Wissey, UK), and that habitat types and quantity are comparable to, and sometimes exceed, those at reintroduction sites in Belgium that have recorded natural recruitment. The Wissey has similar traits to all exemplar sites.

First, it has secondary channels which provide connectivity with the floodplain similar to Scheps and Viersels Gebroekt drains. Secondly, it possesses smaller CFAs that could provide spawning and larval nursery areas like Scheps. And thirdly, it has fewer embankments than Straalmolen, which still has recorded adult burbot, as well as larvae in the secondary channel systems. Thus, considering physical habitat only, it can be concluded that the Wissey has similar lateral habitat to the exemplar Belgian reintroduction sites where burbot are found. The key concerns are access to floodplain spawning habitat and spatial fragmentation of instream spawning habitat. Hence, removal or modification of flood barriers to promote channel-floodplain connectivity, is recommended prior to a burbot release to maximise the chances of reintroduced burbot survival and long-term persistence. Equally instream habitat restoration, especially the introduction of large wood pieces aimed at increasing shelter and refuge habitat, as well as riverbed scour and the exposure of gravels to increase the quantity and connectivity of instream spawning habitat, particularly in the upper study area, would also be highly beneficial. While these findings on the habitat suitability of the Wissey as a burbot reintroduction site are positive overall, further work is required to confirm that the river might support burbot. This includes assessments of water quality, the routing of water through the floodplain using hydrological and hydraulic modelling, and the temperature regime, both currently and under future climate change.

Chapter 4. Examining current and future thermal suitability across burbot life stages

4.1. Introduction

For many freshwater species, water temperature is one of the dominant factors controlling physiology and behaviour (Harrison et al., 2016). Fish are no exception to this rule and based on physical and behavioural responses to thermal fluctuations, thermal optima for fishes can be discerned. These optima are defined here as temperatures at which a certain process is maximal, such as consumption, respiration, ova maturation, or reproduction (Harrison et al., 2016). Thermal optima are not static in fishes, but can shift seasonally and daily, depending on reproductive, developmental, and energetic state (Golovanov, 2013; Harrison et al., 2016). An example of seasonal shift is spawning migrations undertaken by salmonid species (Juanes, et al., 2004; Miller et al., 2009; Kovach et al., 2015; Di Prinzio et al., 2023). Daily shifts in thermal optima are less commonly studied, but research on diel vertical migrations (Mehner, 2012; Harrison et al., 2013), benthic diel bank migrations along the littoral zone (Cott et al., 2015), and diel horizontal migrations (Pekcan-Hekim et al., 2010; Armstrong et al., 2013) continues to emerge. A key driver of these migrations is differences in temperature across time and space, which fish respond to in order to maximise fitness via a behaviour, such as feeding opportunities or shelter opportunities (Harrison et al., 2016).

When considering the reintroduction of a fish species, an understanding of the behavioural thermoregulation of the candidate reintroduction species and how it can affect habitat selection, as well as short-term and long-term survival, is a necessary consideration. Moreover, it is explicitly specified by the IUCN's Species Translocation Guidelines, that seasonal and episodic variation must be taken into consideration, as well as the typical biological and ecological requirements of the candidate species, when evaluating a candidate reintroduction site (IUCN, 2013).

Climate change is predicted to affect freshwater species through, but not limited to, increasing water temperatures (Watts et al., 2015; House et al., 2017; Radinger et al., 2017; Johnson and Penaluna, 2019; Johnson et al., 2024), altering flow regimes (van Vliet et al., 2013; Hannaford, 2015; Kay et al., 2021), and even affecting riparian vegetation (Capon et al., 2013). Fish species are particularly impacted by the effects of climate change as instream barriers can affect the ability of fish species to migrate to more suitable habitat (Woodward et al., 2010). Moreover, for riverine environments, the exact impacts of climate change are hard to predict with high certainty due to a myriad of interacting factors, which can contribute to positive or negative feedback (White et al., 2023). For example, groundwater input can help regulate riverine temperature, but where groundwater inputs are low, residence time of water and amount of riparian shading can influence water temperatures (White et al., 2023). While climate models contain uncertainties, they can provide a framework for assessing potential future scenarios, which river managers and conservationists can mitigate against (Littell et al., 2011; Finney et al., 2022). Thus, any species reintroduction must consider the population's potential to survive under climate change (IUCN, 2013).

The reintroduction guidelines must be applied when considering and planning the reintroduction of the burbot *Lota lota* to England. For burbot, each life stage has a different thermal optimum meaning that, across its life cycle, it can be vulnerable to inherent spatial and temporal variation in water temperature.

4.1.1. Burbot Background

Within the burbot's global range (Fig. 1.5), there are two subspecies, *Lota lota maculosa* and *Lota lota lota*, with *L. lota maculosa*, which has three subclades (Pacific, Missourian, and Mississippian), distributed across North America to the south of Alaska (Van Houdt et al., 2005). *L. lota lota* spread throughout Europe and Siberia to Alaska and has five distinct subclades: western European, north European, Eurasian, Beringian, and Alaskan (Van Houdt et al., 2005). Burbot are described as cold water top-level predators (Stapanian et al., 2010a; Lecaudey et al., 2019). The burbot has

also been described as stenothermal meaning it can only tolerate a small temperature range (Hardewig et al., 2004). The burbot's life history traits and different requirements across developmental stages, however, are more complicated, particularly in relation to water temperature. Each life stage utilises a specific type of habitat, and also possesses a unique thermal optimum (Fig. 3.1). Further, the thermal optima for each life stage varies depending on genetic subclade (Van Houdt et al., 2003; Van Houdt et al., 2005). For example, the spawning temperature requirements of the north European and western European subclades are different, with north European clade requiring lower winter temperatures to achieve spawning. Despite its classification as a cold water stenotherm, its large global distribution and diversification within Europe (Table 4.1) evidence the burbot's potential adaptability. For example, toward the south of its European range, burbot of the Eurasian subclade in the River Po, Italy can withstand average maximum water temperatures of above 25°C (Soana et al., 2024). Comparatively, burbot of the north European subclade, such as those in the River Kyrönjoki, Finland, persist in average maximum water temperatures of 18°C (Kjellman, 2003). Table 4.1 shows burbot of the western European subclade, found in France, Germany, Belgium, Netherlands, and mainland Denmark, persisting within systems of similar water temperature ranges, approximately 0 - 23°C, but can be as high as 25°C (Brackwehr et al., 2016).

Considering the wide climatic and hydrogeomorphological variations across the burbot's global distribution, variations between biological, ecological, and chemical requirements are noted for the species (Elmer et al., 2008; Cott et al., 2013). When considering a species reintroduction, it is vital that the reintroduced population be obtained from the closest genetic relative (IUCN, 2013), due to the subtle variations in life history traits that may make survival of the reintroduced species difficult or make the species detrimental to other native species. Hence, consideration of subclade is vital in the planning and execution of a burbot reintroduction, as observed for the Belgian reintroduction where the source population was obtained from France (Dillen et al., 2005).

Table 4.1. European distribution of burbot obtained from Stapanian et al. (2010a). Subclade classification from van Houdt et al. (2005). Air temperature classifications obtained from weatherspark.com from nearest possible town to published study noting burbot location. T_w = water temperature, T_a = air temperature. Temperatures are given as averages. * = actual value in data opposed to average. Wissey figures determined from data collected during this study with water temperature obtained from main channel.

Country	Subclade	Location	Lat/Long	Min. T _w	Annual av. T _w	Max. T _w	Min. T _a	Max. T _a	Source
Austria	Eurasian	Traun River	48°13'18"N, 014°14'23"E		9.2		-3	25	Webb and Nobilis (1995); Lahnsteiner et al. (1997)
Bulgaria	Eurasian	Lower Danube	44°03'48"N, 026°50'54"E	0*		20	-4	30	Pekárová et al. (2009); Pandakov et al. (2020)
Czechia	Eurasian	Ohře River	50°20'N, 13°32'E	0*		<15	-2	24	Slavík and Bartoš (2002)
Estonia	Eurasian	River Pärnu	59°01'35"N, 025°41'48"E	1*		18	-9	22	Lajus et al. (2007)
Hungary	Eurasian	Ipel' River	47°49'04"N, 018°52'00"E	0*		25	-4	26	Weiperth et al. (2010); Bajtek et al. (2023)
Italy	Eurasian	River Po	45°04'05"N, 010°57'17"E	3-5	15.95	25-30	-1	30	Stapanian et al. (2010a); Soana et al. (2024).
Latvia	Eurasian	Daugava River	56°48'16"N, 024°35'39"E	1*		18	-7	23	Králová-Hromadová et al. (2021)
Lithuania	Eurasian	Nemunas River	55°19'24"N, 021°23'02"E	2		18	-5	22	Idzelis (1979); Králová-Hromadová et al. (2021)
Poland	Eurasian	Odra River	51°11'36", 016°55'09"E	0-5		>20	-3	24	Kupren et al. (2014); Graf and Wrzesiński (2020)
Slovakia	Eurasian	Slovak-Hungarian Danube	47°53'56"N, 017°26'44"E	0*	10.8	23	-3	27	Pekárová et al. (2009); Guti and Pekarík (2016).
Slovenia	Eurasian	Drava River	46°28'55"N, 015°45'50"E				-4	26	Šlejkovec et al. (2004)
Switzerland	Eurasian	River Aare	46°45'05"N, 008°06'08"E	<6		>18	-4	23	Wedekind and Küng (2010); Person et al. (2014)
Belgium	W. European	Grote Nete	51°09'40"N, 004°59'25"E	0*	14.31	23	1	23	Geeraerts et al. (2007)
Denmark	W. European	Gudenå	56°10'54"N, 009°33'06"E	2		17	-2	21	DTU Aqua (2021)
France	W. European	Meuse River	49°47'03"N, 004°43'34"E				-1	23	Vught et al. (2008)
Germany	W. European	River Lippe	51°29'N, 8°6'E	0*		25	0	23	Brackwehr et al. (2016_.
Netherlands	W. European	River IJssel	52°29'42"N, 006°03'32"E	5	13.8	18	0	22	Bosveld et al. (2015); Centraal Bureau voor de Statistiek et al. (2020)
Finland	N. Eur/Eurasian	River Kyrönjoki	66°N, 22°E	2		18	-10	20	Kjellman (2003)
Norway	N. European	River Rena	61°12'18"N, 011°29'21"E				-11	19	Sandlund et al. (2016)
Sweden	N. Eur/Eurasian	Rickleå	64°20'35"N, 020°31'38"E	0*		15	-12	19	Sandberg (2015)
England		River Wissey	52°33'49"N, 000°41'28"E	0.6*	11.29	21.95*	-9.4*	37.6*	

A burbot reintroduction to England is imminent and has undergone research and planning for at least two decades. Key research has addressed questions in the IUCN reintroduction framework (IUCN, 2013), which relate to identifying the closest genetic relative (Van Houdt et al., 2005; Worthington et al., 2017). A key finding to emerge from past research is that the extirpated English population, despite being genetically distinct due to geographical isolation, was most closely related to the western European subclade (Van Houdt et al., 2005; Worthington et al., 2017). As it is not possible to reintroduce the extinct English fish or investigate further behavioural genetic differences between the English and western European group, we must work on the assumption of similarity. Thus, it is crucial to identify temperature requirements and thermoregulatory behaviours of the western European subclade when assessing the suitability of a candidate English reintroduction site.

4.1.2. Burbot Life Stage Temperature Requirements

By garnering the temperature requirements for each life stage from the existing literature, these thresholds can be applied to assess thermal suitability at the Wissey. There is a bias in the published literature relating to burbot temperature requirements and habitat preferences toward North American lake populations. Hence, where possible this study focuses on findings from western European and wider European river populations, but North American populations are included for context. Tables 4.2, 4.3, and 4.4, which consider adult thermal optima and maxima, spawning optima and ranges, and egg incubation and larval development ranges, respectively, are grouped by life stages and list the temperature ranges observed by different studies by location, showing the variation between genetic subclades. If a subclade is not listed in Tables 4.2 – 4.4, it is because published literature on thermal thresholds for that life stage could not be found. Fig. 4.1 summarises the range of temperatures from Table 4.2 – 4.4.

Table 4.2. Studies identifying thermal optima, maxima, and lethal temperature limits for adult burbot. * denotes a lethal maximum temperature in which total death was observed. Maxima refers to upper thermal limits in which stress behaviours were exhibited, not all studies recorded burbot death and therefore not all maxima are indicated as lethal thermal limits.

Subclade	Location	Optima (°C)	Maxima (°C)	Source
<i>W. European</i>	North Rhine-Westphalia, Germany	12	25	Brackwehr et al. (2016)
	River Oder, Germany	13.5	26	Hardewig et al. (2004)
<i>Eurasian</i>	NA		28	Shodjai (1980)
	Rearing ponds, Czechia		<20	Adámek (2000)
	Lake Päijänne, Finland		27 - 28*	Pääkkönen et al. (2003)
	Lake Päijänne, Finland		23	Pääkkönen and Marjomäki (2000)
<i>Pacific</i>	Koontenai River, US		31*	Terrazas et al. (2017)
	Kinbasket Reservoir, BC, Canada	12 – 14		Harrison et al. (2016)
<i>Missourian</i>	Missouri River, USA		22 - 29	Fisher (2000)
<i>Mississippian</i>	Lake Opeongo, Canada		20	Carl (1995)
	Shebandowan Lake, Canada		27	Ryder and Pesendorfer (1992)
	Oneida Lake, US		21 – 27*	Jackson et al. (2008)
	Lake Constance, US	11.4	26.8 – 31.7*	Hofmann and Fischer (2002)
	Moosehead & Haymock Lake, US	10 - 14		Cooper and Fullman (1945)
	Lake Peonage, Canada	10 - 14		Hackney (1973)
<i>NA</i>	Canada	15.6 – 18.3	23.3	Scott and Crossman (1973)

Table 4.3. Studies identifying ranges and thermal optima for spawning adult burbot.

Subclade	Location	Optima (°C)	Range (°C)	Source
<i>Western European</i>	Meuse, France		4 - 6	Vught et al. (2008)
	French Ardennes, France		5 - 7	Beelen (2009)
	River Lippe, Germany	<2		Brackwehr and Kühlmann (2016)
	North Rhine-Westphalia, Germany		0 - 6	Brackwehr, et al. (2016)
<i>Eurasian</i>	Lake Mondesee, Austria	2		Lahnsteiner et al. (2012)
	Szczeciński Bay, Poland	1 - 2		Żarski et al (2010)
	Lake Baikal, Russia	0		Sorokin (1971)
<i>Pacific</i>	Columbia Lake, Canada	5 - 6		Taylor and McPhail, (2000)
	Kinbasket Reservoir, BC, Canada	< 2		Harrison et al. (2016)
	Koontenai River, US		2 - 6	Ashton et al. (2019)

Table 4.3. Continued...

	Koontenai River, US	<4		Paragamian and Wakkinen (2008)
<i>Missourian</i>	Green River, Wyoming, US	0		Brauer et al. (2020)
<i>Mississippian</i>	Shebandowan Lake, Canada	0.5		Ryder and Pesendorfer (1992)
	Lake Eerie, US	0.6 – 1.7		Stapanian et al. (2010b)
	Minnesota, US		0 - 6	Becker (1983)
	Burntside Lake, US	<4		Cahn (1936)
<i>NA</i>	NA		1 - 7	Jäger et al. (1981)
	NA	0 – 3		Alabaster (1982)
	NA	<4		Mann (1996)

Table 4.4. Studies of burbot egg incubation optima and ranges, as well as larvae growth ranges, grouped by genetic subgroup. In. = Egg incubation, L. = Larvae * indicates an upper lethal threshold.

Subclade	Location	In. Optima (°C)	In. Range (°C)	L. Growth Range (°C)	Source
<i>W. European</i>	Gersfled, Germany			16	Trabelsi et al. (2011)
	Meuse, France	3.8	2.1 – 6.1	4 - 12	Vught et al. (2008)
	River Lippe, Germany	4 - 5	4 - 7	8 - 10	Brackwehr and Kühlmann (2016)
	North Rhine-Westphalia, Germany			6 - 9	Brackwehr, et al. (2016)
	French Ardennes, France	4 - 6	2 – 10*		Vught et al. (2015)
	NA		8 – 9*		Kainz and Gollmann (1996)
	NA		2 – 6		de Gelas et al. (2007)
<i>N.European</i>	NA	3.8	8 – 9*		Shodjai (1977)
	Lake Kuohijärvi, Finland			4 – 18	Kjellman and Eloranta (2002)
<i>Eurasian</i>	Rearing ponds, Czechia			14 - 18	Adámek (2000)
	Traun River, Austria		2 – 6		Lahnsteiner et al. (1997)
	Szczeciński Bay, Poland		1 – 5*		Żarski et al (2010)
	Lake Mondesee, Austria		2 – 9*		Lahnsteiner et al. (2012)
	River Odra, Poland	3 – 4	3 – 6*	10 - 16	Kupren et al. (2014)
<i>Mississippian</i>	Lake Eerie, US	0 - 2			Stapanian et al. (2010b)
<i>Pacific</i>	Koontenai River, US	3	3 – 5*		Ashton et al (2021)
	Columbia Lake, Canada		0 - 7		Taylor and McPhail (2000)
<i>NA</i>	NA	4		8	Jäger et al. (1981)
	NA		? - 12*		Alabaster (1982)

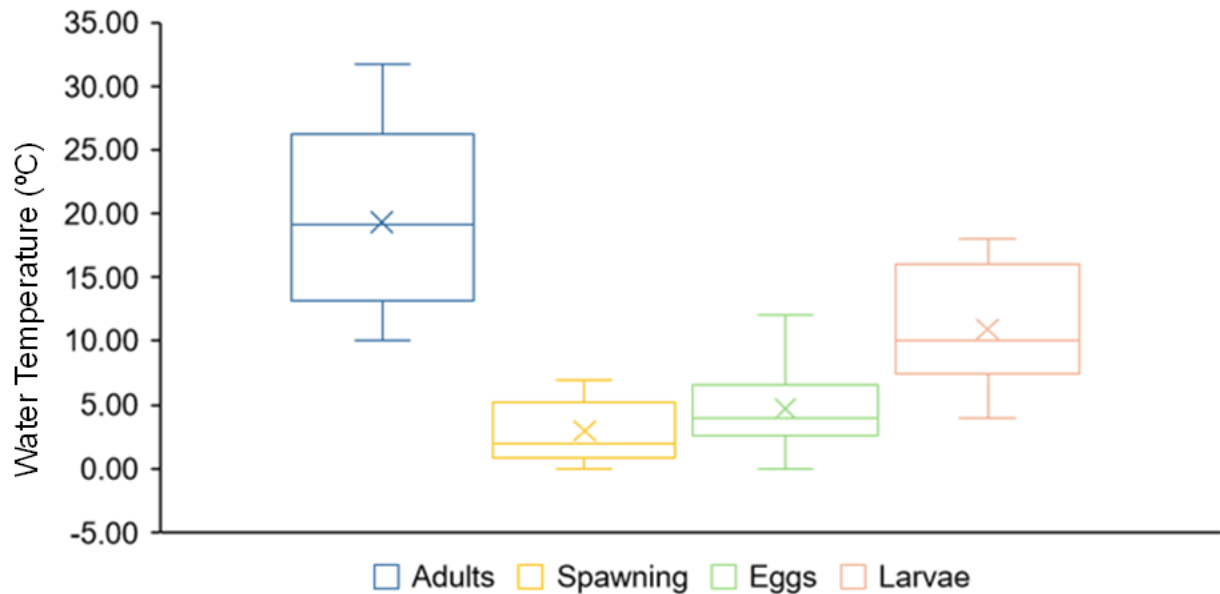


Figure 4.1. Summary of temperature literature showing range of temperatures associated with each burbot life stage. Juveniles are not included as they are regarded as more temperature tolerable than other life stages.

4.1.2.1. Adults

For adults, research shows that, all burbot populations have a tendency to occupy deeper, cooler water (Carl, 1995; McPhail, 1997; Eick, 2013; Jude et al., 2013; Cott et al., 2015; Harrison et al., 2016; Brauer et al., 2020). Those in riverine environments, particularly the western European subclade, are also strongly associated with shelter structures such as large woody pieces and tree roots (Worthington et al., 2012), undercut banks (Dillen et al., 2008), or large substrate (Eick, 2013) which may also afford small-scale thermal refugia. Table 4.2 lists studies of adult burbot thermal optima and critical temperature thresholds. Most studies across the species' range agree that burbot have an optimum between 10 – 14 °C (Cooper and Fuller, 1945; Hackney, 1973; Hofmann and Fischer, 2002; Harrison et al., 2016), including two western European studies which place adult burbot optima temperature at 12 °C (Brackwehr et al., 2016) and 13.5 °C (Hardewig et al., 2004). Comparatively, maximum water temperature tolerances exhibit more variation across the burbot's range. Some studies list the upper threshold as low as 20 °C, but some have identified a upper critical maximum threshold (i.e., temperatures at which fish cannot undergo 10 minutes without exhibiting stress or even death; Hofman and Fischer 2002; Pääkkönen et al., 2003) of between 27 °C and 31 °C (Table 4.2). Some studies have suggested that the

persistence of temperatures above the thermal optimum (i.e., for 30 days or greater) will lead to mortality for burbot populations (Jackson et al., 2008). Under such circumstances, it has been suggested that burbot begin to reduce energy outputs associated with hunting, consumption, and respiration, surviving only on fat reserves (Hardewig et al., 2004) which, if occurring for a significant amount of time, would be detrimental to survival (Pääkkönen and Marjomäki, 2000). This idea needs to be balanced against the ability of adult burbot to avoid high temperatures by migrating to and utilising other cooler habitats, such as the deeper waters of lakes, if available to them (Sorokin, 1971).

For the burbot, due to its classification as a cold water stenotherm, it is considered vulnerable to climate change (Hofmann and Fischer, 2002; Stapanian et al., 2010a). For example, in the Curonian lagoon in Kaliningrad and Lithuania, observed warmer winter temperatures have been linked to declining burbot populations (Švagždys, 2002). In Oneida Lake, USA warmer summer water temperatures have been linked to burbot population decline (Jackson et al., 2008). While some burbot populations in the south of the North American range (i.e., Kansas and Illinois) are considered locally extinct, this was not attributed to rising temperatures, but habitat modification and instream barriers preventing migration (Beard et al., 2017). Despite some observed warming during the last century, most burbot populations have been more directly affected by habitat modification, particularly in Europe (Dillen et al., 2008a; b; Worthington et al., 2010a, 2012; Bosveld et al., 2015; Brackwehr et al., 2016). In terms of future change, for some emissions scenarios, warming over the next century predicted by some climate models could have detrimental impacts for burbot survival due to its likely impact of increasing water temperatures, as estimated for Bulgaria (Pandakov et al., 2020) and British Columbia, Canada (Ashton et al., 2021)

4.1.2.2. Spawning temperatures

The availability of suitable spawning habitat is crucial to the reintroduction of burbot to England and this has a critical temperature component (Worthington et al., 2011b). For western European populations, the most common spawning strategies are on inundated floodplains and back channel habitat (Aarts et al., 2004; Worthington et al.,

2012; Brackwehr et al., 2016). The spawning activity itself is triggered by a drop in temperature, in combination with other factors, depending on the population. For example, in the Ohře River, Czech Republic, burbot spawning migrations have generally been shown to occur during low discharge periods when water temperatures decrease (Slavík and Bartoš, 2002). By contrast Paragamian and Wakkinen (2008) noted it was the drop in temperature in combination with increased water levels that triggered spawning. Decreasing light levels in combination with increasing water levels have also been identified as triggers for burbot spawning (Beelen, 2009). For German burbot, water temperatures dropping to 12°C between September and November is crucial to trigger spawning migrations (Hochleithner, 2020). In Belgium, adult burbot spawning migrations have been triggered by increased water levels and decreased water temperatures in late November and early December (Van den Neucker et al., 2009).

In general, the triggers of burbot spawning events are relatively unstudied and there is a lack of quantitative information on thresholds (i.e., exact figures for temperature decrease or flow increase). The timing of spawning also varies according to local climatic variation. Winter spawning is thought to occur over November to March for *L. lota maculosa* (Paragamian and Wakkinen, 2008), but for a population in Kinbasket Reservoir, British Columbia, Canada, the spawning period is reported as February to April (Harrison et al., 2016). In Germany, as January is the coldest month, the spawning period is determined to be between late December and February (Brackwehr et al., 2016). In Belgium, the recording of spawning events in December and early January was linked to the inundation of floodplains due to the increasing water level, which creates spawning habitat (Van den Neucker et al., 2009). Despite having an extended spawning period, most studies agree the spawning itself takes place over a 2 – 3 week period when conditions are right (Paragamian and Wakkinen, 2008; Brackwehr et al., 2016; J. Auwerx, pers. comms., 2022).

Table 4.3 lists studies that assessed spawning temperature requirements, including the spawning range and if noted, a spawning optimum. It is important to note that most studies have determined these thresholds under laboratory conditions and few have

looked at spawning temperatures and thresholds *in situ*. Most studies, regardless of genetic subclade, identify spawning optima as less than 4°C (Paragamian and Wakkinen, 2008; Żarski et al., 2010; Lahnsteiner, et al., 2012; Brackwehr and Kühlmann, 2016; Harrison et al., 2016). Under real-world conditions, temperatures are unlikely to be consistently maintained at the optimum for any extended period. For example, in the Koontenai River, USA, water temperatures should reach 5°C by the first week of November, until December – February where temperatures should stay between 0 – 4 °C (Paragamian and Wakkinen, 2008). Some studies identify spawning ranges as narrow as 1°C (Żarski et al., 2010) or as great as 6°C (Jäger et al., 1981; Brackwehr et al., 2016). Most studies identify the maximum temperature as 6°C, but two studies have noted spawning occurring at 7°C (Jäger et al., 1981; Beelen, 2009), which includes one western European population in the French Ardennes. Burbot populations in the North Rhine-Westphalia rivers are also noted to spawn between a range of 0 - 6°C (Brackwehr et al., 2016).

The studies synthesised in Table 4.3 show the large range of temperatures in which burbot spawning has been achieved, reflecting a degree of thermal plasticity, and hopefully a future adaptability of the species under climate change. Despite spawning ranges reflecting some flexibility for burbot populations to achieve spawning, some studies have noted that deviations of 2.5°C outside of the spawning range can delay spawning by up to two weeks (Kouřil et al., 1985). While some studies suggest spawning can be achieved at higher temperatures, this needs to be caveated against negative high temperature impacts on spawning success, egg formation and mortality, and spawning period length. For example, Ashton et al. (2019) found that, under experimental conditions, burbot from the Koontenai River, USA (Pacific subclade) could spawn at 6°C, but they shortened the spawning period to 6 days. Further, at the spawning temperatures of 2°C, 4°C, and 6°C, survival of eggs to the eyed embryo stage was 86.7%, 47.9%, and 0.1% respectively (Ashton et al., 2019), clearly reflecting the negative impact of rising water temperatures on likely spawning success.

4.1.2.3. Burbot Egg Incubation and Larval Development

Following spawning, the semi-buoyant eggs of the burbot are easily distributed by currents (Sorokin 1971; Brackwehr et al., 2016), which is why off-channel or low flow floodplain habitat is important for egg incubation as it prevents eggs from being swept out of the system. Similar conditions are needed for larvae nursery habitat before they have developed their swimming physiology (Müller, 1957; Farkas, 1993; Mann, 1996; Worthington et al., 2012; Brackwehr et al., 2016). While egg incubation and egg survival are highly dependent on water temperature (Jäger et al., 1981; Lahnsteiner et al., 1997, 2012; Ashton et al., 2019), once hatched larvae are more vulnerable to predation and hydrological conditions (Brackwehr et al., 2016). Table 4.4 lists studies reporting established egg incubation temperature ranges, as well as temperatures for larval growth ranges, which ranges between 4 °C and 18°C

The optimum temperature for egg incubation throughout the burbot's range is between 3 – 5°C (Table 4.4), with some studies suggesting that egg incubation needs to be between 2 – 6 °C (de Gelas et al., 2007; Kupren et al., 2014; Ashton et al., 2021). Others (e.g. Shodjai, 1980; Kainz and Gollmann, 1996; Lahnsteiner et al., 2012) suggest that incubation could be undertaken in temperatures as high as 9°C, however. Changes in water temperature can affect the length of the egg incubation period , percentage of hatched embryos, and embryo deformity. For example, with eggs from the Eurasian subclade, obtained from burbot from Lake Mondesee, Austria, Lahnsteiner et al (2012) found that under experimental conditions, percentage of ready-to-hatch larvae and normally shaped larvae decreased as temperatures increased with no larvae hatching beyond a constant 9°C treatment, and most larvae hatching at 2°C. Similar findings were observed by Jäger et al. (1981) who found that, while incubation and hatching continued above 4°C, mortality sharply increased above this threshold. Lahnsteiner et al. (2012) also ran experiments in which groups of eggs were spawned at low temperatures (~2°C) and then the water temperatures were increased during incubation, at 8, 16, and 48 days, which is more reflective of the unsteadiness of natural conditions. They found that, at 8 days, an increase from 2°C to 6°C resulted in 92% ready-to-hatch embryos and 85% normally shaped larvae, whilst an increase to 9°C after 8 days resulted in 64% ready-to-hatch embryos and

13% normally shaped larvae. After 16 and 48 days, the negative effect of temperature increase on embryo development was reduced, meaning more eggs hatched in total with lower proportions of deformed larvae. These findings suggest that sudden rises in temperature, while impactful to early stage eggs, may not be lethal to older eggs, especially if the increase can occur two weeks after incubation has begun. Kainz and Gollmann (1996) found similar survival rates under maximum temperatures for egg incubation for eggs from western European populations, which suggest a maximum of between 8 - 9°C as long as this is achieved in the third week of development. A review by Alabaster (1982) found that, for eggs from the western European subclade, eggs can hatch up to 12°C, but observed increasing deformity and mortality with increasing temperature. Similar results have been observed for western European burbot from the River Meuse, France, with maximum egg incubation temperatures observed at 8°C, but with some eggs and larvae surviving beyond this (Vught et al., 2008). Contrastingly, some studies have found less adaptability. For example, Źarski et al. (2010) ran experiments with eggs from Szczeciński Bay, Poland (Eurasian subclade) and found that there was 100% mortality for eggs incubated at 5°C. Ashton et al. (2021) argues that rapid rates of warming (i.e., 0.4°C per day) are more damaging to egg development than gradual warming, while Lahnsteiner et al (2012) found that, once the hatching period had begun, temperature increases did not affect mortality.

Water temperature can shorten the burbot egg incubation period length. For example, Lahnsteiner et al. (2012) found that, at a constant temperature of 2°C, egg development time was 53 days and the hatching period was 19 days, totalling 72 days. Under constant temperatures of 6°C, development time was reduced to 25 days, and the hatching period was 7 days, totalling 32 days. This is similar to the findings of previous studies that have identified the development period between 30 – 75 days (Hochleithner, 2020) or 120 - 160-degree days (Müller, 1957; Wocher, 2010; Donner and Eckmann, 2011). Nagel et al. (2011) also found a difference in length between the hatching period of eggs incubated at 6°C (30 days) and 2°C (41 days).

Alongside an egg incubation and hatching period between 25 to 75 days, burbot larvae also require similar low flow, sheltered, shallow habitats during the first few weeks

post-hatching until their swimming physiology develops, which can be between 11 and 23 days (Clady, 1976; Fischer, 1999). For larvae, while temperatures become less crucial, warmer temperatures can also contribute to faster growth. Table 4.4 captures a distinctive thermal shift for the larval stage, which is higher than the optimum for adults (Table 4.2). Brackwehr et al. (2016) suggest that burbot of the western European subclade need water on floodplains between February to April, raising from 6°C to 9°C for egg incubation and larval growth. Moreover, Jäger et al. (1981) found that larvae do not begin exogenous feeding until water temperatures increase, which they suggest should be above 8°C. The warmer temperatures required by larvae are thought to be linked to the availability of zooplankton (Ryder and Pesendorfer, 1992). The abundance of zooplankton food sources, such as Copepods, as well as the timing of hatching are linked to temperature (Ryder and Pesendorfer, 1992). Overall, the larval stage is determined to last around 60 days (Freyhof and Kottelat, 2007).

After the larval period, juveniles will return to the main channel and inhabit low velocity areas with high macrophyte cover (Fisher, 2000; Dillen et al., 2008b). Their survival rates are more explicitly linked to predation pressure and habitat availability rather than temperature requirements, but burbot would undoubtedly experience stress under extreme thermal conditions (i.e., >30°C). As juvenile burbot grow, it is the need for shelter as well as lower temperature optimum which causes them to shift to deeper habitats and nocturnal activity (Hofmann and Fischer, 2002).

4.1.3. Considering an English Burbot Reintroduction

Overall, previous research shows considerable variation in thermal optima and tolerances for different burbot life stages, which could prevent spawning and long-term survival if these thermal conditions are not met. It is hence extremely important to consider spatial and temporal variations in water temperature to inform a future reintroduction of the western European subclade to eastern England (IUCN, 2013; Worthington et al., 2017), as is proposed. Moreover, considering the potential impacts of future warming under climate change, future variation in temperature must also be considered to evaluate the burbot's potential long-term survival (IUCN, 2013).

In light of published literature on burbot spawning requirements and ahead of the proposed English burbot reintroduction to the River Wissey, Norfolk, the present study aims to assess the suitability of the Wissey, for spawning, egg incubation, larval development, and adult life stages of the burbot by examining (i) observed spatial and temporal variations in water temperature from October 2021 to August 2024, and (ii) estimating potential future water temperature change within the study area to inform evidence-based decision-making in regard to any future reintroduction attempt of the burbot. Juvenile temperature requirements were not considered in this study due to their survival not being dependent on a unique thermal range as they have similar temperature requirements as adults.

4.2. Materials & Methods

4.2.1. Field Site

There are no meteorological data available for the study area (Fig. 2.1). Meteorological data (1979 - 2022) from Denver (TF 59162 00899), 23 km from the top of the study area, show that the month with the highest average maximum air temperature is August (22.27°C), with the maximum daily air temperature recorded as 37.4°C on 20/07/2022. The month with the lowest average minimum temperature is January (1.08°C), with the lowest recorded daily minimum temperature as -15.5°C on 11/02/2012. Average daily minimum and maximum air temperature from Denver for the accepted burbot spawning period determined by the literature (i.e., November to March) (McPhail and Paragamian, 2000) show a large average diurnal temperature range during the winter period (i.e., 5.9°C in January), with average daily maximum temperatures between 8°C to 10°C during the coldest months on average (Fig. 2.5). Further information on the study area is given in Chapter 2.

4.2.2. Temperature Monitoring Network

To achieve the aims of this study and to understand both spatial and temporal temperature variations within the study area relevant to different burbot life stages,

temperature sensors were deployed across the study area (Fig. 4.2). Table 4.5 gives an overview of the temperature sensors displayed in Fig. 4.2, as well as their logging and environmental characteristics, and Fig. 4.3 illustrates how both the HOBO sensors and Arduino sensors were installed.

In October 2021, 23 HOBO Offset 64K Temperature sensors (UA-001-64; <https://www.onsetcomp.com>) were deployed in the study reach. This commercial logger was chosen due to accuracy ($\pm 0.53^{\circ}\text{C}$ from 0° to 50°C), low cost, memory capacity, battery life, and ease of installation. The loggers were installed at ~400 m intervals longitudinally downstream, where accessibility allowed, with seven installed in the side channels, 14 in the main channel, one recording air temperature, and one recording floodplain water temperature. Each submerged logger was covered by a solar radiation shield comprised of a white PVC pipe (Hrachowitz et al., 2010) attached to an angle iron post and hammered directly into the river bed. Each logger was positioned at approximately mid-depth. The locations of the loggers were intended to capture a variety of meso-habitats, including tree roots, riparian shading, and open water habitat, so the exact position in the channel cross-section varied. Environmental parameters for each logger are recorded in Table 4.5. Each HOBO Offset logger was set to measure water temperature at 30-minute intervals. Riparian shading classification was determined from aerial imagery based on the methods of Johnson et al. (2014), but was reduced to two broad categories, unshaded and shaded, rather than four due to the smaller study area compared to Johnson et al. (2014).

In February 2022, 10 additional temperature loggers were installed alongside water depth sensors on the main channel and floodplain in four areas (Fig. 4.2). These loggers were constructed using Arduino microcontrollers and low-cost environmental sensors to increase monitoring capacity in the floodplain, while maintaining high spatial and temporal monitoring resolution. The loggers have been tested for accuracy alongside a manufactured logger, a Solinst® LevelLogger® 5 Junior (<https://www.solinst.com>) and in the study (based on 6 months data logging at hourly intervals), accuracy was determined to be $\pm 0.4^{\circ}\text{C}$ for the observed temperature range, $-2 - 35^{\circ}\text{C}$ (Pearce et al., 2024a). Each temperature logger on the floodplain was set

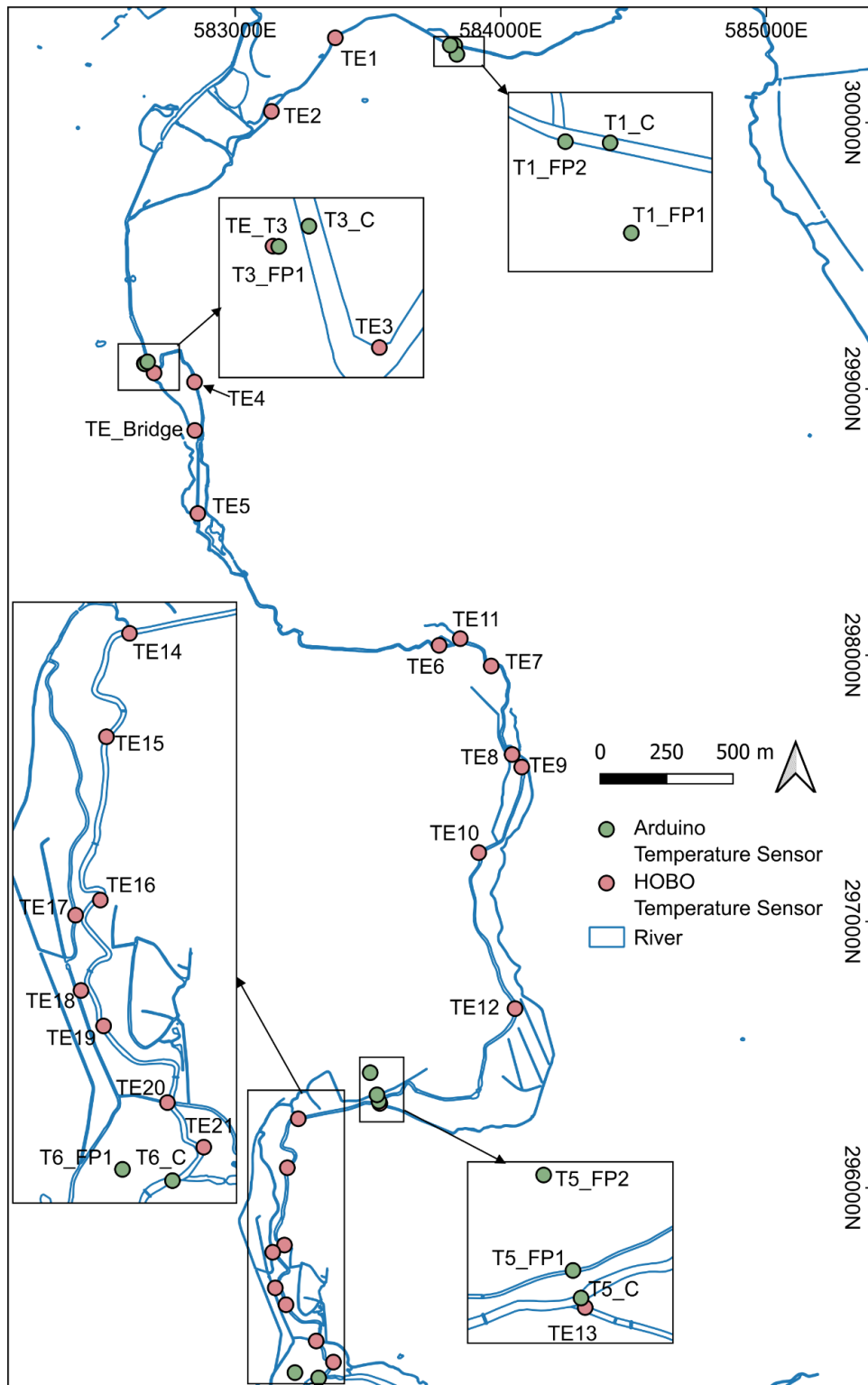


Figure 4.2. Location of HOBOTemperature sensors (red circles) logging at 30-minute intervals and Arduino water depth and temperature sensors (green circles) logging at 60-minute intervals. Inserts in figure show more detail in areas where loggers are placed close together.

Table 4.5. Temperature logger locations and environmental characteristics from 29/10/21 to 07/08/2024. For floodplain loggers, n indicates number of records during inundation.

Name	Easting	Northing	Start	End	Location	Depth from bottom (cm)	Total Depth (cm)	Period (min)	Shading	n
TE1	583378	300317	29/10/21	24/9/22	Main	12	28	30	Shaded	15,784
TE2	583137	300041	29/10/21	28/11/22	Main	20	50	30	Shaded	18,895
TE3	582696	299049	29/10/21	30/6/23	Main	25	45	30	Unshaded	28,550
TE_Bridge	582848	298844	25/11/21	7/8/24	Side	17	23	30	Unshaded	32,504
TE4	582847	299025	29/10/21	29/10/21	Main	20	44	30	Unshaded	0
TE5	582859	298532	29/10/21	30/9/22	Main	10	17	30	Unshaded	12,340
TE6	583769	298034	29/10/21	19/1/23	Main	12	24	30	Unshaded	21,410
TE7	583964	297957	29/10/21	7/8/24	Main	23	63	30	Shaded	23,372
TE8	584043	297624	29/10/21	5/6/23	Air	NA	NA	30	Shaded	25,323
TE9	584080	297578	29/10/21	18/4/24	Main	23	73	30	Unshaded	30,068
TE10	583918	297256	29/10/21	5/6/23	Main	14	49	30	Unshaded	27,975
TE11	583849	298059	29/10/21	7/8/24	Side	5	21	30	Unshaded	38,246
TE12	584054	296671	29/10/21	25/1/23	Main	18	53	30	Unshaded	14,859
TE13	583545	296315	29/10/21	7/8/24	Side	8	36	30	Unshaded	38,247
TE14	583239	296258	29/10/21	5/6/23	Main	14	38	30	Shaded	28,063
TE15	583198	296073	29/10/21	1/10/23	Main	15	42	30	Unshaded	30,787
TE16	583186	295784	29/10/21	5/6/23	Main	25	85	30	Shaded	27,982
TE17	583142	295756	29/10/21	5/6/23	Side	6	30	30	Shaded	27,983
TE18	583152	295622	29/10/21	9/4/23	Side	20	55	30	Shaded	25,235
TE19	583192	295559	29/10/21	19/6/23	Main	20	54	30	Shaded	22,994
TE20	583306	295424	29/10/21	5/6/23	Side	14	28	30	Shaded	25,643
TE21	583371	295344	29/10/21	7/8/24	Side	5	35	30	Shaded	32,234
TE_T3	582662	299093	25/11/21	7/8/24	Floodplain	5	NA	30	Unshaded	32,371
T1_C	583828	300287	23/2/22	7/8/24	Main	30	45	60	Shaded	37,145
T1_FP1	583836	300253	23/2/22	23/7/24	Floodplain	NA	NA	60	Unshaded	13,986
T3_C	582672	299100	10/5/22	7/8/24	Main	NA	NA	60	Unshaded	33,025
T3_FP1	582662	299093	23/2/22	1/8/24	Floodplain	NA	NA	60	Unshaded	17,858
T5_C	583543	296322	23/2/22	7/8/24	Main	27	58	60	Shaded	34,345
T5_FP1	583535	296346	23/2/22	23/7/24	Floodplain	NA	NA	60	Shaded	8,458
T5_FP2	583510	296430	23/2/22	12/3/23	Floodplain	NA	NA	60	Unshaded	328
T6_C	583316	295282	26/11/21	7/8/24	Main	24	73	60	Shaded	35,975
T6_FP1	583227	295304	23/2/22	21/12/22	Floodplain	NA	NA	60	Shaded	862
T1_FP1 Air	583836	300253	5/8/22	7/8/24	Air	NA	NA	30	Unshaded	35,136
T6_FP1 Air	583227	295304	5/8/22	5/6/23	Air	NA	NA	30	Shaded	14,598

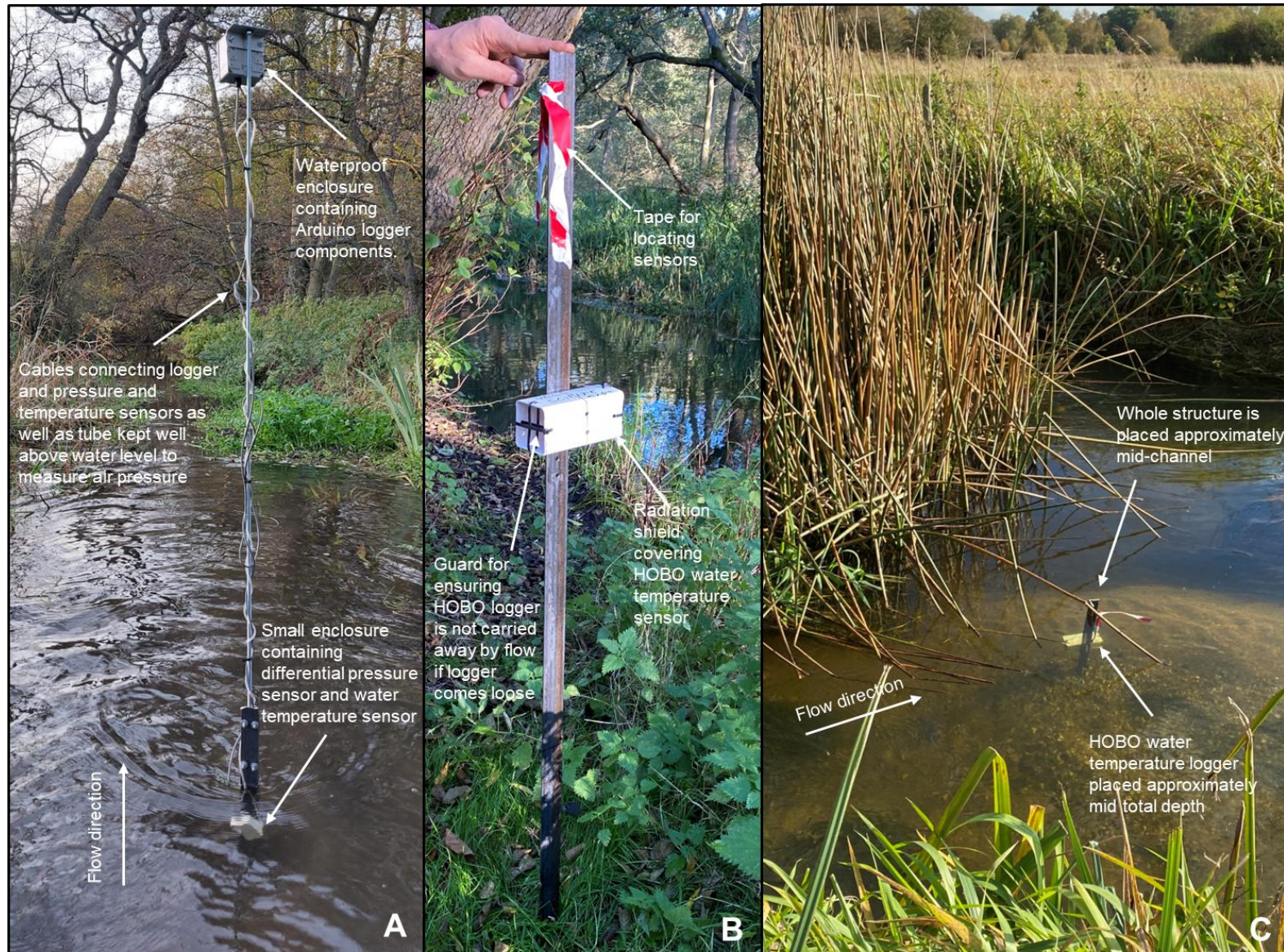


Figure 4.3. Installation of HOBOT and Arduino sensors (A) Arduino water depth and temperature sensor installed at T1_C, design, construction, and testing given in Pearce et al. (2024a); (B) setup of HOBOT temperature sensors, which is a single piece of angle iron with a radiation shield attached to its middle, which contains the HOBOT sensor and (C) an example of an installed HOBOT temperature sensor at TE12 where loggers are placed close together.

to record at ground level and was shielded by a polymer enclosure (Hrachowitz *et al.*, 2010). In the main river channel, the sensor was positioned on the riverbed in the centre of the channel, attached to an angle iron foundation. Each Arduino logger was set to record at 60-minute intervals to reduce power consumption.

Between August – November 2022, the Arduino loggers were replaced with Solinst® LevelLogger® 5 Juniors to increase the battery life and accuracy of the measurements ($\pm 0.1^{\circ}\text{C}$). Alongside these sensors, two barometers, Solinst® Barologger Edge, accuracy $\pm 0.05^{\circ}\text{C}$ (<https://www.solinst.com>) were installed at the top and bottom of the study area, which also recorded air temperature. Each new sensor was set to log temperature at 30 minute intervals. The replacement occurred as the Arduino loggers had more logging and power supply issues compared to the HOBO loggers. For example, T5_FP1 only logged 568 readings compared to T5_C, which logged 6,126 during the same period, excluding T5_FP1 from analysis until a logger replacement on 28/11/2022. Table 4.5 lists the name of all loggers, but due to some loggers being replacements, and thus in the same locations, the names of the Arduino-based loggers is maintained throughout this study (i.e., T1_C, T1_FP1, T3_C, T3_FP1, T5_C, T5_FP1, and T6_C). It should be noted that T5_FP2 and T6_FP1 could not be replaced, so their records are less consistent.

4.2.3. Data Management

The total deployment period for the loggers was from 29/10/2021 until 07/08/2024, covering 2.5 years. For the HOBO loggers, the average number of readings recorded was 23,899, with a maximum of 38,247. During the course of the study, only one logger failed entirely, TE4, so was excluded from analysis. Some loggers had issues with power supply and memory, and thus, over the course of the study, the spatial coverage of the site decreased. Data were organised for analysis into hydrological years, which run from October to September and used in hydrology to calculate precipitation totals. Hydrological years were used here to easily compare the temperature data to the hydrology data collected. During hydrological year 1 (hereafter, HY1; 29/10/21 – 30/09/2022), there were a total of 33 loggers measuring either air or water temperature

at 30 or 60 minute intervals. In hydrological year 2 (hereafter, HY2; 01/10/2022 – 30/09/2023) there were 31 loggers recording in total, and during hydrological year 3 (hereafter, HY3; 01/10/2023 – 07/08/2024), there were 16 loggers. The number of loggers was reduced for HY3 as preliminary analysis of HY1 and HY2 showed spatial homogeneity of the loggers, so some loggers were not redeployed for the final deployment period (TE2, TE5, TE10, TE14, TE16, TE18, TE20). Following this data download, the remaining HOBO loggers were set to record every 60 minutes to conserve memory and battery life, but T1_C, T1_FP1, T3_C, T3_FP1, T5_C, T5_FP1 and T6_C continued logging at 30-minute intervals.

For floodplain loggers, only temperatures that coincided with a water depth of ≥ 10 cm were retained in the dataset for analysis as this is the minimum depth that would allow a spawning-sized fish to swim onto the floodplain (Farkas, 1993) and represents an ecologically relevant threshold. Temperatures where water depth is < 10 cm are irrelevant as an adult fish could not swim onto or off the floodplain and while these depths could support burbot larvae, it would ultimately result in the isolation of larvae and eventual death as water drains or evaporates (Ch. 5).

4.2.4. Data Analysis

All temperature data was combined to test for normality using a Kolmogorov-Smirnov test. The Kolmogorov-Smirnov test revealed the data to be non-normal ($D = 0.99$, $p = < 0.001$). Thus, differences between specific groups (i.e., unshaded vs shaded, main vs side channel) were investigated using a Spearman's rank correlation test, and Kruskal-Wallis tests to compare the medians of each group, both being suitable for non-parametric data, to explore associations between loggers and give an indication of thermal variability across the site. A Levene's test was also conducted to assess the equality of variances across multiple loggers. Exploration of spatial variation was crucial as the burbot uses different habitats at different life stages, so observations in statistical and relative differences needed to be determined.

The spawning thresholds of 2°C, 4°C, 6°C, and 7°C (Table 4.6) were investigated using the literature on burbot from the western European subclade. The water temperature data were compared to these thresholds to assess whether a successful spawning period was observed in each hydrological year with multiple one-way Wilcoxon Signed Rank test were chosen due to the data being non-parametric and having the ability to compare group observations (i.e., floodplains or side channels) against a threshold (μ). As the data is retested for multiple thresholds, the p -values were adjusted using a Benjamini and Hochberg method, which focuses on controlling the false discovery rate rather than controlling the false positive rate as in the Bonferroni method (Jafari and Ansari-Pour, 2019). The 7°C threshold marks an absolute upper threshold for which a low rate of spawning could occur and while sub-optimal, could still facilitate spawning for western European burbot (Jäger et al., 1981; Beelen, 2009). Maximum water temperature was the key variable considered in this study as it can cause burbot mortality at any life stage (Żarski et al., 2010; Lahnsteiner et al., 2012). Weekly rate of change of daily maximum water temperature during the spawning period of the western European subclade (December – February) was also calculated to identify potential spawning windows and an assessment of how variable daily maximum water temperature was. A similar approach was applied to water temperatures for egg incubation, larval stages, and adult optima. All data and statistical analyses were conducted in R (v.4.3.2).

To contextualise the temperatures at the Wissey with a river where burbot are supported, main channel temperatures were compared to the Grote Nete, Belgium for the observation period. Though floodplains and side channels are the main focus of this study for spawning, egg incubation, and larval development, analysis of the main channel temperatures was conducted as no data was available for lateral habitats. Daily average and daily maximum main channel temperatures in the Wissey were compared to available water temperature data for the study period (2021 – 2024) from the Grote Nete (51° 8' 42.2916"N, 5° 0' 13.2084"E), the nearest available monitoring station to the candidate reintroduction area for burbot (De Vlaamse Milieumaatschappij, 2024). Kruskal-Wallis tests were also conducted to compare medians of daily maximum water temperatures for burbot life stage periods (i.e., spawning, egg incubation, and larval development).

Table 4.6. Thermal thresholds for each burbot life stage as determined by the literature from which this study compares Wissey water temperatures and suitability for burbot. * = western European burbot.

Life Stage	Temperatures Investigated (°C)	Maximum Temperature (°C)	Time Period	Source
Spawning	2, 4, 6, 7	7	December - February	Jäger et al. (1981); Beelen (2009)*
Egg Incubation	<9	9	January - April	Shodjai (1977)*; Kainz and Gollmann (1996)*; Lahnsteiner et al. (2012)
Larval Development	<16	16	March - May	Trabelsi et al. (2011)*; Kupren et al. (2014)
Adults	<14, 20 – 30	30	All year	Hardewig et al. (2004)*; Brackwehr et al. (2016)*

4.2.5. Future Temperature Considerations – Climate Projections

To consider the future survival of a reintroduced burbot population, an empirical model for future daily maximum water temperature change in relation to predicted future daily maximum air temperature was produced. Extensive literature has established a relationship between air temperature and water temperature (Webb et al., 2003; Ducharme, 2008; Johnson et al., 2014; Wilby and Johnson, 2020). An empirical modelling approach was chosen here as it offers the advantages of being simple and easily adjusted (Korzukhin, et al., 1996), is based on observational ‘real-world’ data compared to theoretical models (Svensson, et al., 2002), and builds on the extensive climate modelling research that has produced climate projections and methodologies for applying empirical models (Diaz-Nieto and Wilby, 2005; Hrachowitz et al., 2010; Knutti and Sedláček, 2013; Johnson et al., 2014; Wilby et al., 2014; Watts et al., 2015; Wilby and Johnson, 2020). The intention of the empirical model developed here is to act as a sensitivity analysis, for which a potential worst-case future scenario for the context of burbot survival can be discussed (Hansen et al., 1984; Dessai et al., 2005; Imbers et al., 2013). Daily maximum temperature was the chosen variable to investigate due to known lethality when thresholds are exceeded (Jackson et al., 2008; Lahnsteiner et al., 2012).

4.2.5.1. Air-Water Temperature Model Construction

To construct the model, a reference period of observational data is required. Reference periods vary, but 25 – 30 years is common (Diaz-Nieto and Wilby, 2005; Lenderink, et

al., 2007; Wilby and Johnson, 2020; Finney et al., 2022). The water temperature data collected at the Wissey site, however, is not sufficient (i.e., <3 years). There is no extensive water temperature record for the Wissey in close proximity to the study site, but there is, however, an air temperature record for Denver Sluice (TF 59044 00939; hereafter Denver), from 1978 to 2023. The Denver weather station records daily maximum and minimum air temperature and is part of the MetOffice Integrated Data Archive System (MIDAS) Open: UK Land Surface Station Data (Met Office, 2023). The extracted dataset was examined and cleaned for obvious outliers and flagged data, and the remaining data served as a reference period (1981 – 2023) for daily maximum air temperature.

Using this study's observation period at the Wissey (i.e., 29/10/2021 – 07/08/2024), data for daily maximum air and water temperature was extracted from loggers TE8 and TE_T3 for air temperature and from the consistent combined record of TE3 and T3_C for water, which covered the whole study period. A relationship between the two variables was established by logistic regression (Mohseni, et al., 1998, see Eq. 1). Logistic regression was chosen over linear regression as it is known that the linearity between air and water temperature departs near the thermal extremes, with evaporation and latent cooling limiting the upper temperatures that water can reach (Mohseni, et al. , 2002; Johnson, et al., 2014), while hyporheic and phreatic water buffer water temperature during low air temperatures (Crisp and Howson, 1982; Johnson, et al., 2014). A fitted logistic relationship, thus, can offer a more accurate predictive relationship between air and water temperature. The logistic relationship applied to daily maximum air and water temperature was obtained from Mohseni et al. (1981) as:

$$T_w = \frac{\alpha}{(1 + \exp^{\gamma(\beta - T_a)})} \quad (1)$$

where T_w is maximum water temperature, T_a is maximum air temperature, α is the upper asymptote and the maximum T_w the model can predict, β is the inflection point of the curve and the region of T_a with greatest rate of change of T_w , and γ is the gradient of the curve at the inflection point and is the increase of T_w per unit increase in T_a (Mohseni, et al., 1998; Johnson, et al., 2014). The logistic relationship was determined

from the Wissey observational data that was combined to produce daily maximum water and air temperatures from 29/10/21 to 07/08/2024 ($n = 1,014$).

Based on the observational data at the Wissey and at Denver during the same period (though it should be noted the Denver data only extends to 31/12/2023), a relationship between maximum daily air temperature at the Wissey and Denver was established ($r^2 = 0.77$, Fig. 4.4). The strong positive relationship suggests that the Denver dataset could be used as an approximation of air temperature at the Wissey, and in turn as an approximation of air-water temperature relationships at the Wissey study site. Based on this, using the logistic relationship, the water temperature at Denver was hindcast for the period 1981 – 2023. The hindcasted daily maximum water temperature for Denver had a high positive correlation with Wissey daily maximum water temperature during the observational period ($r^2 = 0.9$).

4.2.5.2. Model Validation

Prior to the logistic relationship being used to hindcast maximum daily water temperature at Denver, the model was validated. The observational data from the Wissey were divided randomly into 70% ($n = 710$) and 30% ($n = 304$) subsamples, following the split-sample test framework, which uses 70% of observational records for model calibration and the remainder for validation (Kohavi, 1995; Shen et al., 2022). The split-sample test framework does come with limitations, however, particularly relating to subjectivity when splitting the data (Shen et al., 2022), but this approach has been successfully applied previously to short-term datasets (Johnson et al., 2014). Based on the 70% model subset, the upper asymptote (α) was 20.61°C, β was 12.72°C and γ was 0.14°C. These parameters were used to predict daily maximum water temperature based on the daily maximum air temperature in the 30% subset. The predicted daily maximum water temperature was then compared to the actual observed daily water temperature values. The variables had a correlation of $r^2 = 0.82$, with a root mean square error of 1.85°C, which can be used to contextualise the accuracy of the model predictions.

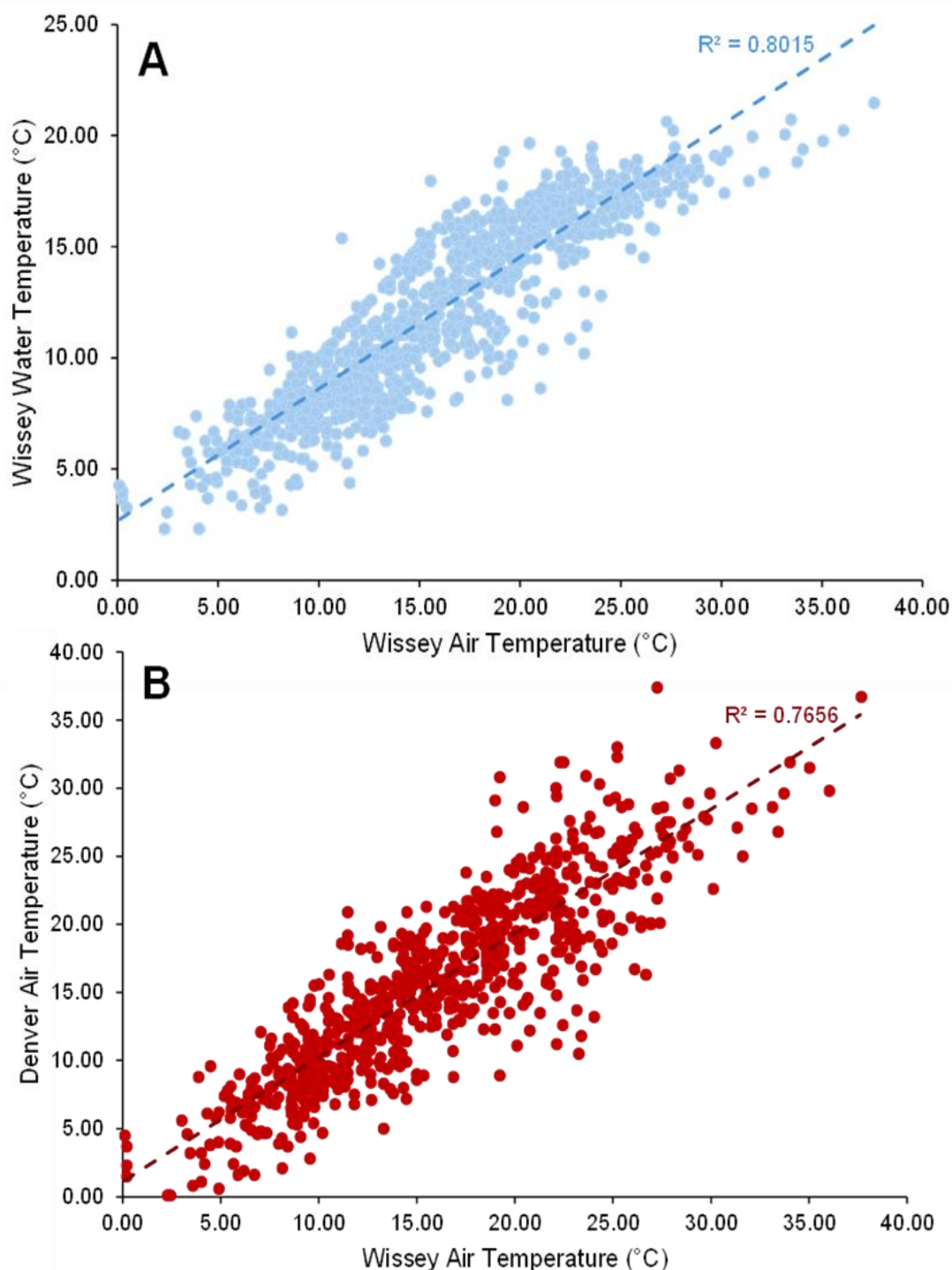


Figure 4.4. (A) Linear relationship between Wissey daily maximum air temperature and daily maximum water temperature (blue) from observational period (29/10/21 to 31/12/23), and (B) linear relationship between Denver daily maximum air temperature and Wissey daily maximum air temperature (red).

4.2.5.3. Climate Projections

Climate projections for Denver daily maximum air temperature were obtained from a regional climate model that is part of the United Kingdom's Climate Projection 2018

(UKCP18) project (Met Office Hadley Centre, 2018). The projections provide estimations for daily maximum air temperature from 1981 to 2080, downscaled to a high resolution (12 km), under a high emissions scenario, RCP8.5 (Met Office Hadley Centre, 2018). This regional climate model was derived from a subset of global climate models based on HadGEM3-GC3, which means it does not include a full range of uncertainty of all possible future climate predictions (Robinson et al., 2023). This regional climate model is considered biased toward drier predictions, and thus less realistic (Aines et al., 2021; Kennedy-Asser et al., 2021; Barnes, et al., 2024). The model, however, represents an extreme warming and drying scenario in which maximum water temperature, and thus the burbot's future can be contextualised as a worst-case scenario. There are limitations to any climate model, which is true here, but this analysis is meant to consider and contextualise the burbot's future survival in the discussion of adaptation and conservation actions.

The data were extracted for TF 58000 06000, which covers the observational station at Denver and contained daily maximum temperature for the period 1981 – 2080. The climate projections produce 12 ensemble members, which are runs with slight adjustments to regional model parameters, giving a range of outcomes. The ensemble members were then bias-corrected using a change factor approach (Diaz-Nieto and Wilby, 2005). For the change factor approach, the difference between the long term averages in daily maximum temperature (1981 – 2023) and the averages in daily maximum temperature for the UKCPs predictions (1981 – 2023) were calculated. The difference in temperature is added to the baseline temperature series. While variability and range remain unchanged, the change factor approach assumes the spatial pattern of the present climate remains unchanged in the future (Diaz-Nieto and Wilby, 2005). Despite using bias correction, the 12 ensembles were not strongly correlated with the observed Denver reference period (average $r^2 = 0.53$). The logistic maximum daily air-water temperature relationship was then applied to the climate projection data for the 2030s (i.e., 2030 – 2039) and the 2070s (i.e., 2070 – 2080) for each ensemble member to predict maximum daily water temperature during those periods.

4.3. Results

Summary statistics for all data across all hydrological years are presented in Table 4.7. The Levene's test revealed that variances in temperature across all loggers were not equal ($F = 1,116.9$, $p = <0.001$). In terms of variation between shaded and non-shaded loggers across all the data, average shaded temperature was $11.0 \pm 4.28^\circ\text{C}$ and for non-shaded it was $10.9 \pm 3.96^\circ\text{C}$. The Kruskal-Wallis test revealed that there was not statistically significant differences between the medians of shaded and non-shaded loggers ($p = 0.16$). Comparatively, average main channel temperature across all hydrological years was $11.0 \pm 4.1^\circ\text{C}$, while average side channel temperature was $10.8 \pm 4.0^\circ\text{C}$. The Kruskal-Wallis test showed that the differences between medians for the main and side channel loggers are statistically significant ($p = <0.001$). The Spearman's rank tests showed there was high correlation between main and side channels ($r^2 = 0.99$, $p = <0.001$).

Overall, the environmental characteristics (i.e., shaded vs open, main channel vs side channel) of the loggers across all years can produce variations in water temperature that have statistically significant differences. Temperature differences between habitat types (i.e., main channel, floodplain, side channel) will be considered in the following sections, due to statistically significant differences observed and due to the biological and ecological significance of burbot using different habitats at different life stages.

4.3.1. Spawning and Egg Incubation Habitat Temperatures

To determine the thermal suitability for the burbot, key thresholds and timings obtained from the literature are considered against the observed data. The spawning period for the western European burbot subclade is from December – February and could occur when daily maximum temperatures are below 7°C for a two-week period. In the following analysis, the spawning period is considered from 1st December – 28th February (Fig. 4.5). While the two-week window is commonly quoted in the literature, it is unclear if this is a minimum requirement or a general rule to allow most spawning to occur. The egg incubation period requires temperatures to rise following spawning, but not exceed 9°C . Similar to the larval period, higher temperatures can reduce the

Table 4.7. Summary statistics for HY1 – HY3.

