THE UNIVERSITY OF HULL

Understanding behavioural ecology of river-resident fish in winter to improve protection at water pumping stations

Being a Thesis submitted for the Degree of
Doctor of Philosophy

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by

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DECLARATION OF AUTHORSHIP

I, Josh Norman (JN)

declare that the work undertaken in this thesis entitled:

“Understanding behavioural ecology of river-resident fish in winter to improve protection at water pumping stations”

and the work presented here in is my own except when work has formed part of jointly authored publications has been included. I confirm that appropriate credit has been given within the thesis where reference has been made to the work of others. The contribution from myself and the other authors to this work has been explicitly indicated below, including; Jon Bolland (JB), Jake Reeds (JR), Rosalind Wright (RW), Andrew Don (AD), Alan Henshaw (AH) and Dan Clark (DC).

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ABSTRACT

Globally, there is a reliance on water pumping stations to manage river levels and prevent flooding in heavily-modified anthropogenic rivers. Pumping stations damage longitudinal and lateral river connectivity and their operation presents a major risk of mortality to river-resident fish via entrainment into pumps, which could have population-level effects. Fish are attracted to pumping stations for refuge from predators in pumped catchments with heavily degraded river habitats. However, the operational management of pumping stations rarely includes ecological considerations for river-resident fish and there is a lack of information on how to protect these species. In order to make informed decisions for mitigating the negative impacts of pumping stations and provide effective protection, a thorough understanding of the behavioural ecology of river-resident and their interactions with pumping stations is required. This study investigated the factors affecting ecological behaviours of river-resident fish at three different pumping stations. The potential for operational management changes and the provision of alternative habitats to provide protection was also investigated.

Multi-beam sonar (Dual-Frequency Identification Sonar: DIDSON) was used at an off-channel flood-relief pumping station on the Yorkshire Ouse to investigate diel movements of river-resident fish in response to temperature, hydrology and pump and flood gate operation, and to determine a fish-friendly operational regime. Lateral movements of fish between the main-river and off-channel area were predominantly during the crepuscular period and daytime. Seasonal and inter-annual variations in diel movements were strongest during a baseline year with no pump operation and was influenced by cooling temperatures. A Generalised Linear Mixed Model (GLMM) suggested fish entered the off-channel area when river levels were stable and not when they were rising or falling. Two years of impact data revealed pump operations severely disrupted the regular ecological functions of local fish populations. Modifying when pumps operate to reduce entrainment and modifying floodgate operations appeared to be a promising management option to prevent immigration of fish into the hazardous off-channel area.

At Bourne Eau (Tongue End) pumping station, which is located at the downstream extent of a heavily degraded single-thread system, the temporal rate of predator-prey interactions, the attack behaviour of predators, and the refuge seeking behaviour of prey was investigated using DIDSON. River-resident fish experienced temporally dynamic species-specific predation risks from two dissimilar predators (i.e., aquatic vs aerial), pike and cormorant. Non-consumptive predation effects were evidenced by quantified changes to shoal structure (density, area) and both shoaling (group aggregation) and schooling (coordinated directional movement), including diurnal migrations and use of a pumping station intake as refuge, were the primary ways in which prey managed predation risk. Consequently, it was concluded that prey fish were paradoxically dependant on a hazardous pumping station for refuge from predators which proposed important considerations for how Flood Risk Management (FRM) on lowland rivers can influence the ecological interactions between piscivorous predators and their prey.

Avian predation at pumping stations could be managed by addressing habitat loss caused by River Maintenance Measures (RMMs) associated with FRM requirements. To investigate the potential for protecting river-resident fish in pumped catchments using habitat restoration techniques, common roach (*Rutilus rutilus*) habitat choice between an artificial habitat and simulated pumping station was tested in controlled conditions with an iterative experimental design. All roach occupied a simulated pumping station rather than open water during baseline observation. Half of the fish did not respond to the provision of artificial habitat and occupancy of artificial habitat was influenced by overhead shelter. After habitat management, i.e., physical exclusion from the pumping station, roach preferred artificial habitat rather than the pumping station and this persisted once access to the pumping station was reintroduced. Therefore, these findings suggest appropriate habitat management is required to accompany habitat restoration plans to protect river-resident fish that occupy pumping stations.

Catchment-wide distribution and abundance of river-resident fish in a pumped flood-relief lowland Fenland drain (North Level Drain) and at artificial habitat designed to provide predator and flow refuge for river-resident fish occupying Tydd pumping station was examined before and after a major flood event using side-scan sonar. Sonar surveys pre-flood found highly abundant aggregations of river-resident fish (approximately 1 km upstream of Tydd pumping station) but North Level Drain was void of fish post-flood. When artificial habitats (installed for predator refuge) were monitored pre-flood, fish abundance followed a crepuscular pattern and was comparable between three different artificial habitat structures. Artificial habitats monitored post-flood were void of fish. Overall, these findings suggest that flood-relief pump operations could significantly alter distribution and abundance of river-resident fish upstream of pumping stations and artificial habitat introduction has the potential to provide protection for river-resident fish.