Logger	HY1					HY2					HY3				
	<i>n</i>	Mean	SD	Max.	Min.	<i>n</i>	Mean	SD	Max.	Min.	<i>n</i>	Mean	SD	Max.	Min.
<i>Main Channel</i>															
TE1	15,784	11.81	4.58	22.71	4.1	-	-	-	-	-	-	-	-	-	-
TE2	16,088	11.88	4.75	30.56	4.2	2,807	11.4	1.64	14.5	7.78	-	-	-	-	-
TE3	16,089	11.41	4.2	21.47	3.79	12,461	9.58	3.38	20.0	1.11	-	-	-	-	-
TE5	12,340	11.95	4.62	20.9	3.68	-	-	-	-	-	-	-	-	-	-
TE6	16,092	11.59	4.47	21.76	3.58	5,319	8.64	3.10	14.1	0.78	-	-	-	-	-
TE7	13,099	10.63	4.14	21.95	3.68	2,795	16.00	1.16	19.9	12.2	7,478	11.07	3.76	20.23	2.84
TE9	16,090	11.28	3.9	20.14	3.68	9,172	10.50	4.12	18.8	2.19	4,806	9.00	2.65	14.9	2.94
TE10	16,091	11.27	3.9	19.85	3.58	11,884	9.34	2.93	16.00	2.19	-	-	-	-	-
TE12	9,251	8.5	2.45	15.57	3.68	5,609	8.52	2.98	13.6	2.09	-	-	-	-	-
TE14	16,176	11.47	4.37	26.78	3.79	11,887	9.27	3.07	18.00	1.66	-	-	-	-	-
TE15	16,093	11.46	4.2	21.38	3.68	14,680	10.5	3.67	19.3	1.66	-	-	-	-	-
TE16	16,093	11.56	4.25	21.86	3.79	11,889	9.34	2.99	15.9	1.55	-	-	-	-	-
TE19	16,176	11.52	4.25	21.76	3.79	6,818	8.52	3.28	18.5	1.44	-	-	-	-	-
T1_C	2,713	15.9	2.7	21.6	9.4	17,469	11.6	4.42	20.6	0.6	14,957	11.1	3.81	19.4	2.9
T3_C	-	-	-	-	-	14,663	11.3	4.30	19.9	1.01	14,957	10.9	3.55	19.0	3.01
T5_C	-	-	-	-	-	14,658	11.4	4.21	19.2	1.67	14,957	10.9	3.65	18.9	2.75
T6_C	2,704	15.6	2.51	20.4	9.5	17,473	11.3	4.08	19.2	1.5	14,957	10.9	3.81	19.7	2.6
<i>Side Channel</i>															
TE_Bridge	14,757	11.41	4.77	24.56	3.16	10,265	9.78	4.80	20.6	0.23	7,482	11.0	3.73	20.3	2.84
TE11	16,091	10.91	3.77	35.22	2.62	14,676	10.01	2.53	19.0	0.67	7,479	10.4	3.56	24.7	0.78
TE13	16,090	11.49	3.99	26.39	3.79	14,679	10.4	2.91	17.0	2.30	7,478	10.7	3.45	18.8	2.62
TE17	16,093	10.48	1.56	13.85	3.89	11,890	10.12	1.18	14.71	3.89	-	-	-	-	-
TE18	16,093	10.42	1.68	14.23	3.79	9,142	9.65	1.27	12.40	3.89	-	-	-	-	-
TE20	16,093	11.46	4.16	21.28	3.89	9,541	8.47	2.50	13.8	1.87	-	-	-	-	-
TE21	16,093	11.94	4.61	23	4.1	8,675	11.1	4.66	21.7	1.98	7,475	11.2	4.04	21.5	3.05
<i>Air</i>															
TE8	13,440	11.38	6.92	37.6	-5.5	11,885	8.14	5.56	26.68	-9.53	-	-	-	-	-

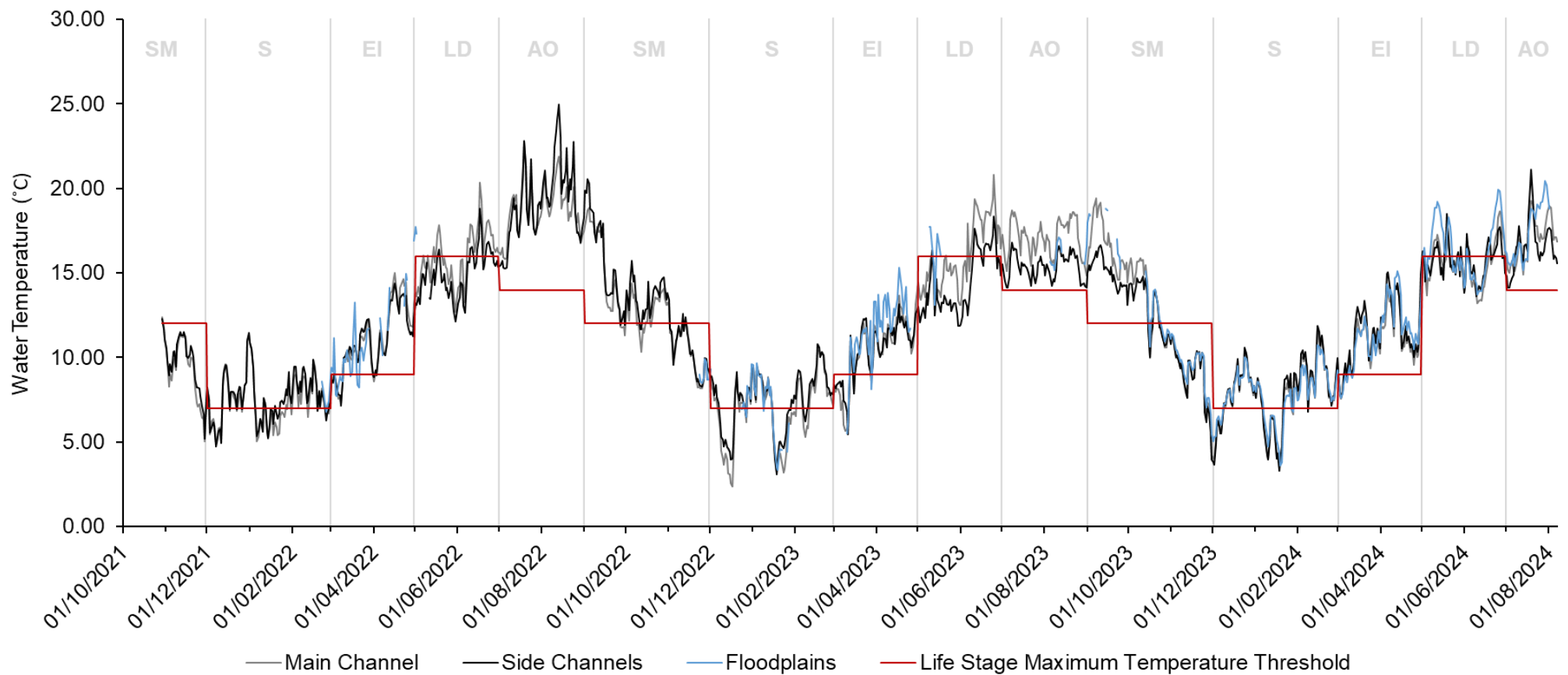


Figure 4.5. Daily maximum temperatures for side channels (black), main channels (grey), floodplains (blue) for entire recording period (29th October 2021 until 7th August 2024). The upper temperature thresholds for spawning (<7°C, S), egg incubation (<9°C, EI), larval development (<16°C, LD), adult thermal optima (14°C, AO) and spawning migration triggers (12°C, SM) are represented by the red line and labelled.

time taken for eggs to incubate, but can increase the chance of egg death or abnormalities in hatched larvae. The egg incubation and hatching period can last 30 – 75 days. In terms of data analysis, the focus is on daily maximum temperature data where water depth is ≥ 10 cm, which would reasonably allow adult fish to swim onto and off the floodplain, as lower depths could result in the isolation of burbot

4.3.1.1. Spawning Migrations

It is clear from Fig. 4.5, that spawning migrations are present in each hydrological year. Despite monitoring beginning in late October in HY1, there is an overall decline in temperature from the beginning of the record to the start of the spawning season in December that could be defined as a pre-spawning drop in temperature. From the start of the record until the beginning of the spawning season, average daily decline in maximum water temperature for the main channel and side channels was $-0.13 \pm 0.81^{\circ}\text{C}$ and $-0.12 \pm 0.75^{\circ}\text{C}$, respectively. In HY1, the greatest daily change in maximum temperature was from 30/11/21 – 1/12/2021 for both the main channel and side channels, which was $+2.28^{\circ}\text{C}$ and $+2.34^{\circ}\text{C}$, respectively. From the start of HY2 until the start of the spawning season on 1/12/2022, average daily decline in maximum water temperature for the main channel and side channels was $-0.07 \pm 0.62^{\circ}\text{C}$ and $-0.09 \pm 0.75^{\circ}\text{C}$, respectively. The greatest daily change in average maximum temperature was observed between 16/10/2022 and 17/10/2022 for the main channel at 1.3°C , while for side channels it was observed between 03/10/2022 and 04/10/2022 at 1.5°C . Interestingly, HY3 contained the most extensive floodplain inundation (Fig. 4.5), beginning 13/10/2023. There was a continuous decline in water temperature for the main channel, side channels, and floodplain after 23/10/2023, which could be defined as a pre-spawning drop. From the start of HY3 until the beginning of the spawning season on 1st December, average daily decline in maximum water temperature for the main channel, side channels, and floodplain was $-0.03 \pm 0.9^{\circ}\text{C}$, $-0.03 \pm 0.93^{\circ}\text{C}$, and $-0.04 \pm 0.7^{\circ}\text{C}$, respectively. The greatest daily change in average daily maximum temperature for all water body types occurred between 24/11/2023 and 25/11/2023, where the main channel experienced a -2.86°C change, the side channels -2.99°C , and the floodplains -2.21°C .

4.3.1.2. Spawning Periods

Floodplain inundation was observed in all hydrological years during the defined spawning period, but this was both spatially and temporally variable. During HY1, across the observed floodplains, water ≥ 10 cm depth was recorded on 46 days. This was not spatially even, with loggers upstream in the study area having less days of floodplain inundation of ≥ 10 cm. For example, T1_FP1 recorded 10 days of floodplain inundation, while T6_FP1 recorded 34 days, which was the maximum consecutive period of inundation. Of the total 46 days across the study site, seven days were within the winter spawning period and the remaining 38 days occurred post-spawning period. Total floodplain inundation increased the following year in HY2, with water depths of ≥ 10 cm recorded on 148 days, with the greatest consecutive period of inundation being 55 days at T5_FP1. Comparatively to HY1, inundation was more spatially even on the uppermost floodplains (T1_FP1 and T3_FP1, 107 and 92 days respectively). Of the total 149 days, 9 were in the pre-spawning period, 39 days were within the winter spawning period, and 101 were in the remainder of the year. HY3 had the most extensive floodplain inundation with a total of 300 consecutive days from 13/10/2023 to 07/08/2024. The extent of the inundation into the summer is attributed to winter flooding deepening the floodplain channel that T5_FP1 is installed in, which remained wetted into August 2024 with a permanent connection to the main channel observed. As for HY1 and HY2, flooding was spatially heterogeneous with T1_FP1 recording 201 days of flooding, T3_FP1 294 days, and T5_FP1 278 days. Of the total 300 days, 49 days were in the pre-spawning autumnal period, 91 days were in the winter spawning period, and 160 in the following in the post-spawning period.

The needed floodplain spawning habitat was created in multiple years during the study, but clear, thermally suitable spawning windows were not observed in every year (i.e., 2-weeks, $< 7^{\circ}\text{C}$ daily maximum temperature). Table 4.8 gives summary statistics for deployed loggers across all spawning periods in each hydrological year, grouped by habitat type: main channel, side channel, floodplain. Across all hydrological years during the spawning periods, there was high correlation between water bodies ($r^2 = > 0.92$, $p = < 0.001$), except for during HY1 where the correlation was lower ($r^2 = 0.85$, $p = < 0.001$) (Table 4.9).

Table 4.8. Summary statistics from the spawning period (December – February) of HY1 – HY3.

Table 10: Summary statistics from the spawning period (December 1, 1997 - February 1, 1998)															
Logger	n	HY1				n	HY2				n	HY3			
		Mean	SD	Max.	Min.		Mean	SD	Max.	Min.		Mean	SD	Max.	Min.
Main Channel															
TE1	4320	6.73	1.48	11.43	4.1	-	-	-	-	-	-	-	-	-	-
TE2	4320	6.78	1.47	11.43	4.21	-	-	-	-	-	-	-	-	-	-
TE3	4320	6.74	1.48	11.33	3.79	4320	6.35	2.07	10.6	1.11	-	-	-	-	-
TE5	3913	6.71	1.55	11.33	3.68	-	-	-	-	-	-	-	-	-	-
TE6	4320	6.62	1.53	11.33	3.58	2391	5.94	2.21	9.57	0.78	-	-	-	-	-
TE7	4320	6.71	1.52	11.43	3.68	-	-	-	-	-	2184	7.23	1.95	12.10	2.84
TE9	4320	6.81	1.48	11.43	3.68	3449	6.13	1.84	9.57	2.19	2184	7.27	1.89	12.00	2.94
TE10	4320	6.81	1.48	11.43	3.58	4320	6.56	1.93	10.5	2.19	-	-	-	-	-
TE12	4320	6.81	1.48	11.43	3.68	2681	6.01	2.02	9.57	2.09	-	-	-	-	-
TE14	4320	6.81	1.47	11.33	3.79	4320	6.52	1.98	10.6	1.66	-	-	-	-	-
TE15	4320	6.76	1.48	11.23	3.68	4320	6.46	1.99	10.6	1.66	-	-	-	-	-
TE16	4320	6.82	1.48	11.33	3.79	4320	6.52	2.01	10.7	1.55	-	-	-	-	-
TE19	4320	6.76	1.48	11.24	3.79	3582	6.07	1.92	9.37	1.44	-	-	-	-	-
T1_C	-	-	-	-	-	4320	6.11	2.14	10.3	0.6	4368	7.19	1.76	11.4	2.9
T3_C	-	-	-	-	-	4320	6.22	2.07	10.5	1.01	4368	7.21	1.80	11.6	3.01
T5_C	-	-	-	-	-	4320	6.39	1.99	10.4	1.67	4368	7.15	1.93	11.8	2.75
T6_C	-	-	-	-	-	4320	6.32	1.99	10.5	1.5	4368	7.03	1.97	11.6	2.6
Side Channel															
TE_Bridge	4320	6.46	1.58	11.43	3.26	4320	5.45	2.48	10.9	0.23	2184	7.25	1.91	11.9	2.84
TE11	4320	7.38	1.79	12.11	3.26	4320	7.84	1.84	11.4	0.67	2184	7.02	2.34	12.20	0.78
TE13	4320	7.49	1.57	11.33	3.79	4320	7.40	1.75	11.1	2.30	2184	7.21	2.00	11.90	2.62
TE17	4320	8.84	1.59	11.24	3.89	4320	9.24	1.56	11.33	3.83	-	-	-	-	-
TE18	4320	8.64	1.51	11.24	3.79	4320	8.9	1.14	11.24	3.83	-	-	-	-	-
TE20	4320	6.79	1.45	11.24	3.89	4320	6.58	1.86	10.2	1.87	-	-	-	-	-
TE21	4320	6.84	1.47	11.24	4.10	2957	6.04	1.93	9.47	1.98	2184	7.30	1.93	11.6	3.05
Air															
TE8	4320	5.82	3.91	15.95	-5.50	4320	4.77	5.22	18.43	-9.53	-	-	-	-	-
T1_FP1 Air	-	-	-	-	-	-	-	-	-	-	4368	6.92	4.3	18.45	-6.29
Floodplain															
T1_FP1	109	6.72	0.96	7.81	4.36	1489	6.61	1.58	9.3	2.2	4368	7.40	1.54	10.3	2.9
T3_FP1	152	6.40	1.72	10.7	2.76	1301	6.35	2.07	9.61	1.19	4368	7.42	1.50	10.4	3.14
T5_FP1	130	6.34	1.01	8.01	4.36	318	6.72	1.27	8.8	3.69	3150	3.81	0.16	4.07	3.49
T5_FP2	105	6.18	1.47	9.36	3.19	42	3.18	3.89	8.1	-1.83	-	-	-	-	-
T6_FP1	133	5.49	0.85	6.92	4.15	122	12.5	0.99	14.4	10.6	-	-	-	-	-

Table 4.9. Spearman's rank correlation between water body types for HY1 – HY3 spawning periods (start December – end February) ($p = <0.001$)

	HY1			HY2			HY3		
	Main	Side	FP	Main	Side	FP	Main	Side	FP
Main		0.969	0.854		0.980	0.954		0.994	0.970
Side	0.969		0.926	0.980		0.943	0.994		0.965
FP	0.854	0.926		0.954	0.943		0.970	0.965	

During HY1, floodplain logger installation in late February meant the spawning season was uncaptured. Hence, spawning suitability in HY1 must be assessed based on side channel temperatures, which are also used as the spawning strategy for some western European burbot populations (Bunzel-Drücke et al., 2004a; Worthington et al., 2012; Brackwehr et al., 2016). Average water temperature for the main channel loggers was $6.79 \pm 1.49^{\circ}\text{C}$, compared to $6.99 \pm 1.62^{\circ}\text{C}$ in the side channels, and $6.14 \pm 1.31^{\circ}\text{C}$ on the floodplains. Comparatively, minimum temperatures for main channel, side channel and floodplain were 3.58°C , 3.26°C , and 2.76°C respectively. During HY2, average floodplain temperature was higher than HY1 at $6.69 \pm 2.15^{\circ}\text{C}$, while the main channel and side channels averaged $6.30 \pm 2.02^{\circ}\text{C}$ and $6.71 \pm 2.18^{\circ}\text{C}$, respectively, which were both lower than HY1. The lowest recorded water temperature average for the winter spawning period in HY2 was from logger TE_Bridge, averaging $5.45 \pm 2.48^{\circ}\text{C}$. This was within the published spawning ranges for western European burbot (Table 4.3; Vught et al., 2008; Brackwehr et al., 2016). TE6 also achieved an average winter water temperature of less than 6°C , at $5.94 \pm 2.21^{\circ}\text{C}$. Three loggers recorded minimum water temperatures during the winter period of $<1^{\circ}\text{C}$: TE6 (0.78°C), TE11 (0.67°C), TE_Bridge (0.23°C). Compared to HY1 and HY2, average water temperatures for all water body types during the spawning period in HY3 were warmer (Table 4.8). Average floodplain water temperature was $7.38 \pm 1.55^{\circ}\text{C}$, while the main and side channels averaged $7.17 \pm 1.88^{\circ}\text{C}$ and $7.19 \pm 2.06^{\circ}\text{C}$, respectively. The lowest recorded water temperature average for the winter spawning period in HY3 was from T5_FP1, which averaged $3.81 \pm 0.16^{\circ}\text{C}$, which is within the published spawning ranges of the western European burbot, and lower than the commonly referenced $<4^{\circ}\text{C}$ figure. All other loggers averaged temperatures above 7°C , which is unsuitable for burbot spawning. Minimum temperatures recorded by all loggers were below 4°C , ranging from 0.78°C (recorded by TE11) and 3.49°C (recorded by T5_FP1).

For the floodplain loggers, one way Wilcoxon Signed Rank tests were used to determine if average daily maximum floodplain temperatures were greater than different spawning thresholds discussed in the literature, namely 2°C, 4°C, 6°C, and 7°C. Table 4.10 shows that for all hydrological years and for all thresholds tested, the average daily maximum floodplain temperature observations were not equal to the thresholds applied, accepting the alternative hypothesis that the observations were greater ($p = <0.05$). The only exception was HY2 and applying the 7°C threshold ($p = 0.38$), which suggests that the null hypothesis is not rejected and the observed floodplain temperatures were not statistically different than the 7°C threshold applied.

Table 4.10. Wilcoxon Signed Rank test results comparing average daily maximum floodplain temperatures to spawning thresholds. * = $p < 0.001$.

Test	HY1			HY2			HY3		
	V	p	Adjusted p	V	p	Adjusted p	V	p	Adjusted p
2	28	0.0078	0.0094	741	*	*	4189	*	*
4	28	0.0078	0.0094	720	*	*	4182	*	*
6	28	0.0078	0.0094	563	0.0022	0.0038	3909	*	*
7	26	0.0234	0.0256	393	0.3762	0.3762	3194	*	*

Fig. 4.6 gives the frequency of daily maximum water temperatures for the side channel, floodplain and main channel loggers (potential spawning areas) across all hydrological years. In HY1, Fig 4.6 shows that for seven days, the Wissey study area was inundated in the winter spawning period, with daily maximum water temperatures between 6.5°C and 9.0°C. It should be noted that these days are also consecutive and extend into the post-spawning period, which is discussed below. For side channel loggers in HY1, Fig. 4.6 shows that the average daily maximum temperatures were most commonly between 7°C and 8°C. For HY2 floodplains, Fig. 4.6 shows that daily maximum water temperatures were between 7°C to 8°C, occurring for 10 days out of the total 39 days of floodplain inundation during the winter period. Similarly, daily maximum water temperatures for the side channels were most commonly between 8°C and 9°C, which occurred on >20 days during the winter period. While similar frequencies of average daily maxima were experienced for both HY1 and HY2 (Fig. 4.6), HY2 had more days where average daily maximum water temperature was >6°C. Comparatively, in HY3, daily maximum floodplain temperatures were between 8 to 9°C during the winter spawning period. Similarly, in the side channels, daily maximum temperatures were most commonly between 8 to 9°C and these temperatures were

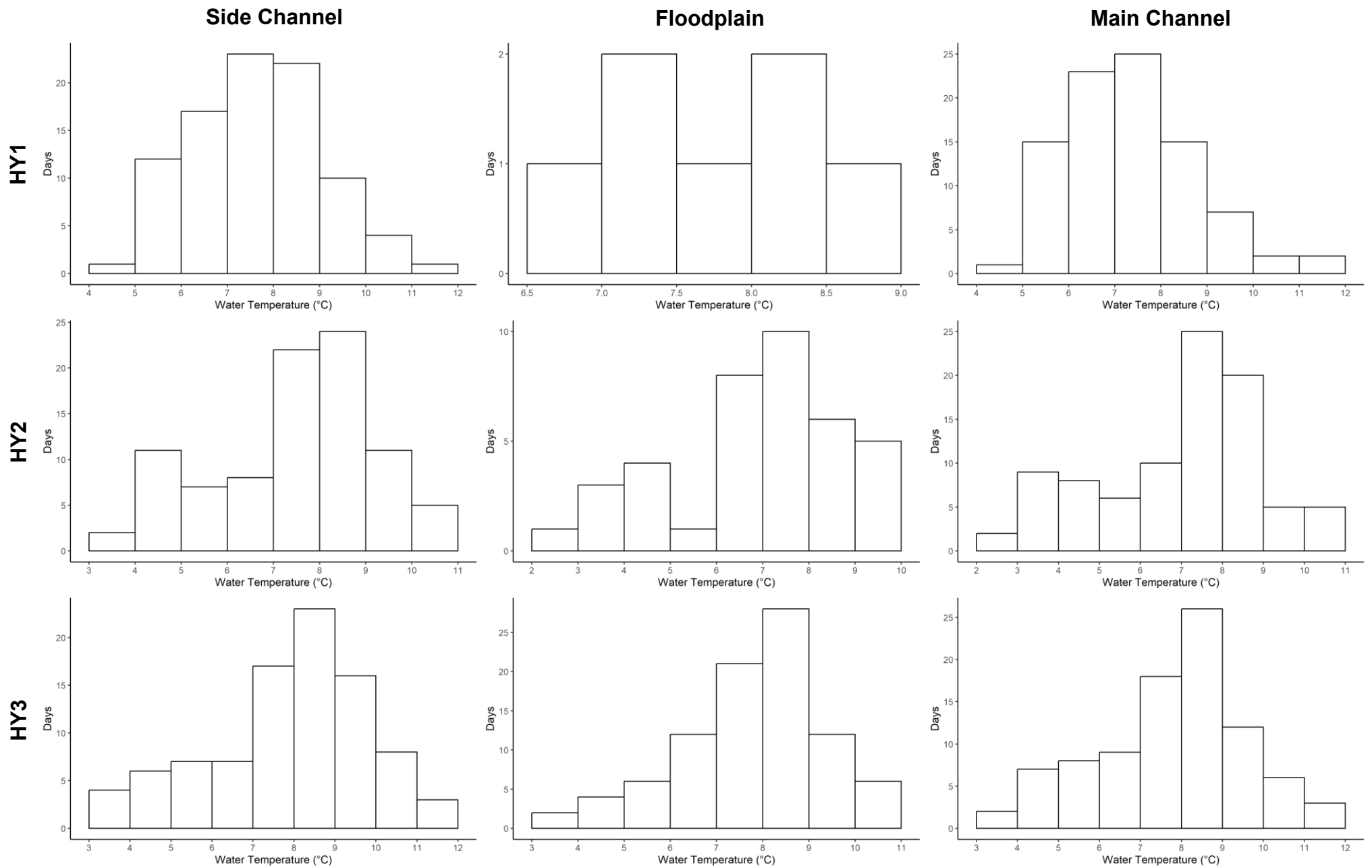


Figure 4.5. Occurrence (number of days) of daily average maximum water temperature for side channels (left), floodplains (middle), and main channel (right) for hydrological year 1 (top), hydrological year 2 (middle), and hydrological year 3 (bottom) during the spawning period (Dec – Feb).

reached on over 20 days. When compared to HY1 and HY2, it was clear that, while HY3 had more days of floodplain inundation, daily maximum water temperatures during the spawning period were often higher in both the floodplains and side channels.

The results show that across all hydrological years, thermally suitable days for spawning are intermittent. Table 4.11 shows the number of consecutive days where daily maximum temperatures for main channel, side channels, and floodplains are below thermal thresholds. Considering burbot spawning habitats only (i.e., side channels and floodplains), there were no thermally suitable spawning windows in HY1, but there was in HY2 in the side channels and in HY3 in both side channels and floodplains.

Table 4.11. Number of consecutive days where average daily maximum temperatures were below 2, 4, 6, and 7 °C for main channel, side channel, and floodplain habitats during the spawning period (Dec – Feb) in each hydrological year.

	HY1			HY2			HY3		
°C	Main	Side	Floodplain	Main	Side	Floodplain	Main	Side	Floodplain
2	0	0	0	0	0	0	0	0	0
4	0	0	0	5	1	3	2	2	2
6	5	6	0	11	10	4	6	6	5
7	14	9	0	17	14	7	15	15	15

The observational data shows that in all hydrological years, temperature is temporally variable across water bodies. In HY1, weekly rate of change calculations between 1/12/21 to 28/2/22 (Fig. 4.7a) showed average change in water temperature for the floodplain, main, and side channels to be 1.7°C, 0.02°C, and 0.02°C respectively. The greatest rate of change observed over the winter period was -4.06°C from 05/01/2022 to 11/01/2022 for main channel average temperature, which responded to a -6.83°C decrease in air temperature that week, while side channels only decreased by -3.92°C. For floodplains, a change of -1.7°C was observed between 16/02/2022 and 28/02/2022, but there is not enough floodplain data to fully assess weekly rate of change in HY1. For HY2, water of at least 10 cm depth was on the floodplains for ~7 weeks out of 12 for the winter period. The average weekly water temperature change, commencing over 1/12/22 - 28/2/23 (Fig. 4.7b), was 0.59°C, -0.02°C, and -0.04°C for

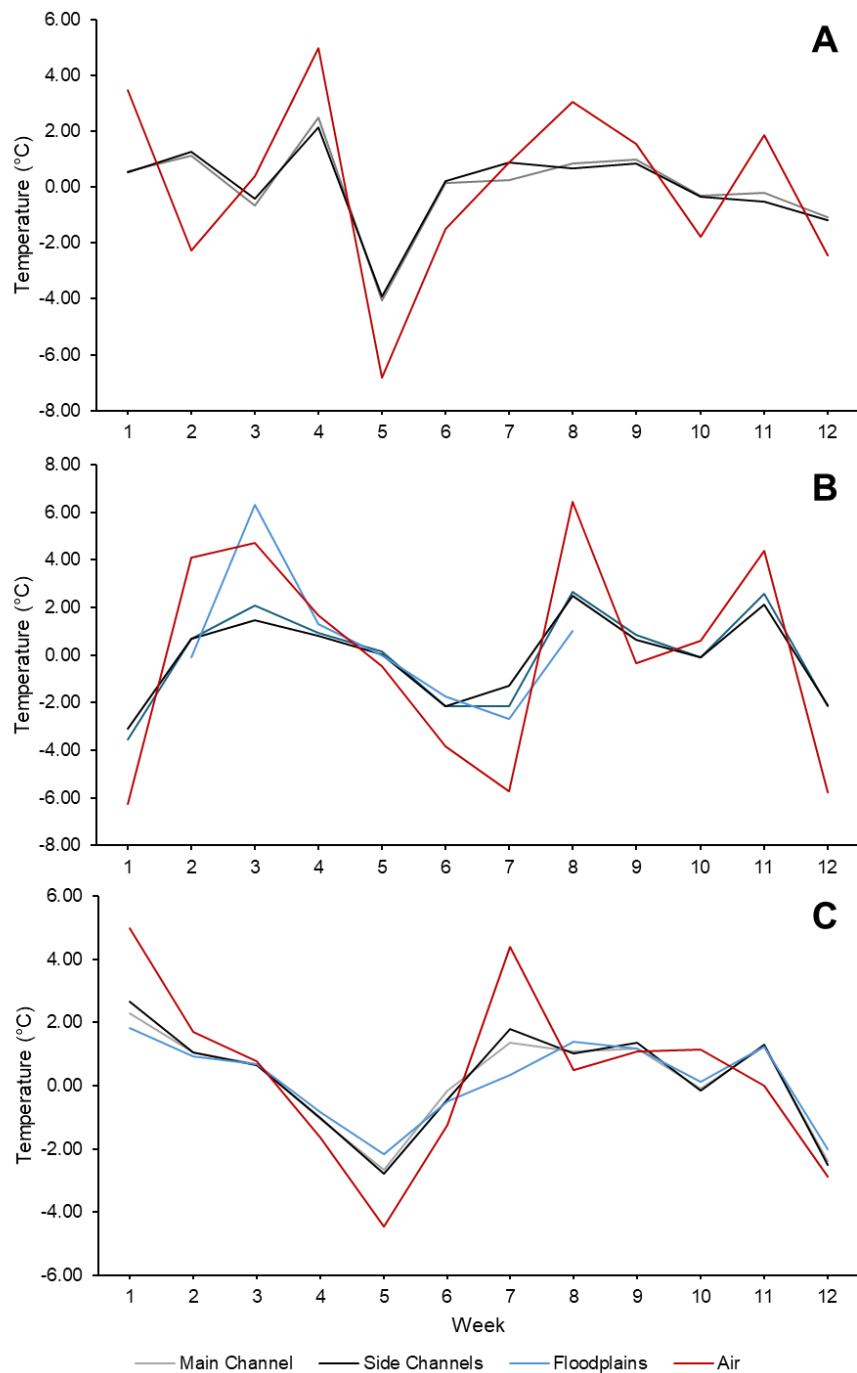


Figure 4.7. Average weekly change in temperature during the winter spawning period for floodplains, the main channel, and side channels (1st December to 28th February) for (A) hydrological year 1, (B) hydrological year 2, and (C) hydrological year 3. Note that floodplain loggers were installed in the last week of February 2021, so (A) has no floodplain data.

the floodplain, main channel, and side channel respectively. The greatest weekly change in temperature was 6.33°C on the floodplains following a 4.72°C increase in air temperature from 15/12/2022 to 22/12/22. Comparatively, the main channels and side channels only increased by 2.08°C and 1.5°C respectively over this same period

(15/12/22 to 22/12/22). For HY3, water was on the floodplain for the full 12 weeks of the spawning period (Fig. 4.7c). The average weekly water temperature change from weeks commencing 1/12/23 to 29/2/24, for the floodplains was 0.18°C, 0.21°C for the main channel, and 0.24°C for the side channels. The greatest weekly change in temperature was -2.18°C for the floodplains, following a -4.47°C decrease in air temperature from 29/12/2023 to 04/01/2024. Comparatively, the main channel and side channels also responded similarly to air temperature change, decreasing -2.66°C and -2.78°C, respectively.

Overall, the data showed that, a potential spawning window on the floodplains is not shown in the captured data in HY1. In HY2, although being towards the upper threshold of burbot spawning capabilities, HY2 had 17 days in the main, 14 days in the side channels, and 8 days on the floodplain where daily maximum temperatures were <7°C. Comparatively, HY3 was warmer on average during the spawning period compared to HY1 and HY2, but there was more extensive flooding, which still provided a 15-day window in the side channels and floodplains at <7°C for burbot to spawn, hence meeting the minimum requirements for a successful spawning period based on the literature.

4.3.1.3. Egg Incubation

As the spawning temperatures observed in the study period were in the upper range (i.e., >6°C) for burbot, based on the literature, the egg incubation period should be < 30 days, as opposed to 30 - 75 days as demonstrated for <4°C (Nagel et al., 2011; Lahnsteiner et al. 2012). In terms of egg incubation, for HY1 (Fig. 4.5) the main and side channels show a 9-day spawning period from 02/12/21 to 11/12/21 and a 14-day spawning period from 5/1/22 to 19/1/22. During this time, temperatures were almost consistently below 7°C, but the two periods were punctuated by a sudden 6°C increase on 11/12/21, rising from 3.9°C to 9.7°C by 15/12/22. If adults had been successful in spawning during the shorter, 11-day spawning window, a sudden increase to 9.7°C could have been fatal to any newly hatched eggs. In HY1, the only floodplain with long-term floodplain inundation was T6_FP1 reaching 34 days from 23/02/22 to 28/03/22. Water was observed to persist on the floodplain for longer following 28/03/22, but

during this period it dropped below 10 cm depth. Daily maximum water temperature on the floodplain did not exceed 9°C until 11/03/22, which provides a 17-day egg incubation period, assuming that spawning had been achieved on the floodplain prior to the installation of the floodplain loggers. Subsequently, 14 out of the 17 following days had temperatures unsuitable for burbot egg development at over 9°C, which would likely result in egg death.

The data showed that for side channels and floodplains, the spawning period in HY2 was followed by an unsuitable egg incubation period as water was held too intermittently on the floodplains and temperatures were too high and would have been lethal to newly hatched eggs (Fig. 4.5). Following the end of the spawning period (28/02), there were only 13 days before water temperatures in all water body types (main channel, side channels, and intermittent floodplain waters) exceeded the 9°C lethal limit for burbot eggs. If time after individual spawning windows is considered, the data still showed unsuitable egg incubation periods due to increasing water temperatures. For example, a 14-day spawning window in the side channels occurs from 15/01/2023 to 28/01/2023, but within 6 days, water temperatures increase to 9.37°C on 02/02/2023, which would be lethal to eggs. There is also a shorter, 11-day window in the side channels that occurs from 08/12/2022 to 18/12/2022, but within two days, temperatures increased to 9.31°C, which would be lethal for new burbot eggs. There was an 8-day suitable spawning window which occurred from 15/01/2023 to 22/01/2023, but it is not the temperature, but a decrease in water level that could threaten new burbot eggs. There is a period of 46 days where water depth is below 10 cm on the floodplains. When water depth increases again on 09/03/2023, daily maximum water temperature is 5.53°C. If burbot eggs could be held in smaller patches of water when floodplain water depths drop until spring floodplain inundation occurs and these small water patches were thermally suitable, there could have been successful egg hatching in HY2, compared to water temperatures in the main and side channels, however, where temperatures increase above 9°C, this may be unlikely.

Similar to HY1 and HY2, the established 15-day spawning window on the floodplains and side channels was also followed by an unsuitable egg incubation period. For

example, for the floodplains, the spawning window occurring from 7/1/24 – 21/1/24, only had 12 days before daily maximum temperature increased to 9.5°C. For the side channels, the 15-day spawning window occurred from 6/1/24 – 20/1/24, but temperatures increased to 9.02°C after only 3 days. For HY3, as well as having a single suitable spawning window within the specified spawning period for western European burbot (i.e., December – February), Fig. 4.5 shows that there was also a shorter (10-day) spawning window from 29/11/2023 to 08/12/2023 on the floodplains where water temperatures were constantly <7°C and ranged between 4.85°C and 6.79°C. Unfortunately, within 9 days, the lethal limit for burbot eggs (i.e., >9°C) was then exceeded, meaning absence of a suitable egg incubation window that might facilitate growth and hatching of burbot eggs. A similar shorter spawning window also occurred in the side channels, with an 11-day spawning window occurring from 28/11/2023 to 08/12/2023, where daily maximum water temperatures were between 3.63°C and 6.85°C. After 9 days following this spawning window, daily maximum water temperature increased to 9.35°C.

4.3.2. Larval Development

The larval growth period is defined by a slow warming to a maximum of 16°C following the winter spawning period (i.e., a two-week period during December – February where temperatures do not exceed 7°C). The literature states that the larval period lasts approximately 60 days, which can be reduced slightly by higher temperatures.

In HY1, the data showed that the floodplains were only inundated for 46 days, which is not sufficient to encompass spawning, egg incubation, and the larval development period before water recedes from the floodplain. If eggs were to incubate and hatch successfully, there is potential that free-floating larvae would be carried into the main and side channel systems where they could potentially find refuge in slack water patches and amongst macrophytes. However, Fig. 4.5 shows that daily maximum average temperatures do not exceed 16°C for the main channel and side channels until 19/05/2022. Following the second potential spawning period in HY1 (22/1/22 – 19/5/22), this provided 87 days for egg incubation and larval development. During that

87-day window, average daily maximum temperature change was $0.09 \pm 0.8^{\circ}\text{C}$ and $0.075 \pm 0.76^{\circ}\text{C}$ for the main and side channels, respectively. The greatest daily change occurred from 14/02/2022 to 15/02/2022 for both main and side channels, which were 1.98°C and 2.02°C , respectively.

For HY2, the floodplains were inundated for 149 days, with 74 days in the spring following the winter spawning period. The floodplain inundation was intermittent, and like HY1, could have resulted in some eggs or newly-hatched larvae being carried into the main and side channels as the inundation receded. At the end of the second spawning event in HY2 (i.e., 01/02/2023), average daily maximum temperatures for the main and side channels did not exceed 16°C until 11/05/2023, affording 99 days for the completion of egg incubation and larval development. During this 99-day window, average daily maximum temperature change was $0.1 \pm 0.83^{\circ}\text{C}$ and $0.09 \pm 0.8^{\circ}\text{C}$ for the main and side channels, respectively. Greatest daily change occurred from 11/03/2023 to 12/03/2023 for both the main and side channels at 2.46°C and 3.24°C , respectively.

During HY3, floodplains were inundated for 300 days, with 160 days of inundation in the spring and summer following the end of the spawning period. Due to this persistent floodplain inundation providing suitable physical habitat, it would be possible for eggs to incubate, hatch and for larval development to occur on the floodplain, if temperatures were suitable. At the end of the second spawning window (i.e., 20/12/2023), average daily maximum temperatures for the floodplains and side channels do not exceed 16°C until 01/05/2024, which provides 133 days to complete egg incubation and larval development. During this window, average daily maximum temperature change was $0.06 \pm 1.01^{\circ}\text{C}$ for the side channels and $0.06 \pm 0.83^{\circ}\text{C}$ for the floodplains. The greatest daily change occurred from 12/02/2024 to 13/02/2024 for both side channels and floodplains at 2.94°C and 2.84°C , respectively.

4.3.3. Adult Temperature Suitability

Compared to the more specific thermal requirements of the egg incubation and spawning stages, adult burbot are more thermally tolerant and have the ability to move to cooler areas. An established thermal optimum for adult burbot is around 14°C, though they can survive at temperatures up to ~30°C. Beyond the thermal optimum, burbot do start to exhibit stress behaviour, and so it is important to assess any reintroduction site by time above and below the thermal optima.

4.3.3.1. Adult Optima

In HY1, the year contained a large proportion of the year where water temperatures were below the thermal optimum for adult burbot (<14°C). On average, daily maximum water temperatures were below 14°C for 64% of all days for all main and side channel loggers (Fig. 4.2). The lowest was TE5, that was only below the thermal optimum on 52% ($n = 133$) of all logging days ($n = 258$), whereas TE17 had daily maximum water temperatures below 14°C on 100% of all logging days ($n = 336$). All main channel loggers show the longest period of consecutive days below 14°C was 166 days during HY1.

Similar to HY1, there was a large proportion of the year in HY2 where water temperatures were below the thermal optimum for burbot. Daily maximum water temperatures were, on average, below 14°C on 76% of all logged days for the main and side channel loggers. The logger with temperature below 14°C for the least amount of days was TE1 at 51% ($n = 122$) out of all logging days ($n = 240$), with the greatest period observed at TE20 and TE18, which both achieved 100% <14°C on all logging days ($n = 199$ and $n = 191$, respectively).

Despite HY3 having fewer loggers recording throughout the study area, similar patterns were observed to the previous hydrological years. On average, daily maximum water temperatures were below 14°C on 69% of all logging days for main and side channel loggers. The logger with the lowest proportion of days where daily maximum water temperature was below 14°C was both TE_Bridge and TE12 at 63%

($n = 196$ and $n = 198$, respectively) out of all logging days ($n = 312$), whereas the highest was TE9 with 92% ($n = 184$), but the high percentage was due to the lower amount of total logging days ($n = 201$).

4.3.3.2. Summer Maxima

Summary statistics for summer maxima across all hydrological years are listed in Table 4.12 for main channel and side channel loggers. In HY1, in terms of upper critical temperatures, the July heatwave 16/7/22 – 19/7/22 saw an air temperature record for the UK. Air temperatures at the Wissey peaked at 37.6°C on 19/07/2022 for TE8 (in a shaded area), and 38.6°C on the same day for TE_T3, representing open, non-shaded conditions on a dry floodplain. For loggers still submerged during July 2022, 7 were shaded (TE1, TE_Bridge, TE7, TE16, TE19, TE20, and TE21) and 7 were unshaded (TE3, TE5, TE6, TE9, TE10, TE13, and TE15) in the main and side channels. Average water temperature for the shaded and unshaded loggers were 17.09°C and 16.64°C respectively. During July 2022, the maximum water temperature recorded by shaded loggers was 23.48°C, compared to 21.76°C for the unshaded loggers. Minimum water temperatures recorded by shaded loggers was 12.3°C, while unshaded loggers recorded a minimum water temperature in July of 12.88°C. During July 2022, there were 10 loggers in the main channel (TE1, TE3, TE5, TE6, TE7, TE9, TE10, TE15, TE16, TE19) and 4 in the side channels (TE_Bridge, TE13, TE20, and TE21; excluding TE17 and TE18 as these loggers represent the lower Wissey side channel, a water body with different thermal characteristics and so were not included in the averages, see below). Average water temperature for the main channel during July 2022 was 16.83°C, while for the side channels it was 17.11°C, and TE17/18 averaged at 11.95°C. Maximum water temperatures were 22.72°C, 23.48°C, and 14.23°C for the main channel, side channel, and TE17/18, respectively. Minimum water temperatures were 12.88°C, 12.3°C, and 10.36°C for the main channel, side channel, and TE17/18, respectively. Overall, the main and side channel temperatures showed high correlation during July 2022 (with $r^2 = 0.96$, $p = <0.001$).

Table 4.12. Summary statistics for July 2022, results from July 2023 and 2024 are given for comparison.

Logger	HY1					HY2					HY3				
	n	Mean	SD	Max.	Min.	n	Mean	SD	Max.	Min.	n	Mean	SD	Max.	Min.
<i>Main</i>															
TE1	1488	17.43	1.75	22.72	13.56	-	-	-	-	-	-	-	-	-	-
TE3	1488	16.63	1.67	21.47	12.88	-	-	-	-	-	-	-	-	-	-
TE5	1488	16.93	1.51	20.9	13.65	-	-	-	-	-	-	-	-	-	-
TE6	1488	17.28	1.67	21.76	14.00	-	-	-	-	-	-	-	-	-	-
TE7	1424	17.12	1.68	21.95	13.75	744	15.80	0.88	17.70	13.80	744	16.1	1.4	20.2	13.6
TE9	1488	16.01	1.37	20.14	13.08	744	15.20	0.78	16.80	13.50	-	-	-	-	-
TE10	1488	16.03	1.35	19.85	13.08	-	-	-	-	-	-	-	-	-	-
TE15	1488	16.84	1.58	21.38	13.37	744	15.40	0.92	17.50	13.30	-	-	-	-	-
TE16	1488	17.02	1.64	21.86	13.46	-	-	-	-	-	-	-	-	-	-
TE19	1488	17.00	1.64	21.76	13.46	-	-	-	-	-	-	-	-	-	-
T1_C	-	-	-	-	-	1488	16.30	0.96	18.30	13.90	1488	16.3	1.22	19.4	14.00
T3_C	-	-	-	-	-	1488	15.30	0.99	17.70	13.30	1488	15.6	1.32	19.00	13.2
T5_C	-	-	-	-	-	1488	15.40	0.86	17.30	13.40	1488	15.7	1.26	18.9	13.6
T6_C	-	-	-	-	-	1488	15.90	0.95	18.30	13.70	1488	16.00	1.43	19.7	13.5
<i>Side</i>															
TE_Bridge	1488	17.12	2.04	23.48	12.3	744	16.00	1.14	18.70	13.00	744	16.00	1.47	20.3	13.1
TE11	-	-	-	-	-	744	12.3	0.59	14.1	10.9	744	14.5	2.70	24.7	11.2
TE13	1488	16.66	1.79	21.47	13.17	744	13.9	0.78	15.7	11.8	744	15.2	1.34	18.8	12.7
TE17	1488	11.87	0.66	13.85	10.36	-	-	-	-	-	-	-	-	-	-
TE18	1488	12.03	0.73	14.23	10.36	-	-	-	-	-	-	-	-	-	-
TE20	1488	16.78	1.57	21.28	13.46	-	-	-	-	-	-	-	-	-	-
TE21	1488	17.86	1.83	23.00	13.75	744	16.7	1.11	19.8	14.1	744	16.8	1.78	21.4	13.9
<i>Air</i>															
TE8	1488	18.46	5.54	37.6	4.31	-	-	-	-	-	-	-	-	-	-
TE_T3	1488	19.19	6.59	38.6	4.52	744	16.5	2.49	23.7	10.5	744	17.1	3.41	28.1	9.46

Individual analysis of daily maximum temperatures in HY1 showed that no loggers achieved consecutive days where daily maximum temperatures reached more than 24°C. It was only at 20°C that more than one logger ($n = 13$) achieves multiple consecutive days with daily maximum exceeding 20°C, with the longest period being 17 days for TE_Bridge. There were still three loggers that achieved no consecutive days where daily maxima exceeded 20°C: TE10, TE17, and TE18. For July 2022, the mean difference between the average main channel temperature and average side channel temperature comparative to the average of TE17/18 was calculated (Fig. 4.8). On average, the difference between TE17 and TE18 and main channel was $-4.89 \pm 1.07^\circ\text{C}$, but on 20/07/2022 at 03:00, the greatest difference between TE17 and TE18 and the main channel was, -7.5°C . Comparatively, TE17 and TE18 were also consistently cooler than average side channel readings, on average, $-5.16 \pm 1.21^\circ\text{C}$ cooler than the other side channels. Maximum difference between TE17 and TE18 and average side channel temperatures was -8.1°C . Unfortunately, both TE17 and TE18 have incomplete records, ending in early summer of HY2 (log period 1/10/2022 – 05/06/2023).

In the summer of HY2, there was no heatwave of a similar magnitude to July 2022. Table 4.12 provides the summary statistics for July 2023 compared with July 2022. The range of mean temperatures across all loggers was narrower than in July 2022. In July 2023, mean water temperature varied between 12.3°C to 16.3°C , while that range in July 2022 was 16.01°C to 17.43°C (excluding TE17 and TE18 data). Maximum water temperature reached in July 2023 was 19.8°C at TE21, compared to 23.0°C for this same logger in July 2022.

For HY2, June had the most consistently high air and water temperatures. Daily maximum air temperatures were above 25°C from 10/06/2023 to 26/06/2023). During this period, air temperatures reached a maximum of 33.12°C at TE_T3, which gives unshaded air temperature. Unfortunately, there was not a logger recording air temperature in shaded conditions at this time due to the loss of data from TE8 (Fig. 4.2; Table 4.5). Of the loggers recording in the main and side channels during this period, four were shaded (TE_Bridge, TE7, TE19, and TE21) and nine were unshaded

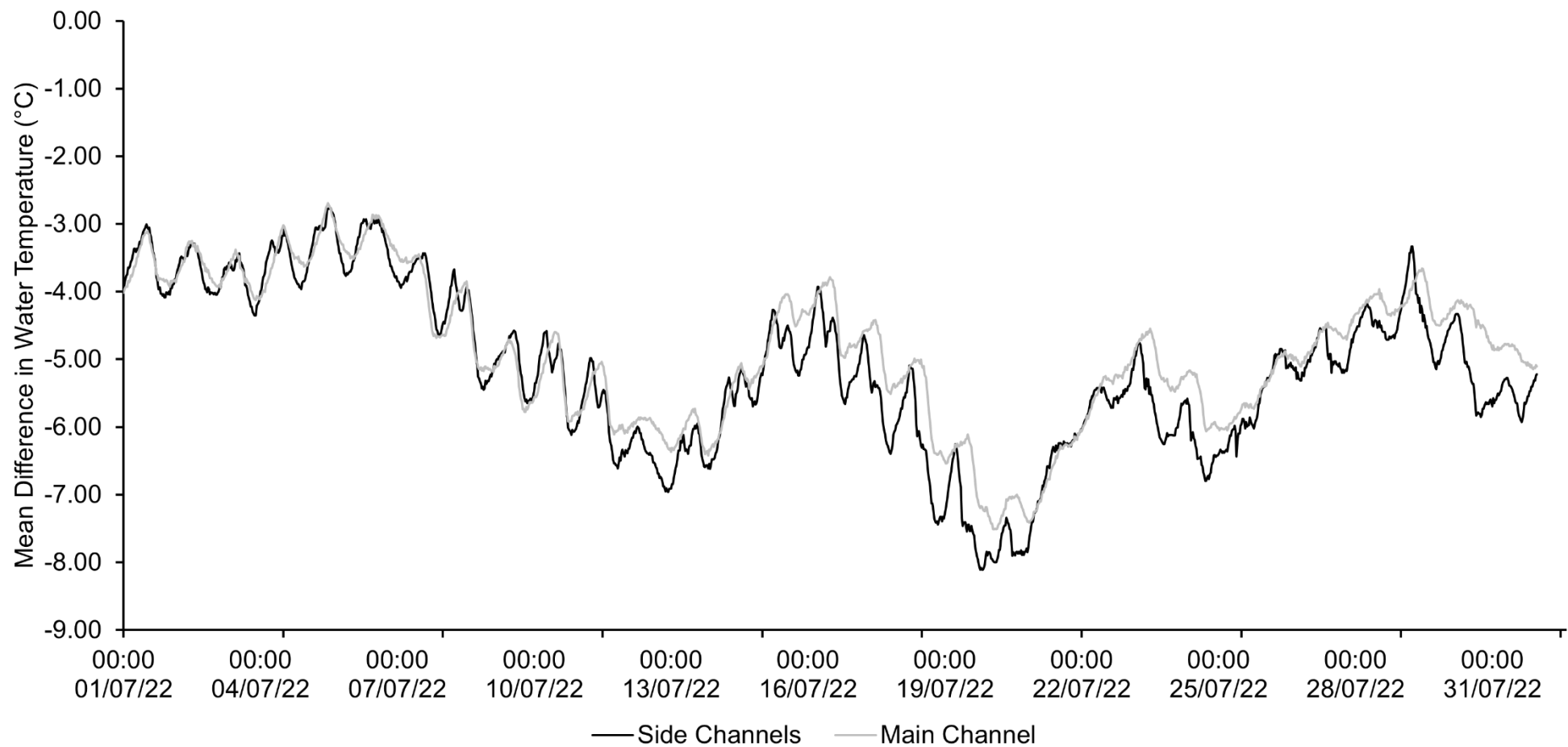


Figure 4.7. Difference between mean measurements for TE17 and TE18 and side channels (black), and TE17 and TE18 and main channel (grey) for July 2022, calculated for 30-minute intervals.

(TE3, TE9, TE11, TE13, TE15, T1_C, T3_C, T5_C, and T6_C). Average water temperature for shaded loggers was $16.6 \pm 1.66^{\circ}\text{C}$ and the average for the unshaded loggers was $15.79 \pm 1.46^{\circ}\text{C}$. The pattern here was similar to HY1 with shaded loggers having higher average temperatures during heatwaves or elevated air temperatures. Shaded and unshaded loggers had high correlation ($r^2 = 0.93$). The maximum water temperatures recorded by shaded loggers was 20.71°C , while for unshaded loggers it was 19.96°C . Minimum water temperatures for both shaded and unshaded loggers were similar at 11.8°C . During this period in June, there were eight loggers in the main channel (TE3, TE7, TE9, TE15, T1_C, T3_C, T5_C, and T6_C) and four in the side channels (TE_Bridge, TE11, TE13, and TE21). Average water temperature for the main channel during this period was $16.15 \pm 1.46^{\circ}\text{C}$ and for the side channels it was $14.95 \pm 1.34^{\circ}\text{C}$. Maximum water temperatures recorded during this period were 19.96°C for the main channel and 18.33°C for the side channel. Minimum water temperatures recorded were 12.1°C and 11.48°C for the main and side channels, respectively. Main channel and side channel temperatures were highly correlated during this period ($r^2 = 0.94$). Unlike HY1, where side channels were often recording warmer temperatures, in HY2 for this June period, side channels were cooler on average than the main channel.

Individual analysis of daily maximum water temperatures for each logger for the entirety of HY2 showed no consecutive days where water temperatures were over 22°C . There was only one logger, T1_C, that reached more than one consecutive day where daily maximum temperature exceeded 20°C , but this was only for three days. Overall, from the summer water temperature from HY2, it is clear that extreme water temperatures were not reached compared to HY1 and thus summer conditions in this year can be deemed suitable for burbot.

In HY3, July 2024 had the warmest temperatures in the observational record (Table 4.12). Compared to HY2, air temperatures in July 2024 reached a higher daily maximum (28.1°C compared to 23.7°C in July 2022). The maximum water temperature reached in July 2024 was 24.7°C at TE11, but this could be measurement error, considering that the next highest value was 20.5°C at TE21 on 19/07/2024.

Though July 2024 had the warmest temperatures, there were only two days in July where air temperatures exceeded 25°C. During this period, unshaded air temperature reached a maximum of 28.1°C at TE_T3. Again, there was no logger recording shaded air temperature. During July 2024, there were three loggers recording shaded water temperature (TE_Bridge, TE7, and TE21) and six loggers recording unshaded water temperature (TE11, TE13, T1_C, T3_C, T5_C, T6_C). Average water temperatures were $16.29 \pm 1.49^{\circ}\text{C}$ and $15.74 \pm 1.33^{\circ}\text{C}$ for shaded and unshaded loggers respectively. Maximum water temperature recorded by shaded loggers was 20.27°C and for unshaded loggers it was 19.95°C. Similar to HY1 and HY2, shaded loggers on average were not cooler than unshaded loggers. Minimum water temperatures for unshaded and shaded loggers were again similar at 13.33°C and 13.63°C respectively. In contrast to HY1 and HY2, however, the correlation between unshaded and shaded loggers was lower ($r^2 = 0.88$). During July, there were five loggers in the main channel (TE7, T1_C, T3_C, T5_C, and T6_C) and four in the side channels (TE_Bridge, TE11, TE13, and TE21). Average temperature for the main channel during this period was $15.92 \pm 1.29^{\circ}\text{C}$ and for the side channels it was $15.64 \pm 1.54^{\circ}\text{C}$. Maximum water temperatures recorded by the main and side channels were 19.27°C and 21.1°C, respectively. Minimum water temperatures recorded by the main and side channels were 13.69°C and 13.1°C, respectively. The main channel and side channels were also less well correlated ($r^2 = 0.84$) compared to HY1 and HY2.

Individual analysis of daily maximum water temperature for each logger over HY3 revealed no consecutive days where water temperatures reached above 24°C for main channel or side channel loggers. TE11 had two consecutive days where daily maximum temperature was above 22°C, and had 6 consecutive days where daily maximum temperature was above 20°C. TE21 also had 12 consecutive days where daily maximum temperature was above 20°C, but the temperature never exceeded 22°C. TE_Bridge was the only other logger that had consecutive days where daily maximum water temperature exceeded 20°C, but this was for two days only. Overall, and similar to HY1 and HY2, summer water temperatures were well suited for adult burbot and temperatures above its thermal optimum do not persist for extensive periods to cause stress or death.

4.3.4. Water Temperature Comparison – Grote Nete, Belgium

A comparison of the Wissey ($n = 1,014$) and the Grote Nete ($n = 847$) daily maximum water temperature datasets showed that water temperatures in the main channel of the Grote Nete reached colder temperatures during the winter spawning period (December – February), while summer temperatures in the Wissey were cooler. Fig. 4.9a and 4.9b show average daily temperature and daily maximum temperature in the main channels of the Wissey and Grote Nete, respectively.

When comparing annual spawning periods for the Grote Nete and Wissey, water temperatures in the main channel of the Grote Nete were often cooler. Fig. 4.10 shows a visualisation of monthly daily maximum temperature variations for the Grote Nete and Wissey main channel. The data showed that on average, daily maximum temperatures in the potential spawning months are higher in the Wissey than in the Grote Nete, while daily maximum temperatures are on average cooler in the Wissey from April to September. The Kruskal-Wallis tests compared the medians of daily maximum temperature for the Wissey and Grote Nete for the spawning period (1st December to 28th February), egg incubation period (1st March to 30th April) and larval development period (1st May – 30th June). The tests for the spawning and larval development period were statistically significant ($p = <0.001$), which would suggest that the medians in daily maximum temperature between the two rivers for the given periods are different. For the egg incubation period, however, the data observations were not found to be significantly different ($p = 0.827$).

In HY1, during the spawning period, the average main channel temperature was $6.79 \pm 1.49^\circ\text{C}$ in the Wissey, with minimum and maximum temperatures of 3.58°C and 11.4°C , respectively. In the Grote Nete, average main channel temperature was $6.1 \pm 1.59^\circ\text{C}$, with minimum and maximum temperatures of 2.64°C and 10°C , respectively. During the spawning period of HY2, the Wissey average temperature in the Wissey main channel was $6.30 \pm 2.02^\circ\text{C}$, with minimum and maximum temperatures of 0.6°C and 10.7°C , respectively. In the Grote Nete, average main channel temperature was $5.49 \pm 2.07^\circ\text{C}$ with minimum and maximum temperatures of 2°C and 9.38°C ,

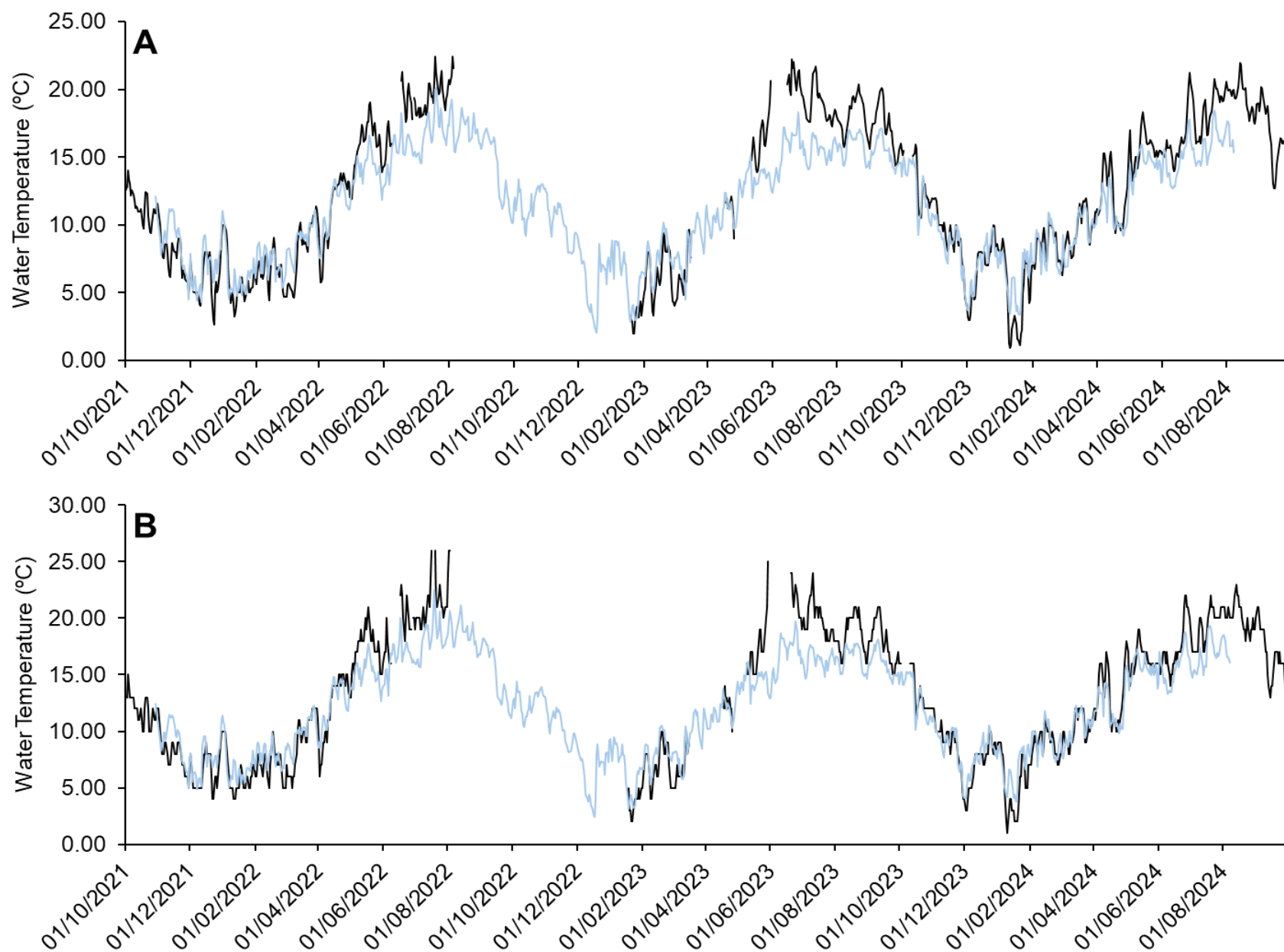


Figure 4.8. (A) Daily average water temperature (°C) and (B) daily maximum water temperature for the Wissey (blue) and Grote Nete (black) from 01/10/2021 to 30/09/2024.

respectively. Finally, in the HY3 spawning period, the average main channel temperature for the Wissey was $7.17 \pm 1.88^{\circ}\text{C}$, with minimum and maximum temperatures of 2.6°C and 12.1°C , respectively. In the Grote Nete, average main channel temperature was $6.64 \pm 0.95^{\circ}\text{C}$, with minimum and maximum temperatures of 0.95°C and 10.32°C , respectively.

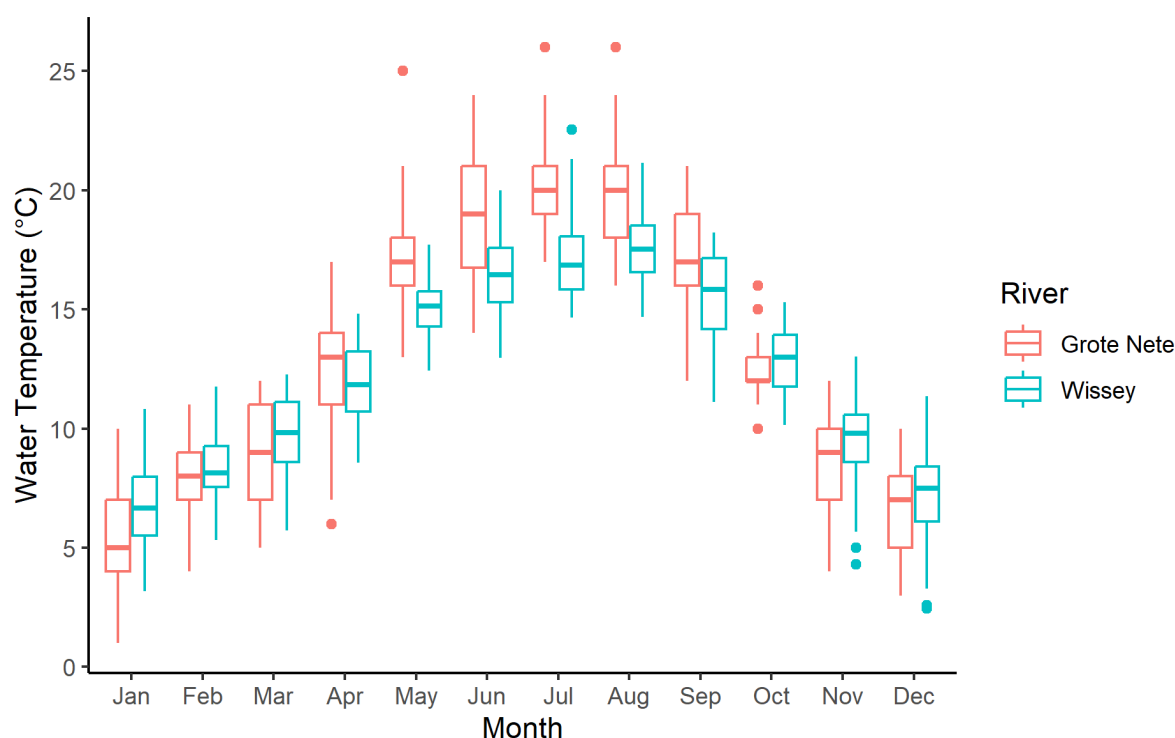


Figure 4.10. Daily maximum water temperature ($^{\circ}\text{C}$) by month for the Grote Nete (red) and River Wissey (blue) from 01/10/2021 to 30/09/2024.

The data showed that for both the Wissey and Grote Nete, the 9°C thermal threshold for egg incubation was exceeded in the spawning period and during the post-spawning period. In HY1, at the Wissey, spawning windows are immediately followed by water temperature increases beyond 9°C , while water temperatures in the Grote Nete increased beyond 9°C after 12 days following the spawning period and remained above 9°C from 11/4/2022. During HY2, at the Grote Nete, average main channel temperatures first exceeded 9°C on the 13/03/22 days but were not consistently above 9°C until 10/5/2023. This 13-day window was similar to the Wissey, which also had a 13-day egg incubation window with suitable conditions. Finally, during HY3, average

water temperature in the main channel of the Grote Nete exceeded 9°C after 3 days post-spawning period and remained consistently above 9°C by 31/02/2024. In the Wissey, the length of suitable egg incubation windows varied from 3 days to 12 days in HY3.

In terms of adult suitability, for the entire Grote Nete record, average main channel temperature was <14°C for 57% of the study period. In comparison, the Wissey's average main channel temperature was <14°C for 67% of the study period. The daily maximum main channel temperature in the Grote Nete during HY1, HY2, and HY3 was 26°C, 24°C, and 23°C, respectively. For the Wissey, daily maximum main channel temperatures for HY1, HY2, and HY3 were 22.72°C, 19.96°C, and 19.27°C, respectively.

4.3.5. Potential Future Water Temperatures Under Climate Change

4.3.5.1. *Historical Climate Record*

The observational years in the current study (2021 – 2024) could be contextualised by comparing the observational air and water temperature data to the air temperature data from the Denver record (1980 – 2023) and the hindcast data for water temperature for Denver. Between 1980 – 2010, a 30-year reference period, average maximum air temperature at Denver was 14.12°C, while average minimum air temperature was 6.12°C. Actual maximum and minimum air temperatures for the same period were 34.7°C and -12.6°C, respectively. During this period, average daily maximum water temperature (based on the hindcast data and thus linked to the air-water temperature relationship at the Wissey) was 11.1°C, with the lowest and highest daily maximum being 1.47°C and 19.7°C, respectively. From 2011 – 2020, average maximum air temperature at Denver was 15.05°C with minimum average air temperature at 6.59°C. Both average maximum and average minimum air temperature exceed the 30-year reference period. Actual minimum and maximum daily air temperature was -15.5°C and 35.6°C, respectively. Daily maximum water temperature for this same period at Denver averaged 11.47°C, also higher than the reference period, with highest daily maximum being 19.81°C and lowest 2°C. There was not a

complete water and air temperature record for the Wissey in 2021, so looking solely at the Denver data, average daily maximum air temperature was 14.52°C and average daily minimum air temperature was 6.4°C, while actual maximum and minimum was 31.2°C and -4.1°C respectively. For the hindcast Denver water temperature values for 2021, average daily maximum water temperature was 11.36°C, while the highest daily maximum estimated was 19.17°C and the lowest 2.87°C. For the Wissey in 2022, based on observed data, average air temperature was 12.2°C, while maximum and minimum values were 37.6°C and -8.7°C, respectively. In terms of water temperature in the main channel, average temperature was 11.6°C, with minimum and maximum of 0.78°C and 21.95°C respectively. Finally, in 2023 average air temperature for the Wissey was 10.93°C, with minimum and maximums of -9.53°C and 28.1°C respectively. For Wissey water temperature data in 2023, the average was 11.41°C, with a minimum and maximum of 1.7°C and 20.1°C, respectively.