1 GENERAL INTRODUCTION

1.1 Overview

Chapter one outlines the main themes of the thesis; in brief, it provides a background on the ecological requirements of river-resident fish, modifications to lowland rivers, the impact of hazardous water pumping stations, remedial measures for protection of river-resident fish at pumping stations and the thesis aims and objectives. The thesis is written and presented in a style suitable for submission and publication in a peer-reviewed journal. As such, the data chapters (Chapters 2 to 5) are presented as individual research papers, which are either submitted or prepared for submission to peer-reviewed journals. This format was chosen to allow for a thorough integration of behavioural ecology with applied management implications. Chapter six concludes the thesis by discussing the implications of the research. References are provided at the end of the thesis to prevent repetition in data chapters.

1.2 The ecological context for habitat selection and habitat use of freshwater fish

Freshwater fish communities rely on access to a wide range of habitats in rivers and the availability of habitat is a critical component controlling the distribution and abundance of fish populations. Habitat is a term regularly used by ecologists to describe both large-scale (e.g., catchment-wide) and small-scale (e.g., physical structures and morphological river features, also referred to as microhabitats Cowx *et al.,* 2004) areas fish live in. Habitats can vary markedly in resource availability (Rosenfeld, 2003; Donelan *et al.,* 2017) and predation risk (Milinski, 1993; Jacobsen *et al.,* 1998; Heithaus *et al.,* 2009) and thus a fish's choice of where to live can have profound effects on its fitness. 'Fitness' is regularly described in the context of reproductive success but must expand its scope to appreciate fish need to acquire energy throughout their ontogeny and survive to maturity. Thus, fish have evolved a diversity of behaviours to attain maximal fitness throughout their life-history (Dugatkin, 2004). Markedly, behaviours including movement, habitat selection and dispersal determine spatial distribution of fish in rivers. Accordingly, fish require different habitats throughout the various stages of their life-history, both for their regular daily movement requirements i.e., access to resources, and seasonal migrations over large distances (Lucas & Baras, 2001).

Migration broadly describes the long-distance movement of fish between distinct habitats on a temporally predictable scale, often for developmental stages, reproduction and spawning (Bronmark *et al.,* 2014). In brief, types of fish spawning migration can be defined as diadromy and potamodromy. Diadromous fish migrate between marine and freshwater, further described as anadromous fish which hatch in freshwater, mature at sea and return to freshwater to spawn (e.g., Atlantic salmon *Salmo salar*) and catadromous fish which hatch at sea, migrate to and mature in freshwater and migrate back to sea to spawn (e.g., European eel *Anguilla Anguilla*). Potamodromous fish spend their entire life in freshwater but make distinct long-distance migrations between freshwater habitats (e.g., Barbel *Barbus barbus*). Conversely, many freshwater fish make regular short-distance movements within rivers and are often described as living within their 'home range' (Lucas *et al.,* 2008). In the UK this typically describes fish from the *Cyprinidae* family, i.e., silver bream (*Abramis bjoerkna*), rudd (*Scardinius erythrophthalmus*), dace (*Leuciscus leuciscus*), chub (*Leuciscus cephalus*) and in particular, the highly abundant and ubiquitous common roach (*Rutilus rutilus*) (Lucas & Baras, 2001; Bolland *et al.,* 2008). These species are referred to as river-resident fish and are the focus of this thesis.

Whether fish migrate at distinct points during their life-history, or on a continuous basis for daily ecological requirements, the decision of which habitats to select, and the spatiotemporal patterns in habitat use, is essential for survival. The Habitat Selection Theory is fundamental for understanding the ecological movements of fish and states that the spatiotemporal distribution of fish across different habitats maximises fitness through active choice of which habitats to select (Fretwell & Lucas 1970; Hughes, 1998; Hughes, 2000; Craig & Crowder, 2002; Lindberg *et al.,* 2006; Komyakova *et al.,* 2021). Although similar, habitat use more closely defines the patterns in when fish occupy habitats i.e., diel habitat use (Craig & Crowder, 2002). Fish use settlement cues (e.g., visual cues like shelter and shade) to select suitable habitats and thus ecological behaviours have evolved for fish to settle in high-quality habitats and avoid low-quality habitats, as described by Adaptive Habitat Selection theory (i.e., Orians & Wittenberger, 1991; Morris, 2003). Accordingly, the ideal free distribution (IFD) and ideal despotic distribution (IDD) models (Fretwell & Lucas, 1970) predict fish will occupy high-quality habitats and only occupy low-quality habitats when density-dependent effects (IFD) or competition (IDD) reduce perceived habitat quality.

Understanding the ecological habitat requirements of fish can be achieved by following the functional unit concept (Cowx & Welcomme, 1998; Cowx *et al.,* 2004), which details habitat requirements for spawning areas for adults and nursery areas for juveniles but is also fundamentally linked to the abiotic-biotic continuum concept (Vannote *et al.,* 1980). Indeed, habitat selection and use are dependent on abiotic factors e.g., temperature, light, hydrology (river level and flow) and river habitat connectivity (longitudinal and lateral) and biotic factors e.g., competition, feeding and predation (Lima & Dill, 1990; Villéger *et al.,* 2017). Low temperatures are associated with reduced swimming performance and thus during winter fish seek habitats which provide low-flow refuge (Allouche *et al.,* 1999), including by moving laterally into off-channel and backwater habitats (Hohausova *et al.,* 2003; Lyon *et al.,* 2010; Tripp *et al.,* 2016). Likewise, the diel light cycle often determines when fish move between different habitats, especially for visual hunters e.g., Northern pike (*Esox Lucius*), which depend on light to see their food (Janac & Jurajda, 2013).