Comparing air temperatures at Denver between 1980 – 2010 and 2011 – 2020, it was clear that average temperatures were warmer, but extremes in minimum air temperatures were still reached. While it was difficult to directly compare the Denver and Wissey records due to differences between the data sources, it was clear that, compared to the Denver climate record, minimum air temperatures were warmer and extreme summer temperatures were higher than for the reference period. The data showed that these warming trends are consistent with some general predictions for climate change in eastern England (Hammond and Pryce, 2007) and also that the observation period in this study covers three warmer years compared to the Denver data.

4.3.5.2. Model Output

Monthly average maximum water temperature was compiled for the reference period at Denver as well as for the 2030s and 2070s (Fig. 4.11a and 4.11b). Fig. 4.11a shows average maximum monthly water temperature compiled for the 12 ensemble members. On average, monthly maximum water temperature will increase from the 2030s to the 2070s comparative to the reference period. Average January monthly maximum water temperature could increase from 6.24°C in the reference period to

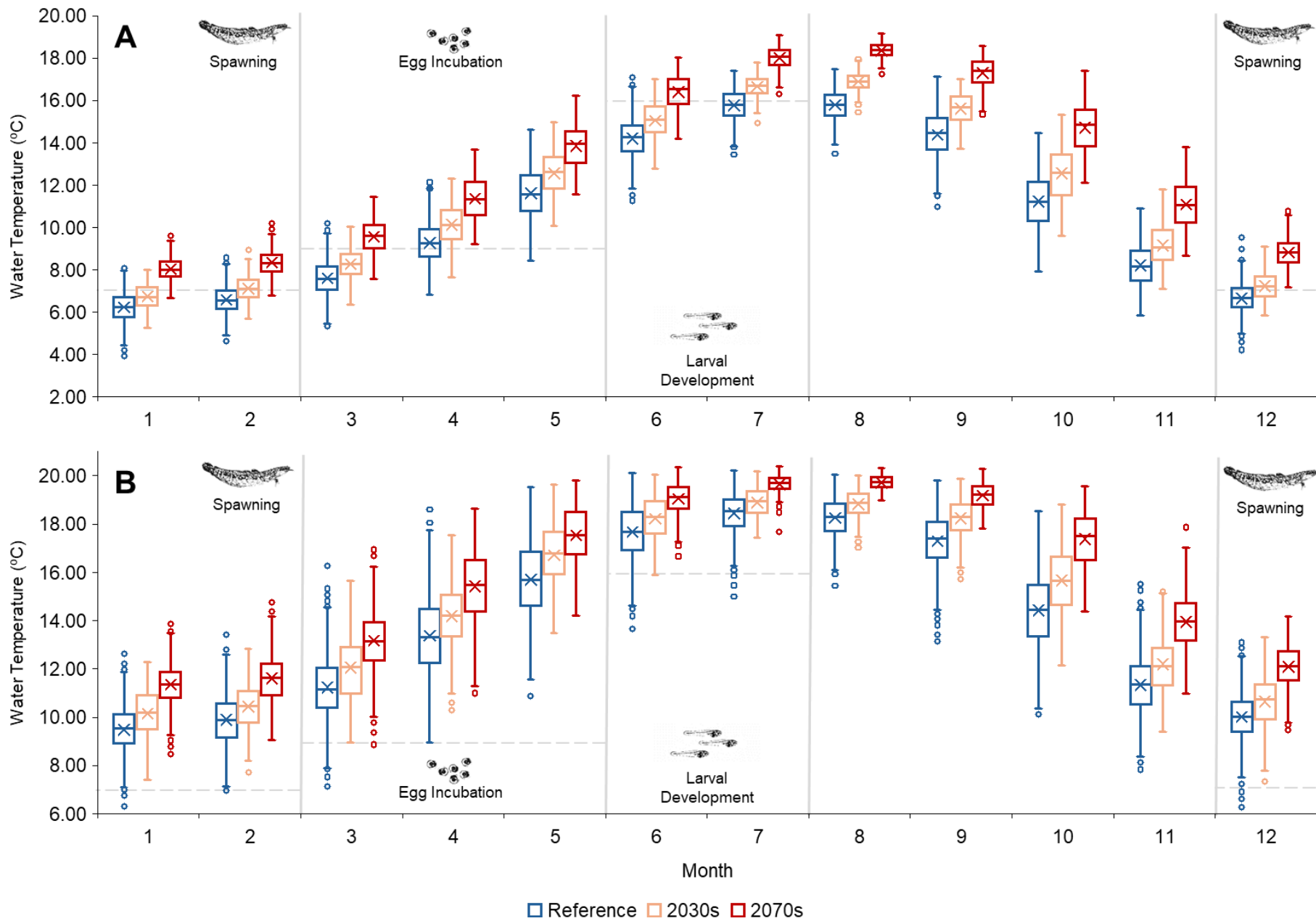


Figure 4.11. Water temperature predictions for Denver (TF 58000 06000) during the reference period (1981 – 2023) (blue), 2030s (orange), and 2070s (red) under emissions scenario RCP 8.5 for (A) average maximum monthly temperature and (B) maximum monthly temperature. Dashed lines represent thermal threshold by life stage: spawning 7°C, egg incubation 9°C, and larval development 16°C.

8.05°C in the 2070s. December faces the greatest potential increase of any winter month from 6.66°C in the reference period to 8.82°C in the 2070s. Average maximum summer water temperatures may also increase. Average maximum monthly water temperature in August may increase from 15.78°C in the reference period, to 16.89°C in the 2030s, and up to 18.37°C in the 2070s.

Fig. 4.11b shows maximum monthly water temperatures obtained from the ensembles and thus a higher range of temperatures. Fig. 4.11b shows that February could contain high monthly maximum water temperatures for the winter based on the ensemble members, with temperatures potentially increasing from an average of 9.90°C during the reference period to 10.44°C in the 2030s, and 11.61°C by the 2070s. The 2070s could have water temperatures as high as 14.37°C in February. Comparatively, in summer, Fig. 4.11b shows maximum monthly water temperature potentially increasing over time, but with less variability. Fig. 4.11b shows that during July in the reference period, maximum water temperatures can range from 13.79°C to 17.42°C, while in the 2070s, the range of maximum water temperature ranges will increase, but become narrower, showing a range of 16.17°C to 19.07°C.

4.4. Discussion

Based on 1,014 days of continuously collected air and water temperature data, this study has evaluated the suitability of the River Wissey for burbot in terms of individual water temperature requirements at each life stage. Importantly, the study has been able to identify the burbot life stages potentially most vulnerable to survival in the Wissey study area and has also investigated one extreme warming scenario relevant to the burbot's future outlook under potential climate change. The data showed that suitable spawning windows exist and that the site provides thermally suitable habitat for larval and adult life stages, but concerns surround temperature spikes that exceed 9°C during winter and early spring, which, according to Shodjai, (1980), Kainz and Gollmann (1996) and Lahnsteiner et al. (2012), would be lethal to burbot eggs.

4.4.1. Spawning Habitat

Overall, the instability and inconsistency of winter air, and thus water temperatures, in the Wissey during the observational study period has weakened the evidence for thermal suitability of the Wissey in terms of supporting a future, naturally reproducing burbot population and has highlighted the importance of the burbot's own potential thermal plasticity and adaptability. The observational data used in this study was, on average, from hotter years with warmer winter maxima compared to the historical air temperature record derived from the Denver station, 23 km downstream from the start of the study area. Nevertheless, all hydrological years possessed an optimal spawning window of at least 14 days in either the main channel, side channel, or floodplains, where daily maximum temperatures were $<7^{\circ}\text{C}$. This conclusion needs to be caveated, however, as while some studies have concluded that spawning is achievable up to 7°C (Jäger et al., 1981; Beelen, 2009) others suggest 6°C as the upper maximum threshold for spawning (Vught et al., 2008; Brackwehr et al., 2016). The literature is not clear whether an entire 14-day window is required for a successful spawning period, or whether it could occur in a shorter window (i.e., 11 days, which occurred in both HY1 and HY2). Under laboratory conditions, Lahnsteiner et al. (2012) used lake water where natural temperatures were $<2^{\circ}\text{C}$, for 35 days, and recorded five spawning events during that period, beginning 21 days after temperatures dropped. Their findings suggest that the two-week window suggested for spawning refers to the maximum window that would allow most reproducing adult burbot to spawn, but spawning events do occur in a shorter period of time. If possible, this would allow spawning adult burbot to take advantage of shorter windows of time where daily maximum water temperatures drop below 6°C at the Wissey, which do occur each year, such as the 6 days observed in the side channels for HY1, 10 and 4 days for the side channels and floodplains, respectively in HY2, and 6 and 5 days for the side channels and floodplains, respectively in HY3.

The observed data also showed that, in HY1, an 9-day spawning and a 14-day spawning period was punctuated by a $\sim 5^{\circ}\text{C}$ increase in water temperature. Kouřil et al. (1985) found that deviations of 2.5°C outside of the burbot's spawning range would result in a delay to spawning of up to two weeks. Based on this, it could be concluded

that burbot would not have spawned in the second 14-day spawning season in HY1. Ashton et al. (2019) showed during an experiment under laboratory conditions with burbot from the Kootenai River (Pacific clade) that each water temperature increase of 1°C would delay spawning by 0.7 ± 0.2 days. Ashton et al. (2019) also showed that the spawning period varied under different temperature treatments: under a continuous 4°C and 6°C, the spawning period was 7 days, while at a constant 2°C it was 18 days. They also found that water temperature did not affect the volume of eggs produced. Their findings suggest that warmer spawning temperatures may result in a shorter spawning period, which the Wissey currently provides as evidenced by short spawning windows in HY1, and across all hydrological years observed.

Overall, compared to observational data in the main channel of the Grote Nete, Belgium, the Wissey spawning temperatures were warmer on average and the spawning periods in this study had higher maximum temperatures reached than observed in the Grote Nete. Though, contextually, it is useful to know that the Wissey would likely sit towards the warmer end of the burbot's requirements, it experiences similar temperatures to the Grote Nete, where they can complete their life cycles, though this is known to occur in off-channel habitat, not the main channel (Vught et al., 2008; Pauwels et al., 2016; Vandamme et al., 2017; Van Wichelen et al., 2018). Though, as the data showed, suitable spawning windows did occur within the Wissey study area in off-channel habitat: side channels and floodplains.

4.4.2. Egg Incubation and Larval Development

The variation of winter temperatures also increases the vulnerability of the egg incubation stage. Some studies suggest that maximum egg incubation temperatures for western European burbot eggs is 9°C (Shodjai, 1977; Kainz and Gollmann, 1996; Table 4.4), but upper tolerance is more commonly listed as <7°C (de Gelas et al., 2007; Vught et al., 2008; Brackwehr and Kühlmann, 2016). Figure 4.5 shows that, for all hydrological years, there was no egg incubation period (i.e., continuous 30-day period with temperatures <9°C) following a spawning period. Laboratory experiments have shown that, for burbot eggs from the Eurasian subclade, eggs held at a constant 9°C

resulted in 100% egg mortality (Lahnsteiner et al., 2012). Hence, based on this commonly cited lethal temperature for burbot eggs, as temperatures exceeded 9°C for the Wissey, theoretically this would have resulted in 100% egg mortality. It is interesting, that the Grote Nete main channel also experiences increases in water temperature beyond 9°C during the spawning period, as shown in Fig. 4.11a and 4.11b. It would be pertinent to determine whether larvae have been observed in the spring following the spawning periods of 21/22, 22/23, and 23/24 in the Grote Nete to determine if these temperatures (>9°C) are detrimental to the life cycle completion of western European burbot.

The thermal tolerance of burbot eggs varies across the incubation stage, however, and could be crucial to burbot egg survival in the Wissey. In a laboratory experiment with western European eggs, hatching rates were tested at constant 2°C, 4°C, 6°C, 8°C, 10°C and results found that hatching occurred under all temperatures except 10°C, which was concluded as the lethal temperature for these burbot eggs (Vught et al., 2015). At 8°C, 18% of eggs developed into healthy viable larvae, which decreased to 0% at 10°C. As 9°C was not tested, it cannot be confidently concluded that 9°C would be lethal for burbot eggs from the western European subclade. Some studies have also shown that depending on when water temperatures increase beyond 9°C, some eggs can hatch, albeit with more abnormalities. For example, Lahnsteiner et al (2012) found that, even during the most vulnerable, initial stage of egg incubation, the morula stage, when water temperature was increased after 8 days from 2°C to 9°C, there were $63 \pm 11\%$ ready-to-hatch embryos and $13 \pm 10\%$ hatched larvae, and only $2 \pm 2\%$ normally shaped larvae. During these experiments, they also found that the switch to high temperatures reduced development time and hatching period. For the egg incubation stage, Ashton et al., (2021) determined that sudden rates of change in water temperature (i.e., 0.4°C per day) were most damaging for eggs rather than gradual change. While for all hydrological years, daily rate of maximum water temperature change in the winter period was low (i.e., 0.06 – 0.1°C), there were nonetheless instances where daily maximum water temperature change was up to 3.42°C. Overall, the literature suggests that without at least an 8-day cold period (ideally 2°C), eggs cannot survive temperature increases beyond 9°C or under rapid daily warming. From Lahnsteiner et al. (2012), their experiments do not consider

temperatures above 9°C, likely due to that being a lethal threshold for burbot eggs, but if a sufficient period (i.e., 8 days) can be provided post-spawning in cool temperatures (i.e., <6°C), there is potential for some eggs to survive. The eggs would likely have large percentages of abnormalities and this, in turn, would reduce the overall quantity and survival chances of burbot larvae post-hatch. What is not determinable, however, is the number of burbot larvae required to survive in order to maintain and expand a healthy, reintroduced burbot population.

The burbot is a long-lived species (10-11 years average, maximum 22; Worthington, 2010), and thus annual successful spawning may not be required every year to ensure population survival and growth expansion. It is unclear whether burbot are similar to other long-lived European species, which can have populations that follow a boom-bust population cycle, such as the crucian carp *Carassius carassius* (C. Sayer pers. comms, 2024). However, to achieve a self-sustaining and stable burbot population in the years following the reintroduction, the right conditions are crucial. Based on the observed data for the Wissey, due to the difficulties that current thermal conditions pose for spawning and egg incubation, which could result in little or no recruitment in some years, any reintroduction programme would have to have a long-term outlook with persistent stocking and post-release monitoring to increase chances of reintroduction success.

Moreover, it is known that burbot are a slow recovery species with a population doubling time of between 4.1 – 14 years (Beelen, 2009). This is confirmed by the reintroduction in Belgium, which started in 2005 and only found its first larvae in 2014 (Vught et al., 2015). Further, long-term studies of burbot translocations into the Beerze river in the Netherlands from 2009 – 2013, show natural reproduction in 2019 only (Beelen et al., 2019). A long-term stocking programme in the German North Rhine-Westphalia region since the 1990s has led to a self-sustaining burbot population in the River Lippe (Bunzel-Drücke et al., 2004b; Bosveld et al., 2015). Thermal conditions in the Grote Nete, Belgium are not ideal every year for burbot, based on established thresholds, and spawning windows can be disrupted by temperature increases above 8°C, but these temperature increases have occurred in 2014 and 2015, where larvae

were spotted in the following spring months (Pauwels et al., 2016, pp.112-116). In contrast to the Wissey, from the data presented in Pauwels et al. (2016, pp. 114 - 115), the unsettled spawning period is followed by at least 30 days where water temperatures in the Grote Nete remained below 9°C each year from 2008 – 2015, which would facilitate egg development. Though, in their study Pauwels et al. (2016) suggest that only 10 days where water temperatures are below 8°C (ideally below 6°C), would provide a sufficient window for some spawning and egg development. They argue that beyond the early stages of the egg development, the eggs become more thermally tolerable, but this study does not specify a maximum temperature threshold. In the Wissey, all hydrological years had ~14-day periods where temperatures were below 7°C, which would facilitate spawning and the development of eggs through their most thermally vulnerable stage based on findings by Pauwels et al. (2016), improving the Wissey's thermal suitability as a candidate reintroduction site.

If egg incubation could be achieved as well as successful hatching of larvae, the observational data showed the Wissey to be suitable for larval development. The maximum threshold of 16°C was not reached in HY1 – HY3 until 87, 99, and 133 days post-spawning period respectively, providing sufficient thermal conditions in the main channel, side channels, and floodplains for larval development. The 300 days of flooding in HY3 was into floodplains with coarse wet-adapted grasses, rushes and sedges along with other wetland plants typical of frequent flood-inundation and/or riparian alder-dominated (*Alnus glutinosa*) woodland both able to provide suitable shelter for burbot larvae. While the literature shows that larvae can be vulnerable to predation and high flow events (Brackwehr et al., 2016), it is less vulnerable than the egg incubation stage. This period of larval development, however, was only provided on floodplains, the ideal nursery habitat for larvae during HY3, which had extensive flooding from autumn to late spring. It would be prudent to find out the frequency of this kind of flooding in further hydrological work at the study site.

In combination with inconsistent winter air and water temperatures was a lack of physical spawning and nursery larval habitat that persists throughout the winter and

spring period in both of HY1 and HY2. Indeed, HY1 and HY2 had short periods of floodplain inundation at 46 and 149 days, respectively. These totals were not consecutive, however, being punctuated by drops in floodplain inundation level of below 10 cm, which could result in the isolation of spawning adults, and later hatched larvae. As the logging period for floodplains began in February 2022 in HY1, the spawning period of HY1 cannot be analysed as extensively. However, it was clear that 38 days of floodplain inundation in spring would have been insufficient to allow completion of egg incubation (~30 days) and larval growth (~60 days), even if temperatures were suitable for egg incubation. For HY2, Fig. 4.5 shows the lowering of floodplain inundation between the winter and spring periods, with only 7 consecutive days in the winter spawning period where floodplain daily maximum temperatures were below 7°C. Conversely, Fig. 4.5 shows that HY3 had extensive floodplain inundation from early autumn to early summer. For HY3, the physical habitat conditions ideal for spawning, egg incubation, and larval development were provided with a total of 300 days of consecutive flooding. The issue, however, was the water temperature, which was too high during the estimated egg incubation period. Even if spawning could occur during the early December window, the high temperature spike between the two estimated spawning windows would have killed any developing eggs. The pattern was clear across all three years, with a consistent spike in water temperature during early January that would be detrimental to any potential eggs developing follow an early winter spawning period.

For two of the three winters observed in the Wissey, after a suitable spawning window, floodplain waters receded into the main channel. Thus, without more data on how frequently long-lasting HY3 equivalent floods occur, burbot egg and larval survival in the Wissey are linked to the assumption that, as winter inundation decreases eggs or larvae could be carried into the side channels where they could develop further. It is estimated that in a river flow of 0.5 m s^{-1} , larvae could be carried as far as 900 km within their development period (Brackwehr et al., 2016), which could carry them to areas where they are vulnerable to predation and pollution. The physical habitat data from this study (Chapter 3) showed the Wissey to be complex with fallen trees, tree roots, high macrophyte cover, meanders, and lateral slack patches that have the potential to shelter larvae if they were carried off the floodplain. Moreover, studies

have shown that shallow lateral slack patches are common areas that larvae are found in (Koporikov and Bogdanov, 2011). However, the literature for the western European burbot subclade, is clear that, under optimal conditions, water would persist on the floodplain into April (Brackwehr et al., 2016) until larvae can develop their swimming physiology and swim off the floodplain. Fig. 4.9b shows that floodplain temperature was highly responsive to air temperature, which means that even if connectivity between the main channel and the floodplains could be maintained for a longer period of time, say from November until the end of February, it may ensure more spawning opportunities, but would not mitigate against warmer spring temperatures that would increase the water temperatures beyond the lethal limit for burbot egg incubation. Overall, for both floodplain and side channel systems, it is important to study the flow characteristics of the Wissey in future work to estimate egg or larvae dispersal during winter and early spring to better estimate chances of survival for burbot eggs and larvae.

Any reintroduced burbot population to the Wissey may be reliant on tight spawning windows, with some years providing no floodplain nursery habitat, meaning that eggs or newly hatched larvae are carried off the floodplain as floodwaters recede and are not stranded, with some eggs and larvae potentially surviving in the main and side channel systems. The extensive side channel systems within the study area could provide potential spawning habitat for a reintroduced burbot population, as they are known to spawn in tributaries of headwaters and in shallow waters (Sorokin, 1971; Farkas, 1993; McPhail and Paragamian, 2000; Aarts et al., 2004; Worthington et al., 2012; Jude et al., 2013; Toivonen et al., 2020), this spawning strategy was also central to the habitat suitability assessment of the Belgian burbot reintroduction in the early 2000s (Dillen et al., 2005). However, in Belgium it is currently known that static floodplain waters are crucial in facilitating natural reproduction in burbot (Vandamme et al., 2021) as eggs and larvae are vulnerable to being swept out of the system by higher flows..

4.4.3. Adult Suitability

Out of all life stages, it was clear that the Wissey is thermally suitable for adult burbot. It could be concluded that the Wissey is more thermally suitable for adult burbot than the Grote Nete, in which they are known to occupy due to the cooler summer temperatures experienced in the main channel comparatively (Fig. 4.11a and 4.11b). Using the July 2022 heatwave as an extreme example, all main channel and side channel loggers had average temperatures below 20°C, with only four loggers recording temperatures above 22°C during the hottest day of 2022. There are few continuous water temperature monitoring stations along eastern flowing rivers in England, but using the Environment Agency's Hydrology Data Explorer (Environment Agency, 2024), maximum water temperatures observed in available rivers that used to contain burbot can be used to contextualise the cooling effect of the Wissey. At Middletonstop (TF 66342 17869), a drain system connected to the River Nar (a tributary to the Great Ouse and a river burbot were known to occupy), water temperatures reached a maximum of 25.15°C during the July 2022 heatwave (Environment Agency, 2024). In the River Witham at Boston (TF 32706 43069), during the July 2022 heatwave, a maximum of 36.08°C was recorded, which could be an error in the record, as maximum temperature recorded the following day (20/7/2022) was 22.99°C (Environment Agency, 2024). The Wissey's ability to maintain water temperatures on average below 22°C during the hottest air temperatures on record, indicates the Wissey is an asset as a thermal refuge for adult burbot as well as other fish species.

Moreover, there was evidence for thermal refugia in the system in the form a spring-fed side channel, as shown by the thermal behaviour of loggers TE17 and TE18. Fig. 4.8 shows that the TE17 and TE18 system was always below average maximum temperatures of the main and side channels in July 2022, averaging at 5.6°C cooler and sometimes ~8°C cooler. The influence of groundwater on water temperature, more specifically the hyporheic temperature gradient, has previously been investigated in the Wissey. A previous study found that, during the summer months, water temperature decreases with increasing depth from the water's surface to below the substratum and in the winter, the water temperature within the substratum can be

similar or warmer than the water's surface (Petts and Bickerton, 1994). The study found that between May and June, the hyporheic temperature can be almost 3°C cooler than the water's surface (Petts and Bickerton, 1994). This pattern is similar to the observations of the lower Wissey side channel that has warmer temperatures in winter compared to the main, side channels and floodplains, but has much cooler temperatures in summer, perhaps indicating a groundwater upwelling. These cooler, thermal refugia may become especially important in the future as summer heatwaves may become increasingly prevalent, which would be beneficial for adult burbot, as well as other fishes.

Regardless of subclade, most literature suggests an upper critical threshold for adult burbot of between 26°C to 30°C (Table 4.2; Fisher, 2000; Pääkkönen et al., 2003; Hardewig et al., 2004; Jackson et al., 2008; Brackwehr et al., 2016). During July 2022, all loggers were below this threshold. Moreover, for the majority of the year in HY1, daily maximum water temperatures were below the adult burbot thermal optimum of 14°C, the commonly regarded thermal optimum for adult burbot (Hofmann and Fischer, 2002; Hardewig et al., 2004; Harrison et al., 2016). Jackson et al. (2008) argue that, for North American burbot (Mississippian clade), persistence of temperatures above the thermal optimum for longer than 30 days can have detrimental effects on burbot. Fig. 4.5 shows a period of approximately two months where average maximum temperature for main and side channels were above the thermal optimum for burbot. The observational data showed, however, that TE17 and TE18 has daily maximum temperatures below 14°C for ~99.85% of the observational record in HY1, evidencing once again the importance of this thermal refugia in the Wissey system.

Comparatively, riparian shading did not have as strong an influence on water temperature as the presence of a spring delivering cooler water (the TE17/18 system). Previous literature has shown that dense blocks of shaded stream (i.e., 1.1 km) can reduce July water temperature values by 1°C in downstream sites, while only 0.5 km of wooded river is needed to achieve the same effect in headwater sites (Johnson and Wilby, 2015). Similarly, Garner et al. (2017) suggested that planting on the southernly bank of a river with an east to west flow direction, with low velocities, would ultimately

achieve the greatest reduction in water temperatures. Under shaded conditions shortwave radiation was found to be 1 - 4 times lower than unshaded sites, resulting in a water temperature reduction of 0.5 - 1°C (Hannah et al., 2008; Dugdale et al., 2018). Short-wave radiation (which can contribute >90% of heating effects observed in summer; White et al., 2023), may be less influential in groundwater dominated systems (Kaandorp et al., 2019) such as the Wissey. However, with increasing anthropogenic demand for water, and thus potential for increases in groundwater abstraction in the area, the Wissey cannot rely on the cooling effect of groundwater inputs alone. Though, research has shown during drought periods, reduced surface water inputs can increase the proportional influence of groundwater inputs (Fennell et al., 2020), so it is hard to predict how groundwater inputs may influence water temperature at the Wissey in the future. Ultimately, the literature shows that the impact of riparian shading on water temperature is influenced by multiple factors, including vegetation density, planting orientation, flow velocities, residence times, water depth, channel width, slope, and energy flux (Johnson and Wilby, 2015; Garner et al., 2017b; Jackson et al., 2021; White et al., 2023). The lack of impact of riparian vegetation on water temperature is most likely driven by the groundwater signature of the Wissey as it is a chalk stream, but it could be linked to the size of the study area, the vegetation density and orientation, or multiple hydrological factors and should be further investigated as natural riparian vegetation regeneration has an important role in providing thermal refugia for fish and other aquatic species, as well as a potential reintroduced burbot population.

Overall, the observational data have provided an assessment of the Wissey's suitability in terms of water temperature requirements for each life stage, a key consideration of the reintroduction guidelines (IUCN, 2013). The data has so far shown that the Wissey meets the thermal requirements for adults and larval development. Spawning and egg incubation temperatures, as well as the provision of suitable spawning, egg development, and larval rearing habitat (i.e., inundated floodplains) were more variable year-to-year. This would ultimately undermine a reintroduced population's chance of survival.

4.4.4. Reintroduction Feasibility

One key aspect that should be considered with regard to a future UK burbot reintroduction, is this study's methodological applications of thermal thresholds. Where possible, this study has determined temperature thresholds for the western European burbot subclade, the genetic relative that is likely to be reintroduced to the Wissey. These studies, however, are few and varied, resulting in ultimately inconclusive thresholds for spawning temperature conditions and egg incubation conditions. The application of these thresholds, often derived from laboratory conditions, can be unrealistic as it can neglect the variability between individual fish and the stochasticity of water temperature in nature. Harrison et al. (2016) used tagging to track diurnal and seasonal movements of a burbot population in Kinbasket Reservoir, British Columbia, Canada and found patterns in burbot occupation of different thermal habitats across time. For example, they found that of all the burbot tracked the average depth of the population often occurred in thermal habitat of $<2^{\circ}\text{C}$, but there were occurrences where the average depth of the population was within thermal habitat of $\sim 10^{\circ}\text{C}$ during pre-spawning and 5°C and 10°C during spawning. This inter- and intrapopulation variability could be key to a reintroduced population's survival as a degree of adaptive plasticity would allow the burbot to cope with current warmer and potential future warming conditions and challenges the common description of a burbot as a stenotherm (Fischer, 2000b; Hofmann and Fischer, 2002; Hardewig et al., 2004; Nagel et al., 2011; Terrazas et al., 2017).

Most burbot populations throughout Europe are in decline or have been previously extirpated (i.e. Belgium and England) with this thought to be due to habitat modification (Worthington et al., 2010a; Bosveld et al., 2015; Wetjen et al., 2020b) rather than temperature increase. Their disappearance from the southernmost part of their North American range in Kansas, has also been attributed to due habitat modification and instream barriers over water temperature (Beard et al., 2017). Nevertheless, declines in burbot populations have been linked to temperature in some studies in Finnish lakes (Saarinen and Kløve, 2012) and water temperature rises are also thought to have contributed to a burbot decline in Bulgaria (Pandakov et al., 2020). Table 4.1 shows that Wissey air and water temperatures are within the same range as countries where

burbot still persist, particularly the western European group, such as in the Grote Nete, Belgium, the Meuse, France, and River Lippe, Germany (Geeraerts et al., 2007; Vught et al., 2008; Brackwehr et al., 2016). To ensure the Wissey's suitability for a reintroduced burbot population, the methodology of Lahnsteiner et al. (2012) can be replicated for a group of western European burbot, where a river temperature regime during a spawning and hatching period was applied to a group of burbot. The experiment could use the November to April temperatures observed during this study to see whether spawning could be initiated and facilitated.

4.4.4.1. The Role of River Restoration and Rewilding

Combined with further research, river managers and conservationists can improve the suitability of the candidate reintroduction site for each life stage through river restoration and rewilding approaches that can influence longitudinal, lateral, vertical and temporal connectivity. By removing instream barriers throughout the Wissey catchment, river restoration could ensure that adult fish could migrate during spawning migrations to reach suitable spawning habitats that are often found higher in the catchment (Dillen et al., 2008a; Jude et al., 2013). Moreover, instream barrier removal could also allow adult fish to migrate to deeper river sections during summer months or during heatwave events, as observed in July 2023. Instream barriers have been shown to have a negative impact on large-bodied fish dispersal under moderate and severe climate change scenarios (Radinger et al., 2017). Aside from existing side channels in the Wissey, river restoration could play a vital role in a successful burbot reintroduction as any work relating to lateral connectivity would help to maintain a longer connection to the floodplain throughout the winter spawning and spring incubation and larval growth periods. Stage zero restoration could be an appropriate choice for preparing a candidate reintroduction site for a burbot reintroduction due to its influence on thermal characteristics across longitudinal, lateral, and vertical space. The approach is typically at valley-scale, up to 10 km longitudinally and between 0.1 – 1 km laterally and aims to achieve base flow connection, valley floor reset and low-intensity land use surrounding the restoration site (Clarke, 2025). By increasing lateral connectivity at base flows, the approach could afford longer periods where potential shallow water habitats are created for spawning burbot. Moreover, stage zero

restoration utilises riparian plant regeneration to lower water temperatures longitudinally and laterally (Flitcroft et al., 2022), which could be beneficial for adult burbot in summer. The restoration of vertical connectivity means that groundwater may help to regulate summer water temperatures also (Clarke, 2025). Though, where shallow channels have formed, it is possible that water temperatures may increase (Bowles et al., 2021).

Any river restoration actions should also consider the impact of potential future air temperature increases of climate change on river water temperature. Any channel alternations, which could affect residence time for example, should be implemented in combination with natural riparian vegetation recovery, such as the restoration of floodplain woodland to produce a shading and potential cooling effect (White et al., 2023). Although, through comparisons of shaded and unshaded loggers at the Wissey, there is no evidence of a current cooling effect by overhead riparian shading. While river restoration projects are not often designed solely on influencing water temperatures, they can highly influence the thermal behaviour of rivers, particularly during extreme air temperatures (Hannah et al., 2008; Johnson et al., 2014; Garner et al., 2017b; White et al., 2023). Though crucially, any river restoration should be delivered in combination with water management policy that is centred on environmental flows to relieve the pressure on riverine systems in the future. Currently, during low flow conditions there can be restrictions or even complete halts to abstraction (Acreman et al., 2008). There is also potential to pump cooler groundwater directly into streams during low flow conditions to reduce temperature (Wilby, 1993b), but this type of stream augmentation is not included in environmental flow approaches (White et al., 2023). Flow augmentation could also have detrimental impacts on cyprinid fishes, though more research is need (Cowx, 2000).

4.4.5. Potential Future Climate Change

As part of the IUCN's reintroduction guidelines, it was important to consider future change as well as current thermal conditions in the Wissey. Climate models, such as those the UKCP18 were calculated from, can provide a potential outlook in the case

of a high emission scenario trajectory. The basic empirical model developed here used a logistic relationship between observed daily maximum air temperature and daily maximum water temperature at the Wissey to create a long-term daily maximum water temperature record for the nearest daily maximum air temperature record (at Denver 1981 – 2023), and from there used bias-corrected climate projections in maximum air temperature at Denver to predict daily maximum water temperature at Denver and then infer potential change at the Wissey.

Overall, Fig. 4.11a and 4.11b show that average monthly maximum water temperature and monthly maximum water temperature will increase over time. The model showed that, even by the 2030s, the monthly maximum water temperatures in winter could exceed the current spawning temperature thresholds applied in this study. Summer maximum water temperatures could also increase, with the length of high temperature periods increasing in June, potentially extending summer-like conditions. Comparatively, the Environment Agency modelled future monthly water temperature for chalk streams nationally for a high emissions scenarios using UKCP18 (Finney et al., 2022). They found that summer maxima were rising $\sim 0.58^{\circ}\text{C}$ per decade above reference levels (1981 – 2005) to 2080. They also found spatial disparities with chalk streams closer to London experiencing greater warming. From their report, it can be estimated that the maximum monthly mean daytime water temperature for the 2070s for the Wissey is between $21 - 22.5^{\circ}\text{C}$ (Finney et al., 2022). This is slightly warmer than temperatures projected in this study, though the report suggests that these projections are an underestimate due to the coarseness of the data used. Other studies suggest, however, that hotter, drier summers have increased over recent decades (Barker et al., 2019) and will continue to increase, with average summer air temperature increases predicted to be as high as 5.4°C by 2070 under the high emission scenario and UKCP18 ensemble members (White et al., 2023). These future predictions follow on from trends in the observational data. Worthington (2010) showed that days where water temperatures for Fenland and Norfolk rivers were $<4^{\circ}\text{C}$ decreased between 1800 and 2000 (see Fig. 2.10). Importantly, however, all predictions emphasise a spatial and temporal variability across the UK and emphasise the influence of interacting factors. Wilby and Johnson (2020), for example, showed annual mean water temperature between 2000 and 2018 has changed -0.4°C per

decade, but mean change in summer water temperature is $+0.6 - 1.1^{\circ}\text{C}$ per decade in parts of central and northern England. Moreover, they found that groundwater inputs can have a stronger influence on water temperature than air temperature, emphasising the spatial-temporal complexity in predicting future changes in water temperature under climate change. Despite trends in the observational record and current future predictions of high temperatures, the likely impact on water temperature in the Wissey specifically is hard to predict due to multiple interacting factors, such as meso-habitat conditions, hydrological factors, water source contributions, and energy flux dynamics as well as ongoing anthropogenic impacts of freshwaters, such as pollution, abstraction, habitat modification, and land use change (Woodward et al., 2010; Johnson and Penaluna, 2019; White et al., 2023).

4.4.5.1. Model Considerations

The empirical model developed here was simple. The aim of application of this model was a sensitivity analysis for the River Wissey and the burbot's long-term survival, drawing on climate projections that are known to be a hot, dry outlier in the catalogue of global and regional climate models available (Aines et al., 2021; Barnes et al., 2024). The assumptions made in constructing the model applied here limits its accuracy and while it could be improved with more observational data, it does, nonetheless, provide a site-specific climate prediction for a candidate burbot reintroduction site. There are several key assumptions made by this model that can influence the accuracy of the model output. First, that the relationship between daily maximum air temperature and maximum water temperature can be described using a logistic relationship. Second, that the daily maximum temperatures at Denver can likely indicate future changes at the Wissey study area. Third, that the logistic relationship between daily maximum water temperature and air temperature remains the same throughout time. Fourth, that the bias in model climate projections is the same throughout time and thus a change factor bias correction can be applied. And finally, that air temperature is the only influencing factor on water temperature. Inaccuracy of the model construction was shown by its prediction for monthly maximum water temperatures into the 2070s. For example, summer monthly water maxima estimations for the 2070s only just exceed 20°C , despite daily maximum air

temperature estimates from some ensemble members exceeding 44°C in July of some years in the 2070s. In July 2022, daily maximum air temperatures reached 38°C, with daily maximum water temperatures reaching between 20 - 23°C varying between individual loggers. As current observational data are exceeding the future predictions for lower air temperatures, it is likely that the predictions for monthly maximum summer temperatures are inaccurate. This is probably due to the small amount of available Wissey data (October 2021 – August 2024) that were used to construct the logistic relationship between daily maximum air and daily maximum water temperatures at the Wissey, which was the core of the model in developing air and water temperature predictions for daily maxima at Denver. It could also be a limitation of applying a logistic relationship to the daily maximum air and water temperature, that despite being more realistic than a linear relationship as it accounts for the evaporative cooling of water (Crisp and Howson, 1982; Mohseni et al., 1998, 2002; Johnson et al., 2014), the small training dataset reduced the accuracy of data prediction for extreme conditions (i.e., summer maxima). Despite this, the model gives a potential worst-case scenario for the future of the burbot in the Wissey system.

4.5. Conclusions

Water temperature is a key influencing factor in fish survival and behaviour in freshwater environments. Different genetic subclades for burbot populations have slightly different thermal requirements, which varies at each life stage. The western European subclade is dependent on floodplain inundation with temperatures below 7°C for spawning, egg incubation temperatures not exceeding 9°C, larval growth temperatures below 16°C, and adult optimum below 14°C and not exceeding 30°C as an absolute critical maximum. This study has utilised a dense spatial network of water and air temperature sensors to determine the thermal suitability of the River Wissey for each life stage of the burbot to determine its appropriateness as a candidate reintroduction site for a reintroduced UK burbot population. The observational data have shown a clear suitability for adults, maintaining maximum daily water temperatures below the optimum for a large portion of the year. The Wissey is also suitable for larval development, with long periods of spring water temperatures remaining below 16°C, enough to allow larvae to develop their swimming physiology.

The main concerns with the thermal suitability of the study area relate to suitable spawning windows that are too short and winter temperatures that are too inconsistent to incubate eggs, with spikes in early February-March reaching above 9°C, which would be lethal to any eggs. These issues are compounded by a lack of floodplain inundation, the known spawning habitat for western European subclade populations, making eggs and larvae vulnerable to either isolation on the receding floodplain waters or carrying into the faster flows of the main channel, which will limit survival.

To ensure that a reintroduced population of burbot has the optimal chance of surviving and achieving natural reproduction there are two key steps that could be taken. First, the winter-spring temperatures observed here should be run under experimental conditions to investigate whether burbot could successfully complete each life stage under these conditions (see Lahnsteiner et al., 2012). Secondly, any research should be done in combination with river restoration to ensure that sufficient physical spawning habitat is available throughout the winter and spring period to offer more chances for spawning and uninterrupted egg incubation and larval development. As well as benefitting a reintroduced burbot population, holistic, catchment-wide river restoration approaches could benefit wider freshwater systems and species by offsetting water temperature extremes and protecting and enhancing other ecosystem services, such as flow and floodwater regulation and biodiversity provision. A future under a high emission scenario based on a simple daily maximum air-water temperature logistic relationship shows that water temperatures could be unsuitable for spawning as early as the 2030s. Overall this heightens the importance of the burbot's possible adaptability and plasticity when it comes to water temperature requirements and the burbot's future in the River Wissey and English rivers.

Chapter 5. Assessing the hydrogeomorphological suitability of the River Wissey for burbot

5.1. Introduction

Floodplains are some of the most threatened ecosystems globally. In Europe and North America, up to 80-90% of floodplains are functionally extinct due to cultivation or development (Tockner and Stanford, 2002; Davidson and Finlayson, 2018). For England, in 2015, agriculture occupied 64% of floodplains, which had increased from 38% in 1990 (Entwistle et al., 2019). The same study found that rare wetland areas, such as fenland, marsh, swamp and bog occupy <0.5% floodplain area on less than 25% of English watercourses, though it is noted that these habitats were already highly degraded before the start of the study assessment (i.e., 1990). The decline in floodplain extent and functioning has been driven flood management and flow control (Abramovitz, 1996; Havrdová et al., 2023). Driven by agricultural intensification and land drainage (Firbank et al., 2007, 2011; McKay et al., 2019), habitat modification in the form of floodplain disconnection from the main river channel via construction of embankments, combined with straightening and dredging of the main channel and drainage systems has facilitated the cultivation and development of floodplains (Tockner and Stanford, 2002). These modifications have been occurring slowly over centuries, but technological advances have meant that the manipulation of riverine systems has intensified. In England, between 1930 – 1980, approximately 8,500 km of rivers were straightened, dredged, embanked and reinforced for flood management and erosion control (Brookes, 1988; Newson et al., 2022). But these modifications resulted in reductions of aquatic diversity, removal of habitat heterogeneity and disconnection of the main channel and floodplain. Similar trends have been observed across Europe, again due to the installation of levees, sluice gates, and embankments (Bunzel-Drüke et al., 2004a; Bosveld et al., 2014).

Research has shown that the decline in floodplain extent and functioning is linked to freshwater biodiversity decline across multiple taxa (Tockner and Stanford, 2002; Havrdová et al., 2023), and improving lateral connectivity to the floodplain is important for the diversity of the freshwater ecosystem, particularly for fish (Copp, 1997b; Grift

et al., 2003; Lasne et al., 2007; Nunn et al., 2007; Zeug and Winemiller, 2007; Peirson et al., 2008; Gorski et al., 2011; Schomaker and Wolter, 2011; Bolland et al., 2012; Pander et al., 2018; Ramler and Keckeis, 2019; Manfrin et al., 2020; Stoffers et al., 2022; Bouloy et al., 2024).

The burbot's extirpation, during the early 1970s in England, coincided with an intense period of river modification and floodplain development (Petts, 1984; Brookes, 1988). Similarly, in Belgium, the burbot was extirpated in the 1960s as river modification increased (Yimer et al., 2023), reducing access to the floodplain and reducing the frequency of floodplain inundation and thus eliminating its known spawning and larval nursery habitat (Vught et al., 2015). In combination with reductions in lateral connectivity in Belgium, loss of longitudinal connectivity within and between watercourses (Parasiewicz et al., 2023; Yimer et al., 2023) ultimately prevented burbot from reaching spawning grounds. This was not only due to the height of the instream structures, but also increased flow velocities in narrowed river channels which would have prevented upstream migration of burbot as they have a low swimming endurance (<10 minutes sprint swimming at 0.25 m s^{-1} , Jones et al., 1974) (Vught et al., 2015). For England, Belgium, and other European countries (see Petts, 1984; Penczak et al., 1998; Van Heezik, 2008; Parasiewicz et al., 2023; Yimer et al., 2023), where burbot have been declining, the severance of the river-floodplain continuum has been detrimental to their survival, which highlights that burbot habitat suitability is dependent on combined hydrogeomorphology.

For each burbot life stage, there are hydrological conditions that need to be met for successful life cycle completion. The most crucial of these stages are spawning, egg development, and larval rearing. Research shows that lateral habitats (i.e., side channels and backwaters) are crucial for both Euro-Beringian and North American burbot spawning and as larval habitat (Fisher, 2000; Dillen et al., 2005). For example, in the Lake Baikal river basin, Russia, lateral connectivity between the main river, lakes, deltas and ponds provide extensive spawning and nursery habitat for the local burbot population (Sorokin, 1971). In Sweden, it has been found that, for rivers connected with off-channel lakes, the burbot population was highest at 500 m directly

above and below the connection to the lake (Degerman and Sers, 1994). Due to a large global distribution, habitat utilisation by life stage can vary and for the western European subclade of burbot (i.e., France, Germany, Belgium, Netherlands, mainland Denmark - see Van Houdt et al., 2005) floodplains play a crucial role in terms of spawning, egg incubation, and larval development. While burbot can still spawn in backwater habitats, rivers that possess functioning floodplains with regular lateral connectivity have a positive influence of burbot recruitment annually (Koporikov and Bogdanov, 2021). The hydrological characteristics that unite habitat utilisation at all early life stages for burbot are slow-flowing and shallow water.

The majority of burbot spawning occurs over a 2-3 week period, but the depths at which burbot spawn are debated, which is likely due to few spawning events being witnessed or recorded. In Burntside Lake, USA, spawning occurs in shallow water at depths between 33 – 132 cm (Cahn, 1936), while in Lake Baikal, Russia, spawning depths are 50 – 80 cm (Sorokin, 1971). In the River Drava, Austria, spawning depths are between 18 – 20 cm (Farkas, 1993). Unfortunately, there are no published studies for floodplains where water depth has been recorded alongside a burbot spawning event. Burbot spawning is undertaken in groups, so it can be assumed that depths across the floodplain must allow the access for, and aggregation of, multiple individuals (between 10 – 12, McPhail and Paragamian, 2000).

The egg stage is clearly the most vulnerable life stage as survival is dependent on a narrow temperature range and low flow conditions. In total, the egg stage can be between 30 – 75 days, dependent on temperature (Hochleithner, 2020). There is debate on where eggs develop. Some studies state that eggs are dispersed by wind and currents, and then get caught up in the shallows or river side arms until they hatch (Meshkov, 1972). Others suggest that the eggs develop directly on the spawning grounds where they are released (Sorokin, 1971; Kainz and Gollmann, 1996; McPhail, 1997). Burbot eggs contain an oil droplet approximately 40% of egg diameter, allowing the egg to stay afloat in velocities of 0.04 m s^{-1} , with velocities of 0.15 m s^{-1} potentially carrying them out the system (Vught et al., 2015). Low flow velocities rather than static water play a crucial role, ensuring that eggs are regularly shaken to free the egg

surface of silt and prevent suffocation by oxygen deficiency (Fabricius, 1954; Sorokin, 1971; McPhail, 1997).

Directly after hatching, burbot larvae settle initially on the bottom and swim up to the surface when disturbed after which they sink back down, headfirst (McPhail and Paragamian, 2000). As for burbot eggs, this behaviour prevents fine substrate covering and suffocating the larvae. Following this early period, burbot larvae are mostly pelagic and immobile, drifting passively in the water column and distributed by the current until they are caught in vegetation in side arms, inlets of backwaters, or in the outer, shallow extent of floodplain waters (Müller, 1957; Koporikov and Bogdanov, 2011; Vught et al., 2015). During this time, the larvae do not have a swim bladder or a mouth, and so feed endogenously on the yolk sac (Vught et al., 2015). While the swim bladder and mouth are developing, it is crucial that burbot larvae remain in almost stagnant water with depths of <20 cm in order for them to reach the surface to fill their swim bladder (Harsányi and Aschenbrenner, 1992; Vught et al., 2015). After the swim bladder is filled, they feed exogenously and are more mobile, shifting away from open water (Taylor and McPhail, 2000). They completely leave the upper water column between 15 – 30 mm length, transitioning toward a benthic life style (Ghan and Sprules, 1993). Once this transition begins, burbot become less vulnerable to currents (Bunzel-Drüke et al., 2004a). The vulnerable endogenous feeding stage lasts between 11 – 23 days (Clady, 1976; Fischer, 1999), but the entire larval stage, approximately 60 days in total, is a vulnerable period, until the full shift to a benthic lifestyle at 31 – 40 mm (Ryder and Pesendorfer, 1992). Brackwehr et al. (2016) suggest that, with currents of 0.5 m s^{-1} , larvae could be carried up to 900 km, emphasising the importance of refuge areas for the burbot's life cycle.

Both the egg and larval stages need almost static hydrological conditions with combined low predation risk. Floodplains that are inundated for 2 -3 months, thus offer ideal habitat for egg and larval development, providing slow flows, and structured wetland plant habitat (often grasses). At the beginning of spring, increasing water temperatures rapidly warm the shallow almost static water, which facilitates an increase in phytoplankton and associated zooplankton development, the latter a key

primary food source for burbot larvae (Vught et al., 2015). In the North Rhine-Westphalia region, Germany, a study found burbot larvae in inundated floodplain vegetation from early March to mid-April (Müller, 1957). In the River Lippe, Germany, during pre- and post-restoration monitoring of a small floodplain, researchers showed a clear increase in the local burbot population post-restoration, linked to increased connectivity to the floodplain area (Bunzel-Drüke et al., 2004a). The greatest recruitment year in the study was in 2000, where the floodplain remained inundated for 35 days from the end of February until the end of March (Bunzel-Drüke et al., 2004a). Kaporikov and Bogdanov (2011) showed that, in years without floodplain inundation, burbot recruitment was greatly reduced compared to years with floodplain inundation. In those years, the larvae relied on flow refugia in riparian vegetation associated with river meanders (Kaporikov and Bogdanov, 2011).

In Belgium, where there is an ongoing reintroduction programme (since 2005), the evidence for where natural recruitment has occurred and where they have found larvae emphasises the importance of suitable hydrological conditions. Burbot have been stocked every year since 2005 into the Grote Nete river system, for which the recorded catch history of larvae and juveniles is highly informative (section 1.4.5; Fig. 1.8, Table 1.4). All larvae and juveniles observed have been found in lateral habitats, not the main river channel. The first juvenile found in 2010 (Van den Neucker et al., 2010) was found in a heavily vegetated part of the Asbeek (Van den Neucker et al., 2010b), a tributary of the Grote Nete known to connect to its floodplain regularly (Van den Neucker et al., 2013) and all larvae (since 2014) have been found in laterally connected ponds in densities as high as 13 individuals per m² (Fig. 1.8; Pauwels et al., 2016). The evidence accumulated by Belgium clearly emphasises the importance of shallow, slow-flowing habitat that often occurs in laterally connected habitats for burbot spawning, egg incubation, and larval development.

Similar importance of floodplains can be evidenced from the translocation of burbot in the Netherlands. From 2009 – 2013, burbot were translocated from a remnant population to the Beerze River (Beelen et al., 2019). Prior to the translocation taking place, the only habitat preparation taken was the restoration of a large floodplain, the

Logstebaan. The first evidence of natural recruitment was recorded in 2019, where juveniles were found on the floodplain amongst vegetation (Beelen et al., 2019). The study compared the floodplain to 'maternity rooms' where the floodplains provide the growth and survival essentials, such as the physical habitat and food sources for young burbot (Beelen et al., 2019).

Overall, existing literature and prior burbot conservation projects demonstrate that inundated floodplains and floodplain waterbodies are crucial for burbot spawning, egg incubation, and larval development (Fig. 5.1). Thus is the combined hydrogeomorphology that is crucial in assessing burbot habitat suitability. In terms of hydrological characteristics, floodplains ideally must remain inundated for 2 – 3 months (Vught et al., 2015), but this can be as low as 35 days (Bunzel-Drüke et al., 2004a). In addition the water needs to be shallow (maximum 20 cm for larvae, Harsányi and Aschenbrenner, 1992) and maintain a connection with the main channel or side channels, with slow flow conditions that do not exceed 0.5 m s^{-1} (Brackwehr et al., 2016). Therefore, any burbot reintroduction must assess the hydrological suitability of candidate reintroduction sites in terms of floodplain functioning, specifically focusing on inundation frequency, extent, depth and duration.

The present study aims to assess the hydrological characteristics within the geomorphological context of the candidate reintroduction site along the upper River Wissey, Norfolk, UK in terms of suitability for burbot spawning, egg incubation and larval development by (i) examining the persistence and extent of floodplain inundation, as well as river-floodplain connectivity from observational data collected from November 2021 until August 2024 (ii) analysing the frequency of flood events that create sufficient floodplain habitat to support burbot spawning-egg-larva development cycles, and (iii) comparing hydrological data with temperature data (Ch. 4) to identify suitable spawning-egg-larva development periods.



Figure 5.1. (A) the inundated Lochstebaan floodplain, the Netherlands where burbot juveniles were found in 2019 (photo from Beelen et al., 2019), (B) a laterally connected pond on the Asbeek, a tributary to the Grote Nete, Belgium where larvae had been found in 2014 - 2017 (photo from Van Wichelen et al., 2018), and (C) an inundated floodplain along the River Wissey, February 2024 (author's own photo).

5.2. Materials and Methods

Study Design

5.2.1.1. Sensor Network

The study was undertaken in the Wissey study area (more detail in Ch. 2, Fig. 2.1). To assess the study area's hydrological characteristics, water depth sensors were installed in transects across the site. Initially, to increase the spatial coverage of data collection, low-cost, open-source sensor designs were used as detailed in Pearce et al. (2024). The sensors recorded water depth (cm) and temperature (°C) every 60 minutes. The sensors were accurate to ± 0.69 cm and $\pm 0.42^\circ\text{C}$ for water depth and temperature, respectively. The low-cost allowed the study to install four transects across the study area with one sensor in the main channel and another floodplain logger in the lowest point of the floodplain (Fig. 4.2). Main channel sensors include: T1_C, T3_C, T5_C, and T6_C, which are paired with floodplain loggers T1_FP1, T3_FP1, T5_FP1 and T5_FP2, and T6_FP1. When discussing the paired sensors together they are hereafter referred to as T1, T3, T5, and T6. Photos from monitoring sites are shown in Appendix 4. The loggers recorded every 60 minutes. Transect widths varied between 12.28 and 111.53 m. Due to accessibility issues only one adjacent floodplain at each transect was studied, with all being on the righthand bank, except T1. Initially, water depth sensors were installed in November 2021, but after one initial failed deployment and two subsequent deployments, the data showed that the low-cost loggers had varying battery life capacities (15 days – 4 months) they were replaced with Solinst® LevelLogger® 5 Juniors by November 2022. The latter have accuracies of $\pm 0.1\%$ of full scale for water level and $\pm 0.1^\circ\text{C}$ for temperature. Alongside these, a Solinst® Barologger 5 Barometric Datalogger (± 0.05 kPa and $\pm 0.05^\circ\text{C}$) was installed at T1_FP1 for atmospheric compensation. From this installation, all loggers recorded every 30 minutes until end of deployment on 07/08/24.

Alongside the water depth sensors, there is an existing stage level sensor at Bodney Bridge (TL 82876 98840), which is operated by the Environment Agency. This gives average daily stage level (mAOD) levels based on 15-minute interval readings. The record extends from 01/03/93 to present day. The record used in this study was for 01/03/93 – 30/08/24 ($n = 11,507$). As the closest gauging station is at Northwold,

approximately 10.34 km downstream from the bottom of the study area, a Streamline Measurement Starflow Ultrasonic Flowmeter (6526H-51; $\pm 0.25 - 0.5$ mm) was installed in November 2022, 1 m upstream of the Bodney Bridge stage level meter to establish a relationship between depth and flow. The flowmeter was recording depth (cm), flow ($\text{m}^3 \text{s}^{-1}$), velocity (m s^{-1}) and water temperature ($^{\circ}\text{C}$) every 2 hours. The flowmeter was logging at a low frequency due to a power supply issue, which also resulted in sporadic data collection, with data collected between 28/11/22 – 28/12/22, 06/06/23 – 29/06/23, and 01/12/23 – 04/02/24.

In combination with the installation of the sensor network, floodplain inundation extent was mapped and depth transect generated. During a period of inundation in February 2022 (survey date: 22/02/2022), flood extent was recorded using GPS (± 3 m) points to outline the inundation at T1 and T3 and this was repeated for a period of inundation in February 2024 (survey date: 23/02/2024). In February 2022, depth transects were taken across the floodplain at all four sensor transects, with water depth recorded every 5 m across to the main channel. From these data, combined with LiDAR data and 1 m resolution Digital Terrain Model (DTM) imagery from 2018 (EDINA Aerial Digimap Service, 2020), a raster volume analysis tool was used in QGIS (v.3.34.1) to calculate flood surface area and volume. The depth transects were also used to calculate flood barrier height along the water depth transects to investigate the hydrogeomorphology and lateral connectivity.

5.2.2. Data Management and Analysis

Observational data from the sensor network was organised into hydrological years, with hydrological year 1 spanning from 26/11/21 – 30/09/22 (hereafter, HY1), hydrological year 2 01/10/22 – 30/09/23 (hereafter, HY2), and hydrological year 3 01/10/23 – 07/08/24 (hereafter, HY3). Some floodplain loggers reported negative readings during the summer months, so the data were cleaned and replaced with 0 cm to reflect the empty floodplain. The negative readings could reflect an issue with a calibration of the sensors or the barometric compensation methodology, but range of negative readings were small (-0.1 to -1.0 cm) and thus not anticipated to impact the

results from the data analysis. Differences in floodplain inundation between observed floodplain sites across hydrological years is tested using a Kruskal-Wallis test due to the data being non-parametric (Kolmogorov-Smirnov test, $p = <0.001$).

For data analysis, life stage thermal requirements (section 4.1.2; Table 4.7) are applied to the hydrological data to identify suitable periods for different life stages. The spawning period is defined as 1st December – 28th February, with any egg incubation and larval development period calculated from the end of a spawning window identified within the observed data. A spawning window is defined as a two-week period where daily maximum water temperatures are $<7^{\circ}\text{C}$ (Jäger et al., 1981; Beelen, 2009). Spawning migration triggers are defined as daily maximum water temperatures $<12^{\circ}\text{C}$ during September-November combined with increases in water level (Hochleithner, 2020). Maximum thermal tolerance for burbot eggs is daily maximum water temperatures $<9^{\circ}\text{C}$ (Lahnsteiner et al., 2012) and $<16^{\circ}\text{C}$ for larvae (Trabelsi et al., 2011).

Unfortunately, due to resource constraints, the floodplain logger at T6_FP1 could not be replaced in 2022, so for the observational data collected ($n = 878$) a relationship was established between the main channel (T6_C) and floodplain (T6_FP1) to predict floodplain inundation for the T6_C record. Interestingly, unlike other transects where the relationship was clearly linear (e.g., T1), the spread of observational data were polynomial, which suggested that the floodplain inundation at T6_FP1 was not just influenced by water depth at T6_C. Nevertheless, based on the distribution of the relationship, a polynomial regression to the 3rd degree was established (Fig. 5.2; Equation 1):

$$y = ax^3 + bx^2 + cx + d \quad (1)$$

Where y is floodplain water depth, a , b , c , and d are correlation coefficients and x is main channel depth. In this case, $a = 0.0018$, $b = 0.5688$, $c = 59.881$, and $d = -2089.6$. The polynomial regression fitted the data well ($r^2 = 0.71$), but due to the polynomial relationship, it likely overestimates values at the extremes of the observed range. Considering floodplain inundation practically and in the current context, accuracy at

the extremes is not crucial at T6_FP1 as the study needs to determine whether the inundation is suitable for burbot (i.e., can they swim on and off the floodplain), which is determined in this study to be depths >10 cm. Due to this issue, outlier predictions of <0 and >90 cm were removed, with the former based on the values being known errors and the latter being improbable readings based on field observations at the location of T6_FP1 and the given distance from the main channel, which would require a large volume of water to exceed 90 cm at that point.

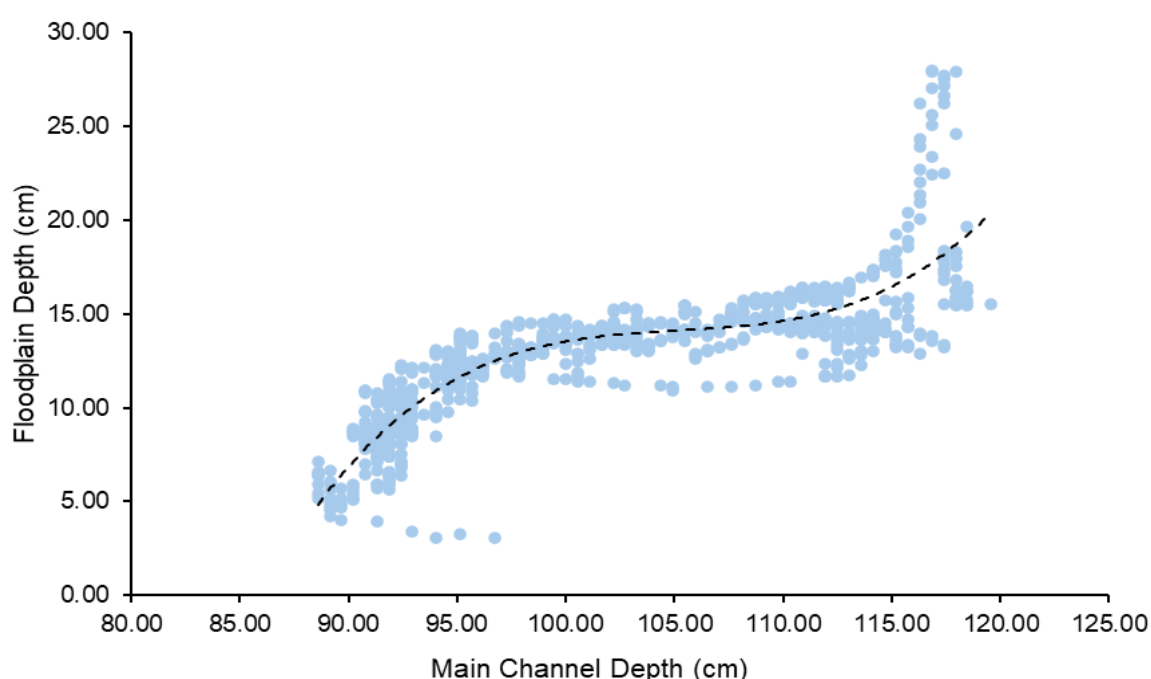


Figure 5.2. Polynomial relationship between hourly main channel water depth (cm) and floodplain water depth (cm) at T6 between 24/02/21 to 02/04/22. Polynomial to 3rd degree trendline displayed.

To establish a depth-flow relationship at Bodney Bridge, observational data from the flow meter and stage gauge record were used. First, stage level was converted to water depth based on field readings of water depth at Bodney Bridge taken across the study and compared to readings from the stage gauge record. The difference between these sets of readings was averaged (18.01 m) and this figure was then subtracted from the stage level record to get actual water depth (m) at Bodney Bridge for the entire record (1993 – 2024). The mean elevation value (18.01 m) was compared to the existing LiDAR data, which gave a similar value (~18 m), but due to accuracy

limitations (~1 m spatial resolution) the observational data were used to calculate actual water depth. Any outliers were deleted ($n = 475$). Based on the newly calculated water depth record for Bodney Bridge, the water depth was compared to the flow recorded by the flow meter during the study period ($n = 770$). A linear relationship was found between the observed depth and flow for the study period ($r^2 = 0.92$) and this was used to hindcast the flow for the existing water depth record at Bodney Bridge (1993 – 2024). From the hindcasted flow record, flood frequency statistics were calculated based on the ranked flow (lowest to highest) of annual maximum flow from each hydrological year for the flow record after Davie (2010). The distribution used for the flood frequency analysis was Gumbel (1941) and was chosen as it is specifically used to model the distribution of the maximum in a dataset and as flood events are extreme events, the Gumbel distribution is well suited to capturing statistical behaviour of extremes (Shaw et al., 2011). The calculations use methods of moments based on the Gumbel distribution (Gumbel, 1941) (Equations 2 – 4):

$$F(X) = e^{-e^{(-x)}} \quad (2)$$

$$a = \bar{Q} - \frac{0.5772}{b} \quad (3)$$

$$b = \frac{\pi}{\sigma_Q \sqrt{6}} \quad (4)$$

Where $F(X)$ is the relative frequency where the probability of the flow being less than the value of X , e is the base number for natural logarithms or the exponential number (≈ 2.7183), $\bar{Q}$ is mean flow, σ_Q is the standard deviation of the annual maximum flow data series, and a and b being parameters that shape the distribution. These equations can be rearranged to estimate the size of flow that might be expected for a given return period (Equation 5):

$$X = a - \frac{1}{b} \ln \ln \left(\frac{T(X)}{T(X)-1} \right) \quad (5)$$

Where X is the estimated flow, $\ln$ is the natural logarithm and $T(X)$ is the given return period (Davie, 2010). Based on these calculations, the frequency of the flow needed to create floods that could support burbot spawning, egg incubation, and larval development (hereafter, burbot life cycle completion) can be determined. All statistical analyses were conducted in R (v.4.3.2) with spatial analyses conducted in QGIS.

To further understand the hydrological years in this study, historical rainfall data were analysed. The daily rainfall data (1975 – 2023) were obtained from the Met Office MIDAS Open: UK Land Surface Stations Data at Denver (TF 59162 00899) (Met Office, 2023), which is 1.88 km from where the Wissey joins the River Great Ouse, approximately 23 km from the uppermost part of the study site. Unfortunately, no rainfall data with an extensive record or more recent monitoring are available any closer to the study site.

5.3. Results

Water depths for main channel sensors, T1_C, T3_C, T5_C, and T6_C, across all hydrological years are presented in Fig 5.3. Summary statistics for all sensors for each hydrological year are listed in Table 5.1. Comparison of observed depth data across each water depth transect and the elevation data extracted from the LiDAR allowed the calculation of minimum depths needed for the main channel to overtop its banks at each transect. Based on these calculations, at T1, when the main channel depths exceeded 84.2 cm and 88.2 cm, overtopping of the lefthand and righthand banks occurred, respectively. At T3, when main channel water depths exceeded 95.3 cm and 91.3 cm then overtopping of the lefthand and righthand banks occurred, respectively. For T5, water depths of 78.7 cm and 118.7 cm were needed in the main channel to overtop the left and righthand banks, respectively. Finally, for T6, water depths of 118.9 cm and 123.8 cm were needed in the main channel to overtop the left and righthand banks respectively. This analysis was also conducted at Bodney Bridge and it was found that main channel water depths of 111 cm and 103 cm were needed to overtop the left and righthand banks, respectively.

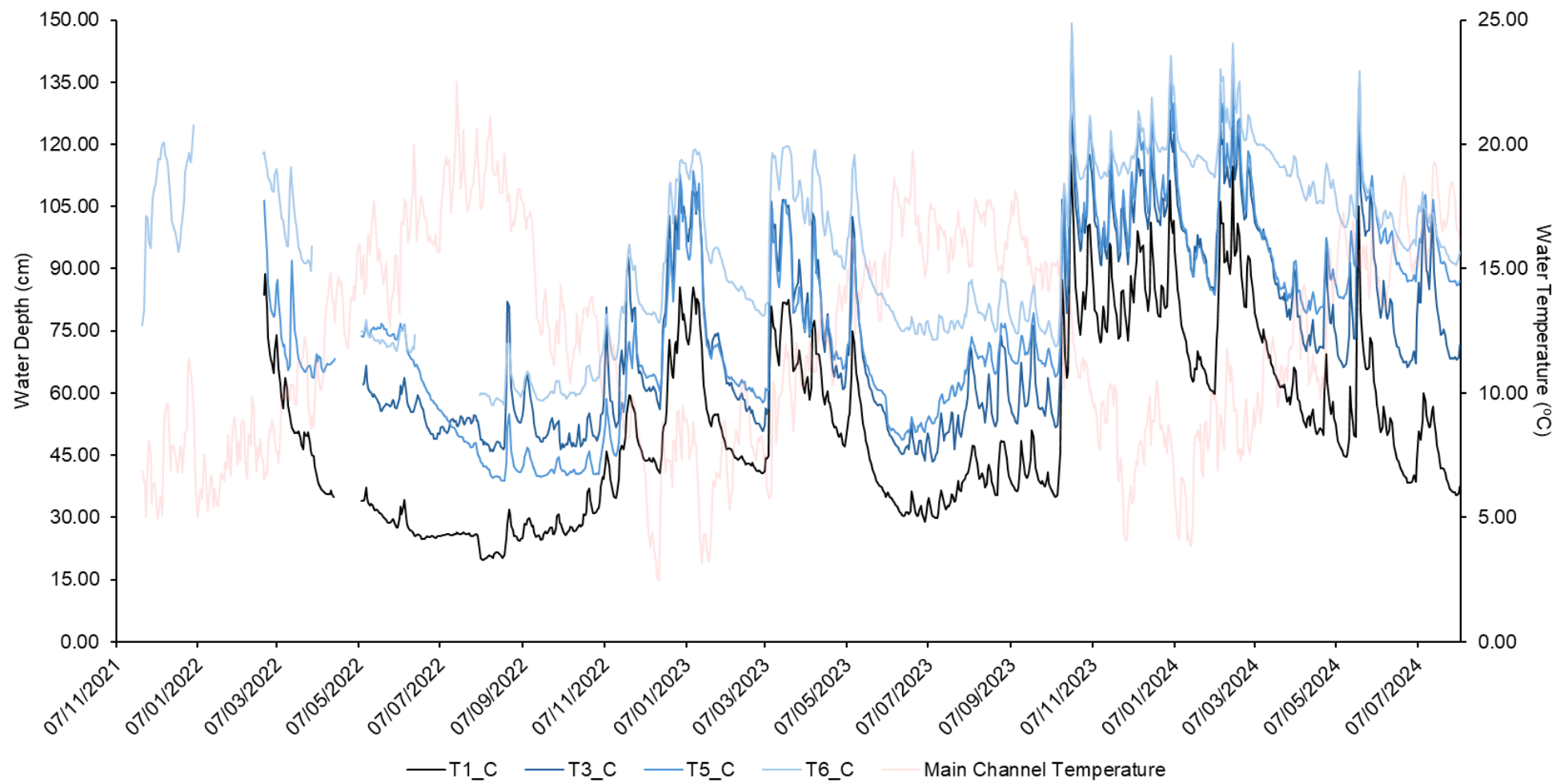


Figure 5.3. Daily average water depth (cm) at main channel sensors with daily average maximum main channel water temperature (°C, light pink) across entire hydrological record (26/11/24 – 07/08/24).