Not only is the selection of suitable habitats important, but fish must also make decisions on how much time and energy to allocate towards fitness associated behaviours i.e., feeding and avoiding predation. Avoiding predators is essential if fish are to survive and breed, yet fish must also feed to avoid starvation. Indeed, the emergence of behavioural adaptations which facilitate ecologically conflicting trade-offs are common adaptations in fish (Hugie & Dill, 1994; Basille *et al.,* 2015; Fu *et al.,* 2015). The risk allocation hypothesis (Lima & Bednekoff, 1999) suggests fish ‘lose-out’ on metabolic gains at the expense of reducing predation risks. Given the fitness implications of predation (i.e., survival time and reproductive opportunities), fish should minimise predation risk whenever possible, although this is dependent on the ecological movements of both predator and prey (Lima & Dill, 1990). Accordingly, the spatiotemporal scales (daily, seasonal) in prey activity and habitat use closely reflect a trade-off between metabolic costs and avoiding the active period of predators (Basille *et al.,* 2015; Fu *et al.,* 2015).

The ability for fish to successfully manage ecologically conflicting trade-offs is determined by abiotic-biotic interactions and the lateral and longitudinal distribution of suitable instream habitats which offer foraging resources and refuge from high flows and predation (Thorp *et al.,* 2006; Wolf *et al.,* 2017). The gradient of physical habitat features differs throughout a river due to the influence of hydro-geomorphological processes (e.g., flooding). Habitat diversity and availability is therefore provided by fluvial processes which create heterogeneity in rivers. Thus, continuity and connectivity between habitats is essential for fish to move between high-quality habitats, enabling functional habitat selection and use.

1.3 Anthropogenic modifications to lowland rivers for flood defence: habitat loss and fragmentation

Flooding in natural lowland rivers with laterally connected floodplains describes the inundation of water during high-flow events which are fundamental to the hydrological regime (see riverine productivity model; Thorp & Delong, 1994). Floods are essential for creating high hydrological connectivity, such as the lateral expansion of main-river bodies into floodplains and backwaters, which provides fish access to previously isolated habitats for refuge, spawning, nursery and feeding (Peirson *et al.,* 2008; David & Closs, 2002; Bolland *et al.,* 2015; Manfrin *et al.,* 2020). Likewise, flooding maintains ecosystem process (e.g., nutrient and sediment movement; Poff *et al.,* 1997). Despite the ecological necessity for natural hydrological processes, flooding in urbanised and agricultural areas can cause significant damage to human society and property and subsequently fluvial morphology has been modified for Flood Risk Management (FRM) (Dudgeon *et al.,* 2006; dos Reis Oliveira *et al.,* 2020).

Anthropogenic river modifications for FRM include the realignment of rivers to single-thread channels which requires channelization along with the conversion of floodplains to agricultural land and the addition of water level management structures including weirs, sluices and water pumping stations (Cowx & Welcomme, 1998; Nilsson *et al.,* 2005; Kruk, 2007; Figure 1.1). For example, there is a global reliance on pumping stations to manage water levels, and in England and Wales there are now over 900 pumping stations which form an essential part of FRM (Baumgartner *et al.,* 2009; Solomon & Wright, 2012). Although not for flood protection, the creation of impoundments and dams for other reasons, such as abstraction, navigation and hydropower, is also relevant when considering river modifications. Throughout Europe there are now at least 1.2 million barriers (Belletti *et al.,* 2020) which have fragmented river habitats and severed hydrological connectivity (Nienhuis & Leuven, 2001; Santos *et al.,* 2006). Consequently, anthropogenic modifications have homogenised riverine ecosystems by altering the spatiotemporal distribution of habitats for fish.

The severance of hydrological connectivity has a profound negative effect on fish species which are well adapted to periodic flooding for movement into spawning, nursery and refuge habitats (Lucas & Baras, 2001). For example, the prevention of lateral movement restricts fish to the main channel and fish are unable to access floodplain and backwater habitats for refuge during floods (Bolland *et al.,* 2015). This problem is further exacerbated by an increase in the severity of high flows in the main channel which can disperse fish downstream towards unfavourable areas (Jurajda *et al.,* 2006). The degradation and loss of refuge habitat can have a profound effect on the distribution of fish (Dudgeon *et al.,* 2006). Given that fish settlement is directly proportional to resource abundance (IFD: Fretwell & Lucas, 1970), a reduced longitudinal or lateral gradient of resources in modified rivers will alter the distribution of fish, resulting in concentrated fish populations at limited resource patches and potential fitness costs. For the above reasons, the homogenisation and loss of critical refuge habitat due to flood defence modifications is now considered a major cause of biodiversity loss in lowland rivers (Dudgeon *et al.,* 2006; Maxwell *et al.,* 2016; Cowan *et al.,* 2021).

Figure 1.1 Reproduced in full (with modifications) from Maab *et al.* (2021). A schematic diagram of anthropogenic modifications to lowland rivers. Pumping stations shown by red squares. PS = pumping station.

1.3.1 The impact of hazardous water intakes on freshwater fish

Hazardous intakes exist in a wide range of applications; for example at drinking water abstractions, cooling water for power stations, wastewater treatment works and hydropower facilities. This thesis concerns the hazardous intake area of water pumping stations for flood protection during winter. Fundamentally, hazardous intakes create impassable barriers which fragment rivers (Nilsson *et al.,* 2005) and can severely impair longitudinal (Baker *et al.,* 2021) and lateral (Tripp *et al.,* 2016) fish migrations and movements (Lucas & Baras, 2001). Whilst the negative effects associated with hazardous intakes are well established for diadromous fish species given the fundamental passage requirement to complete their lifecycle (reviewed in Coutant & Whitney, 2000; Pavlov *et al.,* 2008; Young *et al.,* 2011; Fjeldstad *et al.,* 2018; Tomczyk & Wiatkowski, 2020), the processes and ramifications also apply to potamodromous and river-resident fish species. Weed screens (also referred to as trash racks) are installed at pumping stations to prevent entrainment of debris into pumps. Entrainment describes the process of fish being drawn into pump intakes, frequently with a high likelihood of injury and mortality (Barnthouse, 2013; Piper *et al.,* 2013; Rytwinski *et al.,* 2017; Figure 1.2). When fish pass through pumps they are vulnerable to injury from blade strikes (Krakers *et al.,* 2015), shear stress (Bierschenk *et al.,* 2019) and pressure changes (Van Esch *et al.,* 2012). Many pumping stations are non-operational for long periods of time (months to years), and unlike migrant fish, river-resident fish occupy the forebay and pump intake chambers (behind weed screens) during winter for refuge from predators in modified lowland rivers with degraded winter habitats.

a) European eel *A.anguilla* following turbine entrainment

b) Common roach *R. Rutilus* following turbine entrainment

Ⓒ Adam *et al.,* 2006

Figure 1.2 Reproduced in full from Adam *et al.* (2006). Photographs showing injuries to a) European eel and b) common roach after entrainment through a hydropower turbine.

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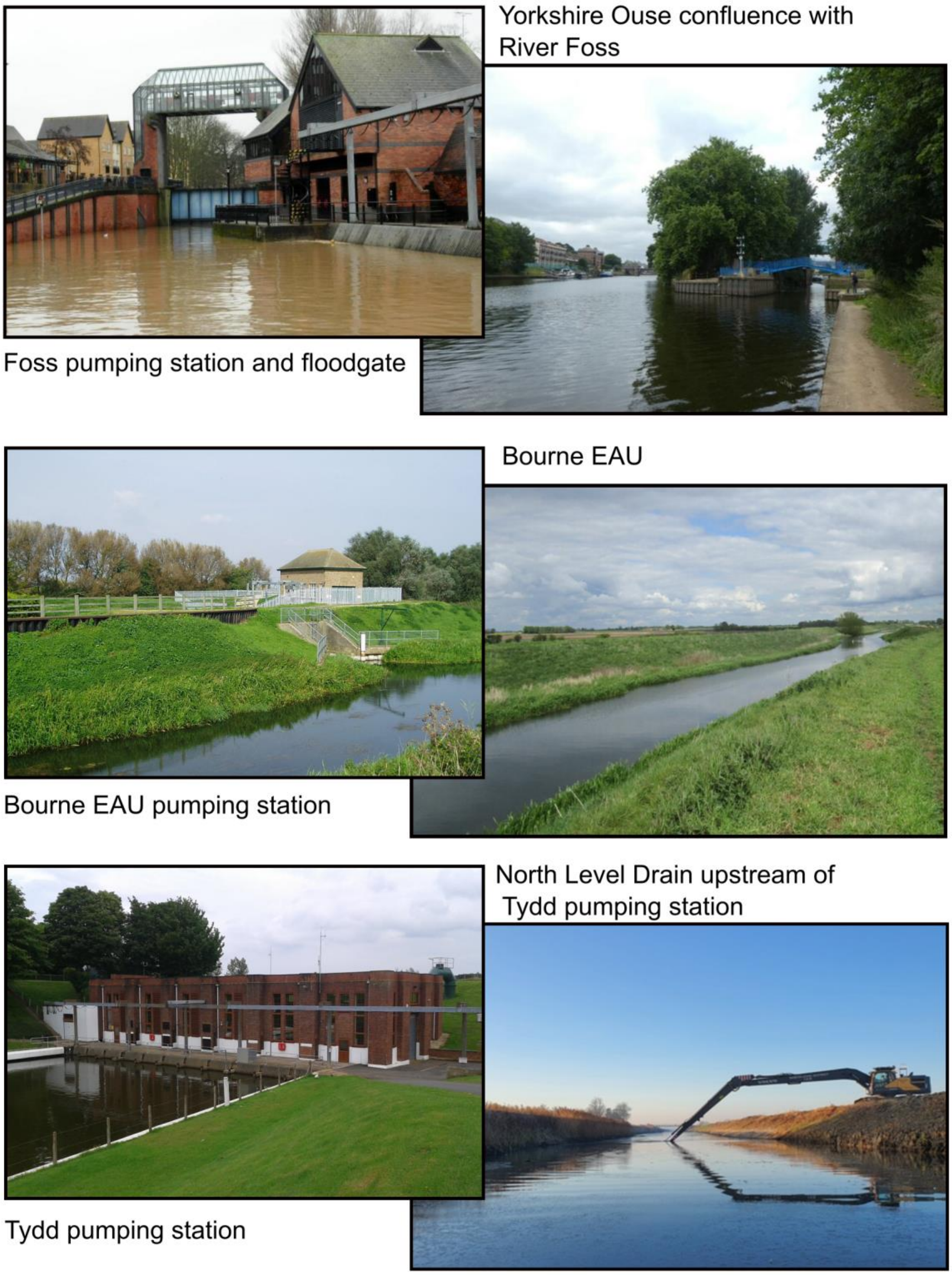
All these factors combined can contribute to significant injury and mortality of migratory fish (i.e., European eel; Bolland *et al.,* 2019), but mortality of entrained river-resident fish may also be as high as 50% (Buysse *et al.,* 2014). Yet, although anecdotal reports exist (Turnpenny & O'Keeffe, 2005; Reeds, 2019), the processes that lead to entrainment of river-resident fish at hazardous intakes remains unquantified and protection is rarely integrated into operational management.