Table 5.1 Summary statistics for water depth (cm) for all sensors across all hydrological years. Bold italicised text indicates summary statistics based on the predicted values for T6_FP1 as there were no observed data. For floodplain loggers, only data points that recorded depths ≥ 10 cm were used for statistical summaries, which is why minima are similar.

Logger	HY1					HY2					HY3				
	N	Mean	SD	Min.	Max.	N	Mean	SD	Min.	Max.	N	Mean	SD	Min.	Max.
T1_C	6,076	31.49	12.73	17.9	90.51	17,468	47.35	14.93	24.9	86.6	14,960	67.2	19.33	34.2	125.8
T1_FP1	164	17.23	5.24	10.06	26.71	4,608	26.17	10.32	10	43.9	9,279	36.26	14.08	10	75.5
T3_C	3,441	54.55	5.9	43.56	84.26	16,069	66.94	17.79	42.31	112.25	14,962	90.92	17.33	50.49	136.9
T3_FP1	381	20.82	7.77	10.09	39.56	3,524	22.55	9.02	10	41.89	14,021	40.04	12.14	10.31	77.59
T5_C	4,734	59.65	14.77	38.24	107.32	16,065	68.97	15.67	39.32	116.64	14,953	98.31	14.94	62.72	160.83
T5_FP1	130	35.52	13.62	10.13	55.61	3,817	16.15	8.96	10	57.67	12,809	38.33	23.61	10.01	121.13
T5_FP2	261	18.29	8.07	10	48.3	0					0				
T6_C	5,461	77.33	20.87	52.7	126.63	17,474	86.48	15.71	58.2	120.4	14,949	111.18	13.14	70.4	157.8
T6_FP1	741	14.50	2.69	10.06	28.02	4,071	11.7	1.53	10.27	88.34	12,967	15.99	10.33	10.02	89.07

Table 5.2. Total days and longest consecutive period (days) of floodplain inundation where daily maximum water depth exceeds 10 cm at each observed floodplain site across all hydrological years.

	HY1								HY2								HY3							
	T1		T3		T5		T6		T1		T3		T5		T6		T1		T3		T5		T6	
	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R
Total days	3	2	NA	NA	16	0	9	4	5	0	47	59	78	0	10	0	80	61	157	175	300	45	90	48
Consecutive Days	3	2	NA	NA	13	0	4	2	3	0	22	27	30	0	6	0	19	18	46	92	300	8	45	18

5.3.1. Floodplain Inundation and Lateral Connectivity

Floodplain inundation varied spatially across all hydrological years (Fig. 5.4 – 5.7). The temporal extent of lateral connection between the main channel and floodplain via overtopping at the main channel observation point also varied spatially (Table 5.2). The Kruskal-Wallis test showed that, for all observational data, differences in days of inundation across floodplain sites were not statistically significant ($p = 0.95$). When comparing interannual variation, however, the differences in total days of floodplain inundation were statistically significant ($p = 0.007$). When considering overall variation in floodplain depths, the Kruskal-Wallis test showed there was statistically significant differences in water depths (>10 cm) across sites ($p = <0.001$). The differences in interannual variation in floodplain depths were also statistically significant ($p = <0.001$).

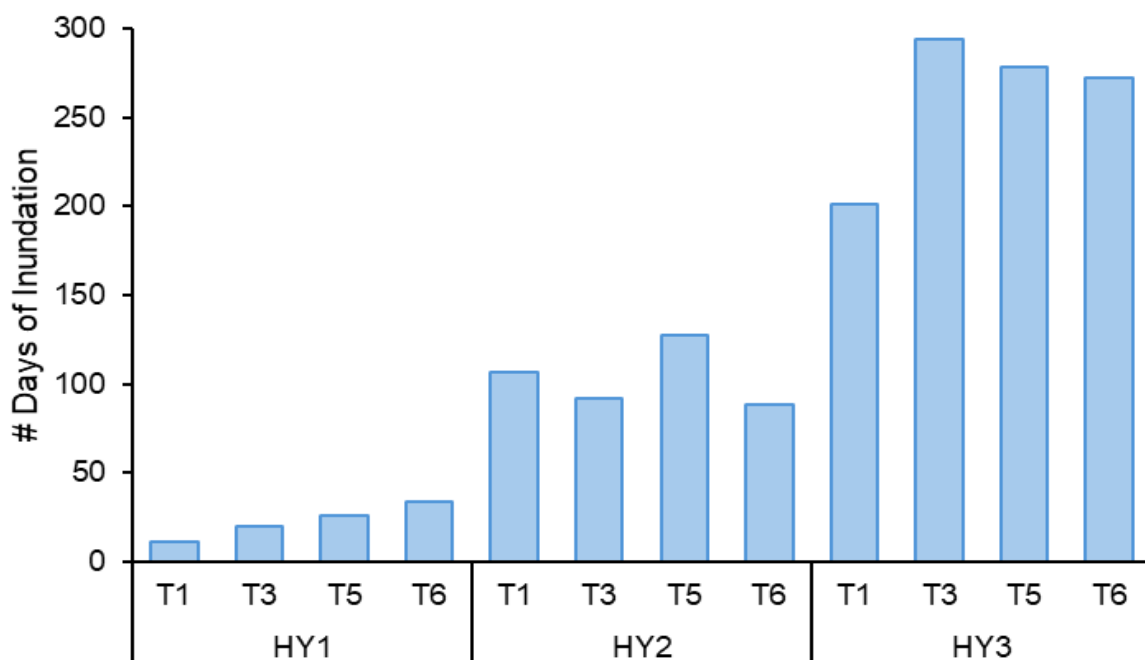


Figure 5.4. Total number of days where water depths on floodplain exceeded 10 cm across all observed floodplains from February 2022 to August 2024.

In HY1, floodplain inundation (i.e. days where daily maximum water depth ≥ 10 cm) was most extensive at T6 (34 days total), but lateral connection was most extensive at T5 where daily maximum water depth exceeded 78.7 cm to overtop the lefthand bank in the main channel at T5 for a total of 16 days (5% of record), and consecutively

for 13 days (4%). At T1_FP1, the number of days in which daily maximum water depth exceeded 10 cm was 11 (Fig. 5.5a). Average depth recorded for T1_FP1 was 17.23 ± 5.24 cm, with a maximum depth of 26.71 cm recorded (Table 5.1). For T3, daily maximum water depth was >10 cm on 20 days total (Fig. 5.5b), but due to the late installation of the T3_C logger, overtopping cannot be calculated for HY1. Average depth recorded for T3_FP1 was 20.82 ± 7.71 cm and maximum depth recorded was 39.57 cm (Table 5.1). For T5, daily maximum water depth at T5_FP2 exceeded 10 cm on 26 days (Fig. 5.5c). For T5_FP1, average depth was 35.52 ± 13.62 cm, while it was 18.39 ± 8.07 cm for T5_FP2. Maximum depths recorded by T5_FP1 and T5_FP2 were 55.61 and 48.3 cm, respectively. For T6, the total number of days that daily maximum water depth exceeded 10 cm on the floodplain at T6_FP1 was 34 in the observed data and 176 days from the predicted record (Fig. 5.5d). Average depth for the observational record at T6_FP1 was 14.50 ± 2.69 cm, with a maximum depth of 28.02 cm.

In HY2, floodplain inundation duration (i.e. days where daily maximum water depth ≥ 10 cm) was longest at T5, with 127 days total inundation, where consecutive lateral connection and total connection was also the most extensive (8% and 21% of logged year, respectively). At T1, daily maximum water depths exceeded 10 cm at T1_FP1 on 107 days during HY2 (Fig. 5.6a). Average depth recorded at T1_FP1 was 26.17 ± 10.32 cm and maximum depth was 43.9 cm (Table 5.1). At T3, daily maximum water depths exceeded 10 cm at T3_FP1 on 92 days (Fig. 5.6b). Average depth at T3_FP1 was 22.55 ± 9.02 cm and maximum depth recorded was 41.89 cm (Table 5.1). At T5, daily maximum water depths exceeded 10 cm at T5_FP1 for 127 days (Fig. 5.6c). Average depth recorded at T5_FP1 was 16.15 ± 8.96 cm and maximum depth was 57.67 cm. At T6_FP1 daily maximum water depths exceeded 10 cm in the observational record on 24 days and the predicted record indicates this to be 88 days in total for HY2 (Fig. 5.6d). Average depth at T6_FP1 based on the predicted record was 11.7 ± 1.53 cm and maximum depth was 88.34 cm.

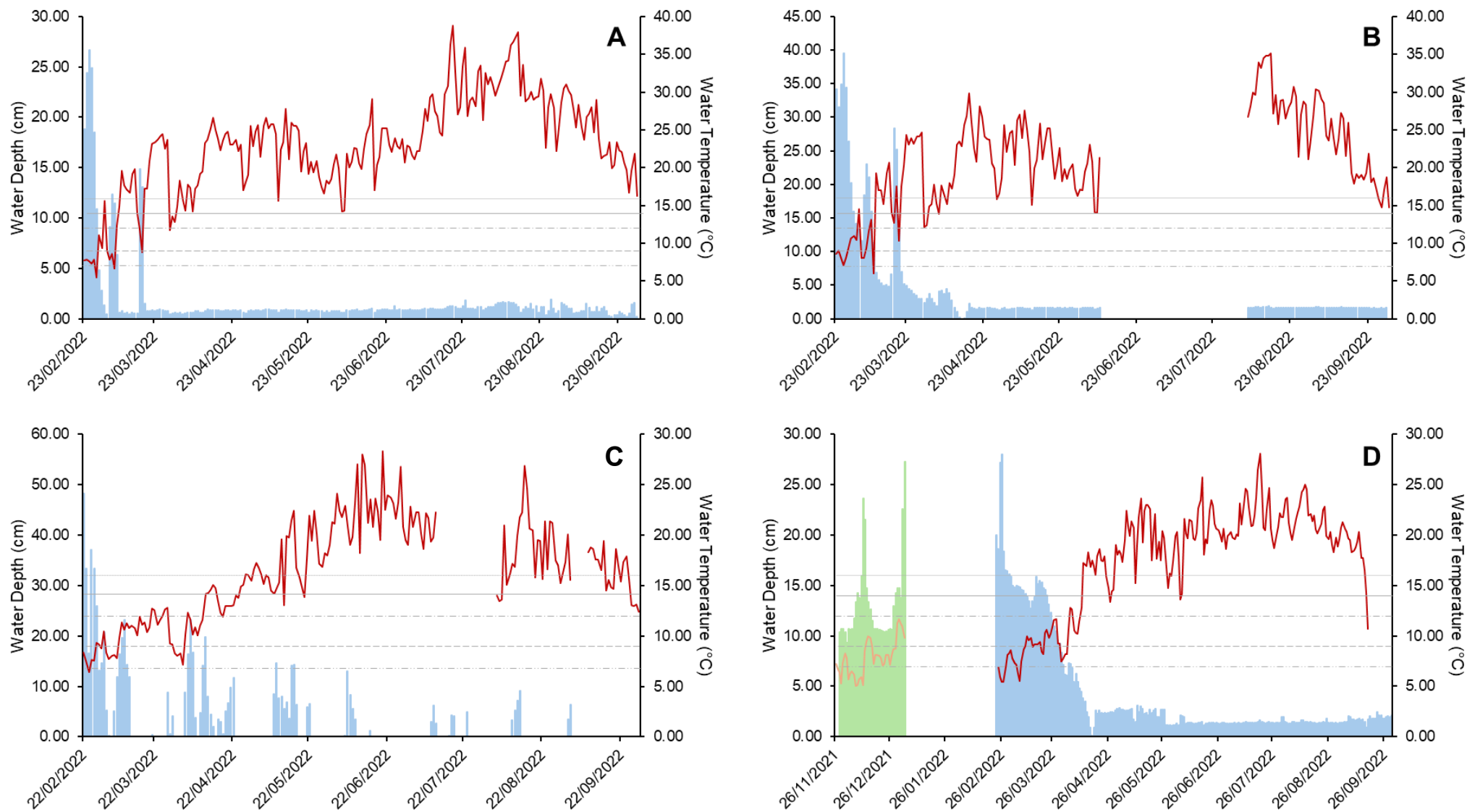


Figure 5.5. HY1 daily maximum floodplain water depth (cm) and daily maximum water temperature (°C) at (A) T1, (B), T3, (C) T5, and (D) T6, where green indicates predicted water levels and orange is the water temperature in the main channel. On each graph the top dotted line is maximum temperature for larval development (16 °C), solid line is adult optimum (14 °C), dot-dash line is spawning migration trigger (12 °C), dashed line is egg incubation lethal temperature (9 °C), and double dot dash is maximum temperature at which some spawning occurs (7 °C).

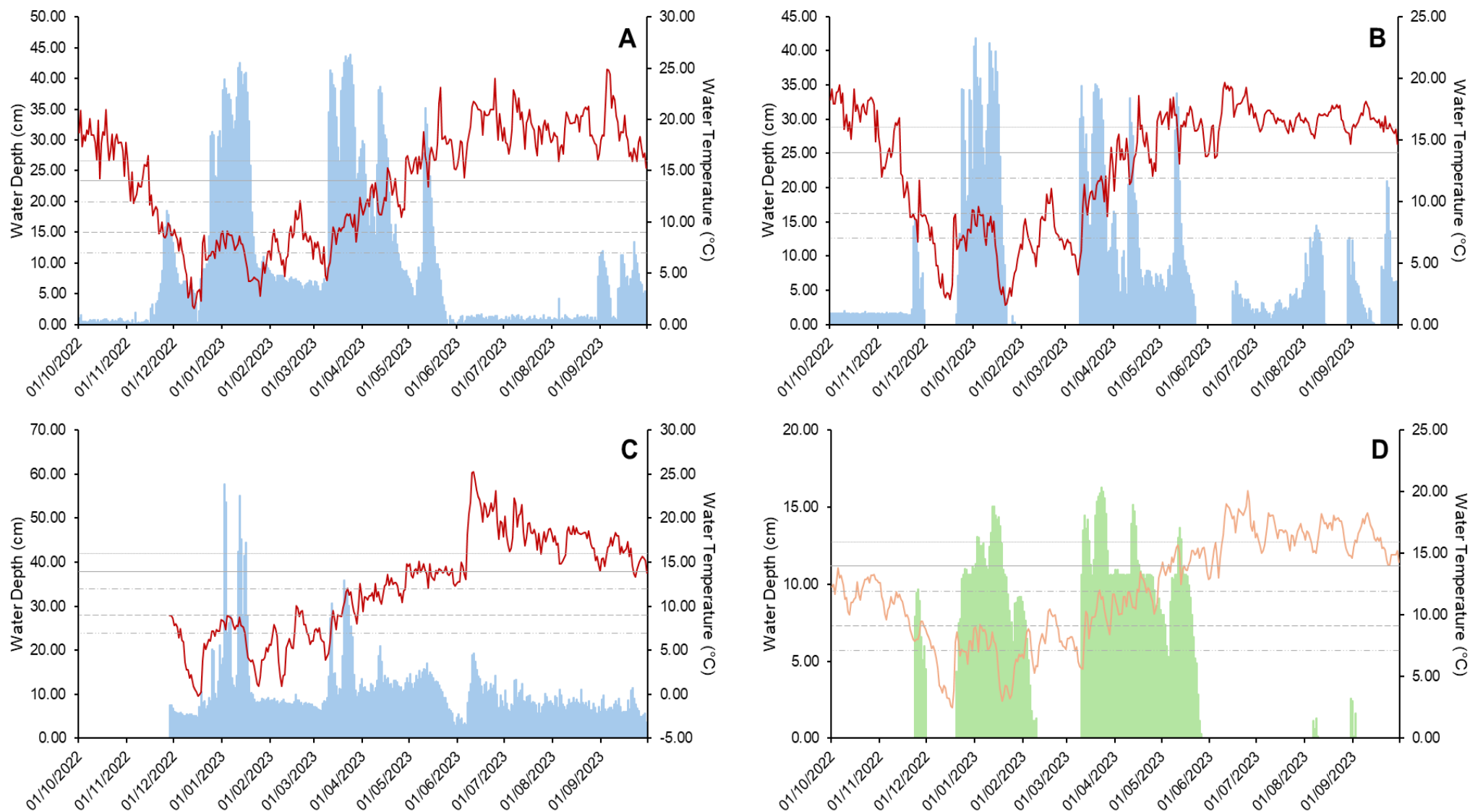


Figure 5.6. HY2 daily maximum floodplain water depth (cm) and daily maximum water temperature (°C) at (A) T1, (B) T3, (C) T5, and (D) T6, where green indicates predicted water levels and orange is the water temperature in the main channel. On each graph the top dotted line is maximum temperature for larval development (16 °C), solid line is adult optimum (14 °C), dot-dash line is spawning migration trigger (12 °C), dashed line is egg incubation lethal temperature (9 °C), and double dot dash is maximum temperature at which some spawning occurs (7 °C).

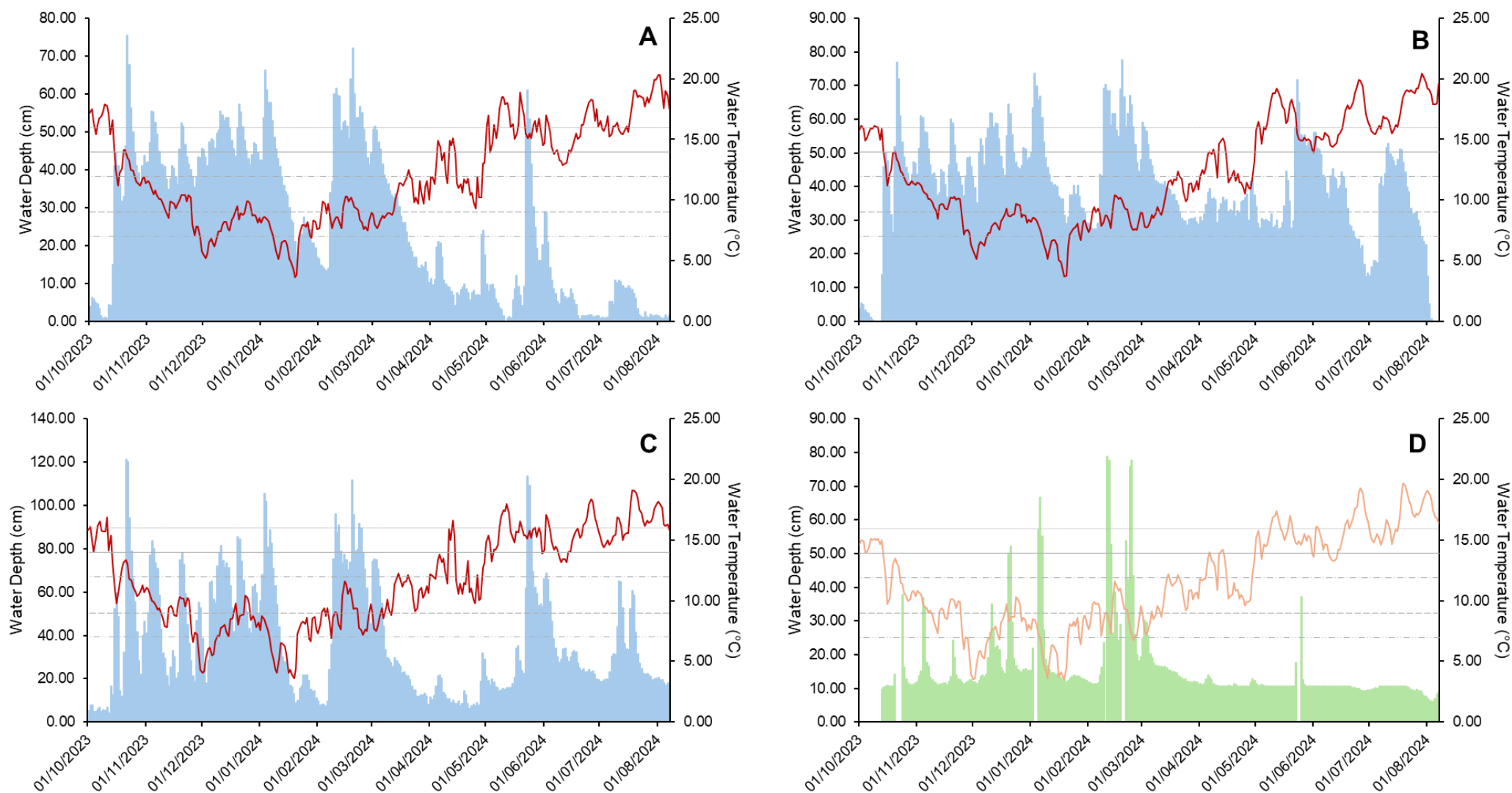


Figure 5.7. HY3 daily maximum floodplain water depth (cm) and daily maximum water temperature (°C) at (A) T1, (B) T3, (C) T5, and (D) T6, where green indicates predicted water levels and orange is the water temperature in the main channel. On each graph the top dotted line is maximum temperature for larval development (16 °C), solid line is adult optimum (14 °C), dot-dash line is spawning migration trigger (12 °C), dashed line is egg incubation lethal temperature (9 °C), and double dot dash is maximum temperature at which some spawning occurs (7 °C).

In HY3, floodplain inundation duration (i.e. days where daily maximum water depth ≥ 10 cm) was longest out of all hydrological years, reaching a maximum of 294 days at T3. Longest total and longest consecutive lateral connection occurred at T5, however (both 96% of logged days; Table 5.2). At T1, daily maximum water depth exceeded 10 cm at T1_FP1 on 201 days during HY3 (Fig. 5.7a). Average depth recorded at T1_FP1 was 36.26 ± 14.08 cm, with a maximum depth of 75.5 cm (Table 5.1). At T3, daily maximum water depth exceeded 10 cm at T3_FP1 on 294 days (Fig. 5.7b). Average depth at T3_FP1 was 40.04 ± 12.14 cm and maximum depth was 77.59 cm. At T5, daily maximum water depths exceeded 10 cm at T5_FP1 for 278 days (Fig. 5.7c). Average depth recorded at T5_FP1 was 38.33 ± 23.61 cm with a maximum depth of 121.13 cm. At T6, daily maximum predicted water depth exceeded 10 cm at T6_FP1 on 272 days (Fig. 5.7d). For the predicted record at T6_FP1, average water depth was 15.99 ± 10.33 cm and maximum depth was 89.07 cm.

5.3.2. Flood Volume

Flood volume could not be calculated for each observed floodplain in every hydrological year, but the available data gives an early indication at the volume of water stored and thus available spawning habitat for burbot at the Wissey. In February 2022, the extent of floodplain inundation was mapped in three areas: the lefthand back of T1, a smaller area close to TE2 on the lefthand bank (Fig. 4.2), and the righthand bank at T3. For T1, geospatial analysis showed that the floodplain extent at T1 was $10,957 \text{ m}^2$ and stored $2,127 \text{ m}^3$ of water. At TE2, the area was $3,738 \text{ m}^2$ and stored 965 m^3 of water. Finally, the righthand bank flooded at T3 was $16,129 \text{ m}^2$ and stored $5,841 \text{ m}^3$ of water.

In February 2024, floodplain extent was mapped again at T1 and T3, but also at an additional site in the field on the lefthand bank upstream of T1 (hereafter, Upper Watton Brook). At the Upper Watton Brook site, the surface area of the flood extent was $16,217 \text{ m}^2$ and flood volume was $7,095 \text{ m}^3$. At T1, the surface area of the flood was $17,445 \text{ m}^2$ and the flood volume was $3,264 \text{ m}^3$. Compared to HY1, the surface area of flooding at T1 in HY3 was 1.59 times greater and the flood volume was 1.53 times greater. At

T3, the flooding was continuous across the fields downstream to Bodney Bridge. Total surface area of flooding on the righthand bank was 55,607 m² and flood volume was 29,759 m³ for all fields. Compared to HY1, the surface area of flooding at T3 in HY3 was 3.45 times greater and the flood volume was 5.01 times greater.

5.3.3. Velocity

For the available observational period (across HY2 and HY3), velocity was recorded in the main channel near Bodney Bridge. The flow meter at Bodney Bridge was deployed for two periods in HY2, 28/11/22 – 28/12/22 and 06/06/23 – 29/06/23. Average velocity in the winter deployment ($n = 354$) was $0.7 \pm 0.12 \text{ m s}^{-1}$. Maximum and minimum velocities recorded during this period were 0.93 m s^{-1} and 0.11 m s^{-1} , respectively. The greatest observed change in the 2-hourly dataset was 0.56 m s^{-1} between 14:00 and 16:00 on 05/12/22. There were 12 occurrences where the 2-hourly change in velocities exceeded 0.25 m s^{-1} . During this period, instream velocity exceeded 0.25 m s^{-1} for 99% of the record. During the summer deployment ($n = 273$), average velocity was $0.13 \pm 0.14 \text{ m s}^{-1}$ and maximum and minimum recorded velocities were 0.48 m s^{-1} and 0.0 m s^{-1} , respectively. The greatest observed change in the 2-hourly dataset was 0.3 m s^{-1} between 00:00 and 2:00 on 21/06/23. There were five occurrences where the 2-hourly change exceeded 0.25 m s^{-1} . In total, instream velocity exceeded 0.25 m s^{-1} for only 24% of the time for the dataset.

During HY3, the flow meter at Bodney Bridge was deployed from 01/12/23 – 04/02/24 ($n = 778$). Average velocity was $0.66 \pm 0.11 \text{ m s}^{-1}$. Maximum and minimum velocities in this period were 1.09 m s^{-1} and 0.49 m s^{-1} , respectively. During this period, the greatest 2-hourly change in velocity was 0.07 m s^{-1} between 22:00 on 02/01/24 and 00:00 on 03/01/24. For this deployment, instream velocity exceeded 0.25 m s^{-1} for 100% of the period.

5.3.4. Combined Hydrology and Temperature

5.3.4.1. Spawning Migrations

In HY1, there was not a clear trigger for potential spawning, where water levels increase and water temperatures drop between 12 - 10°C, except at T6_FP1, due to when the study period began. Fig. 5.5d shows that, on the 26/11/21, when the record began, water was on the floodplain and temperatures in the main channel were well below 12°C. Considering spawning migration in HY2, Fig. 5.5 shows that main channel water depths slowly increased from early September. Temperatures only dropped below 12 °C in mid to late November, with water levels increasing in the main channel in early November (Fig. 5.3) and on the floodplains only in early December (Fig. 5.6a-d). Interestingly, for T1_FP1, T3_FP1, and T5_FP1, water depth increased again before the end of HY2 at 30/09/23, which is reflected in the main channel sensors, which recorded increased depths from August 2023 (Fig. 5.3). With water depths increasing before the end of HY2, the triggers of potential spawning migrations are earliest in HY3. By mid-October, all floodplains had increasing water depths, which was combined with a drop in water temperature for all floodplains below 12 °C before 1st November (Fig. 5.7a-d).

5.3.4.2. Spawning Periods and Egg Incubation

In HY1, temperatures dropped below the 7°C maximum temperature threshold combined with water on the floodplain (Fig. 5.3), which could suggest that there was a potential spawning window in late November, but unfortunately, due to logger deployment failure, there is no clear spawning period on the floodplains during HY1.

For HY2, Chapter 4 identified that there is no two-week spawning window on the floodplain where daily maximum water temperatures were <7°C on the floodplain with sufficient water depths (≥10 cm). Periods where daily maximum water temperatures were <7°C and water depths (≥10 cm) were from 16/01/23 – 22/01/23 (7 days) for T1_FP1, 16/01/23 – 20/01/23 (5 days) for T3_FP1, and 15/01/23 – 19/01/23 (5 days) for T5_FP1. Though suitable temperatures extended for more days, inconsistent water levels were the primary cause of unsuitable spawning windows in HY2 (Fig. 5.6a-d).

If spawning adults could survive in shallow depths and utilise the full window of suitable temperatures (14 – 19 days), then by 03/02/23, daily maximum water temperatures exceeded 9°C, which would be lethal to any eggs that were produced.

HY3 offers potentially the longest window of hydrological suitability for spawning, egg incubation, and larval development of all hydrological years in this study. The temperatures, however, as discussed in Chapter 4 are warmer compared to HY1 and HY2, reducing the extent of thermally and hydrologically suitable windows. At T1_FP1, a 14-day spawning window occurred 08/01/24 – 21/01/24, but daily maximum temperatures exceeded 9°C by 03/02/24, providing 13 days for egg incubation. At T3_FP1, a 15-day spawning window occurred from 07/02/24 – 21/01/24, but daily maximum temperatures also exceeded 9°C on 03/02/24, providing only 13 days for egg incubation. At T5_FP1, a 15-day spawning window occurred from 06/02/24 – 20/01/24, but daily maximum temperatures also exceeded 9°C on 03/02/24, providing only 14 days for egg incubation.

5.3.4.3. Larval Development

Due to a lack of suitable spawning windows in HY1, larval development windows were not evaluated for HY1. In HY2, however, daily maximum water temperatures did not exceed 16°C until late April on the floodplains, providing ~2 months of suitable thermal conditions for larval development, but Fig. 5.6b and d show that floodplain inundation was intermittent, which could have resulted in death of any potential larvae and once more emphasises the hydrological unsuitability of HY2. Comparatively, with the extensive floodplain inundation in HY3, the observed data showed that all floodplains exceed daily maximum water temperatures of 16°C by the beginning of May, providing almost three months of suitable larval development temperatures.

5.3.5. Historical Data

5.3.5.1. Depth and Flow

At Bodney Bridge, on 1/12/24 water depth was 84 cm, and at this point, flooding was observed at all transects. While the depth was not enough for overtopping at Bodney Bridge, it is clear that at depths of 84 cm at Bodney Bridge there would be overtopping elsewhere in the Wissey. When analysing the entire depth record for Bodney Bridge (1993 – 2024), depths over 84 cm have been recorded in 29 years out of 32 (91%). Direct overtopping at Bodney Bridge, which would be main channel depths over 111 cm for the lefthand bank and 103 cm for the righthand, has been achieved in 14 and 22 years out 32, respectively.

The hindcast flow record in Fig. 5.8 shows the maximum monthly flow for each hydrological year in the record. From the hindcast flow data for the Bodney Bridge record, a flow duration curve can be generated (Fig. 5.9a and b), which can be used to characterise the Wissey's flow from the hindcast record. From the flow duration curve, flow statistics were obtained. Q_5 was $0.525 \text{ m}^3 \text{ s}^{-1}$, Q_{50} was $0.115 \text{ m}^3 \text{ s}^{-1}$, and Q_{95} was $0.025 \text{ m}^3 \text{ s}^{-1}$. From the flood frequency analysis that used the hindcast flow data at Bodney Bridge, the annual maximum flow for HY1 was $0.67 \text{ m}^3 \text{ s}^{-1}$, while for HY2 it was $0.51 \text{ m}^3 \text{ s}^{-1}$, and in HY3 it was $0.81 \text{ m}^3 \text{ s}^{-1}$. Using the Gumbel distribution, average recurrence interval ($T(X)$) was calculated for each year. For the 32 year record, HY1 had an average recurrence interval of 2.62 years, while it was 1.25 years for HY2, and 6.61 years for HY3. The probability of exceedence ($P(X)$), the probability that the annual maximum flow for each hydrological year could be exceeded in any given year was 38% for HY1, 80% for HY2, and 15% for HY3.

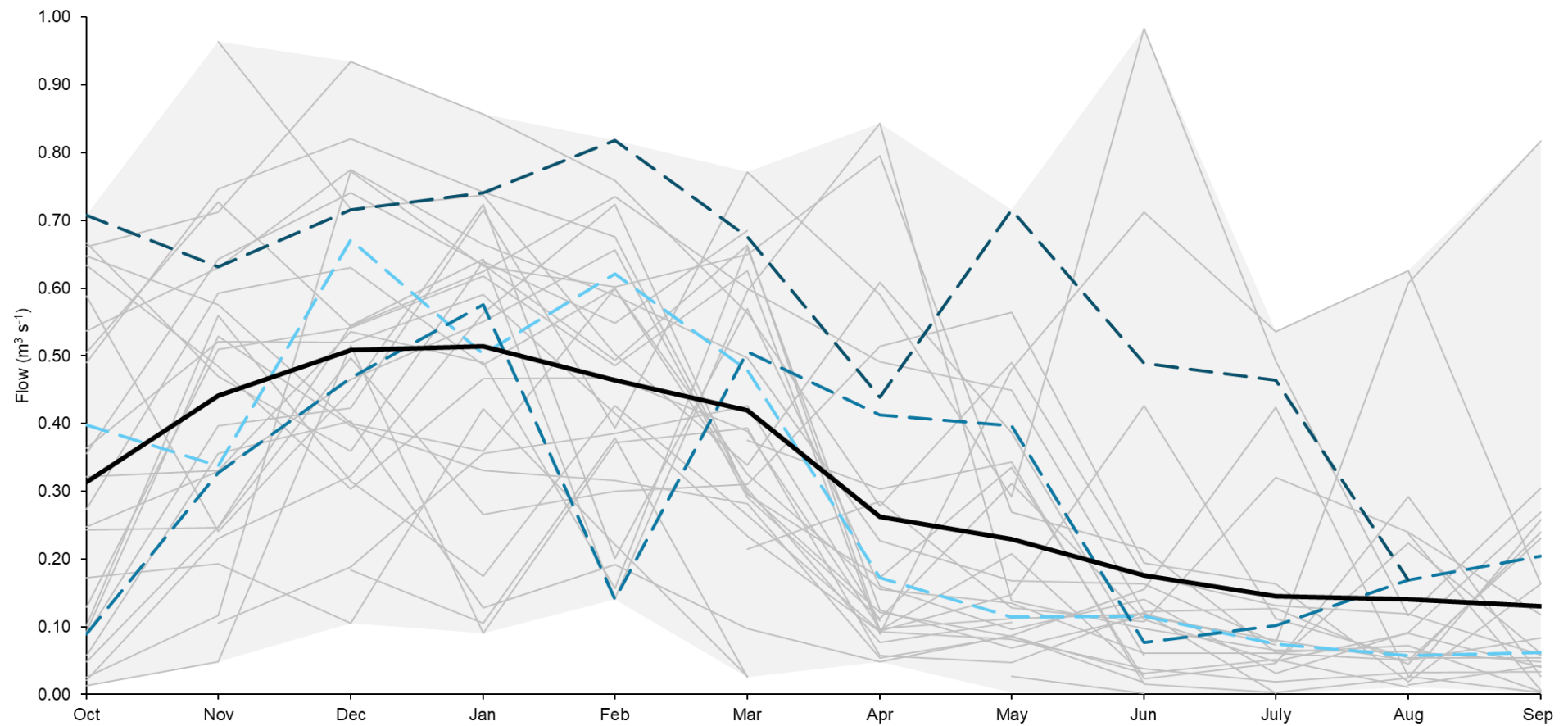


Figure 5.8. Bodney Bridge hindcast monthly maximum flow record (1993 – 2024). Average monthly maximum flow is indicated by the solid black line. Individual monthly maximum flow records are in light grey. Grey shading on graph delineates maximum and minimum monthly flow bounds for entire record. Dashed lines highlight hydrological years from this study with HY1 (21/22) in light blue, HY2 (22/23) in blue, and HY3 (23/24) in dark blue.

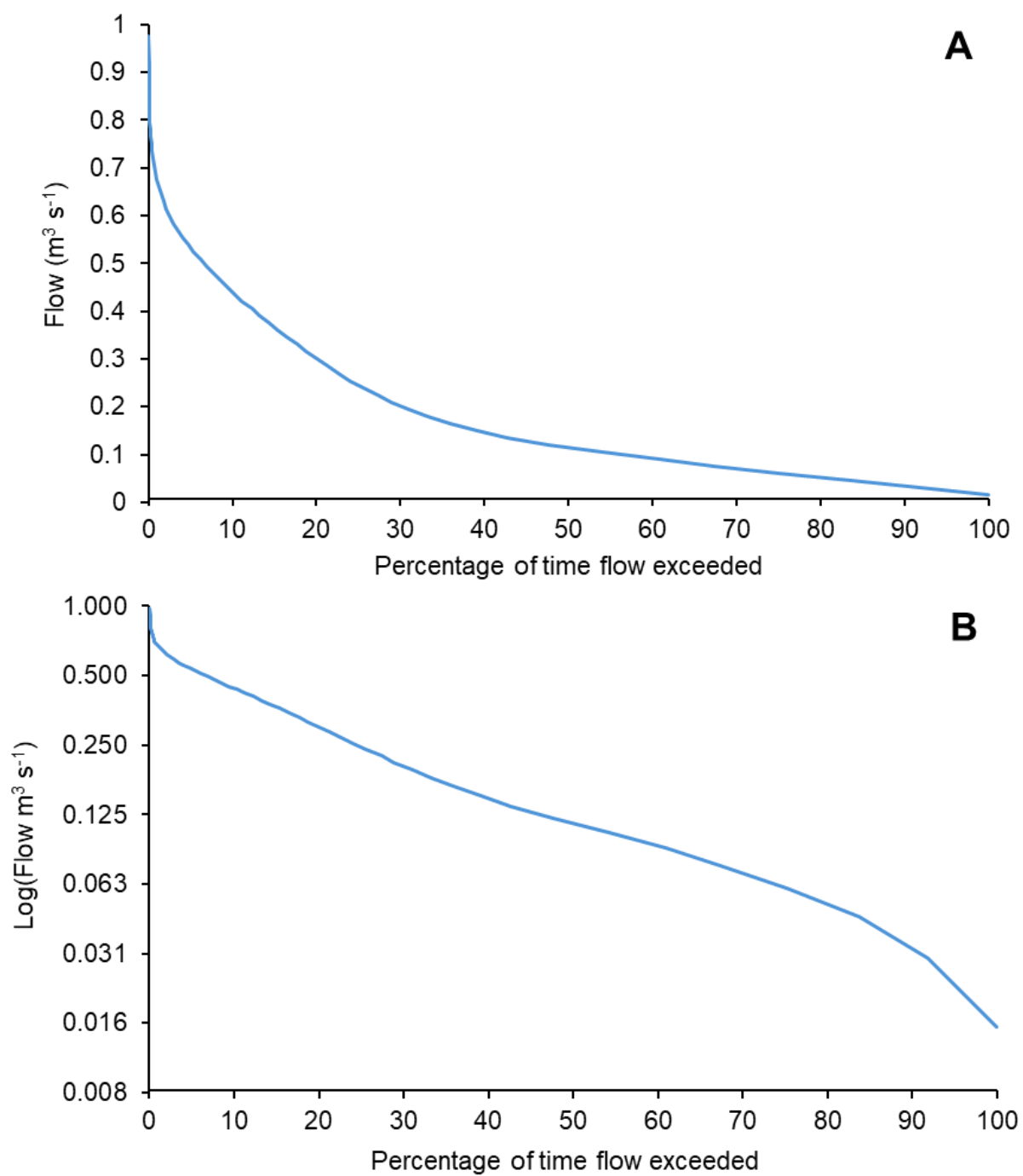


Figure 5.9. (A) flow duration curve for Bodney Bridge record (1993 - 2024) and (B) flow duration curve plotted on log base 2 scale for better visualisation.

5.3.5.2. Rainfall

The rainfall record for Denver 1975 – 2023 is given in Fig. 5.10. Rainfall was highly variable across the record, particularly from March – August, where there can be high rainfall events. For HY1, average monthly rainfall was 39.1 ± 23 mm, with monthly rainfall maximum and minimum of 71 mm and 5.3 mm, respectively. HY2 averaged 93.5 ± 49 mm per month, with monthly rainfall maximum and minimum of 182.9 mm and 21.6 mm, respectively. Comparatively, the average monthly rainfall across hydrological years from 1975/76 to 2020/21 was 50.3 ± 27.9 mm. Across the same period maximum and minimum monthly rainfall were 166 mm and 0 mm, respectively. Unfortunately, there were no data available for 2024, and so it was not possible to compare HY3. The available data from early in HY3, October – December 2023, show that total monthly rainfall was 205.2 mm, 130.4 mm, and 330.1 mm, respectively, which was well above monthly averages for the existing record (Fig. 5.10). Fig. 5.10 also shows that rainfall during HY1 was below average for much of the year, except in December, February, and June.

During HY2, there was above average rainfall for much of the year, except for December and February, with a large increase in spring and summer rainfall events. The culmination of these rainfall events, combined with increased amounts of rainfall in early HY3, likely contributed to above average flows in HY3 (Fig. 5.8). Total rainfall from November – February in HY1 and HY2 was 175 mm and 220 mm, respectively. From the predicted water depth data at T6_FP1, HY1 had 176 days of floodplain inundation, which in theory could facilitate spawning, egg incubation, and larval development as well as a burbot-suitable flood year. If total rainfall from November – February is compared across all hydrological years from 1975 – 2023, 30 out of 48 (63%) had at least 175 mm of total rainfall between November and February, which could contribute to burbot-suitable flood years.

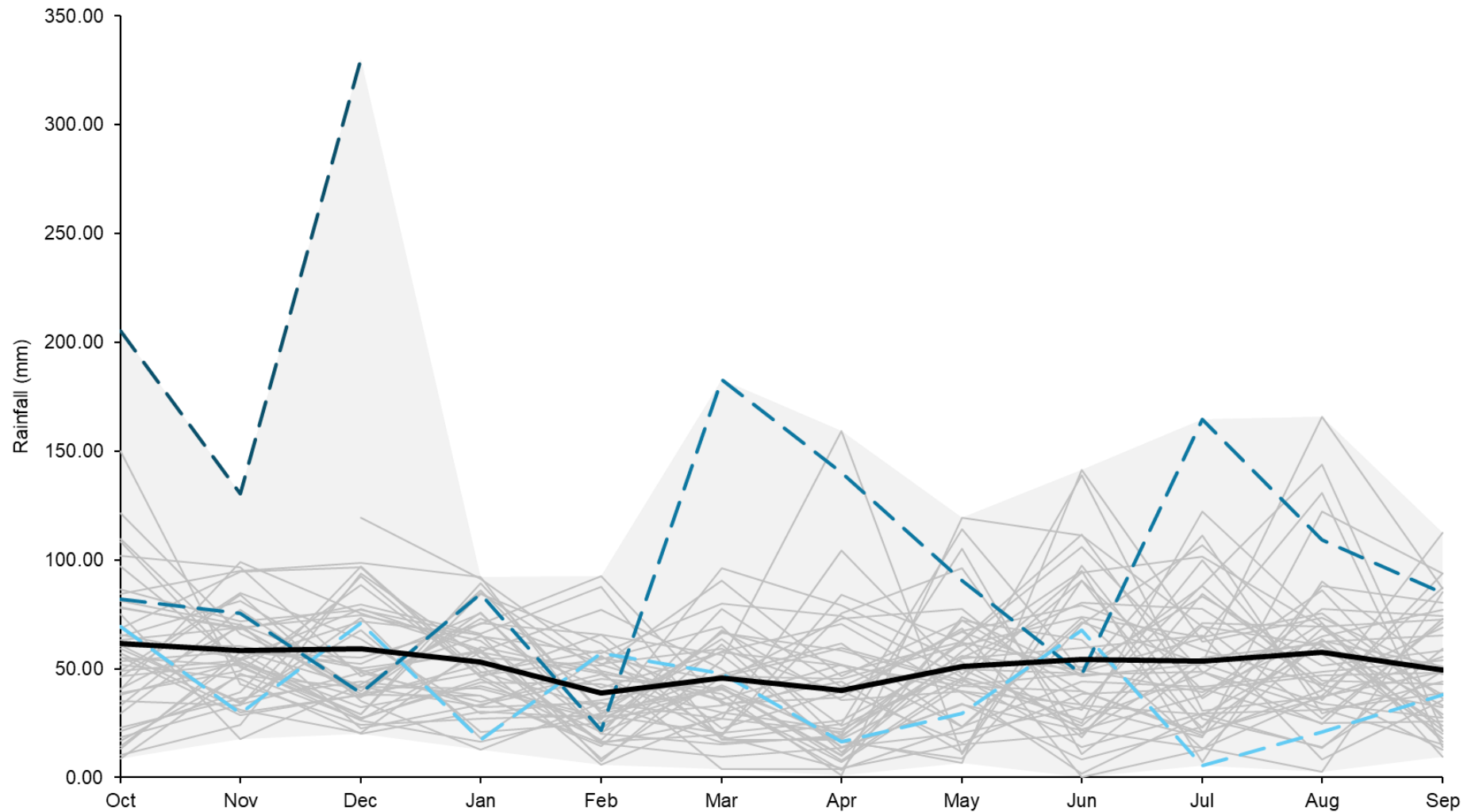


Figure 5.10. Total monthly rainfall at Denver (TF 59162 00899) across hydrological years beginning 1975/76 to 2023/24. Average total monthly rainfall is indicated by the black line. Individual grey lines indicate each hydrological year. Grey shading on the graph delineates maximum and minimum monthly rainfall for entire record. Dashed lines highlight hydrological years from this study with HY1 (21/22) in light blue, HY2 (22/23) in blue, and HY3 (23/24) in dark blue.

5.4. Discussion

Based on the hydrological data collected from November 2021 – August 2024, this chapter has evaluated river-floodplain hydrological characteristics, and thus, the suitability of the Wissey to support burbot across all life stages, with a particular focus on burbot life cycle completion. Using the observational and historical data, it has been possible to describe and quantify the hydrological years observed, determine their frequency of occurrence, and assess flood inundation extent, and thus, potential burbot spawning habitat availability. This study has shown that each hydrological year in this study provides a window in which the hydrological conditions are suitable for burbot life cycle completion. One concern that remains, however, is that the duration of connection between main channel and floodplain does not extend into summer and there are no permanent floodplain water bodies in which isolated burbot (that did not get back to the river as flood waters receded) could persist in until the following autumn or winter floods. The exception to this annual drying is T5_FP1, as during HY3 it was observed to be connected to the main channel as a result of winter flood erosion, now connecting the main channel to the beginning of a network of side channels in which larvae or fry could access the main river channel (Fig. 4.2).

5.4.1. Spawning, Egg, and Larval Suitability

Observed inundated floodplain extent varied from 3,738 m² (TE2, February 2022) to 55,607 m² (T3, February 2024). Floodplain inundation extent can positively influence numbers of burbot larvae (Koporikov and Bogdanov, 2021). In the Sob River, Russia, floodplain water bodies of various sizes (1.2 km² – 16 km²) connect during winter flooding to provide spawning, egg incubation, and larval development habitat to produce an average of 7.3 million burbot larvae annually (Koporikov and Bogdanov, 2021). In the River Oder, Poland, 28 burbot were found in a high flow period (March 2010) across multiple floodplain water bodies, totalling 3.5 km² (Tonolla et al., 2012). Though, in a study of a German section of the River Oder in 1997, across a series of floodplain polders (totalling 54 km²), it was found that the relative abundance of burbot increased in these polders following high flood conditions from 0% to 0.07% ($n = 1,531$). In a 2002 study of the floodplains of the River Oder, Germany, (between 4000 m² and 190,000 m²), burbot were more commonly found in main channel sites (24

individuals recorded, mean relative abundance 15.9%, maximum relative abundance 42.5%), compared to the floodable polder sites in which there were 12 in total (Schomaker and Wolter, 2011). Across these sites, only 10 individuals were caught with a mean relative abundance of 0.9%, and a maximum relative abundance of 2.9% (Schomaker and Wolter, 2011). In Belgium, burbot larvae are found in small floodplain waterbodies, connected to the Grote Nete, which are <50 m in diameter at their widest point. Despite their small sizes, larvae densities up to 13 individuals/m³ have been found, which are similar to densities observed in Oneida Lake, New York, USA (Ghan and Sprules, 1993). The size of floodplain water bodies observed in the Wissey are larger than these pools, and hence are inferred to be large enough to facilitate burbot spawning and larval development. Based on these observations, the size of the floodplains created at the Wissey across all hydrological years would not appear to be a limiting factor for a reintroduced burbot population. Moreover, the annual available spawning habitat presented here does not consider potential side channel, back water, and other lateral habitat and is hence an underestimate of spawning habitat availability. As shown in Chapter 3, there are 16.04 km of secondary channels and 4.7 km of drains, which could also be potential spawning, egg incubation, and larval development habitat. Overall, this study would conclude that physical or hydrological habitat would not be a limiting factor to the burbot reintroduction.

Duration of floodplain inundation varied both temporally across hydrological years and spatially between observed floodplain areas within each hydrological year. The total number of days in a hydrological year where daily maximum depth was over 10 cm on a single floodplain ranged between 11 and 294 days. For spawning, a period of 14 days is needed, eggs incubate for between 30 – 75 days (Hochleithner, 2020), and the larval stage is approximately 60 days (Ryder and Pesendorfer, 1992). Both the egg incubation and the larval development stage can be shortened by warmer temperatures (Nagel et al., 2011; Lahnsteiner et al., 2012). Based on the literature, the spawning, egg, and larval stages could take a maximum of 149 days (~5 months) or as little as 86 days (14 days spawning, 30 days egg incubation from Lahnsteiner et al. (2012), and 42 days larval development from Kupren et al. (2014), depending on temperature conditions.

In HY1, the longest period of floodplain inundation, where water depth was over 10 cm, was at T6 for 35 days, which would not be sufficient. However, based on the predicted data at T6, it is possible that an inundation period of 176 days was observed in total with an earlier inundation event in November and December (Fig. 5.5d), which would provide the hydrological conditions for burbot life cycle completion under the minimum and maximum development time scenarios. From the observational data of HY2, no floodplain inundation was consistent enough to provide the hydrological conditions needed for a long-term development scenario, but all floodplains provided the hydrological conditions required for a short-term development scenario.

In HY3, which has the most consistent record over the winter and spring flooding period, T1 retained water of over 10 cm depth for the least amount of time (201 days compared to 294 days in T3), but all floodplains provided the hydrological conditions for a long-term development scenario. This was driven by high rainfall from early autumn until late spring. HY3 is the only year in this study where overtopping occurred for both banks for consecutive days (8 – 300 days) at all transects. At T3, the river was continuously connected with the floodplain on the righthand bank for 92 days that would allow adults to spawn and swim off, as well as eggs to hatch and larvae to develop and swim off the floodplain, assuming that water temperatures were appropriate. This also occurs at T5 with the lefthand bank, which saw continuous river-floodplain connection for 300 days. In other years, this continuous window of river-floodplain connectivity is much lower, meaning fish would likely be isolated on the floodplain in HY1 and HY2. Overall, the floodplain inundation at the Wissey observed in this study is considerably more extensive than some floodplains in which burbot are known to spawn. For example, in the Klostermersch floodplain along the River Lippe, Germany, the best recruitment year for burbot on record was during a year where the floodplain remained inundated for 35 days between the end of February to the end of March (Bunzel-Drücke et al., 2004a).

The observational data showed that each year floodplain connectivity at the Wissey could have facilitated spawning, egg incubation, and larval development, but in a practical sense, these processes are controlled by several parameters, which both strengthen and weaken the Wissey's suitability as a candidate reintroduction site. Despite a shorter period of floodplain inundation in HY2, as floodwaters retreat to the main channel, larvae can be carried off and caught in early spring vegetation, meanders, woody pieces, and lateral slack water (Müller, 1957; Vught et al., 2015), all of which the Wissey possesses in high densities. The maximum annual flow rates that occurred during HY1, HY2, HY3 at Bodney Bridge have probabilities of being exceeded in any given year at 38%, 80%, and 15%, respectively based on the 32-year flow record. In this record, HY2 was ranked seventh for lowest maximum annual flow rates. The lowest annual maximum flow occurred in the 2011-2012 hydrological year and was $0.32 \text{ m}^3 \text{ s}^{-1}$, with a corresponding maximum depth of 74 cm at Bodney Bridge. When analysing time series data for HY2, comparing all floodplain loggers and the flow and depth data from Bodney Bridge, floodplain inundation of at least 10 cm occurred on the 24/12/22 for all floodplains when corresponding depth at Bodney Bridge is 57.2 cm and the daily average flow is $0.28 \text{ m}^3 \text{ s}^{-1}$.

The depth and flow at Bodney Bridge during HY2, compared to 2011-2012, would suggest even in the hydrological year with the lowest annual maximum flow, there could have been some floodplain inundation. Without hydraulic modelling of this event, however, full extent and duration of the flood cannot be calculated, so it is not possible to assess whether this level of inundation is hydrologically suitable for burbot. The data would suggest, however, that there is some level of lateral connectivity within the Wissey study area each year. With further research into the extent of these low flow condition floods, river restoration work specifically targeting more permanent lateral floodplain connections could help to ameliorate the impact of low flood years on a reintroduced burbot population.

It is not just hydrology, that controls spawning, egg incubation and larval development, however. Temperature plays a crucial role. When considering the above short-term development example (i.e., 86 days), it should be noted that such a short egg

incubation stage is the result of higher temperatures, which reduce the percentage of eggs that hatch and affect the percentage of larvae that are normally shaped (Lahnsteiner et al., 2012). The survival rate from burbot egg to benthic lifestyle is approximately 1% (Carl, 1992), so ensuring that conditions (i.e. temperature, hydrology, habitat) are suitable to have high rates of spawning and normally hatched larvae is key to any burbot reintroduction.

Currently, the key remaining barrier for a potential burbot reintroduction is temperature. As shown in Chapter 4, it is possible that if early spring temperatures are too high this would be lethal for any developing eggs. Burbot life cycle completion at the Wissey would depend on early winter spawning and subsequent development before temperatures exceed the lethal threshold for eggs (Lahnsteiner et al., 2012). As if to mitigate unsuitable conditions itself, not every adult burbot spawns every year, with up to 63% not spawning annually (Pulliainen and Korhonen, 1993). In terms of life expectancy, some populations have recorded a burbot age of 22 years (Yukon and Tanana rivers, Alaska, USA; Chen, 1969), but the standard age of survival seems to be 10 – 11 years (Clemens, 1951b; McCrimmon and Devitt, 1954; Hewson, 1955; Weber, 1976; Katzman and Zale, 2000). With most burbot in a population reaching sexual maturity at, on average, 3 – 4 years (Worthington, 2010), there are between 6 – 8 potential spawning years in an average burbot's lifetime. In each burbot lifetime, the fish is likely to experience an extensive hydrologically suitable flood, such as that observed in HY3 once, with other suitable floods almost annually. The thermal conditions, however, may not be suitable each year, which, in combination with the slow population doubling time (Beelen, 2009) and the low survival rate, means any reintroduced burbot population will have a slow growth. Considering this, any attempted reintroduction should release large numbers of individuals (likely larvae) annually for a long period, perhaps 5 – 10 years or more, similar to the Belgium reintroduction (Van den Neucker et al., 2009; Vught et al., 2015; Vandamme et al., 2024). This, of course, requires extensive resources and investment to cover hatchery infrastructure and research, as well as post-release monitoring and surveys to monitor population recovery.

Beyond temperature and hydrology, further research is also needed into fish use of the floodplain at the candidate reintroduction site to assess how the existing fish community is using the floodplain, as well as the ecological and environmental drivers of the fish floodplain community. From this, predation pressure and prey availability for burbot larvae could also be assessed as well as the gathering of baseline data on the fish community to assess the impact of a burbot reintroduction on local ecology.

5.4.2. Adult Suitability

Though less vulnerable to the hydrological conditions compared to eggs and larvae, the hydrological suitability of the Wissey for adult fish should also be carefully considered. First, in HY2 and HY3, there was a clear increase in water depth in the main channel combined with a decrease in water temperature below 12°C (Fig. 5.3), which is the needed trigger of burbot spawning migrations as described by Hochleithner (2020). Despite HY3 not having a complete record for the full hydrological year, the end of Fig. 5.5 shows greater water depths for all main channel loggers in July 2024 than in July 2023, but especially in comparison to July 2022. In July 2022, there was a heatwave, precipitated by notably dry months from March - May (Fig. 5.10). Across 2022, Norfolk received only 75% of its usual annual rainfall (Kendon et al., 2023). This lack of winter-spring rainfall is likely linked to the low flows displayed in August 2022 (Fig. 5.5), where water depth at T1_C was ~20 cm and ~58 cm for T6_C, compared to ~35 cm for T1_C and ~91 cm for T6_C in August 2024. Low summer flows can lead to lower autumnal flows, that could interfere with fish spawning migrations (Stubbington et al., 2022). Indeed, this may have occurred in HY2, where, during the autumn, main channel water depths were slow to rise in comparison to the following year. The specific in-channel depths required to trigger and facilitate burbot spawning migrations are little understood, but it is likely that earlier peaks in instream water levels will lead to earlier connections between the river and floodplain, and thus potentially provide a longer period of spawning suitability.

Adult burbot have a low swimming endurance, being unable to sprint swim longer than 10 minutes at velocities of 0.25 m s⁻¹ (Jones et al., 1974). Velocity data collected in

June 2023 show that during summer, instream velocities are suitable for the burbot for the majority of the period. Further, from Chapter 3 it is evident that the Wissey has frequent lateral slack patches, instream wood, pools, and instream structures to offer refuge during any changes in velocities. During winter in HY3, for the existing data, however, 0.25 m s^{-1} was exceeded for 100% of the period. Little is known about burbot migrations including how far an adult can travel at high flow during 10 minutes of sprint swimming. Hence, it is hard to conclude whether during these high flow conditions, the Wissey could be classified as unsuitable hydrologically, especially considering the frequent refuges and slower flow back-channel systems that adults would have access to.

5.4.3. Hydrological Suitability and Reintroduction Feasibility

The data collected have shown that, though annually variable, there is hydrological connectivity between the main stream and floodplains along the Wissey. HY3 had the highest proportion of the year where overtopping occurred, which was true for all main channel loggers. The highest proportion was 96% of the logging period in HY3 at T5_C with the lowest in that year being 15% at T6_C. Thus, when considering a candidate reintroduction site for a burbot reintroduction, whose hydrological requirements are linked to high water depths the Wissey is a strong candidate. It is important to recognise, however, that the Wissey's suitability as a candidate reintroduction is dependent on more than hydrogeomorphology, but also temperature and ecological variables (i.e., prey-predator and wider ecosystem interactions).

In combination with any future research, it is important that river restoration is conducted before a reintroduction is attempted. This river restoration should focus on enhancing lateral connectivity to facilitate the creation of permanent and semi-permanent connections to the floodplain. Consecutive days of overtopping in HY1 and HY2 were considerably less in the Wissey compared to HY3, which potentially indicates the need for river restoration focused on river-floodplain connectivity. For example, flood bank removal along the Wissey, would help maintain the river-floodplain connection during high flows (Clilverd et al., 2016; Höckendorff et al., 2017;

Thompson et al., 2017). In the River Lippe, Germany, though no quantitative data are given on number of individuals caught or floodplain water body size, the relative abundance of burbot was higher in floodplain habitats that were permanently connected to the main channel compared to those within the main channel, or temporarily connected and isolated floodplain water bodies (Manfrin et al., 2020). In some cases, the addition of large woody pieces, such as fallen trees could also beneficially influence sediment and flow dynamics and facilitate the breaching of the main channel during higher flows (Abbe and Montgomery, 1996; Parker et al., 2017; Harvey et al., 2018; Cashman et al., 2019; Cashman et al., 2021). Trees are ecosystem engineers and their influence of flow dynamics could create spawning and larval nursery habitats, but also could over time scour side channels, which could be occupied by juvenile and larval fish. The most important intervention associated with the burbot recovery in Belgium has been to restore natural floodplain dynamics where possible and to connect a spectrum of lateral aquatic habitats (i.e., back channels, ponds, wetland and swamp habitats; Vught et al., 2015). Similar broad-scale, laterally focused habitat restoration has occurred in Germany and has been proven to boost burbot populations in the River Lippe (Bunzel-Drücke et al., 2004b). Where large scale restoration of floodplains is not possible, Belgian researchers suggest the connection of temporary shallow ponds directly to the main channel as they have frequently found burbot larvae in these types of floodplain water bodies (Pauwels et al., 2016).

In the Wissey study area, when analysing the frequency of overtopping at each floodplain transect, the data showed that overtopping is not even between each bank due to the presence of flood barriers that prevent lateral connectivity at that point. For example, at T5, the righthand bank is 23.4 cm higher than the lefthand bank, suggesting some anthropogenic modification, which could be removed. Moreover, it is in years of low floods, such as HY2, that these flood barriers will be most problematic by increasing the chances of fish becoming marooned on the floodplain. At the sites monitored in this study, no floodplain possessed a permanent floodplain water body and all water either drained or evaporated, which would result in the death of any stranded fish. It is therefore, important to enhance these floodplain habitats via river-floodplain restoration with more permanent connections to the main river channel to increase the chance of burbot larvae returning to the main channel. Stage zero

restoration increases lateral hydrological connectivity at base-flow and at a large spatial scale (Clarke, 2025) and thus may be appropriate for sites considering a burbot reintroduction. Though, considering the Wissey is a low energy, low gradient chalk stream, this stream type may not be appropriate for stage zero restoration (D. Sear, pers. comms., 2025). As well as river restoration, water management policy related to environmental and ecological flows (Poff and Zimmerman, 2010; McKenna Jr. et al., 2018; Książek et al., 2019) are also crucial. Reducing abstraction in the catchment could help to ensure floodplain inundation. Further research could calculate the required summer base-flows to ensure that sufficient winter floodplain inundation is achieved for burbot. Not only would this action help the burbot reintroduction, but it would benefit the wider riverine ecosystem (Gwinn et al., 2016; Arthington et al., 2024).

A limitation of this study was the inability to study the whole floodplain as covering both banks would better determine lateral connectivity across the entire floodplain. Further hydraulic modelling using LiDAR data at higher spatial resolution, perhaps obtained using drone or UAVs (Langhammer and Vacková, 2018; Schumann et al., 2019) could better estimate flood extent, duration, and connectivity across the entire floodplain for a more detailed assessment of hydrological suitability in the candidate reintroduction area. Moreover, due to issues with equipment, there was only limited flow data collected at Bodney Bridge, which was used to determine the depth-flow relationship and hindcast flow for the entire depth record. The low quantity of data weakens this relationship and the relationship assumption is simple, i.e., depth is the only explanatory variable for flow at that given point. Estimated annual maximum flows at Bodney Bridge ($0.67 \text{ m}^3 \text{ s}^{-1}$, $0.51 \text{ m}^3 \text{ s}^{-1}$, and $0.81 \text{ m}^3 \text{ s}^{-1}$ for HY1, HY2, and HY3, respectively) are similar to previous study conducted at Bodney Bridge where maximum flow observed 1991 – 1992 was $0.64 \text{ m}^3 \text{ s}^{-1}$, which were classed as drought years (Petts and Bickerton, 1994). Interestingly, the maximum flow exceeds that estimated for HY2 from the hindcast Bodney Bridge data, despite HY2 not being classified as a drought year for the region. The discrepancy could be due to a weakness in the relationship between depth and flow at Bodney Bridge. Similar issues regarding low data quantity to generate predictive variables are found for the predicted depths at T6_FP1. This could be improved with the collection of more flow data and depth data at both T6_C and T6_FP1, which ideally should be from multiple years.

When considering the rainfall record, HY2 and potentially HY3, were wetter years when compared to average monthly rainfall at Denver. In particular, across 2023, March, July, October and December were all in the top ten wettest months since 1836 (Kendon et al., 2024). While Chapter 4 showed that, in terms of temperature, the study years have been warmer on average, the data presented in this chapter show that, while HY1 was a low flow and drier year, HY2 and HY3 had increased flows and rainfall. This suggests that drivers of floodplain inundation are complex, and that assessments of burbot suitability cannot be simplified to a specified amount of rainfall or flow level. A combination of the hydrological (i.e., rainfall, flow), climatological (i.e., temperature, drought), and anthropogenic (i.e., water abstraction) will influence the Wissey's annual ability to produce floodplain inundation suitable for the burbot. For example, HY2's winter floodplain inundation was less extensive likely due to low summer flows in HY1 caused by the heatwave in July 2022 (which could likely have resulted in increased abstraction from groundwater nearby, lowering flow levels further) combined with low levels of rainfall in the early autumn of HY2. By contrast, continued extensive rainfall from March 2023 onwards, extending potentially into 2024, contributed to the high flow levels and extensive inundation experienced in HY3. Encouragingly, despite variations in hydrological characteristics, floodplain inundation was experienced across all hydrological years, providing habitat for burbot spawning. From a hydrological perspective, policy that could minimise abstraction across the catchment to maintain a certain level of flow in the summer could increase the likelihood of inundation in the following winter, and thus increase the chance of a reintroduced burbot population's spawning success.

5.5. Conclusions

Each burbot life stage has hydrological requirements, as well as for physical habitat and temperature. Except for adult burbot, which require deeper water and slow flow conditions (i.e., $<0.25 \text{ m s}^{-1}$), the spawning, egg incubation, and larval development hydrological requirements are similar in that shallow, slow flowing habitat is required. For the western European burbot, successful reproduction is associated with inundated floodplains, with a longer period of inundation positively influencing larvae numbers. Overall, the study has shown that, over a long period (e.g. a burbot life time)

there would be years where hydrological conditions are suitable to facilitate reproduction, egg incubation, and larval development. Thus, in terms of hydrology, results would suggest conditions are favourable to support a reintroduced burbot population in the Wissey. All hydrological years showed a distinct drop in temperature coinciding with increasing water levels in the main channel and floodplains, which would trigger spawning migrations. All hydrological years, at least at one of the floodplains studied, provided inundation for the 2-week required spawning window and beyond. Though there was only potential thermally suitable spawning windows in HY2 and HY3, which combined with required water levels. Moreover, there was no period of required floodplain inundation with the needed temperatures to facilitate egg incubation in any of the hydrological years. Extensive floodplain inundation was observed in HY3, which provided extensive larval nursery habitat in all the floodplains observed, which combined with suitable temperatures for larvae also.

When analysing historical data, it is likely that the Wissey has some level of floodplain inundation each year. Encouragingly, even during years of low levels of floodplain inundation, such as HY2, there are hydrologically suitable windows for spawning. The flood frequency analysis demonstrated that for HY2, there is an 80% chance of the maximum flow that occurred in HY2 would occur in any given year, meaning there is high probability that burbot-suitable floodplain inundation would occur each year. As well as hydrological suitability, there are early indicators that ecological factors on the floodplains, such as prey abundance, are also suitable for larval development. The remaining concern is temperature and whether increases in water temperature in early spring will be lethal to any potential developing eggs (as discussed in Chapter 4). Further research should focus on assessing hydrological connectivity across the entire floodplain using hydraulic modelling at a larger scale across the site combined with research into the floodplain plankton, macroinvertebrates and fish communities.

Chapter 6. Summary, key findings, and future directions

6.1. Summary

Freshwater ecosystems are heavily pressured ecosystems (Dudgeon et al., 2006) that are experiencing extensive declines in biodiversity (Vörösmarty et al., 2010; He et al., 2023). Species reintroductions have emerged as conservation tools to help restore biodiversity losses (Jachowski et al., 2016; Hale and Koprowski, 2018). Despite vast potential, however, species reintroductions have several challenges, including: funding and investment, post-release monitoring, release site quality, and future environmental change, which can often result in their failure (Cochran-Biederman et al., 2015; Carter et al., 2017; Berger-Tal et al., 2020). Thus, any species reintroduction considered must be planned and implemented from a strong scientific evidence base, which follows the IUCN's Species Translocation Guidelines (IUCN, 2013). Aside from being carefully planned, species reintroductions also have windows of opportunity, which are periods time following local species extinction when the species can still be reintroduced, before the ecological community enters a closed, resistive state that would result in reintroduction failure (Tielke et al., 2020; Tielke and Vos, 2024). These windows of opportunity can sometimes be extended by management opportunities, such as undertaking simultaneous reintroductions of primarily and secondarily lost species is more successful than sequential reintroductions (Tielke and Vos, 2024). The windows of opportunity concept provides an interesting framework to consider the findings of the burbot reintroduction in England. Do windows of opportunity persist for the burbot in the Wissey?