FRM necessitates a requirement for River Maintenance Measures (RMMs) which aim to reduce variability in river flow upstream of pumping stations and mitigate extreme flood events (Baczyk *et al.,* 2018). RMMs include dredging river channels and the winter removal of macrophytes, woody debris and other river obstructions which maintain heterogeneous fish habitats. Consequently, winter habitats for river-resident fish in pumped catchments have been heavily degraded (see examples of systems studied in Figure 1.3), which has led to overall declines in fish abundance and biodiversity (Baczyk *et al.,* 2018). There is a distinct lack in information on how multi-species lowland river-resident interact with pumping stations and the subsequent effects of winter flood-relief pump operations on lowland fish communities (but see Martins *et al.,* 2014). The reduced diversity and spatial distribution of winter refuge habitats in pumped catchments affects the regular ecological functions of river-resident fish outlined in section 1.2, i.e., diel movement between habitats, prey interactions with predators and refuge, habitat use and preference and catchment-wide distribution. Indeed, maladaptive habitat selection processes may occur in anthropogenic rivers where fish encounter previously reliable settlement cues, which counterintuitively attract them to hazardous structures for winter refuge (Hale *et al.,* 2015). This is exemplified at pumping stations when they are not operational during the summer, as they provide river-resident fish with physical structure, shelter and protection from predators (during winter) but present a high risk of entrainment during operation.

1.4 Remedial measures for protection of river-resident fish at water pumping stations

1.4.1 Legislation

Effective protection for fish at hazardous intakes cannot be implemented without legislation; the following examples are considered most important for the context of this thesis. The passability of hazardous intakes is an essential prerequisite for maintaining fish communities and freshwater biodiversity and achieving good ecological status (or potential) by 2027 according to the EU Water Framework Directive (WFD; 2000/60/EC). The Conservation of Habitats and Species Regulations 2010 (The Habitat Regulations) currently enforces the Habitats Directive (HD; 92/43/EEC).


Yorkshire Ouse confluence with River Foss

Foss pumping station and floodgate

Bourne EAU

Bourne EAU pumping station

North Level Drain upstream of Tydd pumping station

Tydd pumping station

Figure 1.3 Example photographs of the pumping stations and river systems studied in this thesis. From top to bottom, chapter 2, chapter 3 and chapter 5. *Image reproduced under Creative Commons licence (CC0 1.0).*

The Habitats Directive aims to protect, conserve and restore essential fish habitats and maintain biodiversity in heavily modified rivers, such as those in pumped catchments. The European Floods Directive (FD; 2007/60/EC) aims to manage flood risk and is enacted under the UK Flood and Water Management Act (FWMA; 2010 c.29) in the UK and requires development of FRM plans. Although not a river-resident fish, the Eel Recovery Plan (Council Regulation No 1100/2007) is considered relevant here as The Eels (England and Wales) Regulations 2009 (Eels Regulations) Statutory Instrument states pump operators are required to screen intakes that abstract more than 20 m^3s^{-1} of water a day.

1.4.2 Determining suitable solutions for river-resident fish

Fine-mesh physical screens are frequently installed at hazardous intakes to prevent entrainment of diadromous fish and/or aid in directing fish towards bypass facilities (Sheridan *et al.,* 2014). The general principles of screening intakes for diadromous fish are well established (reviewed in Adam & Scwevers, 2020); in brief, physical screens can be adapted to target different species, developmental life-history stages and relative swimming capabilities of migratory fish with high success (Amaral *et al.,* 2003; Russon *et al.,* 2010; Fjeldstad *et al.,* 2013). Alternatively, behavioural guidance systems including velocity barriers, electrical guidance, acoustic and light deterrents were previously used to prevent migratory fish entering hazardous areas and guide towards bypasses (Notach & Suski, 2012), but can perform poorly in real-world scenarios (Kühne & Schwevers, 2016).

Extensive research on fish passage over the past few decades has shown that focusing exclusively on diadromous species does not meet the necessary requirements for biodiversity and conservation (Katopodis & Williams, 2012). Behavioural deterrents will be ineffective for protecting fish with no alternative winter refuge habitats, and for the same reason physical screening is expected to increase the severity of predation risks for river-resident fish. Additionally, installing fine-mesh screens at pumping stations to protect river-resident fish would not be cost-effective and pump operators have expressed major concerns for water conveyance during winter flood-relief pump operations. Instead, the approach to successfully protect river-resident fish at pumping stations could be improved by understanding the individual ecological processes and behaviours of river-resident fish which predispose them to encountering and occupying pumping stations during winter. This thesis considers two approaches: changing operational management of pumping stations to incorporate fish-friendly operations and providing safe alternative predator refuge habitat for river-resident fish.

1.4.3 Fish-friendly operational management of pumping stations

Conservation practices in which fish behaviour is used to inform decision making and solve conservation issues is being increasingly considered by operational managers (Cooke *et al.,* 2014; Brooker *et al.,* 2016). Accordingly, operations can be adjusted to incorporate 'fish-friendly operational management' (Adam & Scwevers, 2020), although this has focused on diadromous species. For example, sluice gate operation has been modified to facilitate downstream European eel movement at pumping stations (Egg *et al.,* 2017; Baker *et al.,* 2021). Similarly, turbines and pumps have been shut down during diadromous winter migrations (Gilligan & Schiller 2003; Trancart *et al.,* 2013). River-resident fish residing in the vicinity of hazardous structures have an increased vulnerability to entrainment during winter (Martins *et al.,* 2014) and thus a thorough understanding of spatiotemporal frequency in occupancy and predictability of behaviours which lead to this process (i.e., abiotic-biotic factors) could inform when to operate. Several authors have alluded to the potential of operational changes for river-resident fish protection (Baumgartner *et al.,* 2009; Reckendorfer *et al.,* 2018; Knott *et al.,* 2019). However, to this end, there exists only one peer-reviewed example of this being incorporated into long-term management (at a power plant intake) (Kühne & Schwevers, 2016); physical and behavioural barriers were deemed unsuitable and an alternative 'fish protecting' operation mode timed to avoid maximal diel fish presence reduced fish occupancy during operation.

1.4.4 Habitat restoration and providing alternative artificial habitat

Pumped catchments are commonly characterised by a high degree of river modifications and subsequent habitat degradation during winter (section 1.3). Thus, there is a high demand in these systems to alleviate the negative anthropogenic impacts on habitat, which could be achieved through improvements to physical habitat availability and distribution (Pander & Geist, 2013). Indeed, restoration ecology aims to produce well-designed projects that improve the quantity and quality of habitats available to fish, in turn re-establishing natural ecological processes (Cowan *et al.,* 2021). Whilst there is potential for operational changes to mitigate the impacts of hazardous intakes on river-resident fish, alone this does not address the winter habitat degradation present in pumped catchments. In brief, fish which are prevented access to hazardous intakes require suitable alternative refuge habitats or will be vulnerable to increased predation risk and downstream displacement during high-flow events. Indeed, river-resident fish may avoid occupying hazardous areas entirely if alternative habitats are available. However, restoration of natural habitats (e.g., riparian vegetation) is not possible in pumped catchment due to frequent anthropogenic disturbance, i.e., seasonal RMMs and natural winter die-off.

A potential solution for this problem is the use of artificial fish habitats; a strategy commonly applied for restoration and improvement of habitat for fish in aquatic ecosystems (reviewed in Cowan *et al.,* 2021; Paxton *et al.,* 2021; Song *et al.,* 2022; Watchorn *et al.,* 2022). In marine environments this includes the creation of artificial reefs from concrete structures, addition of rocks and boulders and sinking decommissioned ships; all of which have shown potential to increase fish abundance and enhance species biodiversity (reviewed in Song *et al.,* 2022). Artificial habitats have also been used to provide refuge for freshwater cyprinids, including river-resident species of concern in this thesis (Russell *et al.,* 2008; Orpwood *et al.,* 2010; Lemmens *et al.,* 2016). Russell *et al.* (2008) used steel cages with overhead cover and interstitial spacing created with wood to provide roach protection from cormorants (*Phalarcrocorax carbo*) and demonstrated a 79% reduction in fish loss in a pond with artificial habitats compared to one without. Using similar habitat designs, Orpwood *et al.* (2010) experimentally demonstrated the importance of overhead cover in artificial habitat designs for protection from avian predators. Lemmens *et al.* (2016) expanded on this suggesting artificial habitats could be used to reduce frequency of predator-prey interactions between roach and rudd and cormorants and pike. Elsewhere, Baumann *et al.* (2016) uniquely assessed four different artificial habitat designs (Figure 1.4) and found all were effective for increasing fish abundance compared to control sites without habitat, but the enclosed habitat (Figure 1.4a) performed best.