The extirpation of the burbot in England is regarded as a potentially reversible case, with discussions of reintroduction as early as the 1990s (Pearce et al., 2024b). Since, research has continued to build the evidence-base for the feasibility of reintroducing the burbot to England. This thesis specifically builds on the PhD research of Worthington (2010), who highlighted the potential of the Great Ouse, Norfolk, UK and its tributaries in terms of a burbot reintroduction. Considering the findings of Worthington (2010), as well as the wider literature on burbot declines in Europe (Bosveld et al., 2015; Pauwels et al., 2016; Wetjen et al., 2020b), this thesis focused

on the River Wissey, Norfolk at a fine spatial scale, to contribute to evidence-based decision-making regarding current discussions and planning of a potential burbot reintroduction.

The overall aim of this thesis was to determine the spatial and temporal extent of suitable habitat for the burbot in the upper River Wissey system, Norfolk, UK. To answer the overall research aim, Chapters 3-5 focused on physical and geomorphological (Chapter 3), thermal (Chapter 4), and hydrological (Chapter 5) characteristics of the proposed reintroduction site. These analyses were grounded in available knowledge of the biological and ecological requirements of the western European burbot. This was overwhelmingly important to the thesis as a whole, due to the known leading cause of failure of species reintroductions being a lack of understanding on the candidate species' biology and ecology (Cochran-Biederman et al., 2015; Berger-Tal et al., 2020). This final chapter summarises the key findings of individual chapters, discusses how they relate to each other, and recommends future directions regarding research, reintroduction implementation, and policy.

6.2. Key Findings

6.2.1. Instream and Floodplain Habitat Availability

It is crucial that any candidate reintroduction site be assessed to ensure that drivers of original population decline have been ameliorated (IUCN, 2013). Previous research into habitat suitability for the burbot across its historic range in England has only been to catchment level (Worthington et al., 2012). Thus, the need for a site-specific assessment was apparent. Concurrently, the literature on species reintroduction success showed that not fully understanding the candidate release habitat, as well as the species biology and ecology, has frequently contributed to reintroduction failure (Cochran-Biederman et al., 2015; Berger-Tal et al., 2020). Considering these aspects, there was a key need for site-specific assessment, grounded in burbot biology and ecology, which incorporated both instream and floodplain habitat with a consideration of each burbot life stage (Research Objective 1, [RO1]). Based on a thorough literature review, there was not an existing river-floodplain habitat methodology that captured

the required burbot-relevant features that distinguished physical habitat use for each life stage (section 3.1, Table 3.1). Thus, a custom walkover survey was designed to capture burbot relevant features across all life stages, as well as characterising the broader riverine environment. The literature extensively emphasised that lack of spawning habitat is a key remaining barrier for any reintroduced burbot population or recovery for current declining populations (Worthington et al., 2011a, 2012; Bosveld et al., 2015; Brackwehr and Kühlmann, 2016; Brackwehr et al., 2016; Pauwels et al., 2016). Thus, the custom walkover survey was applied in combination with an *ex-situ* floodplain habitat classification that focused specifically on spawning and larval nursery habitat availability. In order to better contextualise the Wissey as a suitable candidate reintroduction site, the *ex situ* analysis was also conducted on three Belgium burbot reintroduction sites (RO4).

The results showed that instream habitat was available for all burbot life stages, but was most suitable for adult burbot based on the criteria used in this study. There was a low proportion of instream spawning habitat, but this was to be expected given the western European burbot's preference for floodplain spawning (Worthington et al., 2012; Brackwehr et al., 2016; Auwerx et al., 2019; Beelen et al., 2019). The *ex situ* floodplain classification showed that the Wissey possessed extensive secondary channel systems that can be utilised for spawning as well as large potential areas of river-connected floodplain. When compared to the Belgian reintroduction sites, it was clear that there were similarities in terms of extent of hydrological pathways into the floodplain (drains in Belgium and secondary channels in the Wissey) and areas of potential floodplain connectivity. The presence of these secondary channels or off-channel habitats are crucial as in Belgium newly hatched larvae have been frequently found in off-channel pools (Vught et al., 2015; Pauwels et al., 2016; Vandamme et al., 2017, 2020, 2021, 2024; Van Wichelen et al., 2018). Chapter 3 overall suggests that suitable physical habitat is available to every life stage and that the Wissey is comparable, physically, to the habitats utilised by burbot in Belgium, where they are known to reproduce naturally (Vandamme et al., 2021, 2024).

6.2.2. Temperature

Unsuitable temperatures can be lethal to many freshwater species, including fish. The existing literature on burbot is biased toward North American burbot populations, which as part of a different genetic subclade, have different thermal requirements at each life stage compared to the Euro-Beringian, and especially, to the western European burbot subclade (see Tables 4.2 – 4.4). Published studies on the thermal tolerances of different western European burbot life stages are few (section 4.1.2), but despite this, it is important to assess any candidate reintroduction site for current and future (under possible climate change scenarios) suitability based on known water temperature thresholds (RO2, RO4). To do this, a water temperature network, at high spatial and temporal resolution was established in main channel, side channel, and floodplain habitats across three hydrological years. The observed data were then analysed in comparison to thermal thresholds for each burbot life stage obtained from the existing literature on western European burbot. To assess future suitability under climate change, a logistic relationship between observed air and water temperature was used to predict potential warming of water temperatures from predicted air temperatures at downstream Denver under the UKCP18 scenarios. These models are known to be drier, warmer predictions, representing a potential worse-case for a burbot reintroduction in the Wissey.

From the collected data across the hydrological years, it was clear that the Wissey is highly suitable for burbot adults (and inferred juvenile burbot) and larvae. The study captured the July 2022 heatwave, which recorded record air temperatures across the country, yet water temperatures did not exceed 24°C, and these maximum temperatures were not homogenous across the site. These findings are not only encouraging for the burbot reintroduction, but for wider freshwater biodiversity, as it emphasises the Wissey's (and chalk streams more generally) importance as thermal refugia during summer heatwaves. The results from this chapter also show that suitable thermal spawning conditions were achieved in each hydrological year. Unfortunately, there was no window of thermal suitability for egg incubation, based on the thresholds applied in this study, as late winter temperatures quickly exceeded the upper thermal limit of 9°C for eggs (Lahnsteiner et al., 2012). In comparison to data

and studies available on Belgian river temperatures, the Grote Nete (the key burbot reintroduction river) often has average and maximum main channel temperatures cooler than the Wissey for the observation period in this study (section 4.3.5; Fig. 4.9; Pauwels et al., 2016). Water temperatures did exceed 9°C in the Grote Nete during the spawning period in these observational years, but it is currently unknown if burbot larvae were found in the spring period following these winters. If so, it could be crucial to fully determining the Wissey's thermal suitability for all burbot life stages as it would show that 9°C is not a lethal temperature.

The investigation into potential future change in water temperatures showed that while average water temperatures for the spawning period could still be suitable for the burbot in the 2030s, average monthly maximum water temperature exceeds 7°C by the 2070s. Based on this model, the Wissey could be unsuitable for eggs as soon as the 2030s, but findings from the observational data would suggest that it is already occurring. These findings are similar to models run by Finney et al. (2022) that show predicted chalk stream water temperature under future climate change scenarios, where warming is expected, to the detriment of brown trout. Overall, Chapter 4 showed that temperature is a potential barrier to burbot life cycle completion and thus, a barrier to reintroduction success in achieving a self-sustaining population in the long-term.

6.2.3. Hydrological Suitability

The spawning success of western European burbot is linked to floodplain inundation (Bunzel-Drüke et al., 2004a; Brackwehr et al., 2016; Pauwels et al., 2016), with inundation extent and lateral connectivity being shown to positively influence larvae numbers for a Eurasian population (Koporikov and Bogdanov, 2021). Multiple life stages (spawning, egg development, and larvae) are dependent on floodplain waters (Worthington et al., 2011a), which is why historical habitat modification through embankments and channelisation was detrimental to burbot in England (Worthington et al., 2010a, 2011b) and throughout Europe (Bosveld et al., 2015; Pauwels et al., 2016). Thus, through the assessment of the hydrogeomorphological characteristics of Wissey floodplains, the extent and location of suitable spawning and larval habitat can

be identified and quantified (RO3). To achieve this, once more, the hydrological requirements of each burbot life stage was obtained from the existing literature (RO4). As part of the sensor network, four water depth transects were established throughout the site that measured in-channel and floodplain water depth continuously across three hydrological years. The collected data were assessed against known burbot hydrological requirements.

The results showed that, across all hydrological years, there was sufficient inundation for burbot spawning to be achieved. In hydrological year 2, there was also extensive enough inundation for egg and larval development to be achieved under a short development window scenario: <86 days, based on Lahnsteiner et al., (2012) and Kupren et al., (2014). The most persistent flooding was observed in hydrological year 3, which could have facilitated the spawning, egg, and larval development stages, even under a long development window scenario: 149 days, based on Nagel et al. (2011) and Lahnsteiner et al. (2012). The duration of floodplain inundation observed in this study exceeds the required inundation duration for a burbot population in the River Lippe, Germany (i.e., 35 days, Bunzel-Drücke et al., 2004a). From the observational data, it was clear that there was temporal variation of floodplain inundation across the sites studied. The lack of overtopping in some areas where there was water on the floodplain would suggest that there are flood banks present at all sites studied, which can often prevent direct overtopping, but water can still connect to the floodplain elsewhere. The study observed that permanent water bodies do not persist on the observed floodplains as water is removed through soil infiltration and evaporation (though definitively cannot be determined by this study), except at T5_FP1, which is in a side channel system, suggesting that there is a risk, due to the presence of flood banks, of newly hatched larvae becoming isolated and hence dying on the floodplain. Overall, this would impact a reintroduced burbot population's recovery time.

6.3. Overall Findings

To answer the overall research aim, it is important to consider the findings of the thesis as a whole to fully assess the habitat suitability of the Wissey to inform any future reintroduction (RO4).

From Chapter 5, not every year will provide floodplain inundation sufficient for spawning, egg, and larval development. If floodwaters recede however, the findings from Chapter 3 show that eggs or larvae are likely to be carried into back channel, off-channel, or shallow water, edge habitats that they can survive in (Müller, 1957; Meshkov, 1972; Farkas, 1993; Koporikov and Bogdanov, 2011, 2021). Unlike previous studies that have shown a lack of spawning and larval nursery habitat to limit recovery in burbot populations (Vught et al., 2015; Pauwels et al., 2016), this study has shown that this is not the case, with suitable habitat available each year in this study. Further, the past depth record from Bodney Bridge would suggest that floodplain inundation could be expected each year, but whether the thermal, flow, depth, and ecological conditions would facilitate a full spawning, egg, and larval development window is unknown. It is not crucial for inundation to occur every year due to the burbot's high fecundity (Miller, 1970; Roach and Evenson, 1993) and longevity (Chen, 1969; Katzman and Zale, 2000) and, in fact, in some populations, not all burbot spawn every year (Pulliainen and Korhonen, 1993) meaning that not every year is crucial for recruitment. Moreover, with the estimates from the *ex situ* floodplain habitat classification, and the mapped flood inundation extent from the Chapter 5, the site likely has more suitable spawning and larval nursery habitat available than has been evidenced in this study. From Chapter 4, it is clear that the Wissey maintains thermal regulation that can buffer high summer air temperatures, which emphasises the importance of the Wissey and chalk streams more generally for both adult burbot and the wider aquatic community. Additionally, the results from the hydrology and temperature chapter combined show suitable spawning windows being achieved annually in the preferred spawning habitats, floodplains and side channels, for western European burbot. Considering all these aspects, the evidence-base for selecting the Wissey as a candidate reintroduction site is strong, and suggests that windows of opportunity for the burbot reintroduction persist currently at the Wissey.

There are remaining uncertainties, however, that must be considered to obtain a full assessment of the suitability of the proposed Wissey candidate reintroduction site, and its recommendation, thus, for the burbot reintroduction. The key findings of this study, in this respect, are the thermal unsuitability of the Wissey for egg incubation, it is important to emphasise that the threshold temperatures obtained during this study were most often obtained from laboratory-based studies. Further, the 9°C lethal limit comes from a study of Eurasian subclade burbot, from the Traun River, Austria (Lahnsteiner et al., 2012). Vught et al. (2015) suggest that temperatures beyond 9°C may be suitable for egg incubation, and that the lethal limit is at 10°C, and these are findings from western European burbot. The variation in thermal thresholds attests to the individual- and population-level variation and adaptability of burbot.

Another key uncertainty is future climate change. In Chapter 4, this study predicted a potential future scenario for the River Wissey, based on an empirical model of a logistic relationship, generated from a low quantity of data. This approach increases the uncertainties of any conclusions regarding potential warming trends in Wissey water temperature under UKCP18 scenarios. Further still, the range of predictions for Norfolk, and more widely East Anglia, across a range of climate models also adds uncertainty. Some predictions suggest winters will get wetter (Met Office, 2019a; Hanlon et al., 2021), which would be beneficial for floodplain inundation and thus burbot, but also warmer, which would negatively impact the burbot. Under the IUCN's Translocation Guidelines (2013), future climate change must be considered. For future winter scenarios, air temperatures are warming, which is not positive for a fish that is currently spawning toward the upper end of its thermal tolerance in Belgium (Vught et al., 2015; Pauwels et al., 2016). Thus, this thesis may have identified a barrier to any potential burbot reintroduction based on the thermal thresholds applied from the current existing literature. Overall, reviewing the thermal evidence, it may suggest that the window of opportunity for reintroducing the burbot to the Wissey may have closed considering the thermal thresholds applied in this study. For winter temperature, there are not many management practices that could extend this window of opportunity, especially considering future climate change. It does not mean, however, that the window of opportunity for the burbot in England has closed as more sites could be considered and thus further research is required.

6.4. Future Directions

6.4.1. Further Research

Chapters 3-5 have highlighted issues regarding the current research and offered recommendations for further research within individual chapters, including: laboratory experiments with observed temperatures with western European burbot to see if they spawn, and whole floodplain hydraulic modelling to quantify total floodplain inundation. Through these discussions, these chapters have also indicated further research areas beyond those approached in this study that are needed to implement a burbot reintroduction to English rivers, including at the Wissey candidate reintroduction site.

First, it was outside the ability of this thesis to study the local ecology, or further, water chemistry parameters at the candidate reintroduction site to give a more detailed assessment of site suitability. Baseline data, such as that collected for water depth and temperature in this study, is crucial to assess the progress or the potential causes of failure of a reintroduction. Before any reintroduction can be attempted, baseline data in local ecology (i.e., fish and macroinvertebrate communities) at a finer temporal and spatial resolution to that currently provided by the UK's Environment Agency (see Ch. 2) is required. These data are crucial in determining predation pressure and whether the site is productive enough to support a reintroduced burbot population (Vught et al., 2015). Further, more water chemistry data could be collected, specifically related to dissolved oxygen, which is important for burbot survival (Maitland and Lyle, 1991). These factors were not included in the present study as existing data, though in low quantity and monitoring frequency, would indicate that prey abundance, predation pressure, and other water chemistry parameters are not an issue within the candidate reintroduction site (see Chapter 2). Before any actual reintroduction, however, local ecology and water chemistry should be further investigated.

Ecological data collection, particularly of fish and macroinvertebrate species across a variety of instream and lateral habitats, including floodplains, is crucial for post-release monitoring of the impact of burbot. The literature suggests that burbot can co-exist with fish species present in the Wissey (Hensler et al., 2008; Jude et al., 2013; Vught

et al., 2015), but it is important to understand baseline conditions to understand exactly how a new species is impacting the ecosystem. Further, while conservation actions often recommended in Chapters 3-5 promote lateral connectivity, which follows broader recommendations in the riverine conservation and ecology field (Bolland et al., 2012; Keruzoré et al., 2013b; Brown et al., 2018; Sayer et al., 2018, 2024; Manfrin et al., 2020), it is important to note that not all species benefit from such changes. For example, it has been documented in a study of beaver habitat creation mimicry in Long Creek, Montana, USA that beaver habitats may negatively affect Arctic grayling *Thymallus arcticus*, but can result in the increased abundance of dace *Rhinichthys cataractae* and white sucker *Catostomus commersonii* (Albertson et al., 2022). While it is not possible to anticipate the impact of the burbot on all species, baseline monitoring can at least observe trends to a species level that can become clear over time as the reintroduction is ongoing. Importantly, with the river-floodplain restoration recommendations, the actions reverse historic anthropogenic modifications, which overall, should benefit local freshwater biodiversity, but a more detailed study on floodplain ecology would be beneficial, to understand more specifically how the restoration work affects river-floodplain fish communities.

While this study has contributed to the evidence base that could lead to a burbot reintroduction in England, specifically regarding habitat suitability of a proposed reintroduction site, there are some gaps that remain, which relate to wider burbot population dynamics and ecological interactions. Species reintroductions can be classified as successful if a self-sustaining population can be evidenced (Robert, 2009). In terms of burbot, there is no clear published literature to suggest how productive a site needs to be to support burbot, the extent to which predators can pressure burbot populations into decline, how many burbot are needed to maintain a viable population considering potential recruitment rates versus mortality, and what the estimated period of time needed to supplement the populations to enable the reintroduced population to gain a foothold would be. It is unknown to what extent the current study area (~7.34 km) has these attributes, but this knowledge would be crucial to a reintroduced population's success (Robert, 2009) and important for any reintroduction planning.

Finally, it is important to consider the reintroduction beyond the candidate reintroduction site. Suitability assessments must be undertaken in other rivers within the historical range of the burbot. The connectivity between these sites must also be studied due to the burbot's low swimming endurance (Jones et al., 1974), as they are easily prevented from passing instream barriers (Vokoun and Watrous, 2009). Instream fragmentation is high across England (Jones et al., 2019), and thus a potential study into migration pathways for fish is needed for the Wissey catchment (similar to Harwood et al., 2022) and in the burbot's wider historical range. Considering that the STANTA river stretch in the study site has been relatively unmanaged since the 1940s, it is possible that observed hydrological and physical habitat features have been similar for decades. Thus, the question of why the burbot ever was extirpated from this area is important. Their disappearance could be linked to an unknown factor, perhaps water chemistry, or it could be due to the inability of burbot to access the area because of the presence of instream barriers, combined with dwindling populations elsewhere preventing spawning and population recovery. Based on the reviewed life history information in this study, combined with findings from the Belgian reintroduction, which have also identified instream barriers and connectivity as bottlenecks for their recovering burbot population (Vught et al., 2015), it is strongly recommended that longitudinal and lateral connectivity be further assessed within and beyond the study area.

6.4.2. Policy Recommendations

From the findings of the present study, some potential policy recommendations have emerged. From Chapter 5, an examination in the average monthly flows in the hydrological years compared to the hindcast flow record at Bodney Bridge showed that the later floodplain inundation experienced in HY2 was due to the low flows of summer 2022, which could have occurred due to low rainfall, the heatwave, and water abstraction. Stronger policy, potentially to catchment level, aimed at reducing groundwater and direct river abstraction could reduce pressures on chalk stream during low flow conditions and could potentially increase the likelihood of winter inundation as river management, such as abstraction, has been shown to impact floodplain wetlands and inundation frequency (Groom et al., 2000; Frazier and Page,

2006; Mukhwana, 2016). Such policy would benefit burbot, but also the wider aquatic ecology. Moreover, the policy would be more beneficial for overall chalk stream health during stress periods and could contribute to positive groundwater recharge rates.

More generally, from the overall conclusions of this study, it is clear that catchment-based approaches to river conservation and management need to continue to show the importance of lateral and longitudinal riverine conservation and restoration at a landscape-scale. This work is compatible with England's non-statutory targets of restoring 75% of water bodies to good ecological condition (Wilkes et al., 2025). The clear importance for each burbot life stage of connected habitats that span a large spatial scope is likely true for other freshwater species, which have thus far been steadily confined to the main channel. These landscape-scale approaches to restoration need to be coupled with rewilding techniques, such as beaver reintroductions as they are more suited wetland managers than humans. A long-term outlook for the current study area, which could now be achieved with recent policy change in England (DEFRA, 2025), is the reintroduction of beavers into the area to develop lateral habitat complexity. There is already extensive evidence for benefits of beavers in terms of lateral extension of wetland habitat (Nummi and Holopainen, 2020; Brazier et al., 2021), flood attenuation and regulation (Puttock et al., 2017) and improving habitat for many species including plants, invertebrates (Law et al., 2016), wetland birds (Nummi and Holopainen, 2020) and bats (Nummi et al., 2011). In creating dams, which create deep pools, and beaver canals, which increase connectivity into the floodplain, beavers may also benefit burbot through direct habitat creation of adult suitable habitat and facilitate access to burbot spawning habitat (Albertson et al., 2022). Thus, a beaver reintroduction to the Wissey and other sites could provide a nature-driven rewilding approach to burbot-suitable habitat creation. These types of conservation action link to legislative targets held by the UK government in the Environment Act 2021, which aims to halt the decline of species abundance by 2030 (Wilkes et al., 2025). The Integrated Plan for Water in England sets out actions to achieve these targets and more specifically establishes a new Water Restoration Fund (DEFRA, 2023), but there is no current basis for prioritising actions (Wilkes et al., 2025), but nature-based solutions, such as rewilding approaches, must be included.

6.4.3. Potential Outputs: Burbot Reintroduction Monitoring and Assessment Guidelines and Restoration Plan

The below is an example draft of a guidance document that aims to assist river managers and NGOs who would be interested in participating in the burbot reintroduction. The guide would cover data required to assess suitability, proposed methodologies to collect data, and potential outputs generated, including an exemplar restoration plan, which is presented below.

6.4.3.1. Draft Plan

6.4.3.1.1. Background and Guidance Aims

The reintroduction of the burbot (*Lota lota*), a freshwater cod (Gadidae), is under consideration in England. Considered extirpated in the 1970s, the burbot was distributed in the eastern flowing rivers of England. Research has suggested that the key cause of decline was habitat modification, specifically the loss of connectivity between habitats used at each life stage, as well as some links to increasing water temperatures and water quality changes (Worthington, 2010; Worthington et al., 2010a, 2011b). To meet the IUCN's Translocation Guidelines (IUCN, 2013) and afford the burbot reintroduction every chance of success, habitat suitability must be considered in view of: the species' survival requirements across its life stages and any episodic or seasonal variation now and in the future. Thus, based on previous research and the undertaking of a habitat assessment at the River Wissey, Norfolk for its suitability as a candidate reintroduction site, it is the aim of these guidelines to (i) detail the required data to assess a candidate reintroduction for the suitability of a burbot reintroduction, (ii) provide guidance on methodologies to collect baseline data, and (iii) highlight the potential outputs that can be generated from gathered data, specifically to formulate restoration and management recommendations to improve the suitability of the candidate reintroduction site.

6.4.3.1.2. Methodologies and Baseline Data Collection

Baseline data collection is centred on known barriers to a potential burbot reintroduction as established by previous research. These barriers include: habitat

availability, particularly spawning habitat, which is a combination of hydrology, geomorphology, and water temperature; daily winter water temperature and summer maximum water temperature; in channel hydrology; hydrological connectivity between the river and floodplain; water quality, and prey availability and predation pressure. A total list of survival requirements is given in *Example Appendix 1* (within this thesis it is Table 6.1). An overview of data required for assessing the suitability of the candidate reintroduction site is given in Table (6.)¹. Methodologies for collecting primary data employ monitoring approaches already employed by NGOs and the Environment Agency where possible.

Table 6.1. Example table listing research avenues, the data required to answer research questions, primary methodologies and secondary data sources required.

Investigating	Data Required	Primary Data Methodologies	Secondary Data	Sources
Instream and floodplain habitat availability	River habitat survey data at reach scale; Remote sensing data for entire floodplains (aerial imagery, LiDAR)	River Habitat Survey Modular River Habitat Survey Physical Habitat Survey Drone surveys	DigiMap	(Environment Agency, 2003; England et al., 2017; EDINA Aerial Digimap Service, 2020)
Winter and summer maximum water temperatures Instream hydrology	Daily maximum water temperature from floodplain and instream Hourly change in velocity and flow data	Temperature sensor network installation Flow/velocity meter	National River Flow Archive/ Environment Agency Hydrology Data Explorer Digimap LiDAR data	(UKCEH, 2023; Environment Agency, 2024)
Hydrological connectivity between river and floodplain	Hourly change in water depth in the main channel and floodplain; Channel barriers location	Water depth sensor installation; River Habitat Survey or Modular River Physical Habitat Survey	Environment Agency Hydrology Data Explorer Digimap LiDAR data	(Environment Agency, 2003; England et al., 2017; EDINA Aerial Digimap Service, 2020)
Water quality	Water quality data	Routine spot sampling (temperature, pH, dissolved oxygen, TN, TP)	Environment Agency Hydrology Data Explorer Environment Agency Ecology and Fish Data Explorer	(Environment Agency, 2023b, 2024)
Prey availability and predation pressure	Macroinvertebrate data; fish survey data	Unit-area or unit-time invertebrate surveying; Electric fishing or eDNA sampling		(Environment Agency, 2023a)

6.4.3.1.2.1. Instream and floodplain habitat availability

The main methodologies applied to identify and assess instream and floodplain habitat availability for each life stage are a form of river habitat survey combined with a geospatial analysis of floodplain habitat using secondary data. The river habitat survey

must be at reach-scale (i.e. >5 km), so the Modular River Physical Habitat survey (MoRPh) upscaled to cover multiple kilometres (MoRPh10) (England et al., 2017) would be appropriate. These in-channel focused methodologies can be supplemented with drone surveys to establish spatial relationships between recorded instream features (Coveney and Roberts, 2017; Klein Hentz et al., 2018). It is recommended that floodplain habitat assessment cover the entire length of the instream habitat reach to assess connectivity between the instream and the floodplain. Though biogeomorphology evolves constantly over micro- and macro- spatial and temporal scales it is a challenge to capture such variability. Thus, physical habitat surveys could be repeated every few years in a monitoring programme, but should definitely be repeated following large flood events. To finalise habitat suitability for each life stage, findings must also be combined with thermal and hydrological data.

6.4.3.1.2.2. Water Temperature

Due to the burbot occupying a different habitat and thermal niche at each life stage, it is important to collect data from different habitats (i.e. main channel, side channel, and floodplains). A temperature network should be established using temperature loggers (logging every 60 minutes) spaced 500 m – 1 km. Distance can be determined based on budgetary requirements. Baseline temperature data should be collected for a minimum of 5 years to capture a variation of annual thermal regimes and establish a minimum reference period that could be used to undertake climate modelling. Using a logistic relationship between daily maximum water and air temperature, regional climate models like UKCP18 (Kennedy-Asser et al., 2021) can be used to forecast potential future change in water temperature at the candidate reintroduction site being assessed, providing insight into the future survival of a reintroduced population.

6.4.3.1.2.3. Hydrology – Instream and Floodplain Connectivity

To assess the suitability of the candidate reintroduction site for different life stages (i.e. upper adult swimming capacity, minimal velocities to prevent egg suffocation, floodplain inundation and extent for spawning and larval habitat), more monitoring infrastructure should be installed. An instream flow meter capable of recording flow and velocity is beneficial depending on budgetary requirements. The most crucial

equipment is the installation of instream and floodplain water depth sensors across the site to monitor connectivity between the floodplain and main channel. Water depth sensors should record at least hourly. The flow data and water depth data can be used to verify hydraulic modelling, which can estimate flood extent at whole-floodplain scale for given flood events, and based on a flow record, can estimate occurrence of burbot suitable flood inundation years.

6.4.3.1.2.4. Water Quality

Though temperature is a key barrier to a reintroduced population's survival, water quality should also be monitored due to the burbot depending on high dissolved oxygen conditions (Worthington, 2010). Secondary data provided by the Environment Agency (Environment Agency, 2023b, 2024) can initially indicate if there are issues and if so, regular spot sampling for the parameter of concern should be investigated. If budgets allow, spot sampling could be undertaken anyway as this has also been part of burbot suitability assessments in Belgium and the Netherlands (Dillen et al., 2005; Verdonschot and Verdonschot, 2012).

6.4.3.1.2.5. Ecology

It is crucial to collect data on baseline ecology to indicate habitat suitability, but also to monitor the impact of the reintroduction. Initially, the Environment Agency's Ecology Data Explorer can be consulted to check prey sources crucial to each burbot life stage. If there is no existing evidence for food sources, then routine macroinvertebrate sampling should be undertaken following a unit-time or unit-area approach (Murray-Bligh, 1999). Predation pressure can only be evaluated from targeted fish surveying in spawning and larval fishing habitats (i.e. floodplains). There is a lack of methodologies for surveying floodplain fish communities and approach would depend on land use type. For example, fyke netting would not be suitable in wet woodland due to snagging on woody pieces. The sampling should be undertaken at the beginning of the floodplain inundation period, mid-inundation, as flood waters are receding, and in summer, to understand the full riverine fish community and its spatial variations. From this, predation pressure can be calculated and annual monitoring can create a before-

after understanding of the impact of the burbot reintroduction on the existing fish community.

6.4.3.1.3. Outputs and Restoration Planning

The outputs generated from the data collection vary, including, but not limited to: baseline data sets (temperature, hydrology), hydraulic models, and climate models. Some of the most useful outputs from the combination of the data collected is the formulation of targeted restoration plans. Fig. 6.1 presents data from the instream and floodplain habitat analysis conducted at the Wissey in 2021, showing the extent of modifications. Fig. 6.2 is an example of how collected biogeomorphological, hydrological, and thermal data can inform a recommended restoration plan to improve the site for the burbot reintroduction and also wider aquatic diversity. Fig. 6.3 gives an indication of the impact the restoration actions could have over time.

6.4.3.1.3.1. Exemplar Reintroduction Plan

The example restoration plan for the Wissey focuses on a site north of Bodney Bridge (52°33'35"N, 000°41'35"E to 52°33'31"N, 000°41'45"E). As observed from the instream and floodplain habitat analysis, the section is heavily modified: extensive embankments on both sides of the main channel with instream sections that are over deepened in large stretches, but with secondary channels present in the LiDAR data. The hydrological data indicated that the area floods annually, with water breaching from a cattle drink at 52°33'43"N, 000°41'33"E, approximately 200 m upstream from the start of Fig. 6.1-6.3. During high flows, the water breaches the main channel on both sides and funnels into the secondary channels re-entering the main channel at 52°33'31"N, 000°41'37"E on the righthand bank and at 52°33'34"N, 000°41'42"E on the lefthand bank. Despite annual connection with the floodplain, the flood banks sever connectivity with the floodplain when water levels drop, reducing the duration of lateral connectivity. For burbot, not only is connection during high flows important, but as flood waters recede in this area, any potential eggs or larvae would be carried into the main channel, which due to the over deepened channel would funnel them out of the system with little instream complexity or hydrological variability to shelter them.

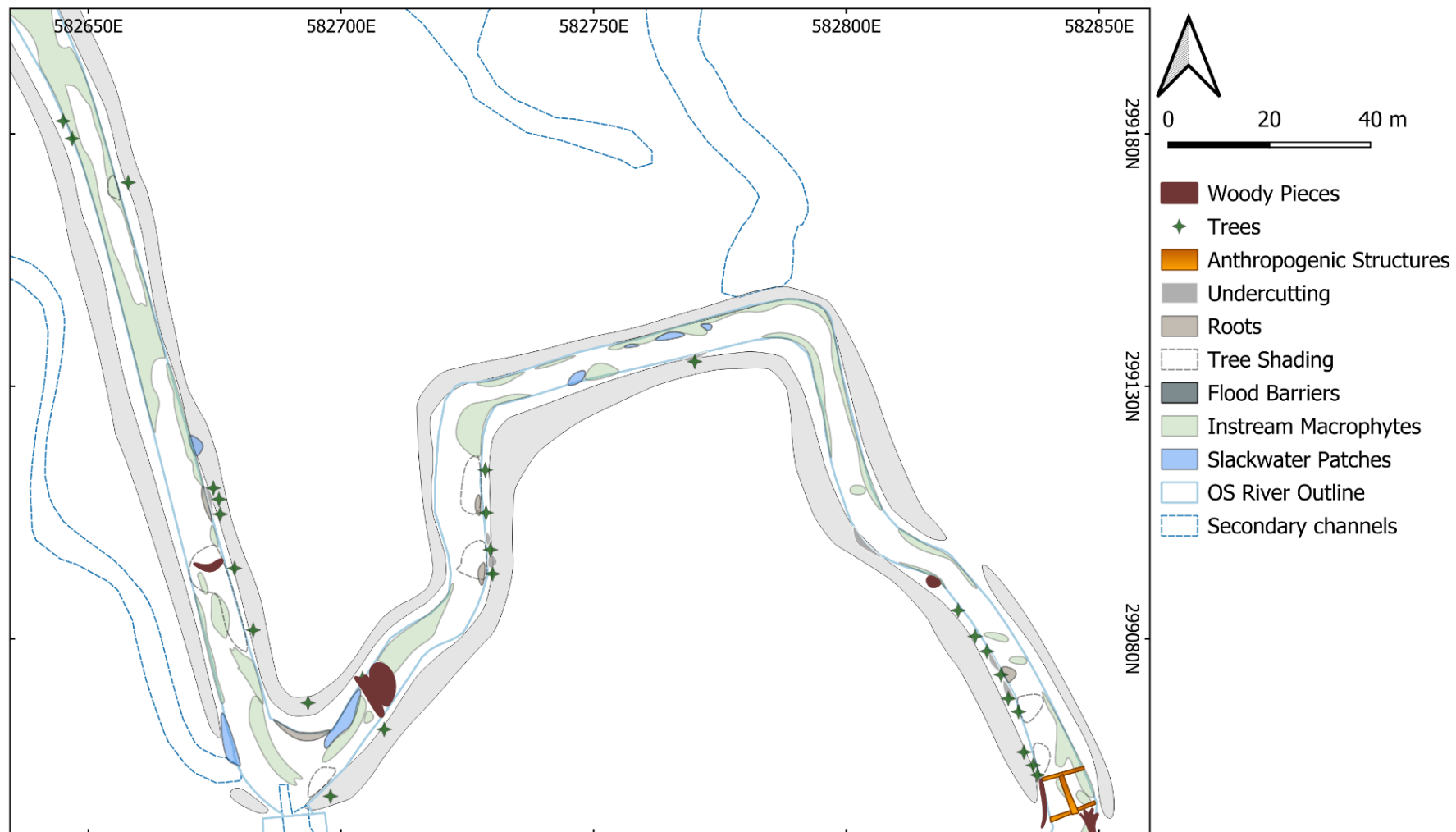


Figure 6.1. Instream and floodplain habitat data used to design restoration plans for River Wissey (52°33'35"N, 000°41'35"E to 52°33'31"N, 000°41'45"E)

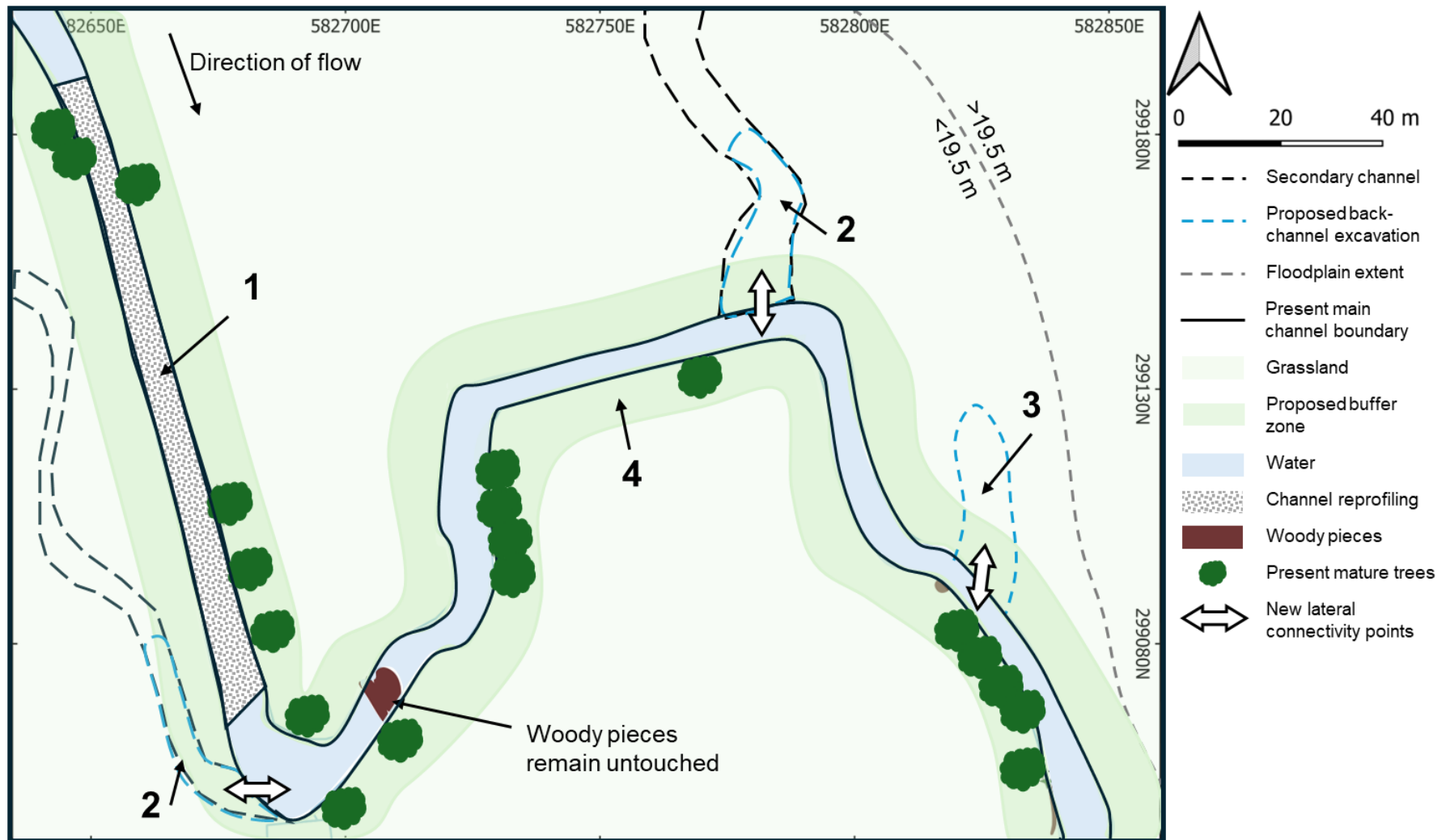


Figure 6.2. Restoration plan for River Wissey (52°33'35"N, 000°41'35"E to 52°33'31"N, 000°41'45"E) based on instream and floodplain habitat analysis, and hydrological and thermal data collection. Potential restoration actions indicated at (1) over deepened channels reprofiled, (2) reconnection with secondary channels, (3) back channel created, and (4) all flood banks removed and 10 m wide natural riparian vegetation buffer zone created. Actions 1-4 are discussed in more detail in the text.

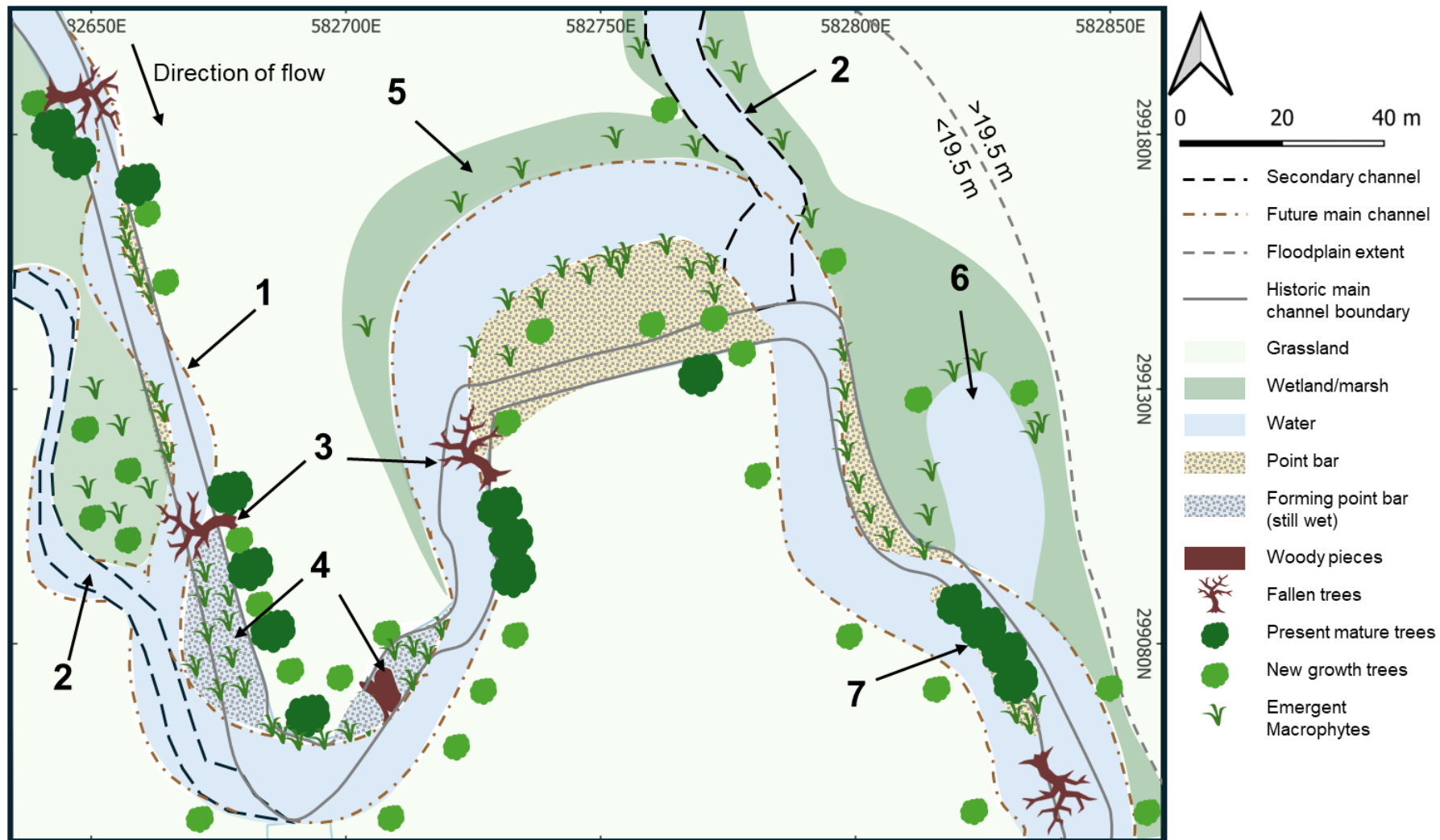


Figure 6.3. Potential future outlook for River Wissey (52°33'35"N, 000°41'35"E to 52°33'31"N, 000°41'45"E) following restoration actions implemented in Fig. 6.2. Future changes anticipated: (1) natural meanders created, (2) activation of secondary channels, (3) fallen trees left, (4) flow redirection from instream complexity creates shallow, depositional environments, (5) expansion of wetland or marsh-like habitat, (6) back waters have expanded, and (7) any mature trees in the original flood banks are left forming instream islands. Actions 1-7 are discussed in more detail in the text.

The proposed exemplar restoration plan, therefore, aims to increase lateral connectivity and its temporal extent while increasing instream complexity of the restoration area to benefit wider aquatic diversity as well as burbot. Fig. 6.2. highlights four main restoration actions: (1) channel reprofiling, (2) reconnection with secondary channels identified from the LiDAR data, (3) creation of a new back channel in a low elevation area, and (4) flood bank removal and creation of a 10 m wide buffer zone focused on natural riparian vegetation regeneration. These actions will also be undertaken upstream to confluence with the Watton Brook to facilitate approximately 1.5 km of laterally connected river-floodplain habitat.

Channel reprofiling in the over deepened sections (or installation of pool-riffle-run sequences) combined with flood bank removal will allow the river to move and carve its own path through the floodplain. To facilitate this, where possible, existing woody jams and large woody pieces will be left, as well as any future woody piece inputs into the section. Instream woody pieces will redirect flow (Wohl et al., 2019; Cashman et al., 2021) causing natural meanders to form over time.

While minimal intervention strategies have been chosen to allow natural dynamics to shape the restoration site, considering the narrow windows of opportunity (Tielke and Vos, 2024) for the burbot reintroduction currently, some direct action to increase lateral connectivity for burbot is also proposed. Increasing permanent connection with secondary channels identified from the LiDAR (2) and the creation of a new back channel (3) in a low elevation area will create permanent, shallow, low flow areas that would be potential spawning habitat in low-flow years and as ideal larval nursery habitat following spawning. Fig. 6.2 highlights that all embankments present within 10 m either side of the main channel will be removed (leaving mature trees where possible) and within the 10 m strip, natural riparian vegetation recovery will be encouraged. The growth of vegetation will provide shading (Kalny et al., 2017), but also a future source of woody pieces that can help maintain instream complexity over time (Wohl, 2020).

The actions proposed here are minimal interventions, removing human influence to restore a more natural dynamic in order to allow nature to carve its own path (Sayer et al., 2018, 2024), which will potentially create more diverse habitats beneficial to the wider aquatic community. Thus, the timescale for achieving ecosystem-wide, ecologically impactful restoration is likely decadal (Haase et al., 2013; Kail et al., 2015; Dolman, 2024; White et al., 2025). Despite this, Fig. 6.3 provides a potential future outlook of the restoration site, which shows habitat heterogeneity created from interactions of biogeomorphological processes across multiple spatial scales.

In Fig. 6.3, the channel reprofiling in combination with natural tree fall and thus the input of woody pieces, which alters hydrological and sediment flows (Cashman et al., 2021) has created a series of natural meanders, creating small depositional point bars and points for macrophyte growth (1, 3). Natural tree fall can have variable effects on flow redirection, creating scour and pools around the fallen tree (Abbe and Montgomery, 1996; He et al., 2009). It can also redirect large proportions of the flow, creating new channels, but some water will continue to filter through the complex woody structures, creating shallow small-scale braiding downstream of the woody structures over time (4), increasing habitat heterogeneity (Gray and Harding, 2007). Flood barrier removal upstream as well as channel reprofiling could allow reactivation of the secondary channels on the right- and lefthand banks (2). Overall, where flood banks have been removed and the cross-sectional elevation between the main channel and floodplain is more uniform and where riparian vegetation has been allowed to regenerate naturally, the riparian zone could expand creating more marsh-like or wetland habitats (Bornette et al., 1998; Pusey and Arthington, 2003; Mitsch et al., 2015) (5).

Over time, it is likely that the created back channel will expand, increasing the area of permanently connected burbot spawning and larval nursery habitat (6). Finally, where mature trees in flood banks were left, it is likely that instream islands will form also influencing the hydrogeomorphology (Wyrick and Klingeman, 2011) (7). Overall, with time, the proposed restoration actions can help to allow natural biogeomorphological dynamics to emerge at the reintroduction site, increasing freshwater biodiversity, and

improving resilience under climate change where riparian shading has increased (Kalny et al., 2017; Dugdale et al., 2018; Jackson et al., 2021) and where flow has been slowed to hold water for longer in the catchment (Nislow et al., 2024).

6.5. Concluding Remarks

This study has assessed the physical habitat, thermal, and hydrological suitability of the River Wissey as a candidate reintroduction for burbot. As well as providing a timely, detailed analysis of the site to a fine spatial and temporal scale, the research has highlighted the key remaining gaps that need to be addressed before a burbot reintroduction can be attempted. From the findings of this study, it is clear that due to temperature, a reintroduced burbot population would face challenges surviving in the Wissey due to the water temperatures not being cool enough to facilitate the full spawning-egg-incubation-larval development window in combination with needed floodplain inundation. It is not completely certain that current temperatures would be lethal for eggs but considering that they would be spawning at the upper end of their thermal tolerance, and combined with potential future climate change, the ethical implications of reintroducing burbot must be considered by any reintroduction planner. If a reintroduction goes ahead, as observed in Belgium, investment into the reintroduction needs to be long-term due to the challenges at the candidate reintroduction site and the slow population doubling time (Beelen, 2009). If a reintroduction cannot secure enough investment, which should include between 10 – 20 years of fish rearing, releasing, and population monitoring, then perhaps the reintroduction should not be attempted. The failure of any species reintroductions inevitably makes it harder for any subsequent reintroduction to be attempted (Berger-Tal et al., 2020). Investment and further research are required to ensure that the burbot reintroduction has an increased chance of success. Even with investment, temperature, unlike floodplain inundation, cannot be controlled as easily, and ultimately, the success of a reintroduced burbot population to England, and the survival of burbot elsewhere, is dependent on individual- and population-level plasticity and adaptability under climate change.

The restoration of floodplain habitats is beneficial for the burbot reintroduction, but regardless of the burbot reintroduction or which climate change scenario England will follow, functioning floodplain and wetland ecosystems are fundamentally important to society and freshwater biodiversity. Functioning floodplains will not only contribute to natural flood management and flow regulation but have the potential to contribute to net biodiversity gain. These ecosystems must be restored to help mitigate climate change impacts as well as reduce freshwater biodiversity loss. The burbot, a dependant on floodplain inundation, could be the flagship species for promoting this kind of landscape-scale, laterally-encompassing riverine conservation and restoration.

References

Aarts, B.G.W., Brink, F.W.B.V.D. and Nienhuis, P.H., (2004) Habitat loss as the main cause of the slow recovery of fish faunas of regulated large rivers in Europe: the transversal floodplain gradient. *River Research and Applications*, 201, pp.3–23.

Abbe, T.B. and Montgomery, D.R., (1996) Large Woody Debris Jams, Channel Hydraulics and Habitat Formation in Large Rivers. *Regulated Rivers: Research & Management*, 122–3, pp.201–221.

Åberg, E.U. and Tapsell, S., (2012) Rehabilitation of the River Skerne and the River Cole, England: A Long-Term Public Perspective. In: *River Conservation and Management*. [online] John Wiley & Sons, Ltd, pp.249–259. Available at: <https://onlinelibrary.wiley.com/doi/abs/10.1002/9781119961819.ch20> [Accessed 13 May 2025].

Abramovitz, J., (1996) Imperiled waters, impoverished future: the decline of freshwater ecosystems. Introduction: the biodiversity deficit–Reconstructing the rivers–What we take out, what we put in–Fisheries mismanagement–Alien invaders–Habitat degradation–Reconnecting the fragments. *Worldwatch paper (USA)*. no. 128.

Acreman, M., Blake, J., Mountford, O., Stratford, C., Prudhomme, C., Kay, A., Bell, V., Gowing, D., Rothero, E., Thompson, J., and others, (2011) Guidance on using wetland sensitivity to climate change tool-kit. A contribution to the Wetland Vision Partnership.

Acreman, M. and Dunbar, M., (2010) *Ecologically acceptable flows in chalk rivers*. [online] Wallingford: UK Centre for Ecology and Hydrology, p.27. Available at: <https://nora.nerc.ac.uk/id/eprint/10308/> [Accessed 26 Nov. 2024].

Acreman, M., Dunbar, M., Hannaford, J., Mountford, O., Wood, P., Holmes, N., Cowx, I., Noble, R., Extence, C., Aldrick, J., and others, (2008) Developing environmental standards for abstractions from UK rivers to implement the EU Water Framework Directive/Développement de standards environnementaux sur les prélèvements d'eau en rivière au Royaume Uni pour la mise en œuvre de la directive cadre sur l'eau de l'Union Européenne. *Hydrological Sciences Journal*, 536, pp.1105–1120.

Adámek, Z., (2000) The applicability of feed mixtures in burbot, *Lota lota*, farming. *Krmiva*, 422, pp.71–76.

Addy, S., Cooksley, S., Dodd, N., Waylen, K., Stockan, J., Byg, A. and Holstead, K., (2016) *River restoration and biodiversity*. IUCN Gland, Switzerland.

Agentschap Digitaal Vlaanderen, (2021) *Bodembedekkingskaart (BBK), 1m resolutie, opname 2018*. Available at: <https://www.geopunt.be/> [Accessed 25 Sep. 2023].

Aines, E., Simpson, C., Munro-Faure, A. and Shuckburgh, E., (2021) *Preliminary report on climate risk in the Cambridgeshire & Peterborough region, 2020-2099*. Available at: <https://www.cambridge.org/engage/coe/article-details/60e5c340338e9276f508c58e> [Accessed 27 Feb. 2024].

Al Rawahi, Q., Mijangos, J.L., Khatkar, M.S., Al Abri, M.A., AlJahdhami, M.H., Kaden, J., Senn, H., Brittain, K. and Gongora, J., (2022) Rescued back from extinction in the wild: past, present and future of the genetics of the Arabian oryx in Oman. *Royal Society Open Science*, 93, p.210558.

Alabaster, J.S., (1982) 3 - WATER TEMPERATURE. In: J.S. Alabaster, ed., *Water Quality Criteria for Freshwater Fish (Second Edition)*. [online] Butterworth-Heinemann, pp.47–84. Available at: <https://www.sciencedirect.com/science/article/pii/B9780408108492500071> [Accessed 2 Feb. 2024].

Albertson, L.K., Ouellet, V., Reinert, J.H., Korb, N. and Jaeger, M., (2022) Influence of beaver mimicry restoration on habitat availability for fishes, including Arctic grayling (*Thymallus arcticus*). *Aquaculture, Fish and Fisheries*, 22, pp.104–115.

Angold, P.G., Gurnell, A.M. and Edwards, P.J., (1995) Information from River-Corridor Surveys. *Water and Environment Journal*, 95, pp.489–498.

Armstrong, J.B., Schindler, D.E., Ruff, C.P., Brooks, G.T., Bentley, K.E. and Torgersen, C.E., (2013) Diel horizontal migration in streams: Juvenile fish exploit spatial heterogeneity in thermal and trophic resources. *Ecology*, 949, pp.2066–2075.

Armstrong, J.D. and Nislow, K.H., (2012) Modelling approaches for relating effects of change in river flow to populations of Atlantic salmon and brown trout. *Fisheries Management and Ecology*, 196, pp.527–536.

Arthington, A.H., Tickner, D., McClain, M.E., Acreman, M.C., Anderson, E.P., Babu, S., Dickens, C.W.S., Horne, A.C., Kaushal, N., Monk, W.A., O'Brien, G.C., Olden, J.D., Opperman, J.J., Owusu, A.G., LeRoy Poff, N., Richter, B.D., Salinas-Rodríguez, S.A., Shamboko Mbale, B., Tharme, R.E. and Yarnell, S.M., (2024) Accelerating environmental flow implementation to bend the curve of global freshwater biodiversity loss. *Environmental Reviews*, 323, pp.387–413.

Ashton, N.K., Jensen, N.R., Ross, T.J., Young, S.P., Hardy, R.S. and Cain, K.D., (2019) Temperature and Maternal Age Effects on Burbot Reproduction. *North American Journal of Fisheries Management*, 396, pp.1192–1206.

Ashton, N.K., Ross, T.J., Hardy, R.S., Stephenson, S.M., Evans, V., Jensen, N.R., Young, S.P. and Cain, K.D., (2021) Effects of Temperature Fluctuation on Burbot Embryos: Implications of Hydropower and Climate Change. *Transactions of the American Fisheries Society*, 1505, pp.605–617.

Astaraie-Imani, M., Kapelan, Z., Fu, G. and Butler, D., (2012) Assessing the combined effects of urbanisation and climate change on the river water quality in an integrated urban wastewater system in the UK. *Journal of environmental management*, 112, pp.1–9.

Auwerx, J., Maes, Y. and Yseboodt, R., (2022) Beheerfocus: nieuwe kansen voor de kwabaal in Vlaanderen. *NatuurFocus*, 211, pp.37–38.

Auwerx, J., Vught, I. and Charleroy, D.D., (2019) Juvenilele kwabaal in de spotlights. *RAVON*, 212, pp.3–7.

Ayres, R.M., Nicol, M.D. and Raadik, T.A., (2009) Establishing new populations for fire-affected Barred Galaxias (*Galaxias fuscus*): site selection, trial translocation and population genetics. *Black Saturday Victoria*.

Baeyens, R., Buysse, D., Van den Neucker, T., Mouton, A., Martens, S., Gelaude, E., Jacobs, Y. and Coeck, J., (2010) Evaluatie ecologische herinrichting oeverzones tappelbeek en klein beek: vastlegging nultoeestand. *Rapporten/Instituut voor Natuur- en Bosonderzoek [Brussel]-Brussel*.

Bagella, S., Gascón, S., Filigheddu, R., Cogoni, A. and Boix, D., (2016) Mediterranean Temporary Ponds: new challenges from a neglected habitat. *Hydrobiologia*, 782, pp.1–10.

Bailly, J.-S., Lagacherie, P., Millier, C., Puech, C. and Kosuth, P., (2008) Agrarian landscapes linear features detection from LiDAR: application to artificial drainage networks. *International Journal of Remote Sensing*, 2912, pp.3489–3508.

Bajomi, B., Tatár, S., Tóth, B., Demény, F., Müllerné, M., Trenovszki, B.U. and Müller, T., (2013) Captive-breeding, re-introduction and supplementation of the European mudminnow in Hungary. *Global Re-introduction Perspectives: 2013. Further case studies from around the globe*, p.15.

Bajtek, Z., Pekárová, P., Jeneiová, K. and Miklánek, P., (2023) Estimation of water temperature changes in the Ipel' River based on future scenarios. *Acta Hydrologica Slovaca*, 242, pp.197–204.

Banks, M.A., Sard, N.M., O'Malley, K.G., Jacobson, D., Hogansen, M. and Johnson, M.A., (2014) A genetics-based evaluation of the spring Chinook salmon reintroduction program above Cougar dam, South Fork McKenzie River, 2007–2013. *US Army Corps of Engineers, Portland District*.

Barker, L.J., Hannaford, J., Parry, S., Smith, K.A., Tanguy, M. and Prudhomme, C., (2019) Historic hydrological droughts 1891–2015: systematic characterisation for a diverse set of catchments across the UK. *Hydrology and Earth System Sciences*, 2311, pp.4583–4602.

Barnes, C.R., Chandler, R.E. and Brierley, C.M., (2024) A Comparison of Regional Climate Projections With a Range of Climate Sensitivities. *Journal of Geophysical Research: Atmospheres*, 1292, p.e2023JD038917.

Barrows, M.G., Koch, R.C., Johnson, J., Koski, M.L. and Bailey, E., (2016) Clackamas River bull trout reintroduction project. *2015 Annual Report. US Fish and Wildlife Service (Columbia River Fisheries Program Office, Vancouver, WA) and Oregon Department of Fish and Wildlife (Corvallis, OR)*.

Basak, S.M., Hossain, M.S., Tusznió, J. and Grodzińska-Jurczak, M., (2021) Social benefits of river restoration from ecosystem services perspective: A systematic review. *Environmental Science & Policy*, 124, pp.90–100.

Batey, C., (2018) *Multi-brooding and breeding season length in the reed warbler*. Lancaster University (United Kingdom).

Baumgärtner, D. and Rothhaupt, K.-O., (2005) The impact of predation by burbot (*Lota lota* L.) on the macroinvertebrate community in the littoral zone of a large lake. *Aquatic Ecology*, 39, pp.79–92.

Beard, Z.S., Quist, M.C., Hardy, R.S. and Ross, T.J., (2017) Survival, Movement, and Distribution of Juvenile Burbot in a Tributary of the Kootenai River. *North American Journal of Fisheries Management*, 37, pp.1274–1288.

Bearman-Brown, L., Saunders, R. and Howse, J., (2018) Attitudes of residents to feral wild boar (*Sus scrofa*) in the Forest of Dean, England. In: *International Society for Anthrozoology Conference 2018: Animals in Our Lives: Multidisciplinary Approaches to the Study of Human–Animal Interactions*.

Becker, G.C., (1983) *Fishes of Wisconsin*. [online] University of Wisconsin. Available at: <https://cir.nii.ac.jp/crid/1130000797995163776> [Accessed 1 Mar. 2024].

Beeck, P., Klinger, H., Jatteau, P. and Chanseau, M., (2008) Re-introduction of allis shad to the River Rhine system: Netherlands, Germany & France. *Global Re-introduction Perspectives: re-introduction case-studies from around the globe*, p.19.

Beelen, P., (2009) *Kennisdocument kwabaal, Lota lota (Linnaeus, 1758)*. Kennisdocument. Bilthoven, Netherlands.

Beelen, P., (2014) *Kwabaal monitoring Beerze 2014*. Bilthoven: Sportvisserij Nederland.

Beelen, P., Scheepens, M. and Auwerx, J., (2019) Hoop voor de kwabaal. *Visionair*, 1354, pp.15–17.

Beeton, A.M., (1956) Food habits of the burbot (*Lota lota lacustris*) in the White River, a Michigan trout stream. *Copeia*, 1956, pp.58–60.

Beheregaray, L., Attard, C., Brauer, C., Whiterod, N., Wedderburn, S. and Hammer, M., (2021) Conservation breeding and reintroduction of pygmy perches in the lower Murray-Darling Basin, Australia: two similar species, two contrasting outcomes. In: *IUCN Global Conservation Translocation Perspectives: 2021 Case studies from around the globe: 2021*. IUCN SSC Conservation Translocation Specialist Group, Environment Agency-Abu ..., pp.26–31.

Belletti, B., Garcia de Leaniz, C., Jones, J., Bizzi, S., Börger, L., Segura, G., Castelletti, A., van de Bund, W., Aarestrup, K., Barry, J., Belka, K., Berkhuisen, A., Birnie-Gauvin, K., Bussetini, M., Carolli, M., Consuegra, S., Dopico, E., Feierfeil, T., Fernández, S., Fernandez Garrido, P., Garcia-Vazquez, E., Garrido, S., Giannico, G., Gough, P., Jepsen, N., Jones, P.E., Kemp, P., Kerr, J., King, J., Łapińska, M., Lázaro, G., Lucas, M.C., Marcello, L., Martin, P., McGinnity, P., O'Hanley, J., Olivo del Amo, R., Parasiewicz, P., Pusch, M., Rincon, G., Rodriguez, C., Royte, J., Schneider, C.T., Tummers, J.S., Vallesi, S., Vowles, A., Verspoor, E., Wanningen, H., Wantzen, K.M.,

Wildman, L. and Zalewski, M., (2020) More than one million barriers fragment Europe's rivers. *Nature*, 5887838, pp.436–441.

Bennett, P.M. and Janz, D.M., (2007) Bioenergetics and growth of young-of the-year northern pike (*Esox lucius*) and burbot (*Lota lota*) exposed to metal mining effluent. *Ecotoxicology and Environmental Safety*, 681, pp.1–12.

Berg, V., Zerihun, M.A., Jørgensen, A., Lie, E., Dale, O.B., Skaare, J.U. and Lyche, J.L., (2013) High prevalence of infections and pathological changes in burbot (*Lota lota*) from a polluted lake (Lake Mjøsa, Norway). *Chemosphere*, 905, pp.1711–1718.

Berger-Tal, O., Blumstein, D.T. and Swaisgood, R.R., (2020) Conservation translocations: a review of common difficulties and promising directions. *Animal Conservation*, 232, pp.121–131.

Bickerton, M., Petts, G., Armitage, P. and Castella, E., (1993) Assessing the ecological effects of groundwater abstraction on chalk streams: Three examples from Eastern England. *Regulated Rivers: Research & Management*, 81–2, pp.121–134.

Biggs, J., Corfield, A., Grøn, P., Hansen, H.O., Walker, D., Whitfield, M. and Williams, P., (1998) Restoration of the rivers Brede, Cole and Skerne: a joint Danish and British EU-LIFE demonstration project, V—short-term impacts on the conservation value of aquatic macroinvertebrate and macrophyte assemblages. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 81, pp.241–255.

BirdLife International, (2021) *Important Bird Areas factsheet: Breckland*. [online] Available at: <http://www.birdlife.org> [Accessed 11 Mar. 2021].

Black, E.C., Fry, F.E.J. and Black, V.S., (1954) The influence of carbon dioxide on the utilization of oxygen by some fresh-water fish. *Canadian Journal of Zoology*, 326, pp.408–420.

Blackman, B., (1997) Arctic grayling habitat use in the Table and Anzac rivers with ancillary information on other associated species. *Peace/Williston Fish and Wildlife Compensation Program Report*, 296, p.34.

Blair, A.H., (2006) *The River Great Ouse and tributaries*. Imray Laurie Norie and Wilson.

Blanchet, R., Willows, N., Johnson, S., Okanagan Nation Salmon Reintroduction Initiatives and Batal, M., (2022) Enhancing cultural food security among the Syilx Okanagan adults with the reintroduction of Okanagan sockeye salmon. *Applied Physiology, Nutrition, and Metabolism*, 472, pp.124–133.

Boardman, J., Vandaele, K., Evans, R. and Foster, I.D.L., (2019) Off-site impacts of soil erosion and runoff: Why connectivity is more important than erosion rates. *Soil Use and Management*, 352, pp.245–256.

Boets, P., Gobeyn, S., Dillen, A., Poelman, E. and Goethals, P.L., (2018) Assessing the suitable habitat for reintroduction of brown trout (*Salmo trutta forma fario*) in a lowland river: A modeling approach. *Ecology and Evolution*, 810, pp.5191–5205.

Bolland, J., Nunn, A., Lucas, M. and Cowx, I., (2012) The importance of variable lateral connectivity between artificial floodplain waterbodies and river channels. *River Research and Applications*, 288, pp.1189–1199.

Bolland, J.D., Nunn, A.D., Lucas, M.C. and Cowx, I.G., (2015) The habitat use of young-of-the-year fishes during and after floods of varying timing and magnitude in a constrained lowland river. *Ecological Engineering*, 75, pp.434–440.

Boon, P. j., (1998) River restoration in five dimensions. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 81, pp.257–264.

Boon, P. j., Wilkinson, J. and Martin, J., (1998) The application of SERCON (System for Evaluating Rivers for Conservation) to a selection of rivers in Britain. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 84, pp.597–616.

Bornette, G., Amoros, C. and Lamouroux, N., (1998) Aquatic plant diversity in riverine wetlands: the role of connectivity. *Freshwater Biology*, 392, pp.267–283.

Bosveld, J., Kranenbarg, J. and Lenders, H., (2014) Recente toename van Kwabbaal in de IJssel-Vechtdelta: goed of slecht nieuws voor herstel van relictpopulaties? *De Levende Natuur*, 115, p.184.

Bosveld, J., Kranenbarg, J., Lenders, H.J.R. and Hendriks, A.J., (2015) Historic decline and recent increase of Burbot (*Lota lota*) in the Netherlands. *Hydrobiologia*, 7571, pp.49–60.

Bouloy, A., Olivier, J.-M., Riquier, J., Castella, E., Marle, P. and Lamouroux, N., (2024) Spatio-temporal dynamics of habitat use by fish in a restored alluvial floodplain over two decades. *Science of The Total Environment*, 906, p.167540.

Bovee, K.D., (1982) *A guide to stream habitat analysis using the instream flow incremental methodology*. Western Energy and Land Use Team, Office of Biological Services, Fish and

Bowes, M.J., Gozzard, E., Johnson, A.C., Scarlett, P.M., Roberts, C., Read, D.S., Armstrong, L.K., Harman, S.A. and Wickham, H.D., (2012) Spatial and temporal changes in chlorophyll-a concentrations in the River Thames basin, UK: Are phosphorus concentrations beginning to limit phytoplankton biomass? *Science of The Total Environment*, 426, pp.45–55.

Bowles, F., Clarke, S., Eardley, B., Jeffries, R. and Stone, P., (2021) The Stage Zero approach—lessons from North America on restoring river, wetland and floodplain habitats. *Conservation Land Management*, 194, pp.21–28.

Boyer, L.F., Cooper, R.A., Long, D.T. and Askew, T.M., (1989) Burbot (*Lota lota*) biogenic sedimentary structures in Lake Superior. *Journal of Great Lakes Research*, 151, pp.174–185.

Brackwehr, L., Bunzel-Drücke, M., Detering, U., Jacobs, G., Kühlmann, M., Kuss, S., Lampert, K.P., Möhlenkamp, M., Peinert, B. and Petruck, A., (2016) Die Quappe (*Lota*

lota) im Einzugsgebiet der Lippe: Ökologie, Schutzmaßnahmen, Zucht und Wiederansiedlung.

Brackwehr, L. and Kühlmann, M., (2016) Künstliche Vermehrung der Quappe. In: L. Brackwehr, M. Bunzel-Drüke, U. Detering, G. Jacobs, M. Kühlmann, S. Kuss, K.P. Lampert, M. Möhlenkamp, B. Peinert, A. Petruck and M. Scharf, eds., *Die Quappe (Lota lota) im Einzugsgebiet der Lippe: Ökologie, Schutzmaßnahmen, Zucht und Wiederansiedlung*.