A problem often not considered when designing and implementing artificial habitat restoration programmes is the potential for maladaptive habitat selection processes to occur in environments vulnerable to frequent change, such is that of rivers with anthropogenic modifications (Hale & Swearer, 2016; Hale *et al.,* 2017). The phenomenon of an ‘ecological trap’ may occur when low-quality habitats are selected over high-quality habitats (Robertson & Hutto, 2006). This process is the result of the uncoupling of settlement cues fish use to select high-quality habitats, for example where previously high-quality habitats are degraded by anthropogenic activity, e.g., winter RMMs in pumped catchments. Alternatively, maladaptive habitat selection processes can lead to fish avoiding high-quality restored habitats and counterintuitively becoming more attracted to historically poor-quality habitats (i.e., a perceptual trap; Pattern & Kelly, 2010). For these reasons there remains uncertainty towards the effectiveness of introducing artificial habitats to degraded pumped catchments where fish occupy pumping stations. Thus, thorough testing of fish response to artificial habitat is required to determine the suitability of this method for providing protection at pumping stations.

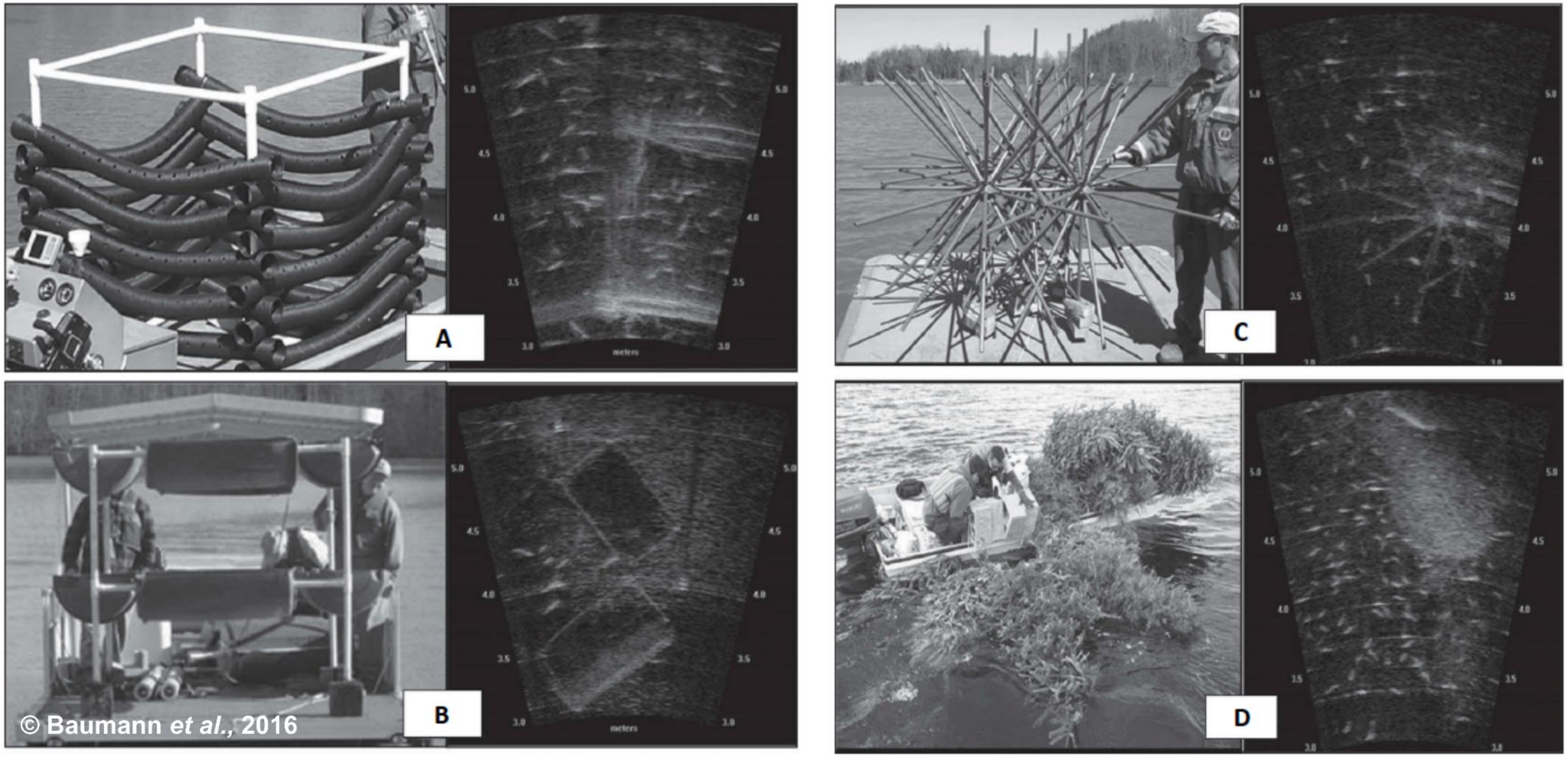


Figure 1.4 Reproduced in full from Baumann *et al.* (2016). Four artificial fish habitat designs shown as photographs (left panels) and sonar image outputs (right panels). The four designs were (A) PVC frame with plastic pipes, (B) separated plastic barrels, (C) Porcupine PVC structure, (D) evergreen trees.