Bradford, R.G., Themelis, D., LeBlanc, P., Campbell, D.M., O'Neil, S.F. and Whitelaw, J., (2015) *Atlantic whitefish (Coregonus huntsmani) stocking in Anderson Lake, Nova Scotia*. Canadian Technical Report of Fisheries and Aquatic Sciences. [online] Ottawa, Canada: Department of Fisheries and Oceans. Available at: <https://policycommons.net/artifacts/3628642/atlantic-whitefish-coregonus-huntsmani-stocking-in-anderson-lake-nova-scotia-by-rg/4433211/> [Accessed 6 Jul. 2024].

Bradshaw, A.D., (1996) Underlying principles of restoration. *Canadian Journal of Fisheries & Aquatic Sciences*, 53, pp.3–9.

Bradter, U., Ozgul, A., Griesser, M., Layton-Matthews, K., Eggers, J., Singer, A., Sandercock, B.K., Haverkamp, P.J. and Snäll, T., (2021) Habitat suitability models based on opportunistic citizen science data: Evaluating forecasts from alternative methods versus an individual-based model. *Diversity and Distributions*, 2712, pp.2397–2411.

Brand, J., (2007) The status of White-clawed crayfish *Austropotamobius pallipes* in the River Wissey, and the potential of ark sites for translocation.

Brauer, T.A., Quist, M.C., Rhea, D.T., Laughlin, T.W. and Waring, E., (2020) Movement Dynamics of Nonnative Burbot in the Upper Green River System and Implications for Management. *North American Journal of Fisheries Management*, 405, pp.1161–1173.

Brazier, R.E., Puttock, A., Graham, H.A., Auster, R.E., Davies, K.H. and Brown, C.M.L., (2021) Beaver: Nature's ecosystem engineers. *WIREs Water*, 81, p.e1494.

Breiman, L., (2017) *Classification and regression trees*. Routledge.

British Geological Society, (2019) *BGS Parent Material Map V6.1*.

Brooker, M.P., (1985) The Ecological Effects of Channelization. *The Geographical Journal*, 1511, p.63.

Brookes, A., (1987) Restoring the sinuosity of artificially straightened stream channels. *Environmental Geology and Water Sciences*, 101, pp.33–41.

Brookes, A., (1988) *Channelized Rivers: Perspectives for Environmental Management*. Chichester: John Wiley & Sons.

Brookes, A., (1990) Restoration and enhancement of engineered river channels: Some european experiences. *Regulated Rivers: Research & Management*, 51, pp.45–56.

Brookes, A., Gregory, K.J. and Dawson, F.H., (1983) An assessment of river channelization in England and Wales. *Science of the total environment*, 272–3, pp.97–111.

Brooks, E.G.E. and Freyhof, J., (2011) *European Red List of freshwater fishes*. [online] Luxembourg: IUCN. Available at: <https://policycommons.net/artifacts/1376333/european-red-list-of-freshwater-fishes/1990594/> [Accessed 6 Jul. 2024].

Brown, A.G., Lespez, L., Sear, D.A., Macaire, J.-J., Houben, P., Klimek, K., Brazier, R.E., Van Oost, K. and Pears, B., (2018) Natural vs anthropogenic streams in Europe: History, ecology and implications for restoration, river-rewilding and riverine ecosystem services. *Earth-Science Reviews*, 180, pp.185–205.

Brown, M.J.F., Sainsbury, A.W., Vaughan-Higgins, R.J., Measures, G.H., Jones, C.M. and Gammans, N., (2017) Bringing Back a Healthy Buzz? Invertebrate Parasites and Reintroductions: A Case Study in Bumblebees. *EcoHealth*, 14S1, pp.74–83.

Bryson, G.E., Kidd, K.A. and Samways, K.M., (2022) Food web incorporation of marine-derived nutrients after the reintroduction of endangered inner Bay of Fundy Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 796, pp.875–882.

Brzezinski, M., Romanowski, J., Kopczynski, L. and Kurowicka, E., (2006) Habitat and seasonal variations in diet of otters, *Lutra lutra* in eastern Poland. *Folia Zoologica*, 554, pp.337–348.

Buckton, S.T. and Ormerod, S.J., (1997) Use of a new standardized habitat survey for assessing the habitat preferences and distribution of upland river birds. *Bird Study*, 443, pp.327–337.

Bunnell, D.B., Madenjian, C.P. and Claramunt, R.M., (2006) Long-term changes of the Lake Michigan fish community following the reduction of exotic alewife (*Alosa pseudoharengus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 6311, pp.2434–2446.

Bunzel-Drücke, M., Scharf, M. and Zimball, O., (2004a) Die Quappe in Nordrhein-Westfalen – Bestandssituation und Schutz eines vom Aussterben bedrohten Auenfisches. *LÖBF-Mitteilun-gen*, 3, pp.12–17.

Bunzel-Drücke, M., Scharf, M. and Zimball, O., (2004b) Zur Biologie der Quappe–Ein Literaturüberblick und Feldstudien aus der Lippeaue. *Naturschutz und Landschaftsplanung*, 3611, pp.334–340.

Butler, J.R.A., Radford, A., Riddington, G. and Laughton, R., (2009) Evaluating an ecosystem service provided by Atlantic salmon, sea trout and other fish species in the River Spey, Scotland: The economic impact of recreational rod fisheries. *Fisheries Research*, 962, pp.259–266.

Butlin, R., (1990) Drainage and land use in the Fenlands and Fen-edge of northeast Cambridgeshire in the seventeenth and eighteenth centuries.

Cahn, A.R., (1936) Observations on the Breeding of the Lawyer, *Lota maculosa*. *Copeia*, 19363, pp.163–165.

Campana, D., Marchese, E., Theule, J.I. and Comiti, F., (2014) Channel degradation and restoration of an Alpine river and related morphological changes. *Geomorphology*, 221, pp.230–241.

Capon, S.J., Chambers, L.E., Mac Nally, R., Naiman, R.J., Davies, P., Marshall, N., Pittock, J., Reid, M., Capon, T., Douglas, M., Catford, J., Baldwin, D.S., Stewardson, M., Roberts, J., Parsons, M. and Williams, S.E., (2013) Riparian Ecosystems in the 21st Century: Hotspots for Climate Change Adaptation? *Ecosystems*, 163, pp.359–381.

Carl, L.M., (1992) The response of burbot (*Lota lota*) to change in lake trout (*Salvelinus namaycush*) abundance in Lake Opeongo, Ontario. *Hydrobiologia*, 2431, pp.229–235.

Carl, L.M., (1995) Sonic Tracking of Burbot in Lake Opeongo, Ontario. *Transactions of the American Fisheries Society*, 1241, pp.77–83.

Carl, L.M. and McGuinness, F., (2006) Lake Whitefish and Lake Herring Population Structure and Niche in Ten South-Central Ontario Lakes. *Environmental Biology of Fishes*, 753, pp.315–323.

Carmona-Catot, G. and Moyle, P.B., (2013) Re-establishment of the natural life histories of Eagle Lake rainbow trout, USA. In: *Global Re-introduction Perspectives: 2013. Further case studies from around the globe*, Global Re-introduction Perspectives. Luxembourg: IUCN, p.21.

Carrie, J., Wang, F., Sanei, H., Macdonald, R.W., Outridge, P.M. and Stern, G.A., (2010) Increasing Contaminant Burdens in an Arctic Fish, Burbot (*Lota lota*), in a Warming Climate. *Environmental Science & Technology*, 441, pp.316–322.

Carter, I., Foster, J. and Lock, L., (2017) The Role of Animal Translocations in Conserving British Wildlife: An Overview of Recent Work and Prospects for the Future. *EcoHealth*, 141, pp.7–15.

Carver, S., Convery, I., Hawkins, S., Beyers, R., Eagle, A., Kun, Z., Van Maanen, E., Cao, Y., Fisher, M., Edwards, S.R., Nelson, C., Gann, G.D., Shurter, S., Aguilar, K., Andrade, A., Ripple, W.J., Davis, J., Sinclair, A., Bekoff, M., Noss, R., Foreman, D., Pettersson, H., Root-Bernstein, M., Svenning, J., Taylor, P., Wynne-Jones, S., Featherstone, A.W., Fløjgaard, C., Stanley-Price, M., Navarro, L.M., Aykroyd, T., Parfitt, A. and Soulé, M., (2021) Guiding principles for rewilding. *Conservation Biology*, 356, pp.1882–1893.

Cashman, M.J., Harvey, G.L. and Wharton, G., (2021) Structural complexity influences the ecosystem engineering effects of in-stream large wood. *Earth Surface Processes and Landforms*, 4610, pp.2079–2091.

Cashman, M.J., Wharton, G., Harvey, G.L., Naura, M. and Bryden, A., (2019) Trends in the use of large wood in UK river restoration projects: insights from the National River Restoration Inventory. *Water and Environment Journal*, 333, pp.318–328.

Castañeda, R.A., Mandrak, N.E., Barrow, S. and Weyl, O.L.F., (2020) Occupancy dynamics of rare cyprinids after invasive fish eradication. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 307, pp.1424–1436.

Castella, E., Béguin, O., Besacier-Monbertrand, A., Hug Peter, D., Lamouroux, N., Mayor Siméant, H., McCrae, D., Olivier, J. and Paillex, A., (2015) Realised and predicted changes in the invertebrate benthos after restoration of connectivity to the floodplain of a large river. *Freshwater Biology*, 606, pp.1131–1146.

Catalano, M.J., Bozek, M.A. and Pellett, T.D., (2007) Effects of dam removal on fish assemblage structure and spatial distributions in the Baraboo River, Wisconsin. *North American Journal of Fisheries Management*, 272, pp.519–530.

Centraal Bureau voor de Statistiek, Planbureau voor de Leefomgeving, Rijksinstituut voor Volksgezondheid en Milieu and Wageningen University and Research, (2020) *Temperatuur oppervlaktewater, 1910 - 2019*. [online] Available at: <https://www.clo.nl/indicatoren/nl056605-temperatuur-oppervlaktewater-1910-2019>.

Chambers, P.A., Brown, S., Culp, J.M., Lowell, R.B. and Pietroniro, A., (2000) Dissolved oxygen decline in ice-covered rivers of northern Alberta and its effects on aquatic biota. *Journal of Aquatic Ecosystem Stress and Recovery*, 81, pp.27–38.

Chapman, N.G., (2021) History of introduction of Reeves' muntjac in Great Britain and ecological characteristics facilitating expansion of feral populations. *European Journal of Wildlife Research*, 673, p.33.

Chen, L.-C., (1969) *The biology and taxonomy of the burbot, Lota lota leptura, in interior Alaska*. University of Alaska. Institute of Arctic Biology.

Chilcott, S., Freeman, R., Davies, P.E., Crook, D.A., Fulton, W., Hamr, P., Jarvis, D. and Sanger, A.C., (2013) Extinct habitat, extant species: lessons learned from conservation recovery actions for the Pedder galaxias (*Galaxias pedderensis*) in south-west Tasmania, Australia. *Marine and Freshwater Research*, 649, p.864.

Clady, M.D., (1976) Distribution and Abundance of Larval Ciscoes, *Coregonus Artedii*, and Burbot, *Lota Lota*, in Oneida Lake. *Journal of Great Lakes Research*, 22, pp.234–247.

Clarke, S.J., (2025) Full floodplain connectivity: Realising opportunities for 'Stage 0' river restoration. *River Research and Applications*, 411, pp.152–158.

Clemens, H.P., (1951a) The food of the burbot *Lota lota maculosa* (LeSueur) in Lake Erie. *Transactions of the American Fisheries Society*, 801, pp.56–66.

Clemens, H.P., (1951b) The growth of the burbot *Lota lota maculosa* (LeSueur) in Lake Erie. *Transactions of the American Fisheries Society*, 801, pp.163–173.

Clilverd, H.M., Thompson, J.R., Heppell, C.M., Sayer, C.D. and Axmacher, J.C., (2016) Coupled Hydrological/Hydraulic Modelling of River Restoration Impacts and Floodplain Hydrodynamics. *River Research and Applications*, 329, pp.1927–1948.

Cluer, B. and Thorne, C., (2014) A Stream Evolution Model Integrating Habitat and Ecosystem Benefits. *River Research and Applications*, 302, pp.135–154.

Cochran-Biederman, J.L., Wyman, K.E., French, W.E. and Loppnow, G.L., (2015) Identifying correlates of success and failure of native freshwater fish reintroductions. *Conservation Biology*, 291, pp.175–186.

Collins, R., Johnson, D., Crilly, D., Rickard, A., Neal, L., Morse, A., Walker, M., Lear, R., Deasy, C., Paling, N., Anderton, S., Ryder, C., Bide, P. and Holt, A., (2020) Collaborative water management across England – An overview of the Catchment Based Approach. *Environmental Science & Policy*, 112, pp.117–125.

Comte, L. and Olden, J.D., (2017) Evolutionary and environmental determinants of freshwater fish thermal tolerance and plasticity. *Global Change Biology*, 232, pp.728–736.

Conallin, J., Boegh, E. and Jensen, J.K., (2010) Instream physical habitat modelling types: an analysis as stream hydromorphological modelling tools for EU water resource managers. *International Journal of River Basin Management*, 81, pp.93–107.

Conservation Translocation Specialist Group, (2021) *Introduction: IUCN SSC Conservation Translocation Specialist Group*. [online] Available at: <https://iucn-ctsg.org/about-us/> [Accessed 4 Sep. 2021].

Contreras-MacBeath, T., Mojica, H.M., González, M.R. and Chino, I.P., (2016) Re-introduction of the Morelos minnow in the "Barranca de Chapultepec" protected area, Cuernavaca, Morelos, Mexico. In: *Global Re-introduction Perspectives: 2016. Case-studies from around the globe*, Global Re-introduction Perspectives. Luxembourg: IUCN, p.25.

Cooper, G.P. and Fuller, J.L., (1945) *A biological survey of Moosehead lake and Haymock lake, Maine*. Maine Department of Inland Fisheries and Game.

Copp, G.H., (1989) The habitat diversity and fish reproductive function of floodplain ecosystems. *Environmental biology of fishes*, 26, pp.1–27.

Copp, G.H., (1997a) Importance of marinas and off-channel water bodies as refuges for young fishes in a regulated lowland river. *Regulated Rivers: Research & Management*, 133, pp.303–307.

Copp, G.H., (1997b) Microhabitat use of fish larvae and 0+ juveniles in a highly regulated section of the River Great Ouse. *Regulated Rivers: Research & Management*, 133, pp.267–276.

Copp, G.H., Edmonds-Brown, V. and Cottey, R., (1998) Behavioural interactions and microhabitat use of stream-dwelling sticklebacks *Gasterosteus aculeatus* and *Pungitius pungitius* in the laboratory and field. *FOLIA ZOOLOGICA-PRAHA*, 47, pp.275–286.

Cornacchia, L., van de Koppel, J., van der Wal, D., Wharton, G., Puijalon, S. and Bouma, T.J., (2018) Landscapes of facilitation: how self-organized patchiness of aquatic macrophytes promotes diversity in streams. *Ecology*, 994, pp.832–847.

Costa, M.J., Duarte, G., Segurado, P. and Branco, P., (2021) Major threats to European freshwater fish species. *Science of the Total Environment*, 797, p.149105.

Costanza, R., d'Arge, R., Groot, R. de, Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P. and Belt, M. van den, (1997) The value of the world's ecosystem services and natural capital. *Nature*, 3876630, pp.253–260.

Costanza, R., De Groot, R., Braat, L., Kubiszewski, I., Fioramonti, L., Sutton, P., Farber, S. and Grasso, M., (2017) Twenty years of ecosystem services: How far have we come and how far do we still need to go? *Ecosystem Services*, 28, pp.1–16.

Cott, P.A., Guzzo, M.M., Chapelsky, A.J., Milne, S.W. and Blanchfield, P.J., (2015) Diel bank migration of Burbot (*Lota lota*). *Hydrobiologia*, 7571, pp.3–20.

Cott, P.A., Hawkins, A.D., Zeddies, D., Martin, B., Johnston, T.A., Reist, J.D., Gunn, J.M. and Higgs, D.M., (2014) Song of the burbot: Under-ice acoustic signaling by a freshwater gadoid fish. *Journal of Great Lakes Research*, 402, pp.435–440.

Cott, P.A., Johnston, T.A. and Gunn, J.M., (2011) Food web position of burbot relative to lake trout, northern pike, and lake whitefish in four sub-Arctic boreal lakes: Food web position of burbot. *Journal of Applied Ichthyology*, 27, pp.49–56.

Cott, P.A., Johnston, T.A. and Gunn, J.M., (2013) Stability in Life History Characteristics among Burbot Populations across Environmental Gradients. *Transactions of the American Fisheries Society*, 1426, pp.1746–1756.

Cotton, J., Wharton, G., Bass, J., Heppell, C. and Wotton, R., (2006) The effects of seasonal changes to in-stream vegetation cover on patterns of flow and accumulation of sediment. *Geomorphology*, 773–4, pp.320–334.

Council Directive 91/271/EEC of 21 May 1991 concerning urban waste-water treatment. 91/271/EEC. [online] Available at: <https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:31991L0271>.

Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora. 92/43/EEC. [online] Available at: <https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A31992L0043>.

Coveney, S. and Roberts, K., (2017) Lightweight UAV digital elevation models and orthoimagery for environmental applications: data accuracy evaluation and potential for river flood risk modelling. *International journal of remote sensing*, 388–10, pp.3159–3180.

Cowx, I.G., (2000) Potential impact of groundwater augmentation of river flows on fisheries: a case study from the River Ouse, Yorkshire, UK. *Fisheries Management and Ecology*, 71–2, pp.85–96.

Cowx, I.G. ed., (2003) *Interactions Between Fish and Birds: Implications for Management*. 1st ed. [online] Wiley. Available at: <https://onlinelibrary.wiley.com/doi/book/10.1002/9780470995372> [Accessed 7 Jun. 2024].

Crawford-Brown, D., Gossé, J.-B., and others, (2015) Collective Finance Models for Sustainable Water Projects. *Journal of Environmental Protection*, 605, p.477.

Crisp, D. t. and Howson, G., (1982) Effect of air temperature upon mean water temperature in streams in the north Pennines and English Lake District. *Freshwater Biology*, 124, pp.359–367.

Dadson, S.J., Hall, J.W., Murgatroyd, A., Acreman, M., Bates, P., Beven, K., Heathwaite, L., Holden, J., Holman, I.P., Lane, S.N., O'Connell, E., Penning-Rowsell, E., Reynard, N., Sear, D., Thorne, C. and Wilby, R., (2017) A restatement of the natural science evidence concerning catchment-based 'natural' flood management in the UK. *Proceedings of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 4732199, p.20160706.

Darby, H.C., (1956) *The drainage of the Fens*. Cambridge University Press.

Darby, H.C., (1983) *The Changing Fenland*. Cambridge, UK: Cambridge University Press.

Darby, H.C., (1986) *Domesday England*. 1st pbk. ed ed. Cambridge [Cambridgeshire]: Cambridge University Press.

David, S.R., Edmonds, D.A. and Letsinger, S.L., (2017) Controls on the occurrence and prevalence of floodplain channels in meandering rivers. *Earth Surface Processes and Landforms*, 423, pp.460–472.

Davidson, N.C. and Finlayson, C.M., (2018) Extent, regional distribution and changes in area of different classes of wetland. *Marine and Freshwater Research*, 6910, p.1525.

Davie, T., (2010) Streamflow Analysis and Modelling. In: *Fundamentals of hydrology*, Routledge fundamentals of physical geography series, 2. ed., repr. (twice). London: Routledge.

Dawson, M.N., (2012) Species richness, habitable volume, and species densities in freshwater, the sea, and on land. *Frontiers of Biogeography*, 43.

Dawson, Q., Kechavarzi, C., Leeds-Harrison, P.B. and Burton, R.G.O., (2010) Subsidence and degradation of agricultural peatlands in the Fenlands of Norfolk, UK. *Geoderma*, 1543, pp.181–187.

De Vlaamse Milieumaatschappij, (2024) *Geel/Grote Nete (L10_077)*. Available at: https://waterinfo.vlaanderen.be/station/01L10_077 [Accessed 10 Jul. 2024].

DEFRA, (2018) *A Green Future: Our 25 Year Plan to Improve the Environment*. [online] UK: DEFRA. Available at:

https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/693158/25-year-environment-plan.pdf [Accessed 24 Mar. 2021].

DEFRA, (2023) *Plan for water: Our integrated plan for delivering clean and plentiful water*. [online] Available at: <https://www.gov.uk/government/publications/plan-for-water-our-integrated-plan-for-delivering-clean-and-plentiful-water/plan-for-water-our-integrated-plan-for-delivering-clean-and-plentiful-water> [Accessed 20 May 2025].

DEFRA, (2025) *Wild release and management of beavers in England*. [Policy Paper] DEFRA. Available at: <https://www.gov.uk/government/publications/wild-release-and-management-of-beavers-in-england/wild-release-and-management-of-beavers-in-england> [Accessed 15 Jul. 2025].

Degerman, E. and Sers, B., (1994) The effect of lakes on the stream fish fauna. *Ecology of freshwater fish*, 33, pp.116–122.

Demars, B. and Gornall, R., (2003) Identification of British species of Callitriche by means of isozymes. *Watsonia*, 243, pp.389–400.

Demars, B.O. and Harper, D.M., (2005) Distribution of aquatic vascular plants in lowland rivers: separating the effects of local environmental conditions, longitudinal connectivity and river basin isolation. *Freshwater Biology*, 503, pp.418–437.

Demars, B.O., Kemp, J.L., Friberg, N., Usseglio-Polatera, P. and Harper, D.M., (2012) Linking biotopes to invertebrates in rivers: biological traits, taxonomic composition and diversity. *Ecological indicators*, 23, pp.301–311.

Dessai, S., Lu, X. and Hulme, M., (2005) Limited sensitivity analysis of regional climate change probabilities for the 21st century. *Journal of Geophysical Research: Atmospheres*, [online] 110D19. Available at: <https://onlinelibrary.wiley.com/doi/abs/10.1029/2005JD005919> [Accessed 27 Feb. 2024].

Di Prinzio, C.Y., Arismendi, I. and Olivos, J.A., (2023) Revealing a rapid shift in the phenology of the adult spawning migration of an introduced Chinook salmon population in Patagonia. *Aquatic Ecology*. [online] Available at: <https://doi.org/10.1007/s10452-023-10066-2> [Accessed 22 Feb. 2024].

Diaz-Nieto, J. and Wilby, R.L., (2005) A comparison of statistical downscaling and climate change factor methods: impacts on low flows in the River Thames, United Kingdom. *Climatic Change*, 692, pp.245–268.

Digitaal Vlaanderen, (2014) *Digitaal Hoogtemodel Vlaanderen II, DTM, raster, 1 m*. Available at: <https://metadata.vlaanderen.be/srv/dut/catalog.search#/metadata/f52b1a13-86bc-4b64-8256-88cc0d1a8735> [Accessed 2 Jun. 2023].

Digitaal Vlaanderen, (2021) *Orthofotomozaïek, middenschalig, winteropnamen, kleur, 2021, Vlaanderen*. Available at: <https://metadata.vlaanderen.be/srv/dut/catalog.search#/metadata/5f429f28-2d6b-4f3d-831a-492bd86bec1a> [Accessed 2 Jun. 2023].

Dillen, A., Coeck, J. and Monnier, D., (2008a) Habitat use and seasonal migrations of burbot in lowland rivers in north France. In: *American Fisheries Society Symposium*. American Fisheries Society, p.29.

Dillen, A., Martens, S., Baeyens, R. and Coeck, J., (2005) *Onderzoek naar de biologie van de kwabaal (Lota Lota L.), ter voorbereiding van het herstel van de soort in het Vlaamse Gewest*. Brussels: Instituut voor Natuurbehoud.

Dillen, A. and Vlietinck, K., (2008) Recovery programmes for endangered freshwater fish in Flanders, Belgium. EIFAC Symposium on Interactions Between Social, Economic and Ecological Objectives of Inland Commercial and Recreational Fisheries and Aquaculture. .

Dillen, A., Vught, I., De Charleroy, D., Monnier, D. and Coeck, J., (2008b) A preliminary evaluation of reintroductions of burbot in Flanders, Belgium. In: V.L. Paragamian and D.H. Bennet, eds., *Burbot: ecology, management and culture*., American Fisheries Society Symposium. Bethesda, pp.55–77.

Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. 2000/60/EC. [online] Available at: <https://eur-lex.europa.eu/eli/dir/2000/60/oj>.

Directive 2007/60/EC of the European Parliament and of the Council of 23 October 2007 on the assessment and management of flood risks. 2007/60/EC. [online] Available at: <https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:32007L0060>.

Directive 2009/147/EC of the European Parliament and of the Council of 30 November 2009 on the conservation of wild birds. 2009/147/EC. [online] Available at: <https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A32009L0147>.

Diver, T.A., Mussmann, S.M., Durst, S.L. and Franssen, N.R., (2021) Effective number of breeders and reconstructed sibships reveal low reproductive output by a reintroduced population of endangered fish. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 3112, pp.3416–3428.

Dixon, C.J. and Vokoun, J.C., (2009) Burbot resource selection in small streams near the southern extent of the species range. *Ecology of Freshwater Fish*, 182, pp.234–246.

Dixon, C.J. and Vokoun, J.C., (2010) Population Structure and Diet of Burbot (*Lota lota*) in Small Streams Near the Southern Extent of the Species' Range. *Journal of Freshwater Ecology*, 251, pp.49–58.

Dockerty, T., Lovett, A., Sünnerberg, G., Appleton, K. and Parry, M., (2005) Visualising the potential impacts of climate change on rural landscapes. *Computers, Environment and Urban Systems*, 293, pp.297–320.

Dolman, L.A., (2024) *The ecological effects of physical habitat restoration in English chalk streams*. [phd] University of Southampton. Available at: <https://eprints.soton.ac.uk/487564/> [Accessed 23 May 2025].

Domínguez, O.D., Morales, R.H., Nava, M.M., Herrerías, Y.H., Venegas, T.D., Jiménez, A.L.E., Vázquez, L.H.E. and García, G., (2018) Progress in the reintroduction program of the tequila splitfin in the springs of Teuchitlán, Jalisco, Mexico. In: *Global reintroduction perspectives: 2018. Case studies from around the globe*. Abu Dhabi: IUCN SSC Conservation Translocation Specialist Group & Environment Agency, pp.38–42.

Domisch, S., Jähnig, S.C. and Haase, P., (2011) Climate-change winners and losers: stream macroinvertebrates of a submontane region in Central Europe. *Freshwater Biology*, 5610, pp.2009–2020.

Donner, M.T. and Eckmann, R., (2011) Diel vertical migration of larval and early-juvenile burbot optimises survival and growth in a deep, pre-alpine lake. *Freshwater Biology*, 565, pp.916–925.

Downs, C.C. and Fredenberg, C.R., (2016) *Glacier National Park Fisheries Monitoring and Management Report*. West Glacier, Montana: National Parks Service.

DTU Aqua, (2021) *Fiskepleje.dk*. [online] Fiskepleje.dk. Available at: <https://kort.fiskepleje.dk/>.

Ducharne, A., (2008) Importance of stream temperature to climate change impact on water quality. *Hydrology and Earth System Sciences*, 123, pp.797–810.

Dudgeon, D., (2010) Prospects for sustaining freshwater biodiversity in the 21st century: linking ecosystem structure and function. *Current Opinion in Environmental Sustainability*, 25–6, pp.422–430.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A., Soto, D., Stiassny, M.L.J. and Sullivan, C.A., (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, 812, pp.163–182.

Dugdale, S.J., Malcolm, I.A., Kantola, K. and Hannah, D.M., (2018) Stream temperature under contrasting riparian forest cover: Understanding thermal dynamics and heat exchange processes. *Science of the Total Environment*, 610, pp.1375–1389.

Dunnigan, J.L. and Sinclair, C.L., (2007) Home Range and Movement Patterns of Burbot in Kootenai Reservoir, Montana, USA. In: *American Fisheries Symposium*. American Fisheries Society. .

Eaton, J.W., (1989) Ecological Aspects of Water Management in Britain. *Journal of Applied Ecology*, 263, pp.835–849.

Edgar, P., Foster, J. and Baker, J., (2010) *Reptile habitat management handbook*. Bournemouth: Amphibian and Reptile Conservation.

EDINA, (2023) *1:2500 County Series 1st Edition [TIFF geospatial data], Scale 1:2500, Tiles: norf-08307-1, Updated: 30 November 2010, Historic, Using: EDINA Historic Digimap Service*. Available at: <https://digimap.edina.ac.uk> [Accessed 27 Nov. 2023].

EDINA Aerial Digimap Service, (2020) *Lidar Composite Digital Terrain Model England 1m resolution*. Tiles: tl89sw, tl89nw, tf80sw. Available at: <https://digimap.edina.ac.uk> [Accessed 6 Feb. 2023].

EDINA Aerial Digimap Service, (2021) *High Resolution (25cm) Vertical Aerial Imagery*. Tiles: tl8599, tl8598, tl8597, tl8596, tl8595, tl8594, tl8499, tl8498, tl8497, tl8496, tl8495, tl8494, tl8399, tl8398, tl8397, tl8396, tl8395, tl8394, tl8199, tl8198, tl8197, tl8196, tl8195, tl8194, tl8299, tl8298, tl8297, tl8296, tl8295, tl8294, tf8200, tf8100, tf8500, tf8400, tf8300. Available at: <https://digimap.edina.ac.uk>. [Accessed 16 Sep. 2022].

Edsall, T.A., Kennedy, G.W. and Horns, W.H., (1993) Distribution, Abundance, and Resting Microhabitat of Burbot on Julian's Reef, Southwestern Lake Michigan. *Transactions of the American Fisheries Society*, 1224, pp.560–574.

Eick, D., (2013) Habitat preferences of the burbot (*Lota lota*) from the River Elbe: an experimental approach. *Journal of Applied Ichthyology*, 293, pp.541–548.

Elmer, K.R., Van Houdt, J.K.J., Meyer, A. and Volckaert, F.A.M., (2008) Population genetic structure of North American burbot (*Lota lota maculosa*) across the Nearctic and at its contact zone with Eurasian burbot (*Lota lota lota*). *Canadian Journal of Fisheries and Aquatic Sciences*, 6511, pp.2412–2426.

Elton, C.S., Simberloff, D. and Ricciardi, A., (2020) *The ecology of invasions by animals and plants*. Second edition ed. Cham: Springer.

England, J., Angelopoulos, N., Cooksley, S., Dodd, J., Gill, A., Gilvear, D., Johnson, M., Naura, M., O'Hare, M., Tree, A., Wheeldon, J. and Wilkes, M.A., (2021) Best Practices for Monitoring and Assessing the Ecological Response to River Restoration. *Water*, 1323, p.3352.

England, J., Beach, E., Leeming, B.F. and Shuker, L., (2017) Introducing the Modular River Survey. *Transactions of the Hertfordshire Natural History Society*, pp.47–49.

Entwistle, N.S., Heritage, G.L., Schofield, L.A. and Williamson, R.J., (2019) Recent changes to floodplain character and functionality in England. *CATENA*, 174, pp.490–498.

Environment Agency, (1997) *River Habitat Survey, 1997 Field Survey Guidance Manual*. Bristol, UK: Environment Agency.

Environment Agency, (2003) *River Habitat Survey in Britain and Ireland Field Survey Guidance Manual: 2003 Version 1*. [online] Available at: <https://www.riverhabitatsurvey.org/manual/rhs-manuals/> [Accessed 2 Jun. 2023].

Environment Agency, (2015a) *Phosphate Issues Priority for Countryside Stewardship*. [online] Available at: https://magic.defra.gov.uk/Metadata_for_MAGIC/Phosphate%20Issues.html [Accessed 11 Mar. 2021].

Environment Agency, (2015b) *Sediment Issues Priority for Countryside Stewardship*. [online] Available at: https://magic.defra.gov.uk/Metadata_for_MAGIC/Sediment%20Issues.html [Accessed 22 Oct. 2021].

Environment Agency, (2020) *Cam and Ely Ouse abstraction licensing strategy (ALS)*. [online] UK: Environment Agency. Available at: <https://www.gov.uk/government/publications/cam-and-ely-ouse-abstraction-licensing-strategy/cam-and-ely-ouse-abstraction-licensing-strategy>.

Environment Agency, (2022) Resetting our rivers – how taking them back to ‘stage zero’ could help nurture nature. *Environment Agency Blog*. Available at: <https://environmentagency.blog.gov.uk/2022/12/09/resetting-our-rivers-how-taking-them-back-to-stage-zero-could-help-nurture-nature/> [Accessed 26 Jul. 2023].

Environment Agency, (2023a) *Ecology and Fish Data Explorer*. [online] Available at: <https://environment.data.gov.uk/ecology/explorer/> [Accessed 3 Nov. 2024].

Environment Agency, (2023b) *Water quality data archive*. [online] Water quality data archive. Available at: <https://environment.data.gov.uk/water-quality/view/landing> [Accessed 3 Aug. 2024].

Environment Agency, (2024) *Hydrology Data Explorer*. [Data Portal] Hydrology Data Explorer. Available at: <https://environment.data.gov.uk/hydrology/explore> [Accessed 10 Aug. 2024].

Erős, T., Botta-Dukát, Z. and Grossman, G.D., (2003) Assemblage structure and habitat use of fishes in a Central European submontane stream: a patch-based approach. *Ecology of Freshwater Fish*, 122, pp.141–150.

European Commission, (2019) *Report from the Commission to the European Parliament and Council on the implementation of the Water Framework Directive (2000/60/EC) and the Floods Directive (2007/60/EC) Second River Basin Management Plans First Flood Risk Management Plans*. Brussels: European Commission.

European Commission., (2024) *Criteria for identifying free-flowing river stretches for the EU biodiversity strategy for 2030*. [online] LU: Publications Office. Available at: <https://data.europa.eu/doi/10.2760/402517> [Accessed 14 May 2025].

European Environment Agency, (2015) *SOER: The European environment – state and outlook. A comprehensive assessment of the European environment’s state, trends and prospects, in a global context*. State of Environment Report. [online] Copenhagen, Denmark: European Environment Agency. Available at: <https://www.eea.europa.eu/soer/2015>.

European Environment Agency, (2016a) *Flood risks and environmental vulnerability — exploring the synergies between floodplain restoration, water policies and thematic policies*. [online] European Environment Agency. Available at: <http://www.eea.europa.eu/publications/flood-risks-and-environmental-vulnerability/> [Accessed 21 Jun. 2022].

European Environment Agency, (2016b) *Species of European interest*. [online] European Environment Agency. Available at: <https://www.eea.europa.eu/data-and-maps/indicators/species-of-european-interest-2/assessment> [Accessed 5 Apr. 2023].

European Environment Agency, (2018a) *Chemicals in European waters — knowledge developments*. [online] European Environment Agency. Available at: <https://www.eea.europa.eu/publications/chemicals-in-european-waters> [Accessed 21 Jun. 2022].

European Environment Agency, (2018b) *European waters: assessment of status and pressures 2018*. [online] European Environment Agency. Available at: <https://www.eea.europa.eu/publications/state-of-water> [Accessed 21 Jun. 2022].

European Environment Agency, (2018c) *WISE Water Framework Directive data viewer —Surface water*. [online] European Environment Agency. Available at: <https://www.eea.europa.eu/data-and-maps/dashboards/wise-wfd> [Accessed 23 Jun. 2022].

European Environment Agency, (2019) *The European Environment - state and outlook 2020*. State of Environment Report. [online] European Environment Agency. Available at: <https://www.eea.europa.eu/soer/publications/soer-2020> [Accessed 21 Jun. 2022].

Evans, E.C., Greenwood, M.T. and Petts, G.E., (1995) Thermal profiles within river beds. *Hydrological Processes*, 91, pp.19–25.

Evans, G.L., (1999) *Phosphorus and its biological effect in lowland rivers*. University of Leicester (United Kingdom).

Evans, R., (2012) Reconnaissance surveys to assess sources of diffuse pollution in rural catchments in East Anglia, eastern England – implications for policy. *Water and Environment Journal*, 262, pp.200–211.

Evans, R., (2017) Factors controlling soil erosion and runoff and their impacts in the upper Wissey catchment, Norfolk, England: A ten year monitoring programme. *Earth Surface Processes and Landforms*, 4214, pp.2266–2279.

Evenson, M.J., (1988) *Movement, abundance and length composition of Tanana River burbot stocks during 1987*. Alaska Department of Fish and Game, Division of Sport Fish.

Evenson, M.J., (1991) *Age and length at sexual maturity of Burbot in the Tanana River, Alaska*. Alaska Department of Fish and Game, Division of Sport Fish.

Evenson, M.J., (1993) *Seasonal movements of radio-implemented burbot in the Tanana River drainage*. Alaska Department of Fish and Game, Division of Sport Fish.

Everard, M., (2021) *Burbot: conserving the enigmatic freshwater codfish*. 5m Books Ltd.

Fabricius, E., (1954) Aquarium observations on the spawning behaviour of the burbot, *Lota vulgaris* L. *Report of the Institute of Freshwater Research, Drottningholm*, 35, pp.5–57.

Farkas, J., (1993) Zur Biologie der Aalrutte in der oberen Drau und ihren Nebengewässern. *Carinthia II*, 183103, pp.593–612.

Fennell, J., Geris, J., Wilkinson, M.E., Daalmans, R. and Soulsby, C., (2020) Lessons from the 2018 drought for management of local water supplies in upland areas: A tracer-based assessment. *Hydrological Processes*, 3422, pp.4190–4210.

Filipsson, K., Bergman, E., Österling, M., Erlandsson, A., Greenberg, L. and Watz, J., (2019) Effects of temperature and a piscivorous fish on diel winter behaviour of juvenile brown trout (*Salmo trutta*). *Freshwater Biology*, 6410, pp.1797–1805.

Finney, M., Charlton, M., England, J., Khamis, K. and Hannah, D.M., (2022) *River water temperature projections for English Chalk streams*. [online] Bristol, UK: Environment Agency. Available at: https://assets.publishing.service.gov.uk/media/637c92a58fa8f53f41348975/River_water_temperature_projections_for_English_Chalk_streams_-_report.pdf.

Firbank, L., Bradbury, R., McCracken, D., Stoate, C., Goulding, K., Harmer, R., Hess, T., Jenkins, A., Pilgrim, E., Potts, S., and others, (2011) Enclosed farmland.

Firbank, L.G., Petit, S., Smart, S., Blain, A. and Fuller, R.J., (2007) Assessing the impacts of agricultural intensification on biodiversity: a British perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 3631492, pp.777–787.

Fischer, J. and Lindenmayer, D.B., (2007) Landscape modification and habitat fragmentation: a synthesis. *Global ecology and biogeography*, 163, pp.265–280.

Fischer, P., (1999) Otolith microstructure during the pelagic, settlement and benthic phases in burbot. *Journal of Fish Biology*, 546, pp.1231–1243.

Fischer, P., (2000a) An experimental test of metabolic and behavioural responses of benthic fish species to different types of substrate. *Canadian Journal of Fisheries and Aquatic Sciences*, 5711, pp.2336–2344.

Fischer, P., (2000b) Test of Competitive Interactions for Space Between Two Benthic Fish Species, Burbot *Lota lota*, and Stone Loach *Barbatula barbatula*. *Environmental Biology of Fishes*, 584, pp.439–446.

Fischer, P., (2004) Effects of intraspecific competition and predation risk in the littoral-benthic community: a case study of juvenile burbot (*Lota lota*). *Boreal environment research*, 93, p.213.

Fischer, P., Kautz, H., Weber, H. and Obergfell, W., (2001) The use of passive integrated transponder systems (PIT) triggered by infrared-gates for behavioural studies in nocturnal, bottom-dwelling fish species. *Journal of fish biology*, 581, pp.295–298.

Fischer, P. and Öhl, U., (2005) Effects of water-level fluctuations on the littoral benthic fish community in lakes: a mesocosm experiment. *Behavioral Ecology*, 164, pp.741–746.

Fisher, S.J., (2000) Early life history observations of burbot utilizing two Missouri River backwaters. *Burbot biology, ecology, and management. American Fisheries Society, Fisheries Management Section, Publication, Bethesda, Maryland*, pp.96–0.

Fleming, E., (2025) Unveiling Stage Zero Conditions in the New Forest National Park: A UAV-Based Structure-From-Motion Photogrammetry and LiDAR Approach for Reconstructing an Anastomosing Wet Woodland at the Avon Water. *River Research and Applications*, 411, pp.159–176.

Flitcroft, R.L., Brignon, W.R., Staab, B., Bellmore, J.R., Burnett, J., Burns, P., Cluer, B., Giannico, G., Helstab, J.M., Jennings, J., Mayes, C., Mazzacano, C., Mork, L., Meyer, K., Munyon, J., Penaluna, B.E., Powers, P., Scott, D.N. and Wondzell, S.M., (2022) Rehabilitating Valley Floors to a Stage 0 Condition: A Synthesis of Opening Outcomes. *Frontiers in Environmental Science*, [online] 10. Available at: <https://www.frontiersin.org/articles/10.3389/fenvs.2022.892268> [Accessed 17 May 2023].

Folland, C.K., Hannaford, J., Bloomfield, J.P., Kendon, M., Svensson, C., Marchant, B.P., Prior, J. and Wallace, E., (2015) Multi-annual droughts in the English Lowlands: a review of their characteristics and climate drivers in the winter half-year. *Hydrology and Earth System Sciences*, 195, pp.2353–2375.

Fox, P.J.A., Naura, M. and Scarlett, P., (1998) An account of the derivation and testing of a standard field method, River Habitat Survey. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 84, pp.455–475.

Frankland, H.M., (1959) The incidence and distribution in Britain of the trematodes of *Talpa europaea*. *Parasitology*, 491–2, pp.132–142.

Franklin, P. and Baker, C., (2016) Re-introduction of giant kokopu to Nukumea Stream, New Zealand'. In: *Global Re-introduction Perspectives: 2016. Case-studies from around the globe.*, Global Re-introduction Perspectives. Luxembourg: IUCN, p.30.

Fraser, E., Harrington, L., Macdonald, D. and Lambin, X., (2017) Control of an invasive species: the American mink in Great Britain.

Fratt, T.W., Coble, D.W., Copes, F. and Bruesewitz, R.E., (1997) Diet of burbot in Green Bay and western Lake Michigan with comparison to other waters. *Journal of Great Lakes Research*, 231, pp.1–10.

Frazier, A.J., Jensen, N.R., Young, S.P. and Todgham, A.E., (2020) Does a cannibal feeding strategy impart differential metabolic performance in young burbot (*Lota lota maculosa*)? *Conservation Physiology*, [online] 8coaa034. Available at: <https://doi.org/10.1093/conphys/coaa034> [Accessed 6 Apr. 2021].

Frazier, P. and Page, K., (2006) The effect of river regulation on floodplain wetland inundation, Murrumbidgee River, Australia. *Marine and Freshwater Research*, 572, pp.133–141.

Freyhof, J., (2010) *Lota lota* (errata version published in 2018). *The IUCN Red List of Threatened Species*. e.T135675A136563279. [online] Available at: <https://www.iucnredlist.org/species/135675/136563279> [Accessed 4 Jan. 2021].

Freyhof, J. and Kottelat, M., (2007) *Handbook of European freshwater fishes*. [online] Available at: <https://portals.iucn.org/library/node/9068> [Accessed 22 Feb. 2024].

Friberg, N., Angelopoulos, N.V., Buijse, A.D., Cowx, I.G., Kail, J., Moe, T.F., Moir, H., O'Hare, M.T., Verdonschot, P.F.M. and Wolter, C., (2016) Chapter Eleven - Effective River Restoration in the 21st Century: From Trial and Error to Novel Evidence-Based Approaches. In: A.J. Dumbrell, R.L. Kordas and G. Woodward, eds., *Advances in Ecological Research*, Large-Scale Ecology: Model Systems to Global Perspectives. [online] Academic Press, pp.535–611. Available at: <https://www.sciencedirect.com/science/article/pii/S0065250416300253> [Accessed 1 Apr. 2021].

Fuiman, L., (1983) Growth gradients in fish larvae. *Journal of fish biology*, 231, pp.117–123.

Gallagher, C.P. and Dick, T.A., (2015) Winter feeding ecology and the importance of cannibalism in juvenile and adult burbot (*Lota lota*) from the Mackenzie Delta, Canada. *Hydrobiologia*, 7571, pp.73–88.

Gallardo, B. and Aldridge, D.C., (2015) Is Great Britain heading for a Ponto–Caspian invasional meltdown? *Journal of Applied Ecology*, 521, pp.41–49.

Gardunio, E., (2014) *Jumping and swimming performance of burbot and white sucker: Implications for barrier design*. Master's Thesis. Colorado State University.

Garner, G., Hannah, D.M. and Watts, G., (2017a) Climate change and water in the UK: Recent scientific evidence for past and future change. *Progress in Physical Geography: Earth and Environment*, 412, pp.154–170.

Garner, G., Malcolm, I.A., Sadler, J.P. and Hannah, D.M., (2017b) The role of riparian vegetation density, channel orientation and water velocity in determining river temperature dynamics. *Journal of Hydrology*, 553, pp.471–485.

Geeraerts, C., Ovidio, M., Verbiest, H., Buysse, D., Coeck, J., Belpaire, C. and Philippart, J.-C., (2007) Mobility of individual roach *Rutilus rutilus* (L.) in three weir-fragmented Belgian rivers. In: P.R. Almeida, B.R. Quintella, M.J. Costa and A. Moore, eds., *Developments in Fish Telemetry*, Developments in Hydrobiology 195. Dordrecht: Springer Netherlands, pp.143–153.

de Gelas, K., Van Houdt, J.K., Hellemans, B., Charleroy, D., van Vessem, J. and Volckaert, F.A.M., (2007) *Genetische monitoring van bronpopulaties voor herintroductie van de kwabaal in het Vlaamse Gewest: Genetische diversiteit en differentiatie in het Maasbekken*. Linkebeek: Instituut voor Natuur en Bosonderzoek.

George, A.L., Hamilton, M.T. and Alford, K.F., (2013) We all live downstream: engaging partners and visitors in freshwater fish reintroduction programmes. *International Zoo Yearbook*, 471, pp.140–150.

George, A.L., Kuhajda, B.R., Williams, J.D., Cantrell, M.A., Rakes, P.L. and Shute, J.R., (2009) Guidelines for Propagation and Translocation for Freshwater Fish Conservation. *Fisheries*, 3411, pp.529–545.

Ghan, D. and Sprules, W.G., (1993) Diet, prey selection, and growth of larval and juvenile burbot *Lota lota* (L.). *Journal of Fish Biology*, 421, pp.47–64.

Gilvear, D.J., Spray, C.J. and Casas-Mulet, R., (2013) River rehabilitation for the delivery of multiple ecosystem services at the river network scale. *Journal of environmental management*, 126, pp.30–43.

Glińska-Lewczuk, K., Burandt, P., Kujawa, R., Kobus, S., Obolewski, K., Dunalska, J., Grabowska, M., Lew, S. and Chormański, J., (2016) Environmental factors structuring fish communities in floodplain lakes of the undisturbed system of the Biebrza River. *Water*, 84, p.146.

Godwin, H., (1978) *Fenland: its ancient past and uncertain future*. Cambridge, UK: Cambridge University Press.

Godwin, H., (1984) *The history of the British flora: a factual basis for phytogeography*. 2nd ed. Cambridge: Cambridge University Press.

Golovanov, V.K., (2013) Ecophysiological patterns of distribution and behavior of freshwater fish in thermal gradients. *Journal of Ichthyology*, 534, pp.252–280.

Gore, J.A. and Hamilton, S.W., (1996) Comparison of Flow-Related Habitat Evaluations Downstream of Low-Head Weirs on Small and Large Fluvial Ecosystems. *Regulated Rivers: Research & Management*, 124–5, pp.459–469.

Gorski, K., De Leeuw, J.J., Winter, H.V., Vekhov, D.A., Minin, A.E., Buijse, A.D. and Nagelkerke, L.A., (2011) Fish recruitment in a large, temperate floodplain: the importance of annual flooding, temperature and habitat complexity. *Freshwater Biology*, 5611, pp.2210–2225.

Gostner, W., Alp, M., Schleiss, A.J. and Robinson, C.T., (2013) The hydro-morphological index of diversity: a tool for describing habitat heterogeneity in river engineering projects. *Hydrobiologia*, 7121, pp.43–60.

Gozlan, R.E., Karimov, B.K., Zadereev, E., Kuznetsova, D. and Brucet, S., (2019) Status, trends, and future dynamics of freshwater ecosystems in Europe and Central Asia. *Inland Waters*, 91, pp.78–94.

Grabowski, T., Young, S.P. and Cott, P.A., (2020) Looking for love under the ice: Using passive acoustics to detect burbot (*Lota lota*: Gadidae) spawning activity. *Freshwater Biology*, 651, pp.37–44.

Graf, R. and Wrzesiński, D., (2020) Detecting Patterns of Changes in River Water Temperature in Poland. *Water*, 125, p.1327.

Gray, D. and Harding, J.S., (2007) Braided river ecology. *Science for conservation*, 279.

Gregg, W.W. and Rose, F.L., (1982) The effects of aquatic macrophytes on the stream microenvironment. *Aquatic botany*, 14, pp.309–324.

Gregory, S.V., Gurnell, A., Piégay, H. and Boyer, K., (2017) Dynamics of wood. In: *Methods in Stream Ecology*. Elsevier, pp.113–126.

Grift, R., Buijse, A., Van Densen, W., Machiels, M., Kranenbarg, J., Klein Breteler, J. and Backx, J., (2003) Suitable habitats for 0-group fish in rehabilitated floodplains along the lower River Rhine. *River Research and Applications*, 194, pp.353–374.

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borrelli, P., Cheng, L., Crochetiere, H., Ehalt Macedo, H., Filgueiras, R., Goichot, M., Higgins, J., Hogan, Z., Lip, B., McClain, M.E., Meng, J., Mulligan, M., Nilsson, C., Olden, J.D., Opperman, J.J., Petry, P., Reidy Liermann, C., Sáenz, L., Salinas-Rodríguez, S., Schelle, P., Schmitt, R.J.P., Snider, J., Tan, F., Tockner, K., Valdujo, P.H., van Soesbergen, A. and Zarfl, C., (2019) Mapping the world's free-flowing rivers. *Nature*, 5697755, pp.215–221.

Groom, B.P.K., Froend, R.H. and Mattiske, E.M., (2000) Impact of groundwater abstraction on a Banksia woodland, Swan Coastal Plain, Western Australia. *Ecological Management & Restoration*, 12, pp.117–124.

Grosberg, R.K., Vermeij, G.J. and Wainwright, P.C., (2012) Biodiversity in water and on land. *Current Biology*, 2221, pp.R900–R903.

Gumbel, E.J., (1941) The Return Period of Flood Flows. *The Annals of Mathematical Statistics*, 122, pp.163–190.

Gurnell, A., (2014) Plants as river system engineers. *Earth Surface Processes and Landforms*, 391, pp.4–25.

Gurnell, A., England, J. and Burgess-Gamble, L., (2019a) Trees and wood: working with natural river processes. *Water and Environment Journal*, 333, pp.342–352.

Gurnell, A.M., Angold, P.G. and Edwards, P.J., (1996) Extracting information from river corridor surveys. *Applied Geography*, 161, pp.1–19.

Gurnell, A.M. and Bertoldi, W., (2024) Plants and river morphodynamics: The emergence of fluvial biogeomorphology. *River Research and Applications*, 406, pp.887–942.

Gurnell, A.M. and Downs, P.W., (2021) The legacy of river channel modification in wadeable, lowland rivers: Exploring overdeep rivers in England. *Earth Surface Processes and Landforms*, 4615, pp.3016–3025.

Gurnell, A.M., England, J., Shuker, L. and Wharton, G., (2019b) The contribution of citizen science volunteers to river monitoring and management: International and national perspectives and the example of the MoRPh survey. *River Research and Applications*, 358, pp.1359–1373.

Gurnell, A.M., O'Hare, M.T., O'Hare, J.M., Scarlett, P. and Liffen, T.M., (2013) The geomorphological context and impact of the linear emergent macrophyte, *Sparganium erectum* L.: a statistical analysis of observations from British rivers. *Earth Surface Processes and Landforms*, 3815, pp.1869–1880.

Gurnell, A.M. and Shuker, L., (2022) *The MoRPh Survey Technical Reference Manual 2022 version*. [online] Available at: <https://modularriversurvey.org/citizen-science-help/> [Accessed 1 Jan. 2023].

Guthruf, J., Gerster, S. and Tschumi, P.A., (1990) The diet of burbot (*Lota lota* L.) in Lake Biel, Switzerland. *Archiv für Hydrobiologie*, 1191, pp.103–114.

Guti, G. and Pekarík, L., (2016) A brief overview of the long-term changes of fish fauna in the Slovak-Hungarian section of the Danube River. *Opuscula Zoologica (Budapest)*, 472, pp.203–211.

Gwinn, D.C., Beesley, L.S., Close, P., Gawne, B. and Davies, P.M., (2016) Imperfect detection and the determination of environmental flows for fish: challenges, implications and solutions. *Freshwater Biology*, 611, pp.172–180.

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

Hackney, P.A., (1973) *Ecology of the burbot Lota lota with special reference to its role in the Lake Opeongo fish community*. University of Toronto Toronto.

Hale, S.L. and Koprowski, J.L., (2018) Ecosystem-level effects of keystone species reintroduction: a literature review. *Restoration Ecology*, 263, pp.439–445.

Hammer, M.P., Bice, C.M., Hall, A., Frears, A., Watt, A., Whiterod, N.S., Beheregaray, L.B., Harris, J.O. and Zampatti, B.P., (2013) Freshwater fish conservation in the face of critical water shortages in the southern Murray–Darling Basin, Australia. *Marine and Freshwater Research*, 649, pp.807–821.

Hammond, D. and Pryce, A.R., (2007) *Climate change impacts and water temperature*. Environment Agency Science Report. Environment Agency.

Hanlon, H.M., Bernie, D., Carigi, G. and Lowe, J.A., (2021) Future changes to high impact weather in the UK. *Climatic Change*, 1663, p.50.

Hanna, D.E., Tomscha, S.A., Ouellet Dallaire, C. and Bennett, E.M., (2018) A review of riverine ecosystem service quantification: Research gaps and recommendations. *Journal of Applied Ecology*, 553, pp.1299–1311.

Hannaford, J., (2015) Climate-driven changes in UK river flows: A review of the evidence. *Progress in Physical Geography: Earth and Environment*, 391, pp.29–48.

Hannah, D.M., Malcolm, I.A., Soulsby, C. and Youngson, A.F., (2008) A comparison of forest and moorland stream microclimate, heat exchanges and thermal dynamics. *Hydrological Processes: An International Journal*, 227, pp.919–940.

Hansen, J., Lacis, A., Rind, D., Russell, G., Stone, P., Fung, I., Ruedy, R. and Lerner, J., (1984) Climate Sensitivity: Analysis of Feedback Mechanisms. In: *Climate Processes and Climate Sensitivity*. [online] American Geophysical Union (AGU), pp.130–163. Available at: <https://onlinelibrary.wiley.com/doi/abs/10.1029/GM029p0130> [Accessed 27 Feb. 2024].

Hardewig, I., Pörtner, H.O. and van Dijk, P., (2004) How does the cold stenothermal gadoid *Lota lota* survive high water temperatures during summer? *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology*, 1742, pp.149–156.

Hardie, S., (2003) Current status and ecology of the golden galaxias (*Galaxias auratus*).

Hardy, R. and Paragamian, V.L., (2013) A synthesis of Kootenai River Burbot stock history and future management goals. *Transactions of the American Fisheries Society*, 1426, pp.1662–1670.

Hares, C.J., Jonas, J.L. and Leonard, J.B.K., (2015) Diet analysis of burbot (*Lota lota*) from eastern Lake Michigan: 1996–2012. *Hydrobiologia*, 7571, pp.89–99.

Harrison, P.M., Gutowsky, L.F.G., Martins, E.G., Patterson, D.A., Cooke, S.J. and Power, M., (2016) Temporal plasticity in thermal-habitat selection of burbot *Lota lota* a diel-migrating winter-specialist. *Journal of Fish Biology*, 886, pp.2111–2129.

Harrison, P.M., Gutowsky, L.F.G., Martins, E.G., Patterson, D.A., Leake, A., Cooke, S.J. and Power, M., (2013) Diel vertical migration of adult burbot: a dynamic trade-off among feeding opportunity, predation avoidance, and bioenergetic gain. *Canadian Journal of Fisheries and Aquatic Sciences*. [online] Available at: <https://cdnsiencepub.com/doi/abs/10.1139/cjfas-2013-0183> [Accessed 5 Apr. 2021].

Harsányi, A. and Aschenbrenner, P., (1992) Die Rutte *Lota lota* (Linnaeus, 1758)–Biologie und Aufzucht. *Fischer & Teichwirt*, 101992, pp.372–376.

Harvey, G.L. and Bertoldi, W., (2015) Dynamic riverine landscapes: the role of ecosystem engineers. *Earth Surface Processes and Landforms*, 4012, pp.1701–1704.

Harvey, G.L., Henshaw, A.J., Parker, C. and Sayer, C.D., (2018) Re-introduction of structurally complex wood jams promotes channel and habitat recovery from overwidening: Implications for river conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 282, pp.395–407.

Harvey, G.L. and Wallerstein, N.P., (2009) Exploring the interactions between flood defence maintenance works and river habitats: the use of River Habitat Survey data. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 196, pp.689–702.

Harvey, J., Gomez-Velez, J., Schmadel, N., Scott, D., Boyer, E., Alexander, R., Eng, K., Golden, H., Kettner, A., Konrad, C., Moore, R., Pizzuto, J., Schwarz, G., Soulsby, C. and Choi, J., (2019) How Hydrologic Connectivity Regulates Water Quality in River Corridors. *JAWRA Journal of the American Water Resources Association*, 552, pp.369–381.

Harwood, A.J., Perrow, M.R., Sayer, C.D., Piper, A.T., Berridge, R.J., Patmore, I.R., Emson, D. and Cooper, G., (2022) Catchment-scale distribution, abundance, habitat use, and movements of European eel (*Anguilla anguilla* L.) in a small UK river: Implications for conservation management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 325, pp.797–816.

Hauer, C., Skrame, K. and Fuhrmann, M., (2021) Hydromorphological assessment of the Vjosa river at the catchment scale linking glacial history and fluvial processes. *Catena*, 207, p.105598.

Havrdová, A., Douda, J. and Doudová, J., (2023) Threats, biodiversity drivers and restoration in temperate floodplain forests related to spatial scales. *Science of the Total Environment*, 854, p.158743.

Hawkins, S.A., Brady, D., Mayhew, M., Smith, D., Iversen, S.V., Lipscombe, S., White, C., Eagle, A. and Convery, I., (2020) Community perspectives on the reintroduction of Eurasian lynx (*Lynx lynx*) to the UK. *Restoration Ecology*, 286, pp.1408–1418.

Hayes, M.F. and Banish, N.P., (2017) Translocation and reintroduction of native fishes: a review of bull trout *Salvelinus confluentus* with applications for future reintroductions. *Endangered Species Research*, 34, pp.191–209.

He, F., Arora, R. and Mansour, I., (2023) Multispecies assemblages and multiple stressors: Synthesizing the state of experimental research in freshwaters. *WIREs Water*, 103, p.e1641.

He, Z., Wu, W. and Douglas Shields Jr, F., (2009) Numerical analysis of effects of large wood structures on channel morphology and fish habitat suitability in a Southern US sandy creek. *Ecohydrology*, 23, pp.370–380.

Heinrich, W., (2009) Peregrine falcon recovery in the continental United States, 1974–1999, with notes on related programs of the Peregrine Fund. *Peregrine Falcon Populations in the 21st Century*, pp.431–444.

Hellmann, J.J., Byers, J.E., Bierwagen, B.G. and Dukes, J.S., (2008) Five potential consequences of climate change for invasive species. *Conservation biology*, 223, pp.534–543.

Hempel, C.A., Peinert, B., Beermann, A.J., Elbrecht, V., Macher, J.-N., Macher, T.-H., Jacobs, G. and Leese, F., (2020) Using environmental DNA to monitor the

reintroduction success of the Rhine sculpin (*Cottus rhenanus*) in a restored stream. *Frontiers in Ecology and Evolution*, 8, p.497255.

Henderson, R., Chips, M., Cornwell, N., Hitchins, P., Holden, B., Hurley, S., Parsons, S.A., Wetherill, A. and Jefferson, B., (2008) Experiences of algae in UK waters: a treatment perspective. *Water and Environment Journal*, 223, pp.184–192.

Hensler, S.R., Jude, D.J. and He, J., (2008) Burbot growth and diets in Lakes Michigan and Huron: an ongoing shift from native species to round gobies. In: *American Fisheries Society Symposium*. American Fisheries Society, p.91.

Herrera-Pantoja, M., Hiscock, K. and Boar, R., (2012) The potential impact of climate change on groundwater-fed wetlands in eastern England. *Ecohydrology*, 54, pp.401–413.

Hewson, L., (1955) Age, maturity, spawning and food of burbot, *Lota lota*, in Lake Winnipeg. *Journal of the Fisheries Board of Canada*, 126, pp.930–940.

Hickerson, B.T., Grube, E.R., Mosher, K.R. and Robinson, A.T., (2021) Successful Restoration of a Native Fish Assemblage in the Blue River, Arizona. *North American Journal of Fisheries Management*, 413, pp.746–756.

Hirsch, P.E. and Fischer, P., (2008) Interactions between native juvenile burbot (*Lota lota*) and the invasive spinycheek crayfish (*Orconectes limosus*) in a large European lake. *Canadian Journal of Fisheries and Aquatic Sciences*. [online] Available at: <https://cdnsiencepub.com/doi/abs/10.1139/F08-162> [Accessed 22 Dec. 2020].

Hochleithner, M., (2020) *Quappen (Lotidae): Biologie und Aquakultur*. Kitzbühel, Austria: AquaTech Publications.

Höckendorff, S., Tonkin, J.D., Haase, P., Bunzel-Drüke, M., Zimball, O., Scharf, M. and Stoll, S., (2017) Characterizing fish responses to a river restoration over 21 years based on species' traits. *Conservation Biology*, 315, pp.1098–1108.

Hodder, K.H. and Bullock, J.M., (1997) Translocations of native species in the UK: implications for biodiversity. *Journal of Applied Ecology*, pp.547–565.

Hoffmann, C.C., Pedersen, M.L., Kronvang, B. and Øvig, L., (1998) Restoration of the Rivers Brede, Cole and Skerne: a joint Danish and British EU-LIFE demonstration project, IV—implications for nitrate and iron transformation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 81, pp.223–240.

Hofmann, N. and Fischer, P., (2001) Seasonal changes in abundance and age structure of burbot *Lota lota* (L.) and stone loach *Barbatula barbatula* (L.) in the littoral zone of a large pre-alpine lake. *Ecology of Freshwater Fish*, 101, pp.21–25.

Hofmann, N. and Fischer, P., (2002) Temperature Preferences and Critical Thermal Limits of Burbot: Implications for Habitat Selection and Ontogenetic Habitat Shift. *Transactions of the American Fisheries Society*, 1316, pp.1164–1172.

Hofmann, N. and Fischer, P., (2003) Impact of temperature on food intake and growth in juvenile burbot. *Journal of Fish Biology*, 635, pp.1295–1305.

Hogberg, N.P., Skorupski Jr., J.A. and Hochhalter, S.J., (2021) Natural Recruitment Potential of a Reintroduced Shovelnose Sturgeon Population in the Bighorn River, Wyoming. *North American Journal of Fisheries Management*, 415, pp.1288–1298.

Hohensinner, S., Habersack, H., Jungwirth, M. and Zauner, G., (2004) Reconstruction of the characteristics of a natural alluvial river–floodplain system and hydromorphological changes following human modifications: the Danube River (1812–1991). *River Research and Applications*, 201, pp.25–41.

Hoijsink, R., (1998) *Habitat Geschiktheids Indexmodel van de kwabaal (Lota lota)*. MSc. IJsselland University of Applied Sciences.

Holden, J., Haygarth, P.M., Dunn, N., Harris, J., Harris, R.C., Humble, A., Jenkins, A., MacDonald, J., McGonigle, D.F., Meacham, T., Orr, H.G., Pearson, P.L., Ross, M., Sapiets, A. and Benton, T., (2017) Water quality and UK agriculture: challenges and opportunities. *WIREs Water*, 42, p.e1201.

Holmes, N.T.H. and Janes, M., (2012) The History, Development, Role and Future of River Restoration Centres. In: *River Conservation and Management*. [online] John Wiley & Sons, Ltd, pp.285–293. Available at: <https://onlinelibrary.wiley.com/doi/abs/10.1002/9781119961819.ch23> [Accessed 13 May 2025].

Holmes, N.T.H. and Nielsen, M.B., (1998) Restoration of the rivers Brede, Cole and Skerne: a joint Danish and British EU-LIFE demonstration project, I—Setting up and delivery of the project. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 81, pp.185–196.

Holzer, S., (2008) *European fish species: taxa and guild classification regarding fish-based assessment methods*. PhD. University of Natural Resources and Life Sciences.

House, A.R., Thompson, J.R., Roberts, C., de Smeth, K., Old, G. and Acreman, M.C., (2017) Projecting impacts of climate change on habitat availability in a macrophyte dominated Chalk River. *Ecohydrology*, 104, p.e1823.

Howden, N.J.K., Burt, T.P., Worrall, F., Mathias, S.A. and Whelan, M.J., (2013) Farming for Water Quality: Balancing Food Security and Nitrate Pollution in UK River Basins. *Annals of the Association of American Geographers*, 1032, pp.397–407.

Howes, G.J., (1991) Biogeography of Gadoid Fishes. *Journal of Biogeography*, 186, p.595.

Hrachowitz, M., Soulsby, C., Imholt, C., Malcolm, I.A. and Tetzlaff, D., (2010) Thermal regimes in a large upland salmon river: a simple model to identify the influence of landscape controls and climate change on maximum temperatures. *Hydrological Processes*, 2423, pp.3374–3391.

Hudson, L.N., Newbold, T., Contu, S., Hill, S.L.L., Lysenko, I., De Palma, A., Phillips, H.R.P., Alhusseini, T.I., Bedford, F.E., Bennett, D.J., Booth, H., Burton, V.J., Chng, C.W.T., Choimes, A., Correia, D.L.P., Day, J., Echeverría-Londoño, S., Emerson, S.R., Gao, D., Garon, M., Harrison, M.L.K., Ingram, D.J., Jung, M., Kemp, V., Kirkpatrick, L., Martin, C.D., Pan, Y., Pask-Hale, G.D., Pynegar, E.L., Robinson, A.N., Sanchez-Ortiz, K., Senior, R.A., Simmons, B.I., White, H.J., Zhang, H., Aben, J., Abrahamczyk, S., Adum, G.B., Aguilar-Barquero, V., Aizen, M.A., Albertos, B., Alcalá, E.L., Del Mar Alguacil, M., Alignier, A., Ancrenaz, M., Andersen, A.N., Arbeláez-Cortés, E., Armbrrecht, I., Arroyo-Rodríguez, V., Aumann, T., Axmacher, J.C., Azhar, B., Azpiroz, A.B., Baeten, L., Bakayoko, A., Báldi, A., Banks, J.E., Baral, S.K., Barlow, J., Barratt, B.I.P., Barrico, L., Bartolommei, P., Barton, D.M., Basset, Y., Batáry, P., Bates, A.J., Baur, B., Bayne, E.M., Beja, P., Benedick, S., Berg, Å., Bernard, H., Berry, N.J., Bhatt, D., Bicknell, J.E., Bihn, J.H., Blake, R.J., Bobo, K.S., Bóçon, R., Boekhout, T., Böhning-Gaese, K., Bonham, K.J., Borges, P.A.V., Borges, S.H., Boutin, C., Bouyer, J., Bragagnolo, C., Brandt, J.S., Brearley, F.Q., Brito, I., Bros, V., Brunet, J., Buczkowski, G., Buddle, C.M., Bugter, R., Buscardo, E., Buse, J., Cabra-García, J., Cáceres, N.C., Cagle, N.L., Calviño-Cancela, M., Cameron, S.A., Canello, E.M., Caparrós, R., Cardoso, P., Carpenter, D., Carrijo, T.F., Carvalho, A.L., Cassano, C.R., Castro, H., Castro-Luna, A.A., Rolando, C.B., Cerezo, A., Chapman, K.A., Chauvat, M., Christensen, M., Clarke, F.M., Cleary, D.F.R., Colombo, G., Connop, S.P., Craig, M.D., Cruz-López, L., Cunningham, S.A., D'Aniello, B., D'Cruze, N., Da Silva, P.G., Dallimer, M., Danquah, E., Darvill, B., Dauber, J., Davis, A.L.V., Dawson, J., De Sassi, C., De Thoisy, B., Deheuvels, O., Dejean, A., Devineau, J., Diekötter, T., Dolia, J.V., Domínguez, E., Dominguez-Haydar, Y., Dorn, S., Draper, I., Dreber, N., Dumont, B., Dures, S.G., Dynesius, M., Edenius, L., Eggleton, P., Eigenbrod, F., Elek, Z., Entling, M.H., Esler, K.J., De Lima, R.F., Faruk, A., Farwig, N., Fayle, T.M., Felicioli, A., Felton, A.M., Fensham, R.J., Fernandez, I.C., Ferreira, C.C., Ficetola, G.F., Fiera, C., Filgueiras, B.K.C., Firincioğlu, H.K., Flaspohler, D., Floren, A., Fonte, S.J., Fournier, A., Fowler, R.E., Franzén, M., Fraser, L.H., Fredriksson, G.M., Freire, G.B., Frizzo, T.L.M., Fukuda, D., Furlani, D., Gaigher, R., Ganzhorn, J.U., García, K.P., Garcia-R, J.C., Garden, J.G., Garilleti, R., Ge, B., Gendreau-Berthiaume, B., Gerard, P.J., Gheler-Costa, C., Gilbert, B., Giordani, P., Giordano, S., Golodets, C., Gomes, L.G.L., Gould, R.K., Goulson, D., Gove, A.D., Granjon, L., Grass, I., Gray, C.L., Grogan, J., Gu, W., Guardiola, M., Gunawardene, N.R., Gutierrez, A.G., Gutiérrez-Lamus, D.L., Haarmeyer, D.H., Hanley, M.E., Hanson, T., Hashim, N.R., Hassan, S.N., Hatfield, R.G., Hawes, J.E., Hayward, M.W., Hébert, C., Helden, A.J., Henden, J., Henschel, P., Hernández, L., Herrera, J.P., Herrmann, F., Herzog, F., Higuera-Díaz, D., Hilje, B., Höfer, H., Hoffmann, A., Horgan, F.G., Hornung, E., Horváth, R., Hylander, K., Isaacs-Cubides, P., Ishida, H., Ishitani, M., Jacobs, C.T., Jaramillo, V.J., Jauker, B., Hernández, F.J., Johnson, M.F., Jolli, V., Jonsell, M., Juliani, S.N., Jung, T.S., Kapoor, V., Kappes, H., Kati, V., Katovai, E., Kellner, K., Kessler, M., Kirby, K.R., Kittle, A.M., Knight, M.E., Knop, E., Kohler, F., Koivula, M., Kolb, A., Kone, M., Kőrösi, Á., Krauss, J., Kumar, A., Kumar, R., Kurz, D.J., Kutt, A.S., Lachat, T., Lantschner, V., Lara, F., Lasky, J.R., Latta, S.C., Laurance, W.F., Lavelle, P., Le Féon, V., LeBuhn, G., Légaré, J., Lehouck, V., Lencinas, M.V., Lentini, P.E., Letcher, S.G., Li, Q., Litchwark, S.A., Littlewood, N.A., Liu, Y., Lo-Man-Hung, N., López-Quintero, C.A., Louhaichi, M., Lövei, G.L., Lucas-Borja, M.E., Luja, V.H., Luskin, M.S., MacSwiney, G., M.C., Maeto, K., Magura, T., Mallari, N.A., Malone, L.A., Malonza, P.K., Malumbres-Olarte, J., Mandujano, S., Måren, I.E., Marin-Spiotta, E., Marsh, C.J., Marshall, E.J.P., Martínez,

E., Martínez Pastur, G., Moreno Mateos, D., Mayfield, M.M., Mazimpaka, V., McCarthy, J.L., McCarthy, K.P., McFrederick, Q.S., McNamara, S., Medina, N.G., Medina, R., Mena, J.L., Mico, E., Mikusinski, G., Milder, J.C., Miller, J.R., Miranda-Esquivel, D.R., Moir, M.L., Morales, C.L., Muchane, M.N., Muchane, M., Mudri-Stojnic, S., Munira, A.N., Muñoz-Alonso, A., Munyekenye, B.F., Naidoo, R., Naithani, A., Nakagawa, M., Nakamura, A., Nakashima, Y., Naoe, S., Nates-Parra, G., Navarrete Gutierrez, D.A., Navarro-Iriarte, L., Ndag'ang'a, P.K., Neuschulz, E.L., Ngai, J.T., Nicolas, V., Nilsson, S.G., Noreika, N., Norfolk, O., Noriega, J.A., Norton, D.A., Nöske, N.M., Nowakowski, A.J., Numa, C., O'Dea, N., O'Farrell, P.J., Oduro, W., Oertli, S., Ofori-Boateng, C., Oke, C.O., Oostra, V., Osgathorpe, L.M., Otavo, S.E., Page, N.V., Paritsis, J., Parra-H, A., Parry, L., Pe'er, G., Pearman, P.B., Pelegrin, N., Péliissier, R., Peres, C.A., Peri, P.L., Persson, A.S., Petanidou, T., Peters, M.K., Pethiyagoda, R.S., Phalan, B., Philips, T.K., Pillsbury, F.C., Pincheira-Ulbrich, J., Pineda, E., Pino, J., Pizarro-Araya, J., Plumptre, A.J., Poggio, S.L., Politi, N., Pons, P., Poveda, K., Power, E.F., Presley, S.J., Proença, V., Quaranta, M., Quintero, C., Rader, R., Ramesh, B.R., Ramirez-Pinilla, M.P., Ranganathan, J., Rasmussen, C., Redpath-Downing, N.A., Reid, J.L., Reis, Y.T., Rey Benayas, J.M., Rey-Velasco, J.C., Reynolds, C., Ribeiro, D.B., Richards, M.H., Richardson, B.A., Richardson, M.J., Ríos, R.M., Robinson, R., Robles, C.A., Römbke, J., Romero-Duque, L.P., Rös, M., Rosselli, L., Rossiter, S.J., Roth, D.S., Roulston, T.H., Rousseau, L., Rubio, A.V., Ruel, J., Sadler, J.P., Sáfián, S., Saldaña-Vázquez, R.A., Sam, K., Samnegård, U., Santana, J., Santos, X., Savage, J., Schellhorn, N.A., Schilthuizen, M., Schmiedel, U., Schmitt, C.B., Schon, N.L., Schüepp, C., Schumann, K., Schweiger, O., Scott, D.M., Scott, K.A., Sedlock, J.L., Seefeldt, S.S., Shahabuddin, G., Shannon, G., Sheil, D., Sheldon, F.H., Shochat, E., Siebert, S.J., Silva, F.A.B., Simonetti, J.A., Slade, E.M., Smith, J., Smith-Pardo, A.H., Sodhi, N.S., Somarriba, E.J., Sosa, R.A., Soto Quiroga, G., St-Laurent, M., Starzomski, B.M., Stefanescu, C., Steffan-Dewenter, I., Stouffer, P.C., Stout, J.C., Strauch, A.M., Struebig, M.J., Su, Z., Suarez-Rubio, M., Sugiura, S., Summerville, K.S., Sung, Y., Sutrisno, H., Svenning, J., Teder, T., Threlfall, C.G., Tiitsaar, A., Todd, J.H., Tonietto, R.K., Torre, I., Tóthmérész, B., Tscharnkte, T., Turner, E.C., Tylanakis, J.M., Uehara-Prado, M., Urbina-Cardona, N., Vallan, D., Vanbergen, A.J., Vasconcelos, H.L., Vassilev, K., Verboven, H.A.F., Verdasca, M.J., Verdú, J.R., Vergara, C.H., Vergara, P.M., Verhulst, J., Virgilio, M., Vu, L.V., Waite, E.M., Walker, T.R., Wang, H., Wang, Y., Watling, J.I., Weller, B., Wells, K., Westphal, C., Wiafe, E.D., Williams, C.D., Willig, M.R., Woinarski, J.C.Z., Wolf, J.H.D., Wolters, V., Woodcock, B.A., Wu, J., Wunderle, J.M., Yamaura, Y., Yoshikura, S., Yu, D.W., Zaitsev, A.S., Zeidler, J., Zou, F., Collen, B., Ewers, R.M., Mace, G.M., Purves, D.W., Scharlemann, J.P.W. and Purvis, A., (2017) The database of the PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) project. *Ecology and Evolution*, 71, pp.145–188.

Huff, D.D., (2013) Examining genetic diversity, outbreeding depression, and local adaptation with slimy sculpin re-introductions in the southeast Minnesota Driftless Region, USA. In: *Global Re-introduction Perspectives: 2013. Further case studies from around the globe*, Global Re-introduction Perspectives. Luxembourg: IUCN, p.10.

Huisman, F., O'Sullivan, R., Marini, C. and Binnberg, J., (2017) Misreading the marshes: past and present perceptions of the East Anglian Fens, UK.

Hunter, R., (1975) Water moulds of the river Great Ouse and its tributaries. *Transactions of the British Mycological Society*, 651, pp.101–108.

Idzelis, A., (1979) Response of soviet Lithuania to environmental problems in the coastal zone. *Journal of Baltic Studies*, 104, pp.299–308.

Imbers, J., Lopez, A., Huntingford, C. and Allen, M.R., (2013) Testing the robustness of the anthropogenic climate change detection statements using different empirical models. *Journal of Geophysical Research: Atmospheres*, 1188, pp.3192–3199.

Irvine, R.D., (2017) Anthropocene East Anglia. *The Sociological Review*, 651_suppl, pp.154–170.

IUCN, (1987) *IUCN Position Statement on the Translocation of Living organisms: Introductions, Re-introductions, and Re-stocking*. [online] Available at: <http://www.iucnsscrg.org/> [Accessed 5 Jan. 2021].

IUCN, (1998) *Guidelines for Reintroductions*. Gland, Switzerland: IUCN/SSC Reintroduction Specialist Group.

IUCN, (2012) *Lota lota: NatureServe: The IUCN Red List of Threatened Species 2013: e.T135675A18233691*. Available at: <http://www.iucnredlist.org/details/135675/0> [Accessed 4 Jan. 2021].

IUCN, (2013) *Guidelines for Reintroductions and Other Conservation Translocations*. Gland, Switzerland: IUCN/SSC Reintroduction Specialist Group.

Jachowski, D., Slotow, R., Angermeier, P. and Millspaugh, J., (2016) Animal Reintroduction in the Anthropocene. In: D. Jachowski, R. Slotow, P. Angermeier and J. Millspaugh, eds., *Reintroduction of Fish and Wildlife Populations*. Oakland, California: University of California Press, pp.1–4.

Jackson, F.L., Hannah, D.M., Ouellet, V. and Malcolm, I.A., (2021) A deterministic river temperature model to prioritize management of riparian woodlands to reduce summer maximum river temperatures. *Hydrological Processes*, 358, p.e14314.

Jackson, J.R., VanDeValk, A.J., Forney, J.L., Lantry, B.F., Brooking, T.E. and Rudstam, L.G., (2008) Long-term trends in burbot abundance in Oneida Lake, New York: life at the southern edge of the range in an era of climate change. In: *American Fisheries Society Symposium*. American Fisheries Society, p.131.

Jacobs, G.R., Madenjian, C.P., Bunnell, D.B. and Holuszko, J.D., (2010) Diet of lake trout and burbot in Northern Lake Michigan during spring: Evidence of ecological interaction. *Journal of Great Lakes Research*, 362, pp.312–317.

Jafari, M. and Ansari-Pour, N., (2019) Why, When and How to Adjust Your P Values? *Cell Journal (Yakhteh)*, 204, pp.604–607.

Jäger, T., Nellen, W., Schöfer, W. and Shodjai, F., (1981) *Influence of salinity and temperature on early life stages of Coregonus albula, C. lavaretus, R. rutilus and L. lota*. Copenhagen: International Council for the Exploration of the Sea, pp.345–348.

Jarić, I., Lennox, R.J., Kalinkat, G., Cvijanović, G. and Radinger, J., (2019) Susceptibility of European freshwater fish to climate change: Species profiling based

on life-history and environmental characteristics. *Global Change Biology*, 252, pp.448–458.

JNCC, (2023) *UKBI - B7. Surface Water Status*. [online] Available at: <https://jncc.gov.uk/our-work/ukbi-b7-surface-water-status/> [Accessed 24 Mar. 2021].

Jobling, M., (2002) Environmental factors and rates of development and growth. In: P.J.B. Hart and J.D. Reynolds, eds., *Handbook of Fish Biology and Fisheries*. Oxford, UK: Blackwell Science, pp.97–122.

Johnson, M.F., Albertson, L.K., Algar, A.C., Dugdale, S.J., Edwards, P., England, J., Gibbins, C., Kazama, S., Komori, D., MacColl, A.D., and others, (2024) Rising water temperature in rivers: Ecological impacts and future resilience. *Wiley Interdisciplinary Reviews: Water*, 114, p.e1724.

Johnson, M.F. and Wilby, R.L., (2015) Seeing the landscape for the trees: Metrics to guide riparian shade management in river catchments. *Water Resources Research*, 515, pp.3754–3769.

Johnson, M.F., Wilby, R.L. and Toone, J.A., (2014) Inferring air–water temperature relationships from river and catchment properties. *Hydrological Processes*, 286, pp.2912–2928.

Johnson, S.A., Ober, H.K. and Adams, D.C., (2017) Are keystone species effective umbrellas for habitat conservation? A spatially explicit approach. *Journal for Nature Conservation*, 37, pp.47–55.

Johnson, S.L. and Penaluna, B.E., (2019) Climate change and interactions with multiple stressors in rivers. In: *Multiple stressors in river ecosystems*. Elsevier, pp.23–44.

Johnson, T., (1981) Biotopwechsel und lebensweise der quappe (*Lota lota* L.) in der Bottnischen See und einem kuestenfluss. *Oesterreichs Fischerei*, 34, pp.6–9.

Johnstone, D.W.M. and Horan, N.J., (1996) Institutional developments, standards and river quality: A UK history and some lessons for industrialising countries. *Water Science and Technology*, 333, pp.211–222.

Jolly, M.T., Aprahamian, M.W., Hawkins, S.J., Henderson, P.A., Hillman, R., O'Maoiléidigh, N., Maitland, P.S., Piper, R. and Genner, M.J., (2012) Population genetic structure of protected allis shad (*Alosa alosa*) and twaite shad (*Alosa fallax*). *Marine Biology*, 1593, pp.675–687.

Jones, D.R., Kiceniuk, J.W. and Bamford, O.S., (1974) Evaluation of the swimming performance of several fish species from the Mackenzie River. *Journal of the Fisheries Board of Canada*, 3110, pp.1641–1647.

Jones, J., Börger, L., Tummers, J., Jones, P., Lucas, M., Kerr, J., Kemp, P., Bizzi, S., Consuegra, S., Marcello, L., Vowles, A., Belletti, B., Verspoor, E., Van de Bund, W., Gough, P. and Garcia de Leaniz, C., (2019) A comprehensive assessment of stream fragmentation in Great Britain. *Science of The Total Environment*, 673, pp.756–762.

Josefsson, M. and Andersson, B., (2001) The Environmental Consequences of Alien Species in the Swedish Lakes Mälaren, Hjälmaren, Vänern and Vättern. *AMBIO: A Journal of the Human Environment*, 308, pp.514–521.

Juanes, F., Gephard, S. and Beland, K.F., (2004) Long-term changes in migration timing of adult Atlantic salmon (*Salmo salar*) at the southern edge of the species distribution. *Canadian Journal of Fisheries and Aquatic Sciences*, 6112, pp.2392–2400.

Jude, D.J., Wang, Y., Hensler, S.R. and Janssen, J., (2013) Burbot Early Life History Strategies in the Great Lakes. *Transactions of the American Fisheries Society*, 1426, pp.1733–1745.

Kaandorp, V.P., Doornenbal, P.J., Kooi, H., Broers, H.P. and de Louw, P.G., (2019) Temperature buffering by groundwater in ecologically valuable lowland streams under current and future climate conditions. *Journal of Hydrology X*, 3, p.100031.

Kahilainen, K. and Lehtonen, H., (2003) Piscivory and prey selection of four predator species in a whitefish dominated subarctic lake. *Journal of Fish Biology*, 633, pp.659–672.

Kail, J., Brabec, K., Poppe, M. and Januschke, K., (2015) The effect of river restoration on fish, macroinvertebrates and aquatic macrophytes: A meta-analysis. *Ecological Indicators*, 58, pp.311–321.

Kainz, E. and Gollmann, H.P., (1996) Laichgewinnung, Erbrütung und erste Aufzuchtversuche bei Aalrutten (*Lota lota*). *Osterreichs Fischerei*, 49, pp.154–159.

Kaiser, N.N., Feld, C.K. and Stoll, S., (2020) Does river restoration increase ecosystem services? *Ecosystem Services*, 46, p.101206.

Kalny, G., Laaha, G., Melcher, A., Trimmel, H., Weihs, P. and Rauch, H.P., (2017) The influence of riparian vegetation shading on water temperature during low flow conditions in a medium sized river. *Knowledge & Management of Aquatic Ecosystems*, 418, p.5.

Katzman, L. and Zale, A., (2000) Age and growth of an unexploited burbot population in Upper Red Rock Lake, Montana. *Burbot biology, ecology, and management*, pp.139–146.

Kay, A.L., Griffin, A., Rudd, A.C., Chapman, R.M., Bell, V.A. and Arnell, N.W., (2021) Climate change effects on indicators of high and low river flow across Great Britain. *Advances in Water Resources*, 151, p.103909.

Kechavarzi, C., Dawson, Q., Bartlett, M. and Leeds-Harrison, P., (2010a) The role of soil moisture, temperature and nutrient amendment on CO₂ efflux from agricultural peat soil microcosms. *Geoderma*, 1543–4, pp.203–210.

Kechavarzi, C., Dawson, Q. and Leeds-Harrison, P., (2010b) Physical properties of low-lying agricultural peat soils in England. *Geoderma*, 1543–4, pp.196–202.

Keller, E.A., (1976) Channelization: Environmental, Geomorphic, and Engineering Aspects. In: *Geomorphology and Engineering*. Routledge.

Kelly, L.A. and Hassall, C., (2018) The spatial ecology of phytoplankton blooms in UK canals. *Inland Waters*, 84, pp.422–433.

Kendon, M., Doherty, A., Hollis, D., Carlisle, E., Packman, S., McCarthy, M., Jevrejeva, S., Matthews, A., Williams, J., Garforth, J. and Sparks, T., (2024) State of the UK Climate 2023. *International Journal of Climatology*, 44, pp.1–117.

Kendon, M., McCarthy, M., Jevrejeva, S., Matthews, A., Williams, J., Sparks, T. and West, F., (2023) State of the UK Climate 2022. *International Journal of Climatology*, 43S1, pp.1–83.

Kennedy-Asser, A.T., Andrews, O., Mitchell, D.M. and Warren, R.F., (2021) Evaluating heat extremes in the UK Climate Projections (UKCP18). *Environmental Research Letters*, 161, p.014039.

Keruzoré, A.A., Willby, N.J. and Gilvear, D.J., (2013a) The role of lateral connectivity in the maintenance of macrophyte diversity and production in large rivers. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 232, pp.301–315.

Keruzoré, A.A., Willby, N.J. and Gilvear, D.J., (2013b) The role of lateral connectivity in the maintenance of macrophyte diversity and production in large rivers. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 232, pp.301–315.

Kiffney, P.M., Pess, G.R., Anderson, J.H., Faulds, P., Burton, K. and Riley, S.C., (2009) Changes in fish communities following recolonization of the Cedar River, WA, USA by Pacific salmon after 103 years of local extirpation. *River Research and Applications*, 254, pp.438–452.

Kim, K.-R., Kwak, Y.-H., Sung, M.-S., Cho, S.-J. and Bang, I.-C., (2023) Population structure and genetic diversity of the endangered fish black shinner *Pseudopungtungia nigra* (Cyprinidae) in Korea: a wild and restoration population. *Scientific Reports*, 131, p.9692.

Kjellman, J., (2003) *Growth and recruitment of burbot (Lota lota)*. [online] University of Helsinki. Available at: <https://helda.helsinki.fi/server/api/core/bitstreams/79ea681d-79ed-4a92-91bd-5b99a4969f55/content>.

Kjellman, J. and Eloranta, A., (2002) Field estimations of temperature-dependent processes: case growth of young burbot. *Hydrobiologia*, 481, pp.187–192.

Klein Hentz, Â.M., Kinder, P.J., Hubbart, J.A. and Kellner, E., (2018) Accuracy and Optimal Altitude for Physical Habitat Assessment (PHA) of Stream Environments Using Unmanned Aerial Vehicles (UAV). *Drones*, 22, p.20.

Klein, Z.B., Hardy, R.S. and Quist, M.C., (2016a) Diet of juvenile burbot and insight into gape limitation. *Intermountain Journal of Sciences*, 224, pp.55–69.

- Klein, Z.B., Quist, M.C., Rhea, D.T. and Senecal, A.C., (2016b) Population Characteristics and the Suppression of Nonnative Burbot. *North American Journal of Fisheries Management*, 365, pp.1006–1017.
- Klinger, H., Schmidt, G. and Steinberg, L., (1999) Rote Liste der in Nordrhein-Westfalen gefährdeten Fische (Pisces) und Rundmäuler (Cyclostomata). In: LÖBF, ed., *Rote Liste der in Nordrhein-Westfalen gefährdeten Pflanzen und Tiere*. LÖBF/LAfAO, pp.405–412.
- Klinger, H., Schütz, C., Ingendahl, D., Steinberg, L., Jarocinski, W. and Feldhaus, G., (2011) Rote Liste und Artenverzeichnis der Fische und Rundmäuler – Pisces et Cyclostomata – in Nordrhein-Westfalen, Stand Mai 2010. In: LANUV, ed., *Rote Liste der gefährdeten Pflanzen, Pilze und Tiere in Nordrhein-Westfalen*. pp.223–238.
- Knudsen, R., Amundsen, P.-A. and Klemetsen, A., (2010) Arctic charr in sympatry with burbot: ecological and evolutionary consequences. *Hydrobiologia*, 6501, pp.43–54.
- Knutti, R. and Sedláček, J., (2013) Robustness and uncertainties in the new CMIP5 climate model projections. *Nature Climate Change*, 34, p.369.
- Kohavi, R., (1995) A study of cross-validation and bootstrap for accuracy estimation and model selection. In: *Ijcai*. Montreal, Canada, pp.1137–1145.
- Kolozsvary, M.B. and Swihart, R.K., (1999) Habitat fragmentation and the distribution of amphibians: patch and landscape correlates in farmland. *Canadian Journal of Zoology*, 778, pp.1288–1299.
- Kondolf, G.M., Boulton, A.J., O'Daniel, S., Poole, G.C., Rahel, F.J., Stanley, E.H., Wohl, E., Bång, A., Carlstrom, J., Cristoni, C., Huber, H., Koljonen, S., Louhi, P. and Nakamura, K., (2006) Process-Based Ecological River Restoration: Visualizing Three-Dimensional Connectivity and Dynamic Vectors to Recover Lost Linkages. *Ecology and Society*, [online] 112. Available at: <http://www.jstor.org/stable/26266026> [Accessed 8 Jul. 2024].
- Koporikov, A.R. and Bogdanov, V.D., (2011) Spatial and biotopic distribution patterns of semianadromous burbot, *Lota lota* L. (Lotidae), early larvae in the Lower Ob floodplain. *Russian Journal of Ecology*, 424, pp.339–343.
- Koporikov, A.R. and Bogdanov, V.D., (2021) Survival of Early Burbot Larvae (*Lota lota* L., 1758) in the Ob Floodplain. *Russian Journal of Ecology*, 526, pp.486–495.
- Korzukhin, M.D., Ter-Mikaelian, M.T. and Wagner, R.G., (1996) Process versus empirical models: which approach for forest ecosystem management? *Canadian Journal of Forest Research*, 265, pp.879–887.
- Kouřil, J., Linhart, O., Dubsky, K. and Kavasnicka, P., (1985) The fertility of female and male burbot (*Lota lota* L.) reproduced by stripping. *Vodnany Research Institute of Fishery and Hydrobiology*, 14, pp.75–79.

Kovach, R.P., Ellison, S.C., Pyare, S. and Tallmon, D.A., (2015) Temporal patterns in adult salmon migration timing across southeast Alaska. *Global Change Biology*, 215, pp.1821–1833.

Kozfkay, J.R. and Paragamian, V.L., (2002) *Kootenai River Fisheries Investigation, Stock Status of Burbot: Project Progress Report: 2001 Annual Report*. Idaho, US: Department of Fish and Game.

Králová-Hromadová, I., Radačovská, A., Čisovská Bazsalovicsová, E. and Kuchta, R., (2021) Chapter Three - Ups and downs of infections with the broad fish tapeworm *Dibothriocephalus latus* in Europe from 1900 to 2020: Part I. In: D. Rollinson and R. Stothard, eds., *Advances in Parasitology*. [online] Academic Press, pp.75–166. Available at: <https://www.sciencedirect.com/science/article/pii/S0065308X21000336> [Accessed 1 Feb. 2024].

Kreutzweiser, D.P., Good, K.P. and Sutton, T.M., (2005) Large woody debris characteristics and contributions to pool formation in forest streams of the Boreal Shield. *Canadian Journal of Forest Research*, 355, pp.1213–1223.

Kronvang, B., Svendsen, L. m., Brookes, A., Fisher, K., Møller, B., Ottosen, O., Newson, M. and Sear, D., (1998) Restoration of the rivers Brede, Cole and Skerne: a joint Danish and British EU-LIFE demonstration project, III—channel morphology, hydrodynamics and transport of sediment and nutrients. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 81, pp.209–222.

Kruk, A., (2007) Role of habitat degradation in determining fish distribution and abundance along the lowland Warta River, Poland. *Journal of Applied Ichthyology*, 231, pp.9–18.

Kruse, C.G., Clancey, P., Barndt, S., Patten, K. and Shepard, B., (2013) Setting the stage for conservation success: large-scale watershed renovation and re-introduction of cutthroat trout in the Rocky Mountain region of the USA. In: *Global Re-introduction Perspectives: 2013. Further case studies from around the globe*, Global Re-introduction Perspectives. Brussels: IUCN, p.26.

Książek, L., Woś, A., Florek, J., Wyrębek, M., Młyński, D. and Wałęga, A., (2019) Combined use of the hydraulic and hydrological methods to calculate the environmental flow: Wisłoka river, Poland: case study. *Environmental Monitoring and Assessment*, 1914, p.254.

Kupren, K., Trąbska, I., Żarski, D., Krejszeff, S., Palińska-Żarska, K. and Kucharczyk, D., (2014) Early development and allometric growth patterns in burbot *Lota lota* L. *Aquaculture International*, 221, pp.29–39.

Kwiatkowski, S.K. and Targońska, K., (2009) Mass initial rearing of burbot *Lota lota* (L.) larvae under controlled conditions. *Animal Breeding and Husbandry*, p.76.

Ladle, M. and Westlake, D., (2006) River and stream ecosystems of Great Britain. *River and stream ecosystems of the world*. University of California Press, Berkeley. p, pp.343–388.

Lahnsteiner, F., Berger, B., Weismann, T. and Patzner, R., (1997) Sperm motility and seminal fluid composition in the burbot, *Lota lota*. *Journal of Applied Ichthyology*, 133, pp.113–119.

Lahnsteiner, F., Kletzl, M. and Weismann, T., (2012) The effect of temperature on embryonic and yolk-sac larval development in the burbot *Lota lota*. *Journal of Fish Biology*, 813, pp.977–986.

Lahnsteiner, F., Mansour, N. and Berger, B., (2004) The effect of inorganic and organic pollutants on sperm motility of some freshwater teleosts. *Journal of Fish Biology*, 655, pp.1283–1297.

Lajus, J., Ojaveer, H. and Tammiksaar, E., (2007) Fisheries at the Estonian Baltic Sea coast in the first half of the 19th century: What can be learned from the archives of Karl Ernst Baer? *Fisheries Research*, 872, pp.126–136.

Lambert, S., Thomas, K. and Davy, A., (2006) Assessment of the risk posed by the antifouling booster biocides Irgarol 1051 and diuron to freshwater macrophytes. *Chemosphere*, 635, pp.734–743.

Lamothe, K.A., Drake, D.A.R., Pitcher, T.E., Broome, J.E., Dextrase, A.J., Gillespie, A., Mandrak, N.E., Poesch, M.S., Reid, S.M. and Vachon, N., (2019) Reintroduction of fishes in Canada: a review of research progress for SARA-listed species. *Environmental Reviews*. [online] Available at: <https://cdnsiencepub.com/doi/abs/10.1139/er-2019-0010> [Accessed 7 Apr. 2021].

Langhammer, J. and Vacková, T., (2018) Detection and mapping of the geomorphic effects of flooding using UAV photogrammetry. *Pure and Applied Geophysics*, 1759, pp.3223–3245.

Larsson, P.-O., (1985) Predation on migrating smolt as a regulating factor in Baltic salmon, *Salmo salar* L., populations. *Journal of Fish Biology*, 264, pp.391–397.

Lasne, E., Lek, S. and Laffaille, P., (2007) Patterns in fish assemblages in the Loire floodplain: the role of hydrological connectivity and implications for conservation. *Biological Conservation*, 1393–4, pp.258–268.

Laville, S., (2020) Shocking state of English rivers revealed as all of them fail pollution tests. *The Guardian*. [online] Available at: <https://www.theguardian.com/environment/2020/sep/17/rivers-in-england-fail-pollution-tests-due-to-sewage-and-chemicals> [Accessed 24 Mar. 2021].

Law, A., Jones, K.C. and Willby, N.J., (2014) Medium vs. short-term effects of herbivory by Eurasian beaver on aquatic vegetation. *Aquatic Botany*, 116, pp.27–34.

Law, A., McLean, F. and Willby, N.J., (2016) Habitat engineering by beaver benefits aquatic biodiversity and ecosystem processes in agricultural streams. *Freshwater Biology*, 614, pp.486–499.

Lecaudey, L.A., Schletterer, M., Kuzovlev, V.V., Hahn, C. and Weiss, S.J., (2019) Fish diversity assessment in the headwaters of the Volga River using environmental DNA

metabarcoding. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 2910, pp.1785–1800.

Lenderink, G., Buishand, A. and van Deursen, W., (2007) Estimates of future discharges of the river Rhine using two scenario methodologies: direct versus delta approach. *Hydrology and Earth System Sciences*, 113, pp.1145–1159.

Lintermans, M., Lyon, J.P., Hammer, M.P., Ellis, I. and Ebner, B.C., (2015) Underwater, out of sight: lessons from threatened freshwater fish translocations in Australia. In: D. Armstrong, M. Hayward, D. Moro and P. Seddon, eds., *Advances in Reintroduction Biology of Australian and New Zealand Fauna*. Australia: Csiro Publishing, pp.237–253.

Littell, J.S., McKenzie, D., Kerns, B.K., Cushman, S. and Shaw, C.G., (2011) Managing uncertainty in climate-driven ecological models to inform adaptation to climate change. *Ecosphere*, 29, p.art102.

Logez, M., Bady, P. and Pont, D., (2012) Modelling the habitat requirement of riverine fish species at the European scale: sensitivity to temperature and precipitation and associated uncertainty. *Ecology of Freshwater Fish*, 212, pp.266–282.

López, J.A.G. and Mata, P.R., (2008) Re-introduction programme of the Spanish toothcarp “Fartet” in the Valencian region, Spain. In: P.S. Soorae, ed., *Reintroduction Perspectives: Re-introduction Case Studies From Around The Globe.*, Global Re-introduction Perspectives. Abu Dhabi: IUCN, p.284.

Lovett, A., Herrmann, S., Appleton, K. and Winter, T., (2003) Landscape modelling and visualisation for environmental planning in intensive agricultural areas. *Trends in Landscape Modeling*, pp.114–122.

Luhta, P.-L., Huusko, A. and Louhi, P., (2012) Re-building brown trout populations in dredged boreal forest streams: in-stream restoration combined with stocking of young trout. *Freshwater Biology*, 579, pp.1966–1977.

Maddock, I., (1999) The importance of physical habitat assessment for evaluating river health. *Freshwater Biology*, 412, pp.373–391.

Maddock, I., Bickerton, M., Spence, R. and Pickering, T., (2001) Reallocation of compensation releases to restore river flows and improve instream habitat availability in the Upper Derwent catchment, Derbyshire, UK. *Regulated Rivers: Research & Management: An International Journal Devoted to River Research and Management*, 174–5, pp.417–441.

Maddock, I.P., (1994) *Instream habitat assessment: a geomorphological approach*. PhD Thesis. Loughborough University.

Madenjian, C.P., Stapanian, M.A., Rediske, R.R. and O’Keefe, J.P., (2013) Sex Difference in Polychlorinated Biphenyl Concentrations of Burbot *Lota lota* From Lake Erie. *Archives of Environmental Contamination and Toxicology*, 652, pp.300–308.

Madenjian, C.P., Stapanian, M.A., Witzel, L.D., Einhouse, D.W., Pothoven, S.A. and Whitford, H.L., (2011) Evidence for predatory control of the invasive round goby. *Biological Invasions*, 134, pp.987–1002.

Maitland, P.S. and Lyle, A.A., (1991) Conservation of freshwater fish in the British Isles: the current status and biology of threatened species. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 11, pp.25–54.

Manfrin, A., Bunzel-Drücke, M., Lorenz, A.W., Maire, A., Scharf, M., Zimball, O. and Stoll, S., (2020) The effect of lateral connectedness on the taxonomic and functional structure of fish communities in a lowland river floodplain. *Science of the Total Environment*, 719, p.137169.

Mann, R.H.K., (1996) Environmental requirements of European non-salmonid fish in rivers. *Hydrobiologia*, 3233, pp.223–235.

Marjomäki, T.J., Mustajärvi, L., Mänttari, J., Kiljunen, M. and Karjalainen, J., (2022) Indications of polymorphism in the behaviour and morphology of burbot (*Lota lota*) in a European lake. *Hydrobiologia*, 8498, pp.1839–1853.

Marlborough, D., (1970) The status of the burbot *Lota lota* (L.) (Gadidae) in Britain. *Journal of Fish Biology*, 23, pp.217–222.

Marr, J.C., (1956) The 'Critical Period' in the Early Life History of Marine Fishes. *ICES Journal of Marine Science*, 212, pp.160–170.

Marsh, T., Hannaford, J. and Sanderson, F., (2008) *National Hydrological Monitoring Programme: 2006 UK Hydrological Review*. [online] UK: National Environment Research Council. Available at: https://nora.nerc.ac.uk/id/eprint/6357/1/Hydrological_Review_2006.pdf#:~:text=Monthly%20and%20seasonal%20variations%20in%20rainfall%20throughout%202006,the%20continuation%20of%20drought%20conditions%20across%20southern%20Britain.

Marshall, M.R., Francis, O.J., Frogbrook, Z.L., Jackson, B.M., McIntyre, N., Reynolds, B., Solloway, I., Wheeler, H.S. and Chell, J., (2009) The impact of upland land management on flooding: results from an improved pasture hillslope. *Hydrological Processes*, 233, pp.464–475.

Martay, B., Hughes, F. and Doberski, J., (2012) A comparison of created and ancient fenland using ground beetles as a measure of conservation value. *Insect Conservation and Diversity*, 54, pp.251–263.

Mason, C. and Macdonald, S., (1993) Impact of organochlorine pesticide residues and PCBs on otters (*Lutra lutra*) in eastern England. *Science of the total environment*, 1381–3, pp.147–160.

Mason, C.F. and Macdonald, S.M., (2004) Growth in Otter (*Lutra lutra*) Populations in the UK as Shown by Long-term Monitoring. *AMBIO: A Journal of the Human Environment*, 333, pp.148–152.

Mason, R.J., Johnson, M.F., Wohl, E., Russell, C.E., Olden, J.D., Polvi, L.E., Rice, S.P., Hemsworth, M.J., Sponseller, R.A. and Thorne, C.R., (2025) Rebalancing River Lateral Connectivity: An Interdisciplinary Focus for Research and Management. *WIREs Water*, 121, p.e1766.

McCrimmon, H. and Devitt, O., (1954) Winter studies on the burbot, *Lota lota lacustris*, of Lake Simcoe, Ontario. *Canadian Fish Culturist*, 16, pp.34–41.

McDowell, W.G., Benson, A.J. and Byers, J.E., (2014) Climate controls the distribution of a widespread invasive species: implications for future range expansion. *Freshwater Biology*, 594, pp.847–857.

McKay, D.I.A., Dearing, J.A., Dyke, J.G., Poppy, G.M. and Firbank, L.G., (2019) To what extent has sustainable intensification in England been achieved? *Science of The Total Environment*, 648, pp.1560–1569.

McKenna Jr., J.E., Reeves, H.W. and Seelbach, P.W., (2018) Measuring and evaluating ecological flows from streams to regions: Steps towards national coverage. *Freshwater Biology*, 638, pp.874–890.

McPhail, J.D., (1997) *A Review of Burbot, Lota Lota, Life History and Habitat Use in Relation to Compensation and Improvement Opportunities*. British Columbia, Canada: Department of Fisheries and Oceans.

McPhail, J.D. and Lindsey, C.C., (1970) *Freshwater fishes of northwestern Canada and Alaska*. Bulletin (Fisheries Research Board of Canada). [online] Fisheries Research Board of Canada : available by mail from the Queen's Printer. Available at: <https://cir.nii.ac.jp/crid/1130282271595883520>.

McPhail, J.D. and Paragamian, V.L., (2000) Burbot biology and life history. *Burbot: biology, ecology, and management*. American Fisheries Society, Fisheries Management Section, Publication, 1, pp.11–23.

Mehner, T., (2012) Diel vertical migration of freshwater fishes – proximate triggers, ultimate causes and research perspectives. *Freshwater Biology*, 577, pp.1342–1359.

Meshkov, N.M., (1972) *Developmental stages of the burbot (Lota lota (L.))*. p.26.

Met Office, (2019a) *UK Climate Projections: Headline Findings*. [online] Available at: <https://www.metoffice.gov.uk/research/approach/collaboration/ukcp/index> [Accessed 4 Feb. 2021].

Met Office, (2019b) *UKCP18 Science Overview Report - November 2018 (Updated March 2019)*. [online] UK: Met Office. Available at: <https://www.metoffice.gov.uk/pub/data/weather/uk/ukcp18/science-reports/UKCP18-Overview-report.pdf>.

Met Office, (2023) *MIDAS Open: UK daily temperature data, v202308. NERC EDS Centre for Environmental Data Analysis, 04 October 2023*. Available at: <https://catalogue.ceda.ac.uk/uuid/220b9b8ffbed43fcbdd323e739118f6c> [Accessed 27 Mar. 2024].

Met Office Hadley Centre, (2018) *UKCP18 Regional Projections on a 12km grid over the UK for 1980-2080*. Available at: <https://catalogue.ceda.ac.uk/uuid/589211abeb844070a95d061c8cc7f604> [Accessed 27 Feb. 2024].

Milan, D.J., (1994) *Sediment quality characteristics of salmonid spawning grounds*. PhD Thesis. Loughborough University.

Millenium Ecosystem Assessment, (2005) *Ecosystems and human well-being: synthesis*. Washington DC, US: Island Press.

Miller, D.D., (1970) *A life-history study of Burbot in Boysen Reservoir, Ring Lake and Trail Lake*. Cheyenne, Wyoming, US: Wyoming Game and Fish Commission.

Miller, K.M., Schulze, A.D., Ginther, N., Li, S., Patterson, D.A., Farrell, A.P. and Hinch, S.G., (2009) Salmon spawning migration: Metabolic shifts and environmental triggers. *Comparative Biochemistry and Physiology Part D: Genomics and Proteomics*, 42, pp.75–89.

Mitsch, W.J., Bernal, B. and Hernandez, M.E., (2015) *Ecosystem services of wetlands. International Journal of Biodiversity Science, Ecosystem Services & Management*, Taylor & Francis, pp.1–4.

Mohseni, O., Erickson, T.R. and Stefan, H.G., (2002) Upper Bounds for Stream Temperatures in the Contiguous United States. *Journal of Environmental Engineering*, 1281, pp.4–11.

Mohseni, O., Stefan, H.G. and Erickson, T.R., (1998) A nonlinear regression model for weekly stream temperatures. *Water resources research*, 3410, pp.2685–2692.

Mondon, B., Sear, D.A., Collins, A.L., Shaw, P.J. and Sykes, T., (2021) The scope for a system-based approach to determine fine sediment targets for chalk streams. *CATENA*, 206, p.105541.

Moore, H.E., Mercer, T.G., de Alwis Pitts, D., Beagley, S., Naura, M. and Bryden, A., (2021) Assessing the progress of river restoration in the UK: Has biophysical condition improved over two decades of intervention? *River Research and Applications*, 3710, pp.1494–1509.

Moorhouse, T.P. and Macdonald, D.W., (2015) Are invasives worse in freshwater than terrestrial ecosystems? *Wiley Interdisciplinary Reviews: Water*, 21, pp.1–8.

Moss, B., (1983) The Norfolk Broadland: experiments in the restoration of a complex wetland. *Biological Reviews*, 584, pp.521–561.

Moy, K.G., Hammer, M.P., Matin, K.C., Ebner, B.C., Brown, C. and Unmack, P.J., (2021) Conservation introductions of the malanda rainbowfish in the wet tropics bioregion, Australia. In: P.S. Soorae, ed., *Global conservation translocation perspectives: 2021. Case studies from around the globe.*, Global Re-introduction Perspectives. Gland, Switzerland: IUCN SSC Conservation Translocation Specialist Group & Environment Agency, p.353.

Moy, K.G., Schaffer, J., Lintermans, M. and Unmack, P.J., (2018) Conservation introductions of the running river rainbowfish into deception and puzzle creeks, Australia. In: *Global reintroduction perspectives*, Global Re-introduction Perspectives. pp.34–37.

Mukhwana, L., (2016) *Effects of Upstream Water Abstraction on Floodplains Case Study: Ewaso Ng'iro North River*. [Thesis] University of Nairobi. Available at: <http://erepository.uonbi.ac.ke/handle/11295/100238> [Accessed 20 Jan. 2025].

Müller, W., (1957) *Beiträge zur Biologie der Quappe Lota lota L. nach Untersuchungen in Gewässern zwischen Elbe und Oder*.

Murray-Bligh, J., (1999) *Procedures for collecting and analysing macro-invertebrate samples*. Environment Agency.

Nagel, F., Hölker, F. and Wolter, C., (2011) In situ estimation of gastric evacuation and consumption rates of burbot (*Lota lota*) in a summer-warm lowland river. *Journal of Applied Ichthyology*, 275, pp.1236–1241.

Nardi, F., Vivoni, E.R. and Grimaldi, S., (2006) Investigating a floodplain scaling relation using a hydrogeomorphic delineation method. *Water Resources Research*, 429.

National Rivers Authority, (1992) *River corridor surveys: methods and procedures*. National Rivers Authority.

National Soils Research Institute, (2005) *Soilscape (England)*. [online] Available at: https://magic.defra.gov.uk/Metadata_for_MAGIC/magsoilscape.html.

Natural England, (2020) *Priority Habitat Inventory: England*. [online] Available at: <https://data.gov.uk/dataset/4b6ddab7-6c0f-4407-946e-d6499f19fcde/priority-habitat-inventory-england> [Accessed 11 Mar. 2021].

Naura, M., Clark, M.J., Sear, D.A., Atkinson, P.M., Hornby, D.D., Kemp, P., England, J., Peirson, G., Bromley, C. and Carter, M.G., (2016) Mapping habitat indices across river networks using spatial statistical modelling of River Habitat Survey data. *Ecological Indicators*, 66, pp.20–29.

Naura, M. and Robinson, M., (1998) Principles of using River Habitat Survey to predict the distribution of aquatic species: an example applied to the native white-clawed crayfish *Austropotamobius pallipes*. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 84, pp.515–527.

Neachell, E., (2015) *Environmental flows for English rivers: a focus on modified catchments*. PhD Thesis. University of Westminster.

Nelichek, V.A., (1973) The burbot (*Lota lota* (L.)) of the Upper Tuloma Reservoir. *Journal of Ichthyology*, 13, pp.834–840.

Newson, M., Lewin, J. and Raven, P., (2022) River science and flood risk management policy in England. *Progress in Physical Geography: Earth and Environment*, 461, pp.105–123.

Newson, M.D. and Newson, C.L., (2000) Geomorphology, ecology and river channel habitat: mesoscale approaches to basin-scale challenges. *Progress in Physical Geography*, 242, pp.195–217.

Nieminen, P., Mustonen, A.-M. and Hyvärinen, H., (2003) Fasting reduces plasma leptin-and ghrelin-immunoreactive peptide concentrations of the burbot (*Lota lota*) at 2 C but not at 10 C. *Zoological science*, 209, pp.1109–1115.

Nilsen, E.B., Milner-Gulland, E.J., Schofield, L., Myrsterud, A., Stenseth, N.C. and Coulson, T., (2007) Wolf reintroduction to Scotland: public attitudes and consequences for red deer management. *Proceedings of the Royal Society B: Biological Sciences*, 2741612, pp.995–1003.

Nislow, K.H., Magilligan, F.J., Saleeba, M. and Palmer, R.E., (2024) Chapter 26 - Slowing the flow for climate resilience in human-dominated riverine landscapes. In: M. Thoms and I. Fuller, eds., *Resilience and Riverine Landscapes*. [online] Elsevier, pp.545–568. Available at: <https://www.sciencedirect.com/science/article/pii/B9780323917162000029> [Accessed 23 May 2025].

Nock, C.J., Ovenden, J.R., Butler, G.L., Wooden, I., Moore, A. and Baverstock, P.R., (2011) Population structure, effective population size and adverse effects of stocking in the endangered Australian eastern freshwater cod *Maccullochella ikei*. *Journal of Fish Biology*, 781, pp.303–321.

Norfolk Rivers Trust, (2015) *Re-naturalising the Wissey near Bodney*. [online] Available at: <https://norfolkriverstrust.org/project/re-wilding-the-wissey/> [Accessed 27 Apr. 2021].

Norfolk Rivers Trust, (2018) *Stopping the silt: River Wissey restoration & enhancement*. [online] Available at: <https://norfolkriverstrust.org/project/stopping-the-silt-river-wissey-restoration-enhancement/> [Accessed 27 Apr. 2021].

Nuetzel, H.M., Galbreath, P.F., Staton, B.A., Crump, C.A., Naylor, L.M. and Shippentower, G.E., (2023) Improved productivity of naturalized spring Chinook salmon following reintroduction from a hatchery stock in Lookingglass Creek, Oregon. *Canadian Journal of Fisheries and Aquatic Sciences*, 802, pp.375–392.

Nummi, P. and Holopainen, S., (2020) Restoring wetland biodiversity using research: Whole-community facilitation by beaver as framework. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 309, pp.1798–1802.

Nummi, P., Kattainen, S., Ulander, P. and Hahtola, A., (2011) Bats benefit from beavers: a facilitative link between aquatic and terrestrial food webs. *Biodiversity and Conservation*, 204, pp.851–859.

Nunes, A.L., Tricarico, E., Panov, V.E., Cardoso, A.C. and Katsanevakis, S., (2015) Pathways and gateways of freshwater invasions in Europe. [online] Available at: <https://scholar.sun.ac.za:443/handle/10019.1/106336> [Accessed 24 Jun. 2022].

Nunn, A., Harvey, J. and Cowx, I., (2007) Benefits to 0+ fishes of connecting man-made waterbodies to the lower River Trent, England. *River research and applications*, 234, pp.361–376.

O'Hara, K., (2018) A commentary on the current status of the Pine Marten *Martes martes* in Northern England. *Northumbrian Naturalist: Transactions of the Natural History Society of Northumbria*, 85.

O'Hare, J.M., O'Hare, M.T., Gurnell, A.M., Scarlett, P.M., Liffen, T.O.M. and McDonald, C., (2012) Influence of an ecosystem engineer, the emergent macrophyte *Sparganium erectum*, on seed trapping in lowland rivers and consequences for landform colonisation. *Freshwater Biology*, 571, pp.104–115.

Olden, J.D. and Naiman, R.J., (2010) Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. *Freshwater Biology*, 551, pp.86–107.

Olivier, J.M., Carrel, G., Lamouroux, N., Dole-Olivier, M.J., Malard, F., Bravard, J.P. and Amoros, C., (2009) The Rhône river basin. In: K. Tockner, U. Uehlinger and C.T. Robinson, eds., *Rivers of Europe*. London, UK: Academic Press, pp.247–296.

Olsvik, P.A., Berg, V. and Lyche, J.L., (2013) Transcriptional profiling in burbot (*Lota lota*) from Lake Mjøsa—A Norwegian Lake contaminated by several organic pollutants. *Ecotoxicology and Environmental Safety*, 92, pp.94–103.

Ondersteunend Centrum Databank Ondergrond Vlaanderen, (2017) *Digitale bodemkaart van het Vlaams Gewest: bodemtypes*. Available at: www.geopunt.be [Accessed 25 Sep. 2023].

Ordnance Survey, (2021) *Topography. 1: 1250, OS MasterMap® Topography Layer*. Available at: <https://digimap.edina.ac.uk/roam/download/os>.

Pääkkönen, J.-P., Tikkanen, O. and Karjalainen, J., (2003) Development and validation of a bioenergetics model for juvenile and adult burbot. *Journal of fish biology*, 634, pp.956–969.

Pääkkönen, J.-P.J. and Marjomäki, T.J., (2000) Feeding of Burbot, *Lota lota*, at Different Temperatures. *Environmental Biology of Fishes*, 581, pp.109–112.

Padmore, C.L., (1998) The role of physical biotopes in determining the conservation status and flow requirements of British rivers. *Aquatic Ecosystem Health & Management*. [online] Available at: <https://www.tandfonline.com/doi/abs/10.1080/14634989808657003> [Accessed 19 Jan. 2023].

Pain, D., Carter, I., Sainsbury, A., Shore, R., Eden, P., Taggart, M.A., Konstantinos, S., Walker, L., Meharg, A. and Raab, A., (2007) Lead contamination and associated

disease in captive and reintroduced red kites *Milvus milvus* in England. *Science of the Total Environment*, 3761–3, pp.116–127.

Palmer, M.A., Bernhardt, E.S., Allan, J.D., Lake, P.S., Alexander, G., Brooks, S., Carr, J., Clayton, S., Dahm, C.N., Follstad Shah, J., Galat, D.L., Loss, S.G., Goodwin, P., Hart, D.D., Hassett, B., Jenkinson, R., Kondolf, G.M., Lave, R., Meyer, J.L., O'Donnell, T.K., Pagano, L. and Sudduth, E., (2005) Standards for ecologically successful river restoration. *Journal of Applied Ecology*, 422, pp.208–217.

Palmer, M.A., Menninger, H.L. and Bernhardt, E., (2010) River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? *Freshwater Biology*, 55s1, pp.205–222.

Pandakov, P.G., Teofilova, T.M. and Kodzhabashev, N.D., (2020) Status of the burbot (*Lota lota* L.) in the Lower Danube (Bulgaria) – a species threatened by climate change. *ZooKeys*, 910, pp.143–161.

Pander, J., Mueller, M. and Geist, J., (2018) Habitat diversity and connectivity govern the conservation value of restored aquatic floodplain habitats. *Biological Conservation*, 217, pp.1–10.

Paragamian, V.L. and Hansen, M.J., (2009) Rehabilitation Needs for Burbot in the Kootenai River, Idaho, USA, and British Columbia, Canada. *North American Journal of Fisheries Management*, 293, pp.768–777.

Paragamian, V.L. and Wakkinen, V.D., (2008) Seasonal movement of burbot in relation to temperature and discharge in the Kootenai. In: *In Burbot: ecology, management and culture. Edited by V.L. Paragamian and D.H. Bennett. American Fisheries Society, Symposium 59, Bethesda, Md.* pp.55–77.

Paragamian, V.L., Whitman, V., Hammond, J. and Andrusak, H., (2000) Collapse of burbot fisheries in the Kootenai River, Idaho, USA, and Kootenay Lake, British Columbia, Canada. In: V.L. Paragamian and D.W. Willis, eds., *Burbot: Biology, Ecology, and Management*. Bethesda: American Fisheries Society, pp.155–160.

Parasiewicz, P., Belka, K., Łapińska, M., Ławniczak, K., Prus, P., Adamczyk, M., Buras, P., Szlakowski, J., Kaczkowski, Z., Krauze, K., and others, (2023) Over 200,000 kilometers of free-flowing river habitat in Europe is altered due to impoundments. *Nature Communications*, 141, p.6289.

Parasiewicz, P. and Dunbar, M.J., (2001) Physical habitat modelling for fish—. *Arch. Hydrobiol. Suppl.*, 13524, pp.239–268.

Parker, C., Henshaw, A.J., Harvey, G.L. and Sayer, C.D., (2017) Reintroduced large wood modifies fine sediment transport and storage in a lowland river channel. *Earth Surface Processes and Landforms*, 4211, pp.1693–1703.

Pauwels, I., Van Wichelen, J., Vandamme, L., Vught, I., Van Thuyne, G., Auwerx, J., Baeyens, R., De Maerteleire, N., Gelaude, E. and Picavet, B., (2016) Wetenschappelijke onderbouwing en ondersteuning van het visserijbeleid en het visstandbeheer-onderzoeksprogramma visserij 2015.

Peake, S.J., (2008) *Swimming performance and behaviour of fish species endemic to Newfoundland and Labrador: A literature review for the purpose of establishing design and water velocity criteria for fishways and culverts*. [Canadian Manuscript Report of Fisheries and Aquatic Sciences] Canada: Fisheries and Oceans Canada. Available at: https://www.publications.gc.ca/collections/collection_2009/mpo-dfo/Fs97-4-2843E.pdf [Accessed 7 Aug. 2024].

Pearce, R.H., Chadwick, M.A., Main, B., Chan, K., Sayer, C.D. and Patmore, I.R., (2024a) Low-Cost Approach to an Instream Water Depth Sensor Construction Using Differential Pressure Sensors and Arduino Microcontrollers. *Sensors*, 248, p.2488.

Pearce, R.H., Sayer, C.D., Chadwick, M.A., Perrow, M., Worthington, T., Harvey, G.L. and Tosney, J., (2024b) Bringing the Burbot back to English rivers. *British Wildlife*, 361, pp.17–27.

Pearce-Higgins, J.W., Eglington, S.M., Martay, B. and Chamberlain, D.E., (2015) Drivers of climate change impacts on bird communities. *Journal of Animal Ecology*, 844, pp.943–954.

Peirson, G., Bolland, J.D. and Cowx, I., (2008) Lateral dispersal and displacement of fish during flood events in lowland river systems in the UK—implications for sustainable floodplain management: Ecohydrological Processes and Sustainable Floodplain Management. *Ecohydrology & Hydrobiology*, 82–4, pp.363–373.

Pekárová, P., Halmova, D., Miklanek, P., Onderka, M., Pekar, J. and Skoda, P., (2008) Is the water temperature of the Danube River at Bratislava, Slovakia, rising? *Journal of Hydrometeorology*, 95, pp.1115–1122.

Pekárová, P., Onderka, M., Pekár, J., Rončák, P. and Miklánek, P., (2009) Prediction of Water Quality in the Danube River Under extreme Hydrological and Temperature Conditions. *Journal of Hydrology and Hydromechanics*, 571, pp.3–15.

Pekcan-Hekim, Z., Nurminen, L., Ojala, T., Olin, M., Ruuhijärvi, J. and Horppila, J., (2010) Reversed Diel Horizontal Migration of Fish: Turbidity Versus Plant Structural Complexity as Refuge. *Journal of Freshwater Ecology*, 254, pp.649–656.

Penczak, T., Głowacki, Ł., Galicka, W. and Koszaliński, H., (1998) A long-term study (1985–1995) of fish populations in the impounded Warta River, Poland. *Hydrobiologia*, 3681, pp.157–173.

Percy, R., (1975) *Fishes of the outer MacKenzie Delta*. Beaufort Sea Technical Report. [online] Canada: Fisheries and Marine Service. Available at: http://www.restco.ca/BSPTR/BSP_TR08_Percy.pdf [Accessed 7 Aug. 2024].

Person, E., Bieri, M., Peter, A. and Schleiss, A.J., (2014) Mitigation measures for fish habitat improvement in Alpine rivers affected by hydropower operations. *Ecohydrology*, 72, pp.580–599.

Pessenlehner, S., Liedermann, M., Holzapfel, P., Skrame, K., Habersack, H. and Hauer, C., (2022) Evaluation of hydropower projects in Balkan Rivers based on direct sediment transport measurements; challenges, limits and possible data interpretation–

Case study Vjosa River/Albania. *River Research and Applications*, 386, pp.1014–1030.

Pettorelli, N., Barlow, J., Stephens, P.A., Durant, S.M., Connor, B., Böhne, H.S. to, Sandom, C.J., Wentworth, J. and Toit, J.T. du, (2018) Making rewilding fit for policy. *Journal of Applied Ecology*, 553, pp.1114–1125.

Petts, G.E., (1984) *Impounded rivers: perspectives for ecological management*. Wiley.

Petts, G.E., (1988) Regulated rivers in the United Kingdom. *Regulated Rivers: Research & Management*, 23, pp.201–220.

Petts, G.E. and Bickerton, M.A., (1994) *River Wissey: Linking Ecology and Hydrology*. Peterborough: National Rivers Authority, p.105.

Pham, L., Closs, G. and West, D., (2016) Re-introduction of a native galaxiid (banded kokopu), after piscicide treatment, in two small streams and a reservoir, Wellington, New Zealand. In: *Global Re-introduction Perspectives: 2016. Case-studies from around the globe*, Global Re-introduction Perspectives. p.20.

Pilotto, F., Bertoncin, A., Harvey, G.L., Wharton, G. and Pusch, M.T., (2014) Diversification of stream invertebrate communities by large wood. *Freshwater Biology*, 5912, pp.2571–2583.

Pinder, L.C.V., (1997) Research on the Great Ouse: Overview and implications for management. *Regulated Rivers: Research & Management*, 133, pp.309–315.

PlantLife International, (2007) *Fact Sheet for Breckland IPA*. [online] Available at: <https://www.plantlifeipa.org/site/factsheet/1019> [Accessed 11 Mar. 2021].

Poff, N.L. and Zimmerman, J.K.H., (2010) Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology*, 551, pp.194–205.

Prady, J., Austin, S., Dodd, J., White, J., Wilkes, M. and Naura, M., (2025) Special Issue: Scientific Advances in River Restoration. *River Research and Applications*, 411, pp.3–9.

Preston, C.D., Sheail, J., Armitage, P. and Davy-Bowker, J., (2003) The long-term impact of urbanisation on aquatic plants: Cambridge and the River Cam. *Science of The Total Environment*, 314–316, pp.67–87.

Price, M.R.S., (1989) *Animal reintroductions: the Arabian oryx in Oman*. Cambridge University Press.

Price, M.R.S. and Soorae, P.S., (2003) Reintroductions: whence and whither? *International Zoo Yearbook*, 381, pp.61–75.

Pulliainen, E. and Korhonen, K., (1993) Does the burbot, *Lota lota*, have rest years between normal spawning seasons? *Journal of Fish Biology*, 433, pp.355–362.

Pulliainen, E., Korhonen, K., Kankaanranta, L. and Mäki, K., (1992) Non-Spawning Burbot on the Northern Coast of the Bothnian Bay. *Ambio*, 212, pp.170–175.

Purvina, S. and Medne, R., (2018) Reintroduction of sturgeon, *Acipenser oxyrinchus*, in the Gulf of Riga, East-Central Baltic Sea. *Archives of Polish Fisheries*, 261, pp.39–46.

Pusey, B.J. and Arthington, A.H., (2003) Importance of the riparian zone to the conservation and management of freshwater fish: a review. *Marine and freshwater Research*, 541, pp.1–16.

Putland, R.L., Austin, J.A., Hill, C.S. and Mensinger, A.F., (2022) A song of ice and vessels: Seasonal trends in the soundscape of the western arm of Lake Superior. *Journal of Great Lakes Research*, 482, pp.478–488.

Puttock, A., Graham, H.A., Cunliffe, A.M., Elliott, M. and Brazier, R.E., (2017) Eurasian beaver activity increases water storage, attenuates flow and mitigates diffuse pollution from intensively-managed grasslands. *Science of The Total Environment*, 576, pp.430–443.

Radinger, J., Essl, F., Hölker, F., Horký, P., Slavík, O. and Wolter, C., (2017) The future distribution of river fish: The complex interplay of climate and land use changes, species dispersal and movement barriers. *Global Change Biology*, 2311, pp.4970–4986.

Railsback, S.F., (2016) Why It Is Time to Put PHABSIM Out to Pasture. *Fisheries*, 4112, pp.720–725.

Ramler, D. and Keckeis, H., (2019) Effects of large-river restoration measures on ecological fish guilds and focal species of conservation in a large European river (Danube, Austria). *Science of the total environment*, 686, pp.1076–1089.

Rangley-Wilson, C. and Sykes, T., (2021) Chalk stream restoration strategy 2021: Main report.

Raven, P. j., Holmes, N. t. h., Dawson, F. h. and Everard, M., (1998) Quality assessment using River Habitat Survey data. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 84, pp.477–499.

Razzaque, J. and Lester, C., (2021) Why Protect Ancient Woodland in the UK? Rethinking the Ecosystem Approach. *Transnational Environmental Law*, 101, pp.135–158.

Riaz, M., Kuemmerlen, M., Wittwer, C., Cocchiararo, B., Khaliq, I., Pfenninger, M. and Nowak, C., (2020) Combining environmental DNA and species distribution modeling to evaluate reintroduction success of a freshwater fish. *Ecological Applications*, 302, p.e02034.

Ricciardi, A. and Rasmussen, J.B., (1999) Extinction Rates of North American Freshwater Fauna. *Conservation Biology*, 135, pp.1220–1222.

Richardson, B.M., (2015) *A dietary comparison of the reintroduced alligator gar *Atractosteus spatula* and three sympatric Gar relatives (family: Lepisosteidae) in the Clarks River, Kentucky*. [PhD] Murray State University. Available at: <https://www.proquest.com/openview/2154ee884cc0e479f856245f3e4d0167/1?pq-origsite=gscholar&cbl=18750>.

Rinaldi, M., Belletti, B., Bussetini, M., Comiti, F., Golfieri, B., Lastoria, B., Marchese, E., Nardi, L. and Surian, N., (2017) New tools for the hydromorphological assessment and monitoring of European streams. *Journal of environmental management*, 202, pp.363–378.

Ritz, T.A., Jensen, N.R. and Leonard, J.B.K., (2020) Larval morphology of North American burbot (*Lota lota maculosa*) from two spatially separated populations. *Hydrobiologia*, 84714, pp.2981–2998.

River Restoration Centre, (2020) *The Manual of River Restoration Techniques*. [online] Available at: <https://www.therrc.co.uk/manual-river-restoration-techniques>.

Roach, S.M. and Evenson, M.J., (1993) *A geometric approach to estimating and predicting the fecundity of Tanana River Burbot*. Fisheries Data Series. Alaska, US: Alaska Department of Fish and Game, pp.93–98.

Roberge, J.-M. and Angelstam, P., (2004) Usefulness of the Umbrella Species Concept as a Conservation Tool. *Conservation Biology*, 181, pp.76–85.

Robert, A., (2009) Captive breeding genetics and reintroduction success. *Biological Conservation*, 14212, pp.2915–2922.

Robins, C.R. and Deubler, E.E., (1955) *The life history and systematic status of the Burbot, *Lota lota lacustris* (Walbaum) in the Susquehanna River system*. New York, NY, USA: University of the State of New York.

Robins, J.E., Naura, M., Austin, S., Bryden, A., Cullis, J., Prady, J., Shi, F. and Treves, R., (2025) A New Framework for River Restoration Planning at Catchment Scale in the UK. *River Research and Applications*, 411, pp.82–107.

Robinson, E.L., Huntingford, C., Semeena, V.S. and Bullock, J.M., (2023) CHES-SCAPE: high-resolution future projections of multiple climate scenarios for the United Kingdom derived from downscaled United Kingdom Climate Projections 2018 regional climate model output. *Earth System Science Data*, 1512, pp.5371–5401.

Roni, P., Hall, J.E., Drenner, S.M. and Arterburn, D., (2019) Monitoring the effectiveness of floodplain habitat restoration: A review of methods and recommendations for future monitoring. *WIREs Water*, 64, p.e1355.

Rosenfeld, J., (2003) Assessing the Habitat Requirements of Stream Fishes: An Overview and Evaluation of Different Approaches. *Transactions of the American Fisheries Society*, 1325, pp.953–968.

Rosset, V. and Oertli, B., (2011) Freshwater biodiversity under climate warming pressure: Identifying the winners and losers in temperate standing waterbodies. *Biological Conservation*, 1449, pp.2311–2319.

Rotherham, I.D. and Read, D.J., (1988) Aspects of the ecology of *Rhododendron ponticum* with reference to its competitive and invasive properties. *Aspects of Applied Biology*, 16, pp.327–335.

RRC, (1997) *River Restoration Centre. Forward Plan*. Bedford: River Restoration Centre.

Ryder, R.A. and Pesendorfer, J., (1992) Food, growth, habitat, and community interactions of young-of-the-year burbot, *Lota lota* L., in a Precambrian Shield lake. *Hydrobiologia*, 2431, pp.211–227.

Saarinen, T.S. and Kløve, B., (2012) Past and future seasonal variation in pH and metal concentrations in runoff from river basins on acid sulphate soils in Western Finland. *Journal of Environmental Science and Health, Part A*, 4711, pp.1614–1625.

Sandberg, M., (2015) *Life history trade-offs in Anadromous Burbot Lota lota (Linnaeus 1758) from Rickleån and Sävarån, Northern Sweden*. Swedish University of Agricultural Sciences.

Sandlund, O.T., Museth, J. and Øistad, S., (2016) Migration, growth patterns, and diet of pike (*Esox lucius*) in a river reservoir and its inflowing river. *Fisheries Research*, 173, pp.53–60.

Saumure, R.A., Ambos, A., O'Toole, T., Harter, J., Guadelupe, K., Senger, B. and Marshall, Z., (2021) A fish out of water: rewilding the Pahrump poolfish in Las Vegas, Nevada, USA. In: P.S. Soorae, ed., *Global conservation translocation perspectives: 2021. Case studies from around the globe*, Global Re-introduction Perspectives. Gland, Switzerland: IUCN SSC Conservation Translocation Specialist Group & Environment Agency, p.353.

Sayer, C., Bennion, H., Gurnell, A., Goodyer, E., Kotze, D. and Lindsay, R., (2018) Restoration of freshwaters: principles and practice. In: J. Hughes, ed., *In: Hughes, J, (ed.) Freshwater Ecology and Conservation Approaches and Techniques*. (pp. 378-403). Oxford University Press: Oxford, UK. (2018). [online] Oxford, UK: Oxford University Press, pp.378–403. Available at: <https://global.oup.com/academic/product/freshwater-ecology-and-conservation-9780198766384?lang=en&cc=gb> [Accessed 8 Feb. 2023].

Sayer, C., van Biervliet, O., Pearce, R.H. and Mills, T., (2024) In natural processes we trust: rewilding and freshwater-wetland restoration. *British Wildlife*, 35, 4 Feb., pp.262–272.

Sayer, C.D., (2014) Conservation of aquatic landscapes: ponds, lakes, and rivers as integrated systems. *WIREs Water*, 16, pp.573–585.

Schiemer, F., Beqiraj, S., Drescher, A., Graf, W., Egger, G., Essl, F., Frank, T., Hauer, C., Hohensinner, S., Miho, A., and others, (2020) The Vjosa River corridor: a model of

natural hydro-morphodynamics and a hotspot of highly threatened ecosystems of European significance. *Landscape Ecology*, 35, pp.953–968.

Schomaker, C. and Wolter, C., (2011) The contribution of long-term isolated water bodies to floodplain fish diversity. *Freshwater Biology*, 568, pp.1469–1480.

Schreiber, B., Korte, E., Schmidt, T. and Schulz, R., (2018) Reintroduction and stock enhancement of European weatherfish (*Misgurnus fossilis* L.) in Rhineland-Palatinate and Hesse, Germany. *Knowledge & Management of Aquatic Ecosystems*, 419, p.43.

Schreve, D.C., (2006) The taphonomy of a Middle Devensian (MIS 3) vertebrate assemblage from Lynford, Norfolk, UK, and its implications for Middle Palaeolithic subsistence strategies. *Journal of Quaternary Science: Published for the Quaternary Research Association*, 215, pp.543–556.

Schulze, E.-D. and Mooney, H.A. eds., (1994) *Biodiversity and ecosystem function*. Ecological studies. Berlin ; New York: Springer-Verlag.

Schumann, D., Hoback, W., Koupal, K., Schoenebeck, C., Schainost, S. and Wilson, T., (2017) Experimental analysis of reintroduction strategies to conserve the vulnerable plains topminnow *Fundulus sciadicus* in Nebraska. *Endangered Species Research*, 34, pp.349–355.

Schumann, G.J.-P., Muhlhausen, J. and Andreadis, K.M., (2019) Rapid mapping of small-scale river-floodplain environments using UAV SfM supports classical theory. *Remote Sensing*, 118, p.982.

Scott, W.B. and Crossman, E.J., (1973) *Freshwater Fishes of Canada*. Bulletin of the Fisheries Research Board of Canada.

Seddon, P. and Armstrong, D., (2016) Reintroduction and Other Conservation Translocations: History and Future Developments. In: D. Jachowski, J. Millspaugh, P. Angermeier and R. Slotow, eds., *Reintroduction of Fish and Wildlife Populations*. Oakland, California: University of California Press, pp.7–28.

Seddon, P.J., Soorae, P.S. and Launay, F., (2005) Taxonomic bias in reintroduction projects. *Animal Conservation*, 81, pp.51–58.

Shao, X., Fang, Y., Jawitz, J.W., Yan, J. and Cui, B., (2019) River network connectivity and fish diversity. *Science of The Total Environment*, 689, pp.21–30.

Shaw, E.M., Beven, K.J., Chappell, N.A. and Lamb, R., (2011) *Hydrology in Practice*. 4th ed. [online] London: CRC Press. Available at: <https://www.taylorfrancis.com/books/9781315274904> [Accessed 15 May 2025].

Sheail, J., (1979) Documentary evidence of the changes in the use, management and appreciation of the grass-heaths of Breckland. *Journal of Biogeography*, pp.277–292.

Sheail, J., (1988) River regulation in the United Kingdom: An historical perspective. *Regulated Rivers: Research & Management*, 23, pp.221–232.

Shen, H., Tolson, B.A. and Mai, J., (2022) Time to Update the Split-Sample Approach in Hydrological Model Calibration. *Water Resources Research*, 583, p.e2021WR031523.

Shen, M. and Liu, X., (2021) Assessing the effects of lateral hydrological connectivity alteration on freshwater ecosystems: A meta-analysis. *Ecological Indicators*, 125, p.107572.

Shenton, W., Bond, N.R., Yen, J.D.L. and Mac Nally, R., (2012) Putting the “Ecology” into Environmental Flows: Ecological Dynamics and Demographic Modelling. *Environmental Management*, 501, pp.1–10.

Shine, C., Williams, N. and Gündling, L., (2000) *A guide to designing legal and institutional frameworks on alien invasive species*. Luxembourg: IUCN.

Shodjai, F., (1977) *Ein Beitrag zur Embryonal-und Larvalentwicklung der Quappe (Lota lota L.) in Abhängigkeit von der Temperatur*. Christian-Albrechts-Universität Kiel.

Shodjai, F., (1980) *Entwicklungs-, stoffwechsel- und ernährungsphysiologische Untersuchungen an der Aalquappe (Lota lota L.) unter Berücksichtigung ihrer Eignung als Kulturfisch*. [thesis] Christian-Albrechts-Universität Kiel. Available at: <https://oceanrep.geomar.de/id/eprint/41576/> [Accessed 2 Feb. 2024].

Shuker, L.J., Gurnell, A.M., Wharton, G., Gurnell, D.J., England, J., Finn Leeming, B.F. and Beach, E., (2017) MoRPh: a citizen science tool for monitoring and appraising physical habitat changes in rivers. *Water and Environment Journal*, 313, pp.418–424.

Shute, J.R., Rakes, P.L. and Shute, P.W., (2005) Reintroduction of Four Imperiled Fishes in Abrams Creek, Tennessee. *Southeastern Naturalist*, 41, pp.93–110.

Sideleva, V.G., (2003) *The endemic fishes of Lake Baikal*. Leiden, Netherlands: Backhuys Publishers.

Simpson, H., Knightbridge, J. and Nineham, N., (2021) Integrated approaches to phosphorus management in the Watton Brook, UK. *Proceedings of the Institution of Civil Engineers - Water Management*, pp.1–11.

Skempton, A., (1983) Engineering on the Thames navigation, 1770–1845. *Transactions of the Newcomen Society*, 551, pp.153–176.

Skempton, A.W., (1985) *The engineering works of John Grundy (1719-1783)*. Society for Lincolnshire History and Archaeology.

Slavík, O. and Bartoš, L., (2002) Factors affecting migrations of burbot. *Journal of Fish Biology*, 604, pp.989–998.

Slavík, O., Bartoš, L. and Mattas, D., (2005) Does Stream Morphology Predict the Home Range Size in Burbot? *Environmental Biology of Fishes*, 741, pp.89–98.

Šlejkovec, Z., Bajc, Z. and Doganoc, D.Z., (2004) Arsenic speciation patterns in freshwater fish. *Talanta*, 625, pp.931–936.

- Smart, J., Amar, A., Sim, I.M.W., Etheridge, B., Cameron, D., Christie, G. and Wilson, J.D., (2010) Illegal killing slows population recovery of a re-introduced raptor of high conservation concern – The red kite *Milvus milvus*. *Biological Conservation*, 1435, pp.1278–1286.
- Smith, B., Clifford, N.J. and Mant, J., (2014) The changing nature of river restoration. *WIREs Water*, 13, pp.249–261.
- Smith, D.M., Zalasiewicz, J.A., Williams, M., Wilkinson, I.P., Scarborough, J.J., Knight, M., Sayer, C., Redding, M. and Moreton, S.G., (2012) The anatomy of a Fenland roddon: sedimentation and environmental change in a lowland Holocene tidal creek environment. *Proceedings of the Yorkshire Geological Society*, 592, pp.145–159.
- Solomon, D.J. and Lightfoot, G.W., (2008) *Using Science to Create a Better Place: The Thermal Biology of Brown Trout and Atlantic Salmon*. Environment Agency.
- Soorae, P.S., (2003) *Re-introduction NEWS*. Re-introduction NEWS. Abu Dhabi: IUCN/SSC Reintroduction Specialist Group, p.48.
- Sorokin, V.N., (1971) The spawning and spawning grounds of the Burbot, *Lota lota* (L.). *Journal of Ichthyology*, 116, pp.907–915.
- Spence, R. and Hickley, P., (2000) The use of PHABSIM in the management of water resources and fisheries in England and Wales. *Ecological Engineering*, 161, pp.153–158.
- Stanford, J.A., Ward, J.V., Liss, W.J., Frissell, C.A., Williams, R.N., Lichatowich, J.A. and Coutant, C.C., (1996) A General Protocol for Restoration of Regulated Rivers. *Regulated Rivers: Research & Management*, 124–5, pp.391–413.
- Stapanian, M.A., Madenjian, C.P. and Witzel, L.D., (2006) Evidence That Sea Lamprey Control Led to Recovery of the Burbot Population in Lake Erie. *Transactions of the American Fisheries Society*, 1354, pp.1033–1043.
- Stapanian, M.A. and Myrick, C.A., (2015) Ecology, culture, and management of Burbot: an introduction. *Hydrobiologia*, 7571, pp.1–2.
- Stapanian, M.A., Paragamian, V.L., Madenjian, C.P., Jackson, J.R., Lappalainen, J., Evenson, M.J. and Neufeld, M.D., (2010a) Worldwide status of burbot and conservation measures. *Fish and Fisheries*, 111, pp.34–56.
- Stapanian, M.A., Witzel, L.D. and Cook, A., (2010b) Recruitment of burbot (*Lota lota* L.) in Lake Erie: an empirical modelling approach. *Ecology of Freshwater Fish*, 193, pp.326–337.
- Steenvoorden, J., Bartholomeus, H. and Limpens, J., (2023) Less is more: Optimizing vegetation mapping in peatlands using unmanned aerial vehicles (UAVs). *International Journal of Applied Earth Observation and Geoinformation*, 117, p.103220.

Stoessel, D., (2012) *Targeted survey for threatened Murrumbidgee hardyhead (Craterocephalus fluviatilis) in selected water bodies in the Lower Murrumbidgee River system, Victoria*. Melbourne, Australia: Department of Sustainability and Environment.

Stoffers, T., Buijse, A., Geerling, G., Jans, L., Schoor, M., Poos, J., Verreth, J. and Nagelkerke, L., (2022) Freshwater fish biodiversity restoration in floodplain rivers requires connectivity and habitat heterogeneity at multiple spatial scales. *Science of the Total Environment*, 838, p.156509.

Stubbington, R., Dimon, J., England, J. and Watts, G., (2022) *Chalk Streams of the Future Report*. Available at: https://figshare.com/articles/online_resource/Chalk_Streams_of_the_Future_report_pdf/21663269/1 [Accessed 30 Oct. 2024].

Sundermann, A., Stoll, S. and Haase, P., (2011) River restoration success depends on the species pool of the immediate surroundings. *Ecological Applications*, 216, pp.1962–1971.

Švagždys, A., (2002) Growth and Abundance of Burbot in the Curonian Lagoon and Determinatives of Burbot Abundance. *Acta Zoologica Lituanica*, 121, pp.58–64.

Svensson, M.K., Eliasson, I. and Holmer, B., (2002) A GIS based empirical model to simulate air temperature variations in the Göteborg urban area during the night. *Climate Research*, 223, pp.215–226.

Syzdek, D.J., Simons, L.H., Guadalupe, K. and Schwemm, M.R., (2021) Restoration to historic and artificial habitat of a rare desert fish, the Moapa dace in Nevada, USA. In: *Global conservation translocation perspectives: 2021. Case studies from around the globe*, Global Re-introduction Perspectives. Luxembourg: IUCN, p.46.

Tammi, J., Lappalainen, A., Mannio, J., Rask, M. and Vuorenmaa, J., (1999) Effects of eutrophication on fish and fisheries in Finnish lakes: a survey based on random sampling. *Fisheries Management and Ecology*, 63, pp.173–186.

Tatár, S., Bajomi, B., Specziár, A., Tóth, B., Trenovszki, M.M., Urbányi, B., Csányi, B., Szekeres, J. and Müller, T., (2017) Habitat establishment, captive breeding and conservation translocation to save threatened populations of the Vulnerable European mudminnow *Umbra krameri*. *Oryx*, 514, pp.718–729.

Taylor, J.L. and McPhail, J.D., (2000) Temperature, development, and behavior in the early life history of burbot from Columbia Lake, British Columbia. *Burbot biology, ecology, and management. American Fisheries Society, Fisheries Management Section, Publication, Bethesda, Maryland*, pp.30–37.

Taylor, S., (2014) National biodiversity climate change vulnerability model. *Climate Change Adaptation and Mitigation*, p.17.

Temple, S.A., (1978) *Endangered birds: management techniques for preserving threatened species*. University of Wisconsin Press.

Terrazas, M.M., Adams, J.R., Sudheesh, P.S. and Cain, K.D., (2017) Effects of Diel Temperature Fluctuation on Growth, Stress Response, and Immune Function of Burbot. *Transactions of the American Fisheries Society*, 1465, pp.996–1007.

Therneau, T., Atkinson, B. and Ripley, B., (2022) *rpart: Recursive Partitioning and Regression Trees*.

Thevenet, A., Citterio, A. and Piégay, H., (1998) A new methodology for the assessment of large woody debris accumulations on highly modified rivers (example of two French piedmont rivers). *Regulated Rivers: Research & Management: An International Journal Devoted to River Research and Management*, 146, pp.467–483.

Thompson, J.R., Iravani, H., Clilverd, H.M., Sayer, C.D., Heppell, C.M. and Axmacher, J.C., (2017) Simulation of the hydrological impacts of climate change on a restored floodplain. *Hydrological Sciences Journal*, 6215, pp.2482–2510.

Thompson, M.S.A., Brooks, S.J., Sayer, C.D., Woodward, G., Axmacher, J.C., Perkins, D.M. and Gray, C., (2018) Large woody debris “rewilding” rapidly restores biodiversity in riverine food webs. *Journal of Applied Ecology*, 552, pp.895–904.

Thompson, S., Vehkaoja, M., Pellikka, J. and Nummi, P., (2021) Ecosystem services provided by beavers *Castor* spp. *Mammal Review*, 511, pp.25–39.

Tielke, A.-K., Karreman, J. and Vos, M., (2020) Mild cycles open closed communities to ecological restoration. *Restoration Ecology*, 284, pp.841–849.

Tielke, A.-K. and Vos, M., (2024) Successful reintroduction of species: improving on windows of opportunity for biodiversity repair. *Restoration Ecology*, 323, p.e14091.

Tockner, K., Schiemer, F., Baumgartner, C., Kum, G., Weigand, E., Zweimüller, I. and Ward, J.V., (1999) The Danube restoration project: species diversity patterns across connectivity gradients in the floodplain system. *Regulated Rivers: Research & Management*, 151–3, pp.245–258.

Tockner, K. and Stanford, J.A., (2002) Riverine flood plains: present state and future trends. *Environmental conservation*, 293, pp.308–330.

Toivonen, J., Hudd, R., Nystrand, M. and Österholm, P., (2020) Climatic effects on water quality in areas with acid sulfate soils with commensurable consequences on the reproduction of burbot (*Lota lota* L.). *Environmental Geochemistry and Health*, 4210, pp.3141–3156.

Tonolla, D., Wolter, C., Ruhtz, T. and Tockner, K., (2012) Linking fish assemblages and spatiotemporal thermal heterogeneity in a river-floodplain landscape using high-resolution airborne thermal infrared remote sensing and in-situ measurements. *Remote Sensing of Environment*, 125, pp.134–146.

Trabelsi, A., Gardeur, J.-N., Teletchea, F. and Fontaine, P., (2011) Effects of 12 factors on burbot *Lota lota* (L., 1758) weaning performances using fractional factorial design experiment. *Aquaculture*, 3161, pp.104–110.

UKCEH, (2023) *National River Flow Archive*. [online] Available at: <https://nrfa.ceh.ac.uk/data/station/spatial/33006>.

Vaage, B. and Myrick, C., (2021) The effects of acute and chronic exposure of ammonia on juvenile burbot (*Lota lota*) growth and survival. *Aquaculture*, 542, p.736891.

Van den Neucker, T., Gelaude, E., Baeyens, R., Jacobs, Y., De Maerteleire, N., Robberechts, K., Stevens, M., Mouton, A., Buysse, D. and Auwerx, J., (2013) Wetenschappelijke ondersteuning herstelprogramma's kopvoorn, serpeling, kwabaal en beekforel in 2012. *Rapporten/Instituut voor Natuur-en Bosonderzoek [Brussel]-Brussel*.

Van den Neucker, T., Gelaude, E., Baeyens, R., Jacobs, Y., De Maerteleire, N., Stevens, M., Mouton, A., Buysse, D., Auwerx, J., Vught, I., and others, (2012) Wetenschappelijke ondersteuning herstelprogramma's kopvoorn, serpeling, kwabaal en beekforel in 2011. *Rapporten/Instituut voor Natuur-en Bosonderzoek [Brussel]-Brussel*.

Van den Neucker, T., Gelaude, E., Martens, S., Baeyens, R., Jacobs, Y., Stevens, M., Mouton, A., Buysse, D., Auwerx, J., De Charleroy, D., Coeck, J. and van Vessem, J., (2009) *Wetenschappelijke ondersteuning herstelprogramma's kopvoorn, serpeling, kwabaal en beekforel in 2008*. Rapporten van het Instituut voor Natuur- en Bosonderzoek. België: Instituut voor Natuur- en Bosonderzoek.

Van den Neucker, T., Gelaude, E., Martens, S., Baeyens, R., Jacobs, Y., Stevens, M., Mouton, A., Buysse, D., Auwerx, J., De Charleroy, D., Coeck, J. and van Vessem, J., (2010a) *Wetenschappelijke ondersteuning van de herstelprogramma's voor kopvoorn, serpeling, kwabaal en beekforel in 2009*. [online] Brussels: Instituut voor Natuur- en Bosonderzoek. Available at: <https://repository.uantwerpen.be/desktop/irua> [Accessed 6 Dec. 2024].

Van den Neucker, T., Gelaude, E., Martens, S., Baeyens, R., Jacobs, Y., Stevens, M., Mouton, A., Buysse, D., Auwerx, J., Vught, I., De Charleroy, D., Coeck, J. and van Vessem, J., (2010b) *Wetenschappelijke ondersteuning herstelprogramma's kopvoorn, serpeling, kwabaal en beekforel in 2010*. [online] Brussels: Instituut voor Natuur- en Bosonderzoek. Available at: <https://publicaties.vlaanderen.be/view-file/8352> [Accessed 6 Dec. 2024].

Van Heezik, A., (2008) *Battle over the rivers. Two hundred years of river policy in the Netherlands*. van heezik beleidsresearch.

Van Houdt, J.K., Hellemans, B. and Volckaert, F.A.M., (2003) Phylogenetic relationships among Palearctic and Nearctic burbot (*Lota lota*): Pleistocene extinctions and recolonization. *Molecular Phylogenetics and Evolution*, 293, pp.599–612.

Van Houdt, J.K.J., De Cleyn, L., Perretti, A. and Volckaert, F. a. M., (2005) A mitogenic view on the evolutionary history of the Holarctic freshwater gadoid, burbot (*Lota lota*). *Molecular Ecology*, 148, pp.2445–2457.

Van Rees, C.B., Waylen, K.A., Schmidt-Kloiber, A., Thackeray, S.J., Kalinkat, G., Martens, K., Domisch, S., Lillebø, A.I., Hermoso, V., Grossart, H., Schinegger, R., Decler, K., Adriaens, T., Denys, L., Jarić, I., Janse, J.H., Monaghan, M.T., De Wever, A., Geijzendorffer, I., Adamescu, M.C. and Jähnig, S.C., (2021) Safeguarding freshwater life beyond 2020: Recommendations for the new global biodiversity framework from the European experience. *Conservation Letters*, 141, p.e12771.

Van Wichelen, J., Vandamme, L., Pauwels, I., Auwerx, J., Buysse, D., Baeyens, R., De Maerteleire, N., Gelaude, E., Pieters, S., Robberechts, K. and Coeck, J., (2018) *Wetenschappelijke onderbouwing en ondersteuning van het visserijbeleid en het visstandbeheer: Onderzoeksprogramma visserij 2017 - eindverslag*. [online] Instituut voor Natuur- en Bosonderzoek. Available at: [https://pureportal.inbo.be/portal/nl/publications/wetenschappelijke-onderbouwing-en-ondersteuning-van-het-visserijbeleid-en-het-visstandbeheer\(7eaca3e3-7ae5-4f0f-912b-12022c51cbee\).html](https://pureportal.inbo.be/portal/nl/publications/wetenschappelijke-onderbouwing-en-ondersteuning-van-het-visserijbeleid-en-het-visstandbeheer(7eaca3e3-7ae5-4f0f-912b-12022c51cbee).html) [Accessed 11 Jun. 2024].

Van Wichelen, J., Vandamme, L., Pauwels, I., Auwerx, J., Buysse, D., Baeyens, R., De Maerteleire, N., Gelaude, E., Pieters, S., Robberechts, K., Vermeersch, S. and Coeck, J., (2019) *Wetenschappelijke onderbouwing en ondersteuning van het visserijbeleid en het visstandbeheer: Onderzoeksprogramma visserij 2018*. [online] Instituut voor Natuur- en Bosonderzoek. Available at: [https://pureportal.inbo.be/portal/nl/publications/wetenschappelijke-onderbouwing-en-ondersteuning-van-het-visserijbeleid-en-het-visstandbeheer\(575b8c87-bca0-4c4d-9d5c-4df2235cace4\).html](https://pureportal.inbo.be/portal/nl/publications/wetenschappelijke-onderbouwing-en-ondersteuning-van-het-visserijbeleid-en-het-visstandbeheer(575b8c87-bca0-4c4d-9d5c-4df2235cace4).html) [Accessed 11 Jun. 2024].

Vandamme, L., Pauwels, I., Verhelst, P., Buysse, D., Steendam, C., De Maerteleire, N., Gelaude, E., Pieters, S., De Dapper, T., Baeyens, R., Wackenier, M., Auwerx, J., Vermeersch, S. and Coeck, J., (2021) *Wetenschappelijke onderbouwing en ondersteuning van het visserij-beleid en het visstandbeheer: Onderzoeksprogramma visserij 2020 - eindrapport*. [online] Instituut voor Natuur- en Bosonderzoek. Available at: <https://pureportal.inbo.be/nl/publications/wetenschappelijke-onderbouwing-en-ondersteuning-van-het-visserij--3> [Accessed 11 Jun. 2024].

Vandamme, L., Van Wichelen, J., Pauwels, I., Auwerx, J., Vught, I., Buysse, D., Baeyens, R., De Maerteleire, N., Gelaude, E., Picavet, B., Pieters, S., Robberechts, K. and Coeck, J., (2017) *Wetenschappelijke onderbouwing en ondersteuning van het visserijbeleid en het visstandbeheer: Onderzoeksprogramma visserij 2016 - eindrapport*. [online] Instituut voor Natuur- en Bosonderzoek. Available at: [https://pureportal.inbo.be/portal/nl/publications/wetenschappelijke-onderbouwing-en-ondersteuning-van-het-visserijbeleid-en-het-visstandbeheer\(ae5ba158-c435-4d02-ae5d-c46966a1737f\).html](https://pureportal.inbo.be/portal/nl/publications/wetenschappelijke-onderbouwing-en-ondersteuning-van-het-visserijbeleid-en-het-visstandbeheer(ae5ba158-c435-4d02-ae5d-c46966a1737f).html) [Accessed 11 Jun. 2024].

Vandamme, L., Van Wichelen, J., Steendam, C., Brys, R., Pauwels, I., Auwerx, J., Buysse, D., Baeyens, R., De Maerteleire, N., Gelaude, E., Pieters, S., Robberechts, K., Vermeersch, S. and Coeck, J., (2020) *Wetenschappelijke onderbouwing en ondersteuning van het visserijbeleid en het visstandbeheer. Onderzoeksprogramma visserij 2019*. [online] Instituut voor Natuur- en Bosonderzoek. Available at: [https://pureportal.inbo.be/portal/nl/publications/wetenschappelijke-onderbouwing-en-ondersteuning-van-het-visserijbeleid-en-het-visstandbeheer\(e1b1db61-eb55-48f7-b3af-874323293e3e\).html](https://pureportal.inbo.be/portal/nl/publications/wetenschappelijke-onderbouwing-en-ondersteuning-van-het-visserijbeleid-en-het-visstandbeheer(e1b1db61-eb55-48f7-b3af-874323293e3e).html) [Accessed 11 Jun. 2024].

Vandamme, L., Verhelst, P., Pauwels, I., Buysse, D., Broos, S., Auwerx, J., Brys, R., Neyrinck, S., Plaetinck, S., Pieters, S., Rosseel, D., De Maerteleire, N. and Coeck, J., (2024) *Wetenschappelijke onderbouwing en ondersteuning van het visserijbeleid en het visstandbeheer: Onderzoeksprogramma visserij 2021 - 2022*. [online] Instituut voor Natuur- en Bosonderzoek. Available at: <https://pureportal.inbo.be/nl/publications/wetenschappelijke-onderbouwing-en-ondersteuning-van-het-visserijb-12> [Accessed 11 Jun. 2024].

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. and Cushing, C.E., (1980) The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 371, pp.130–137.

Varga, K., Dévai, G. and Tóthmérész, B., (2013) Land use history of a floodplain area during the last 200 years in the Upper-Tisza region (Hungary). *Regional Environmental Change*, 135, pp.1109–1118.

Verdonschot, R.C.M. and Verdonschot, P.F.M., (2012) *Habitat-en systeemgeschiktheid van beeksystemen voor beekvisserij*. Bosschap, bedrijfsschap voor bos en natuur.

Viles, H.A., (2022) Biogeomorphology. *Geological Society, London, Memoirs*, 581, pp.205–212.

Visser, A., Beevers, L. and Patidar, S., (2019) The Impact of Climate Change on Hydroecological Response in Chalk Streams. *Water*, 113, p.596.

Vivash, R., Ottosen, O., Janes, M. and Sørensen, H. v., (1998) Restoration of the rivers Brede, Cole and Skerne: a joint Danish and British EU-LIFE demonstration project, II—the river restoration works and other related practical aspects. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 81, pp.197–208.

van Vliet, M.T.H., Franssen, W.H.P., Yearsley, J.R., Ludwig, F., Haddeland, I., Lettenmaier, D.P. and Kabat, P., (2013) Global river discharge and water temperature under climate change. *Global Environmental Change*, 232, pp.450–464.

Vokoun, J.C. and Watrous, D., (2009) *Determining swim speed performance characteristics for fish passage of burbot using an experimental flume and nature-like fishway*. Connecticut, US: Connecticut Department of Environmental Protection.

Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Liermann, C.R. and Davies, P.M., (2010) Global threats to human water security and river biodiversity. *Nature*, 4677315, pp.555–561.

Voss, R., Hinrichsen, H.-H. and Wieland, K., (2001) Model-supported estimation of mortality rates in Baltic cod (*Gadus morhua callarias* L.) larvae: the varying impact of 'critical periods'. *BMC Ecology*, 11, p.4.

Vught, I., Buysse, D., De Charleroy, D., Jansen, I., Mouton, A., Papadopoulos, I., Pauwels, I., Auwerx, J., Baeyens, R., De Maerteleire, N., Gelaude, E., Picavet, B., Pieters, S., Robberechts, K. and Coeck, J., (2015) *Wetenschappelijke*

onderbouwingen ondersteuning van het visserijbeleid en het visstandbeheer - onderzoeksprogramma visserij 2014: eindrapport. Rapporten van het Instituut voor Natuur- en Bosonderzoek jaar. [online] Brussels: Instituut voor Natuur- en Bosonderzoek. Available at: <https://pureportal.inbo.be/en/publications/wetenschappelijke-onderbouwing-en-ondersteuning-van-het-visserijb-8> [Accessed 6 Nov. 2024].

Vught, I., Harzevilli, A.S., Auwerx, J., De Charleroy, D., Paragamian, V.L. and Bennet, D.H., (2008) Aspects of reproduction and larviculture of burbot under hatchery conditions. In: *American Fisheries Society Symposium*. American Fisheries Society, p.167.

Wagner, W.C., (1972) Utilization of Alewives by Inshore Piscivorous Fishes in Lake Michigan. *Transactions of the American Fisheries Society*, 101, pp.55–63.

Walton, S.E., Nunn, A.D., Probst, W.N., Bolland, J.D., Acreman, M. and Cowx, I.G., (2017) Do fish go with the flow? The effects of periodic and episodic flow pulses on 0+ fish biomass in a constrained lowland river. *Ecohydrology*, 101, p.e1777.

Wang, N. and Appenzeller, A., (1998) Abundance, depth distribution, diet composition and growth of perch (*Perca fluviatilis*) and burbot (*Lota lota*) larvae and juveniles in the pelagic zone of Lake Constance. *Ecology of Freshwater Fish*, 74, pp.176–183.

Ward, J.V., Tockner, K., Uehlinger, U. and Malard, F., (2001) Understanding natural patterns and processes in river corridors as the basis for effective river restoration. *Regulated Rivers: Research & Management*, 174–5, pp.311–323.

Watts, G., Battarbee, R.W., Bloomfield, J.P., Crossman, J., Daccache, A., Durance, I., Elliott, J.A., Garner, G., Hannaford, J., Hannah, D.M., Hess, T., Jackson, C.R., Kay, A.L., Kernan, M., Knox, J., Mackay, J., Monteith, D.T., Ormerod, S.J., Rance, J., Stuart, M.E., Wade, A.J., Wade, S.D., Weatherhead, K., Whitehead, P.G. and Wilby, R.L., (2015) Climate change and water in the UK – past changes and future prospects. *Progress in Physical Geography: Earth and Environment*, 391, pp.6–28.

Wayre, P., (1979) Otter havens in norfolk & suffolk, England. *Biological Conservation*, 161, pp.73–81.

WeatherSpark, (2023a) *Average Weather in Herentals, Belgium*. [online] Available at: <https://weatherspark.com/y/51212/Average-Weather-in-Herentals-Belgium-Year-Round> [Accessed 15 Sep. 2023].

WeatherSpark, (2023b) *Average Weather in Nijlen, Belgium*. [online] Available at: <https://weatherspark.com/y/51189/Average-Weather-in-Nijlen-Belgium-Year-Round> [Accessed 16 Sep. 2023].

WeatherSpark, (2023c) *Climate and Average Weather Year Round at RAF Marham*. [online] Available at: <https://weatherspark.com/y/147885/Average-Weather-at-RAF-Marham-United-Kingdom-Year-Round#Figures-Temperature> [Accessed 14 Jun. 2023].

Webb, B.W., Clack, P.D. and Walling, D.E., (2003) Water–air temperature relationships in a Devon river system and the role of flow. *Hydrological Processes*, 1715, pp.3069–3084.

Webb, B.W. and Nobilis, F., (1995) Long term water temperature trends in Austrian rivers. *Hydrological Sciences Journal*, 401, pp.83–96.

Webb, P.W., (1984) Form and function in fish swimming. *Scientific American*, 2511, pp.72–83.

Weber, J.J., (1976) *Winter observations on the age and growth of the burbot in Lake Winnebago, Wisconsin*. Department of Natural Resources.

Wedekind, C. and Küng, C., (2010) Shift of Spawning Season and Effects of Climate Warming on Developmental Stages of a Grayling (Salmonidae). *Conservation Biology*, 245, pp.1418–1423.

Weidel, B.C., Ackiss, A.S., Chalupnicki, M.A., Connerton, M.J., Davis, S., Dettmers, J.M., Drew, T., Fisk, A.T., Gordon, R., Hanson, S.D., Holden, J.P., Holey, M.E., Johnson, J.H., Johnson, T.B., Lake, C., Lantry, B.F., Loftus, K.K., Mackey, G.E., McKenna, J.E., Millard, M.J., Minihkeim, S.P., O'Malley, B.P., Rupnik, A., Todd, A. and LaPan, S.R., (2022) Results of the collaborative Lake Ontario bloater restoration stocking and assessment, 2012–2020. *Journal of Great Lakes Research*, 482, pp.371–380.

Weiperth, A., Gaebele, T., Potyó, I. and Guti, G., (2010) Long-term changes of fish fauna in the Hungarian section of the Ipel River. In: *Proceedings Volume of the 38th Conference of the IAD*. pp.1–6.

Wells, P. and Heydon, M., (2022) *Reintroductions and Conservation Translocations: Case studies from the UK*. [Natural England Research Report] UK: Natural England. Available at: <https://publications.naturalengland.org.uk/publication/4940855555915776>.

Wentworth, C.K., (1922) A scale of grade and class terms for clastic sediments. *The journal of geology*, 305, pp.377–392.

Wetjen, M., Hübner, D., Seehausen, O. and Schulz, R., (2020a) Genetic diversity of endangered *Chondrostoma nasus* in the River Rhine system: Conservation genetics considerations on stocking and reintroduction. *Knowledge & Management of Aquatic Ecosystems*, 421, p.25.

Wetjen, M., Schmidt, T., Schrimpf, A. and Schulz, R., (2020b) Genetic diversity and population structure of burbot *Lota lota* in Germany: Implications for conservation and management. *Fisheries Management and Ecology*, 272, pp.170–184.

Wharton, G., Cotton, J.A., Wotton, R.S., Bass, J.A., Heppell, C.M., Trimmer, M., Sanders, I.A. and Warren, L.L., (2006) Macrophytes and suspension-feeding invertebrates modify flows and fine sediments in the Frome and Piddle catchments, Dorset (UK). *Journal of Hydrology*, 3301–2, pp.171–184.

White, J.C., Khamis, K., Dugdale, S., Jackson, F.L., Malcolm, I.A., Krause, S. and Hannah, D.M., (2023) Drought impacts on river water temperature: A process-based understanding from temperate climates. *Hydrological Processes*, 3710, p.e14958.

White, J.C., Seddon, E., Hill, M.J., Mathers, K.L., Bridger, M., Hannah, D.M. and Wood, P.J., (2025) Going to the archives: Combining palaeoecological and contemporary data to support river restoration appraisals. *River Research and Applications*, 411, pp.23–36.

Whitehead, P.G. and Robinson, M., (1993) Experimental basin studies—an international and historical perspective of forest impacts. *Journal of Hydrology*, 1453, pp.217–230.

Whitehead, P.G., Wilby, R.L., Battarbee, R.W., Kernan, M. and Wade, A.J., (2009) A review of the potential impacts of climate change on surface water quality. *Hydrological Sciences Journal*, 541, pp.101–123.

Whitesel, T.A., DeHaan, P.W., Doyle, J., Adams, B.A. and Sankovich, P.M., (2022) Evaluating the success of a conservation reintroduction: The case of bull trout in the Wallowa River. *Conservation Science and Practice*, 46, p.e12674.

Wilby, R., (1993a) *Modelling low flows in relation to weather pattern and landuse*. Bristol, UK: National Rivers Authority.

Wilby, R.L., (1993b) *River Ouse augmentation scheme impact on water temperatures*. [Technical Report] Available at: https://www.researchgate.net/publication/346521891_Wilby_1993_FEG_-_River_Ouse_augmentation_scheme_-_impact_on_water_temperatures [Accessed 15 May 2025].

Wilby, R.L. and Johnson, M.F., (2020) Climate variability and implications for keeping rivers cool in England. *Climate Risk Management*, 30, p.100259.

Wilby, R.L., Johnson, M.F. and Toone, J.A., (2014) Nocturnal river water temperatures: Spatial and temporal variations. *Science of The Total Environment*, 482–483, pp.157–173.

Wildlife and Countryside Act 1981. [online] Available at: <http://www.legislation.gov.uk/ukpga/1981/69/contents> [Accessed 27 Dec. 2019].

Wilkes, M.A., Mungee, M., Naura, M., Bell, V.A. and Brown, L.E., (2025) Predicting nature recovery for river restoration planning and ecological assessment: A case study from England, 1991–2042. *River Research and Applications*, 411, pp.68–81.

Wilson, C.J., (2004) Could we live with reintroduced large carnivores in the UK? *Mammal Review*, 343, pp.211–232.

Winfield, I.J., Adams, C.E., Bean, C.W., Durie, N.C., Fletcher, J.M., Gowans, A.R., Harrod, C., James, J.B., Lyle, A.A., Maitland, P.S. and Thompson, C., (2012) Conservation of the vendace (*Coregonus albula*), the UK's rarest freshwater fish. *Advances in Limnology*, 63, pp.547–559.

Winfield, I.J., Fletcher, J.M. and James, J.B., (2004) Conservation ecology of the vendace (*Coregonus albula*) in Bassenthwaite Lake and Derwent Water, UK. *Annales Zoologici Fennici*, 411, pp.155–164.

Woher, H., (2010) Überprüfung der fischart Rutte (*Lota lota* L.) für zwecke der speisefischproduktion.[Validation of the Burbot (*Lota lota* L.) for purposes of aquaculture production.]. *Abschlussbericht des Pilotprojektes II (2007–2010), Bezirk Niederbayern, Fachberatung für Fischerei. LOTAqua-Hatchery, Überlingen, Germany.(In German.)*.

Wohl, E., (2017) Connectivity in rivers. *Progress in Physical Geography*, 413, pp.345–362.

Wohl, E., (2020) Wood process domains and wood loads on floodplains. *Earth Surface Processes and Landforms*, 451, pp.144–156.

Wohl, E., Angermeier, P.L., Bledsoe, B., Kondolf, G.M., MacDonnell, L., Merritt, D.M., Palmer, M.A., Poff, N.L. and Tarboton, D., (2005) River restoration. *Water Resources Research*, 4110, p.2005WR003985.

Wohl, E., Kramer, N., Ruiz-Villanueva, V., Scott, D.N., Comiti, F., Gurnell, A.M., Piegay, H., Lininger, K.B., Jaeger, K.L., Walters, D.M. and Fausch, K.D., (2019) The Natural Wood Regime in Rivers. *BioScience*, 694, pp.259–273.

Wohl, E., Lane, S.N. and Wilcox, A.C., (2015) The science and practice of river restoration. *Water Resources Research*, 518, pp.5974–5997.

Wohl, E., Uno, H., Dunn, S.B., Kemper, J.T., Marshall, A., Means-Brous, M., Scamardo, J.E. and Triantafyllou, S.P., (2024) Why wood should move in rivers. *River Research and Applications*, 406, pp.976–987.

Wolter, C. and Freyhof, J., (2004) Diel distribution patterns of fishes in a temperate large lowland river. *Journal of Fish Biology*, 643, pp.632–642.

Wood, T., (1981) River management. In: *British Rivers*. Routledge, pp.170–195.

Woodget, A.S., Visser, F., Maddock, I.P. and Carbonneau, P.E., (2016) The Accuracy and Reliability of Traditional Surface Flow Type Mapping: Is it Time for a New Method of Characterizing Physical River Habitat? *River Research and Applications*, 329, pp.1902–1914.

Woodward, G., Perkins, D.M. and Brown, L.E., (2010) Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 3651549, pp.2093–2106.

Worthington, T., (2010) *The feasibility of reintroducing the burbot (Lota lota) to England*. PhD. University of Southampton.

Worthington, T., Kemp, P. and Osborne, P.E., (2011a) Factors affecting the population viability of the burbot, *Lota lota*. *Fisheries Management and Ecology*, 184, pp.322–332.

Worthington, T., Kemp, P., Osborne, P.E., Howes, C. and Easton, K., (2010a) Former distribution and decline of the burbot (*Lota lota*) in the UK. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 204, pp.371–377.

Worthington, T., Kemp, P.S., Osborne, P.E., Dillen, A., Coeck, J., Bunzel-Drücke, M., Naura, M., Gregory, J. and Easton, K., (2012) A spatial analytical approach for selecting reintroduction sites for burbot in English rivers. *Freshwater Biology*, 573, pp.602–611.

Worthington, T., Kemp, P.S., Osborne, P.E., Howes, C. and Easton, K., (2011b) A review of the historical distribution and status of the burbot (*Lota lota*) in English rivers. *Journal of Applied Ichthyology*, 27s1, pp.1–8.

Worthington, T., Tisdale, J., Kemp, P., Williams, I. and Osborne, P.E., (2010b) Public and stakeholder attitudes to the reintroduction of the burbot, *Lota lota*. *Fisheries Management and Ecology*, 176, pp.465–472.

Worthington, T.A., Houdt, J.K.J.V., Hull, J.M. and Kemp, P.S., (2017) Thermal refugia and the survival of species in changing environments: new evidence from a nationally extinct freshwater fish. *Ecology of Freshwater Fish*, 263, pp.415–423.

Wright, J.F., Hiley, P.D., Ham, S.F. and Berrie, A.D., (1981) Comparison of three mapping procedures developed for river macrophytes. *Freshwater Biology*, 114, pp.369–379.

Wrona, F.J., Prowse, T.D., Reist, J.D., Hobbie, J.E., Lévesque, L.M. and Vincent, W.F., (2006) Climate change effects on aquatic biota, ecosystem structure and function. *AMBIO: A Journal of the Human Environment*, 357, pp.359–369.

Wu, H.C., Lee, K.C. and Lee, P.F., (2008) Restoration of Formosan landlocked salmon in the Shei-Pa National Park, Taiwan. In: P.S. Soorae, ed., *Global Reintroduction Perspectives: Re-introduction Case Studies From Around The Globe.*, Global Re-introduction Perspectives. Abu Dhabi: IUCN SSC Conservation Translocation Specialist Group, p.284.

WWF, (2024) *Living Planet Report 2024 – A System in Peril*. [online] Gland, Switzerland: WWF. Available at: <https://www.worldwildlife.org/publications/2024-living-planet-report> [Accessed 13 May 2025].

Wyrick, J.R. and Klingeman, P.C., (2011) Proposed fluvial island classification scheme and its use for river restoration. *River Research and Applications*, 277, pp.814–825.

Yimer, E.A., Riakhi, F.-E., Bailey, R.T., Nossent, J. and van Griensven, A., (2023) The impact of extensive agricultural water drainage on the hydrology of the Kleine Nete watershed, Belgium. *Science of The Total Environment*, 885, p.163903.

Young, J., (2018) Re-establishing the three-spined stickleback fish as part of the holistic restoration of an urban lake, California, USA. In: P.S. Soorae, ed., *Global Reintroduction Perspectives: 2018. Case studies from around the globe*, Global Re-introduction Perspectives. Gland, Switzerland: IUCN SSC Conservation Translocation Specialist Group & Environment Agency, p.286.

Yusoff, I., Hiscock, K. and Conway, D., (2002) Simulation of the impacts of climate change on groundwater resources in eastern England. *Geological Society, London, Special Publications*, 1931, pp.325–344.

Żarski, D., Kucharczyk, D., Sasinowski, W., Targońska, K. and Mamcarz, A., (2010) The Influence of Temperature on Successful Reproductions of Burbot, *Lota Lota* (L.) Under Hatchery Conditions. *Polish Journal of Natural Science*, 25, pp.93–105.

Zeug, S.C. and Winemiller, K.O., (2007) Ecological correlates of fish reproductive activity in floodplain rivers: a life-history-based approach. *Canadian Journal of Fisheries and Aquatic Sciences*, 6410, pp.1291–1301.

Živkov, M.T., Trichkova, T.A. and Raikova-Petrova, G.N., (1999) Biological reasons for the unsuitability of growth parameters and indices for comparing fish growth. *Environmental Biology of Fishes*, 541, pp.67–76.

Appendices

Appendix 1. Chapter 2, study area site locations, descriptions, and data sources.

Site Name	Grid Reference	Description	Source
Necton Common	TF 88805 08110	EA water quality monitoring site	https://environment.data.gov.uk/water-quality/view/landing
Swaffham	TF 82122 08707	Town referenced	
Shipdham	TF 96057 06971	Wissey source	
Bradenham	TF 92539 07798	EA water quality monitoring site	https://environment.data.gov.uk/water-quality/view/landing
Browns Lane	TF 87791 06623	EA water quality monitoring site	https://environment.data.gov.uk/water-quality/view/landing
Northern Pickenham	TF 86381 06059	EA water quality, macroinvertebrates, and fish monitoring site	https://environment.data.gov.uk/ecology/explorer/ ; https://environment.data.gov.uk/water-quality/view/landing
Great Cressingham	TF 84971 00983	EA macroinvertebrates monitoring site	https://environment.data.gov.uk/ecology/explorer/
Linghills Farm	TF 83467 00231	EA water quality, macroinvertebrates, and fish monitoring site	https://environment.data.gov.uk/ecology/explorer/ ; https://environment.data.gov.uk/water-quality/view/landing
Hilborough	TF 82191 00176	EA fish monitoring site	https://environment.data.gov.uk/ecology/explorer/
West Tofts	TL 83770 92547	Area referenced	
Munford	TL 80194 93709	EA water quality, macroinvertebrates, and fish monitoring site	https://environment.data.gov.uk/ecology/explorer/ ; https://environment.data.gov.uk/water-quality/view/landing
Ickburgh	TL 81088 94603	EA water quality and fish monitoring site	https://environment.data.gov.uk/ecology/explorer/ ; https://environment.data.gov.uk/water-quality/view/landing
Didlington	TL 78078 96659	Town referenced	
Northwold	TL 75635 96749	Daily gauged flow monitoring site	UKCEH (2023), https://nrfa.ceh.ac.uk/data/station/info/33006
Denver	TF 61450 01398	MetOffice MIDAS Open: UK Land Surface Stations Data, daily maximum and minimum air temperature monitoring station	https://data.ceda.ac.uk/badc/ukmo-midas-open/data/uk-daily-temperature-obs/dataset-version-202308/norfolk/00407_denver/qc-version-1
Hilborough Ford	TF 83313 00778	EA fish monitoring site	https://environment.data.gov.uk/ecology/explorer/
Watton Brook	TF 84020 00275	EA water quality monitoring site	https://environment.data.gov.uk/water-quality/view/landing
Hilborough Mill	TL 82701 99772	EA fish monitoring site	https://environment.data.gov.uk/ecology/explorer/
Bodney Bridge	TL 82873 98798	EA water quality and macroinvertebrates monitoring site; EA stage gauge site	https://environment.data.gov.uk/ecology/explorer/ ; https://environment.data.gov.uk/water-quality/view/landing
Bodney Meadows	TL 83104 98272	EA fish monitoring site	https://environment.data.gov.uk/ecology/explorer/
NRT 2015	TL 83245 98164	NRT fish survey	
Chalk Hall Farm	TL 83499 98069	Petts and Bickerton (1994) monitoring site	Petts and Bickerton (1994)
NRT 2023	TL 83934 96383	NRT fish survey	
Bridge Carr Lake	TL 83589 95218	Area referenced, artificial lake	
Buckenham Tofts	TL 84169 94955	Area referenced	
Langford	TL 83009 94983	Petts and Bickerton (1994) monitoring site	Petts and Bickerton (1994)

Appendix 2. Fish species caught within the upper Wissey catchment from North Pickenham to Mundford. All survey data are obtained from Environment Agency (2023b), except NRT 2015 and NRT 2023, which was obtained from Norfolk Rivers Trust (personal comms., 2023). Each location has a different number of total survey years: Bodney Meadows, 2; Buckenham Tofts Lake, 1; Buckenham Tofts River, 2; Hilborough Ford, 7; Hilborough Mill, 6; Ickburgh Plantation, 2; Linghills Farm, 7; Mundford, 1; North Pickenham, 4; NRT 2015, 1, and NRT 2023, 1.

Species name	Common Name	Locations	Years	# Fish
<i>Abramis brama</i>	Common bream	Buckenham Tofts Lake	2000	6
<i>Anguilla anguilla</i>	European eel	Bodney Meadows	1990	100
			1993	67
		Buckenham Tofts River	1990	133
			1993	3
		Hilborough Ford	1990	40
			1993	24
			1996	4
			2000	3
			2007	1
			2012	4
		Hilborough Mill	1990	83
			1993	7
			1996	8
			2000	19
		Ickburgh Plantation	1990	308
			1993	12
		Linghills Farm	1990	17
			1993	3
			1996	6
			2000	7
			2012	1
			2015	1
		NRT 2015	2015	120
		NRT 2023	2023	31
<i>Barbatula barbatula</i>	Stone loach	Buckenham Tofts River	1990	3
		Hilborough Ford	1990	1
			1993	1
			2000	1
			2007	1
			2012	4
		Hilborough Mill	1990	3
			1996	4
			2007	4
			2012	8
		Ickburgh Plantation	1990	1
		Linghills Farm	1996	2
			2000	3
			2007	21
			2012	8
			2015	4
		North Pickenham	2010	16
			2012	11
			2015	22
			2018	16
		NRT 2015	2015	4
		NRT 2023	2023	2
<i>Cobitis taenia</i>	Spined loach	Bodney Meadows	1993	1
<i>Cottus gobio</i>	European bullhead	Buckenham Tofts Lake	2000	2
		Buckenham Tofts River	1990	7
		Hilborough Ford	1990	1

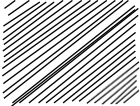
<i>Esox lucius</i>	Northern pike		1993	4
			1996	1
			2000	5
			2007	8
			2012	2
			2015	4
		Hilborough Mill	1996	1
			2000	14
			2007	4
			2012	15
		Ickburgh Plantation	1990	7
			1993	2
		Linghills Farm	1990	3
			1993	1
			2000	8
			2007	3
			2012	48
			2015	9
		Mundford	2013	16
		North Pickenham	2010	21
			2012	38
			2015	7
		NRT 2015	2015	89
		NRT 2023	2023	62
		Buckenham Tofts Lake	2000	3
		Buckenham Tofts River	1990	3
<i>Gasterosteus aculeatus</i>	Three-spined stickleback		1993	2
		Hilborough Ford	1996	5
			2000	5
		Hilborough Mill	2007	1
		Ickburgh Plantation	1990	6
			1993	7
		Linghills Farm	1993	1
			2000	2
		Mundford	2013	3
		Buckeham Tofts Lake	2000	1
		Hilborough Ford	2007	2
			2012	6
			2015	1
		Hilborough Mill	1996	1
			2007	2
			2012	6
<i>Gobio gobio</i>	Gudgeon	Linghills Farm	2012	12
		Mundford	2013	11
		North Pickenham	2010	14
			2012	22
			2015	2
			2018	5
		NRT 2015	2015	53
		NRT 2023	2023	31
		Buckenham Tofts River	1990	7
		Bodney Meadows	1993	13
		Hilborough Ford	1996	8
			2000	1
		Hilborough Mill	1990	20
			1993	6
			1996	2
			2000	6
			2007	7
		Ickburgh Plantation	1990	7
			1993	2
		Linghills Farm	1993	5
			1996	33
			2000	34
			2007	33

			2012	7
		North Pickenham	2010	12
			2018	20
<i>Lampetra planeri</i>	Brook lamprey	Hilborough Ford	2000	4
			2015	2
		Hilborough Mill	2012	1
		NRT 2015	2015	1
		NRT 2023	2023	4
<i>Leuciscus cephalus</i>	European chub	Bodney Meadows	1993	3
		Buckenham Tofts River	1990	1
		Hilborough Mill	1993	3
		Linghills Farm	1993	7
			1996	5
			2000	4
			2012	15
<i>Leuciscus leuciscus</i>	Dace	Mundford	2013	3
		Bodney Meadows	1990	2
			1993	13
		Buckenham Tofts River	1990	14
			1993	70
		Hilborough Ford	1990	56
			1996	58
			2000	8
		Hilborough Mill	1990	26
			1993	42
			1996	5
			2000	4
			2007	4
		Ickburgh Plantation	1990	63
			1993	1
		Linghills Farm	1990	32
			1993	53
			1996	55
			2000	313
			2007	5
		North Pickenham	2010	1
			2012	11
		NRT 2023	2023	1
<i>Perca fluviatilis</i>	European perch	Buckenham Tofts Lake	2000	38
		Hilborough Mill	2000	1
			2007	1
		Linghills Farm	2000	1
<i>Pungitius pungitius</i>	Nine-spine stickleback	Mundford	2013	3
		Mundford	2013	3
		North Pickenham	2015	1
<i>Rutilus rutilus</i>	Common roach	Bodney Meadows	1993	4
		Buckenham Tofts Lake	2000	645
		Buckenham Tofts River	1990	7
			1993	10
		Hilborough Ford	1990	4
			1996	489
			2000	12
		Hilborough Mill	1993	2
			1996	1
		Linghills Farm	1990	10
			1993	14
			1996	3
			2000	5
<i>Rutilus rutilus x Scardinius erythrophthalmus</i>	Roach – rudd hybrid	Linghills Farm	1993	1
<i>Salmo trutta</i>	Brown trout	Bodney Meadows	1990	9
			1993	1
		Buckenham Tofts River	1990	21
			1993	4
		Hilborough Ford	1990	74
			2000	19

<i>Scardinius erythrophthalmus</i>	Common rudd		2007	95
			2012	39
			2015	143
		Hilborough Mill	1990	20
			1993	1
			2000	3
		Ickburgh Plantation	2007	89
			2012	58
			1990	9
		Linghills Farm	1993	20
			1990	14
			1993	22
			1996	40
			2000	9
			2007	22
			2012	51
			2015	195
		Mundford	2013	8
		North Pickenham	2010	6
			2015	7
			2018	15
		NRT 2015	2015	120
		NRT 2023	2023	31
		Bodney Meadows	1993	2
<i>Tinca tinca</i>	Tench	Buckenham Tofts River	1993	1
		Hilborough Mill	1993	6
			1996	1
			1993	14
		Linghills Farm	1996	9
			2000	1
			2007	2
		Buckeham Tofts Lake	2000	1
		Ickburgh Plantation	1990	1

Appendix 3. Key used during the custom walkover instream river habitat survey as part of the methodology for Chapter 3.

Item To Be Recorded * = Take photo of feature	Symbol	Other Notes	Burbot/Project Importance
Measurements			
Photos	Ph_1_12:37		
GPS Locations	GPS_001		
Depth	●	GPS these locations	Depth measurements need to be taken as deep water is where adult burbot will linger during the day, especially in summer to avoid hot temperatures.
Unexpected, interesting feature*	!	Make a note of the feature with a quick description and take a photo Examples: large, instream objects, freefalls, rare macrophyte species	.
Potential Temperature Probe Location	xT	Examples: Backchannels, side channels, floodplain ponds, deeper water locations. GPS these locations.	Back and side channels are important juvenile habitat, so we need to know whether their temperatures are within the survival range of the burbot. Deeper water is important for adults and whether their temperatures are optimal 12-16°C will decide whether adult populations persist in the area or whether the Wissey is a migratory location for spawning.
Obstructions			
Channel spanning barriers* (with height estimation)	===== 0.5m	Examples: weirs, sluices, etc. Note type of passage, take photo, and take GPS location if not listed on the map. If possible note if there is any installed fish passage, height, and other interesting features related to the instream barrier	Any barrier could impact the migration of migratory burbot as their ability to use fish passage effectively is disputed
Adjacent Land/Floodplain Use			
Wooded	O O O O O O O O O O O		Identifying surrounding landuse will be useful to understand relationships between local water chemistry, hydrology, geomorphology, and meteorology. Wooded areas are also likely to provide shading and therefore lower temperature habitats.
Farmland	X X X X X X X X X X X		Identifying surrounding landuse will be useful to understand relationships between local water chemistry, hydrology, geomorphology, and meteorology. Farmland could influence local water quality.

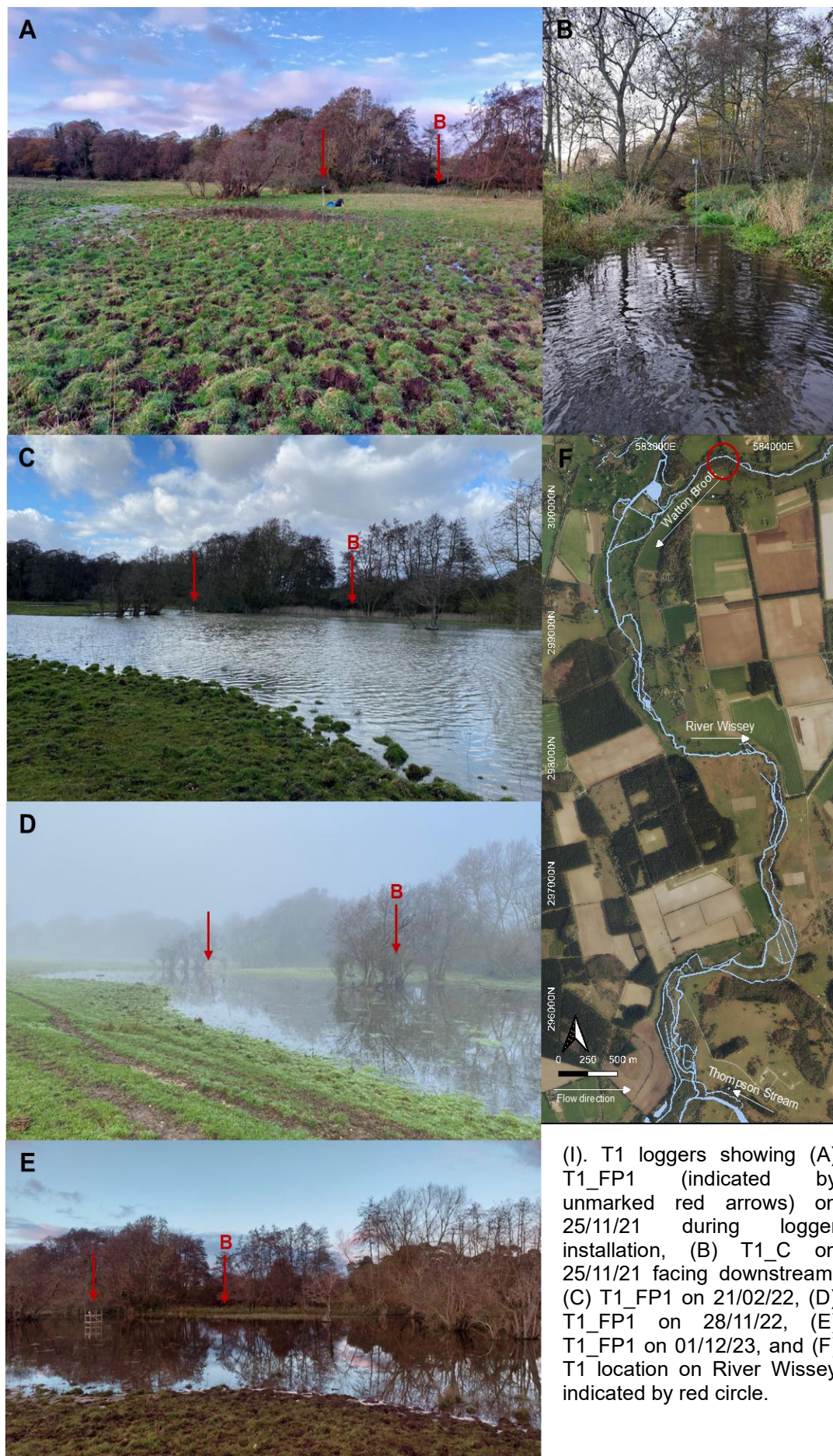
Marshy Ground			Identifying surrounding landuse will be useful to understand relationships between local water chemistry, hydrology, geomorphology, and meteorology.
Grassland/Meadows			
Development		Unlikely to have much development, but odd buildings can be noted using this symbology.	Identifying surrounding landuse will be useful to understand relationships between local water chemistry, hydrology, geomorphology, and meteorology. Developed areas could influence local water quality.
Scrub		Transitional habitat between more open (grassland, meadow) habitat and woodland. Common identifiers: bramble, hawthorn.	Identifying surrounding landuse will be useful to understand relationships between local water chemistry, hydrology, geomorphology, and meteorology.
Floodplain spill*		During the August fieldwork the river is unlikely to breach so it will be harder to spot these. Look for dips in the embankment. GPS these areas.	This will help to understand relationships between the channel and floodplain can help to identify burbot spawning habitat.
Potential Floodplain Spill		GPS these areas.	Potential areas of winter/autumn flooding so it is easier to plan later fieldwork and place the locations of water level meters later in the project.
Ponds		GPS these if possible and not on the map	The identification of valuable floodplain ponds could impact future decisions in river restoration, which could impact burbot.
Side channels*		If not on the map, GPS locations. May be dry during August walkover survey, but delineation here can be checked again at a later date.	Back/side channels are important juvenile habitat that provide shelter. Identifying substrate type, if covered in overhanging vegetation also helps to identify shelter suitability for burbot.
Depressions		These will be hard to spot during the summer, but could indicate winter flooding. GPS these areas.	Depressions will indicate where water will sit and persist on the floodplain during winter flooding. Identifying depressions could influence locations of water level sensors to identify suitable spawning habitat.
Bankside Features			
Flood banks (with height estimation)			If the project concludes a lack of suitable spawning habitat, it could still recommend river restoration techniques (bank removal) that could help connect the main channel to floodplain to create suitable habitat

Trees close to riverbank		This symbol alone will represent a single, isolated tree.	The presence of trees will influence burbot shelter as well as lowering later temperatures through bankside shading, which burbot could use as refuge in summer. Location of trees close to the riverbank could also be used as a suggestion for trees to be felled into the river for future restoration.
		Used in a line it will show trees in a continuous line. In this case, the distance estimation is more important than the number of symbols representing the number of trees.	
		Used in a cluster of 3, the symbol represents clumps of trees. The recorder may estimate and note the total number (optional).	
River shading by trees			Bankside shading will provide cooler areas of refuge for burbot in the summer. The more bankside shading, the greater the chance the burbot has for longevity in the reach under climate change.
Overhanging branches trailing the water		Can be branches, bushes or other vegetation touching the water surface so not just shading	Bankside vegetation touching the water's surface will provide cover and shelter opportunities for juvenile burbot as well as shading.
Geomorphic Features			
Pools		Reflections on water's surface are not distorted, anything on surface (foam or stick or debris) will appear stationary (Newson and Newson, 2000). Occupies full channel width.	Pools are likely to be the most dominant deepwater habitat, which is important habitat for adult burbot who will inhabit it during the day
Other deep-water habitat		Any deepwater habitat that is clearly not part of a pool-riffle-run sequence. Could be produced by instream barriers or woody debris.	Deep water is used by adult burbot during the day. In North America (lakes and rivers), burbot will occupy depths greater than 15m. The Wisconsin is unlikely to have depths greater than 3m, so identification and noting of any of this habitat is important in combination with assessing the longitudinal connectivity of the river.
Glides		Very little surface roughness, small turbulent flow cells are visible and "foam" moves downstream (Newson and Newson, 2000).	A shallow water habitat that will help to map the variations in depth across the study area to help identify habitat suitability
Runs		The surface does not produce waves, but symmetrical ripples which move in a general downstream direction. "A stick placed vertically into the flow creates an upstream facing 'V' (Newson and Newson, 2000)	Shallow-deep transition habitat that will help to map the variations in depth across the study area to help identify habitat suitability
Eddies		Any upwelling will identify eddies, either through vertical boils or horizontal eddies.	Indicative of deep water habitat or an upstream feature that is effecting flow variations throughout the catchment.
Riffles		Identified by unbroken standing waves flow type (Newson and Newson, 2000).	A shallow water habitat that will help to map the variations in depth across the study area to help identify habitat suitability. Help to identify stream bed slope.

Slack Water/ Marginal dead water		Reflections on water's surface are not distorted, any thing on surface (foam or stick or debris) will appear stationary (Newson and Newson, 2000). Located to the side and will not occupy full channel width.	The dead water zones could indicate deep or shallow water that could be of refuge to younger burbot
Bars*		Note the type of bar on the sheet. Examples: pointbars, mid-channel bars, side bars, and whether they are vegetated or non-vegetated	If access to winter floodplain habitat is not available, burbot will use shallow gravel deposits within the main channel habitat or between tributaries.
Undercut banks		Note whether there are exposed tree roots or whether the bank is plain soil and grass on top.	Burbot use undercut banks for shelter.
Bed Material			
Boulders		Boulders here classified by the Wentworth scale (>256mm)	Any sizeable boulders can affect the geomorphology, which could produce deep water habitats
Gravel/Cobble		Note down size estimate using the sediment sorter.	Burbot have been known to spawn in shallow gravel deposits.
Fine Sediments		Examples: sand, silt, clay, mud If possible, record the distinction on the sheet	
Riverbed Not Visible	N	Important for survey continuity and longevity; the survey will be easier to return to and will minimise gaps in data.	
Vegetation			
Fallen Trees*		Note the features of the tree: rate of decay, whether the root ball is in tact, whether there are in stream features (pools or scouring) and if the roots are interacting with the flow, estimate length, whether still attached to bank or how it is anchored. Take GPS location.	Fallen trees could provide key juvenile habitat due to the pools scoured downstream, upstream, and by the root ball.
Woody debris*		Other woody debris that has entered the channel that cannot be classified as a fallen tree. Take GPS location. Estimate length to nearest 0.5m	Any instream features that influence hydrology can influence the location of burbot habitat for all life stages

Submerged macrophyte vegetation		If surveyor can identify the species it can be recorded on the sheet, but not strictly necessary. Photos can be taken for later identification.	Indicative of shallower, faster flowing areas
Emergent macrophyte vegetation		If surveyor can identify the species it can be recorded on the sheet, but not strictly necessary. Photos can be taken for later identification.	Indicative of slower flowing marginal areas with finer sediments. Important for the shelter of juvenile and adult burbot. Worthington et al (2012) says emergent vegetation important for juvenile and adult shelter (good indicator of burbot habitat).
Free floating macrophyte vegetation		If surveyor can identify the species it can be recorded on the sheet, but not strictly necessary. Photos can be taken for later identification.	Indicative of slower flowing water

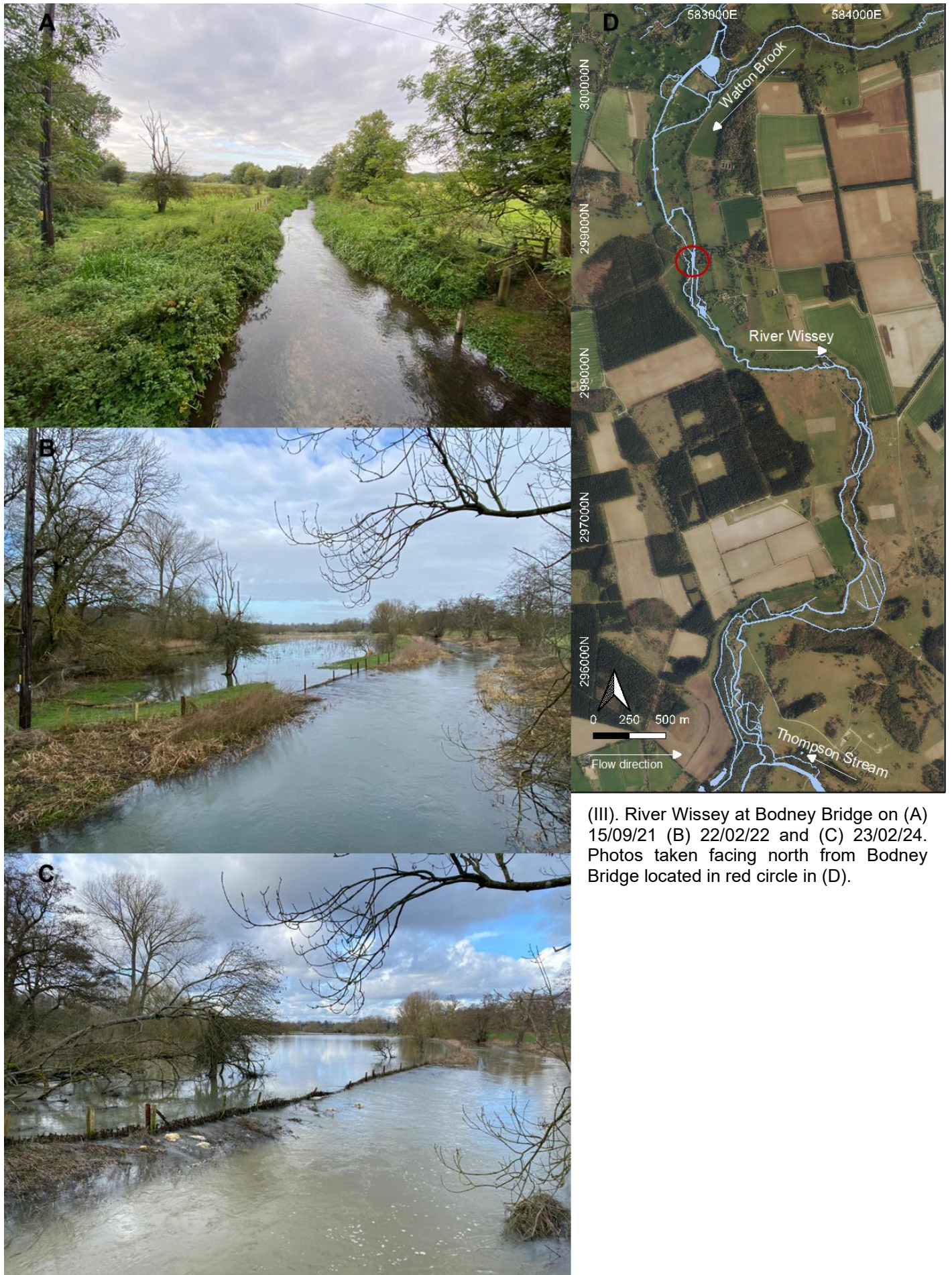
Appendix 4. (I-V) Photographs of study area throughout study period.



(I). T1 loggers showing (A) T1_FP1 (indicated by unmarked red arrows) on 25/11/21 during logger installation, (B) T1_C on 25/11/21 facing downstream, (C) T1_FP1 on 21/02/22, (D) T1_FP1 on 28/11/22, (E) T1_FP1 on 01/12/23, and (F) T1 location on River Wissey indicated by red circle.



(II). T3 loggers showing (A) T3_FP1 on 21/02/22 facing upstream (T3_C is not yet installed) (B) T3 on 01/12/23 facing upstream (loggers are not visible), (C) T3 on 01/12/23 facing downstream, (D) T3 on 23/02/24 facing downstream, and (E) T3 location on River Wissey indicated by red circle.



(III). River Wissey at Bodney Bridge on (A) 15/09/21 (B) 22/02/22 and (C) 23/02/24. Photos taken facing north from Bodney Bridge located in red circle in (D).





(V). T6 on River Wissey showing (A) T6_C in high flow 22/02/22 and approximate direction of T6_FP1, (B) T6_FP1 on 01/12/23 and approximate direction of T6_C, (C) T6 floodplain on 01/05/24 showing spring inundation and wetland vegetation with approximate locations of main channel and floodplain loggers shown, and (D) Location on T6 indicated by red circle.