1.5 Thesis aims and objectives

This chapter emphasises that knowledge, legislation and protection for fish interacting with hazardous intakes during winter (in this thesis – pumping stations) has been established for conservation-status diadromous species i.e., the catadromous European eel, but knowledge on river-resident fish behaviour at hazardous intakes and how to provide protection for these species during winter is lacking. Despite the lack of conservation status for these fish, legislation necessitates operational managers must provide protection but ecological considerations for these fish are rarely implemented into management. This is largely because there remain important knowledge gaps in the ecological behaviours of river-resident fish at pumping stations, especially in how behaviour of these fish could inform safe operation and the suitability of alternative remedial measures for their protection. At present, the majority of research on river-resident fish concerns spring and summer spawning behaviour and there remains a dearth of research into the winter behaviour of these fish. Further, despite winter aggregations of fish being a common occurrence in lowland rivers, there is considerable uncertainty concerning how and why fish aggregate around hazardous structures in anthropogenic settings. State of the art multi-beam and side-scan sonar surveys during winter (i.e., October – February), and experimental testing in laboratory conditions were employed to fill these knowledge gap. Such research is essential for management and conservation of river-resident fish which are vulnerable to interacting with pumping stations year-round, but especially during winter when anthropogenic pressures exacerbate naturally challenging ecological conditions for fish.

The overall aim of this thesis is therefore to develop an understanding of the behavioural ecology of lowland river-resident fish species at water pumping stations, to inform safe operation and provide suitable remedial solutions. The thesis is divided into key topics that are addressed in chapters 2 to 6. Specific research questions, hypothesis and aims and objectives are provided in each chapter.

Chapter 2 quantifies the temporal periodicities in river-resident fish presence and lateral movement between the main-river Yorkshire Ouse and a tributary (River Foss) with a flood-relief pumping station. It investigates the influence of river level, temperature, pump operation and floodgate operation over three years with different hydrological conditions on the temporal variability of river-resident fish presence. Finally, it provides management recommendations for operational changes to provide a low-cost entrainment solution.

Chapter 3 establishes an ecological context for predator-prey interactions at pumping stations. It provides a novel insight into non-consumptive predation of river-resident fish, by both instream and avian predators at a lowland pumping station with heavily channelised upstream river and degraded in-channel and riparian habitats. It investigates the temporal rate of predation, the attack behaviour of predators, the prey shoal response and the use of a pumping station as predator refuge. The necessity for providing protection for prey in habitat degraded pumped catchments is discussed.

Chapter 4 investigates the effectiveness of providing artificial habitat as a safe alternative for river-resident fish which occupy pumping stations for refuge. The remedial measure is explored using an iterative experimental process where habitat choice of roach was manipulated by providing a simulated reed bed and pumping station before testing habitat preference by preventing access to the pumping station at different stages throughout the experiment. The necessity for physical exclusion is discussed in the context of ecological and perceptual traps.

Chapter 5 determines the catchment-wide distribution and abundance of river-resident fish in a channelised, pumped, flood-relief lowland drain and at artificial habitats designed to provide predator and flow refuge for river-resident fish occupying a pumping station intake. The data are considered in context of two years before and one year after a major flood-relief pump operation. The concern for an increasing rate of major rainfall events during climate change and subsequent catastrophic pump operations, and the necessity for pump operators to provide artificial habitats for flow refuge is discussed.

Chapter 6 summarises the findings from chapters 2 – 5 and integrates them into a final discussion chapter. Management implications generated throughout chapters 2 – 5 are discussed and future research recommendations are provided.

1.5.1 Impact of COVID-19 on the PhD programme

The experimental data collection for chapter 3 was originally attempted at Hull University but was incomplete when COVID-19 lockdown was enforced. Subsequently, the experiment was moved to an experimental facility at a fish farm. Additionally, temporally robust data collection at artificial fish habitats (Chapter 5) was limited by lockdown periods and thus alternative data were provided by the Environment Agency. The original PhD project outline included a fifth data chapter, which would have tracked lateral and longitudinal movements of river-resident fish in pumped catchments using passive integrated transponder tags. Although significant effort had gone into designing this study, lockdown prevented data collection. An alternative study site was planned for in 2020, but flooding prevented data collection.

1.6 Method statement: multi-beam sonar

Understanding the ecology of fish in rivers using traditional technologies (i.e., angling, netting and electrofishing) is difficult, time consuming and does not allow the behaviour of fish to be studied. Telemetry techniques are regularly used to fill this knowledge gap (Abecasis *et al.,* 2018). However, such techniques are expensive (~£2000 per fish), the fish must be caught, and acoustic transmitters surgically implanted, which is dependent on target species, body weight and size, and multiple acoustic receivers must be deployed in a river to track signals from tagged fish (see review: Abecasis *et al.,* 2018). The invasive procedures required for telemetry investigations are undesirable for studying fish behaviour, and both the cost of tags and species-specific nature of the technology make telemetry-based investigations poorly suited for understanding the behaviour of large multi-species fish communities.

Alternatively, hydroacoustic methods provide a quantitative, non-invasive and low-cost approach to long-term aquatic monitoring and for gathering research data (Martignac *et al.,* 2015). Acoustic echosounders use sound reflections instead of light reflections to produce images, and thus image visibility is not limited by light (Belcher & Lynn, 2000).

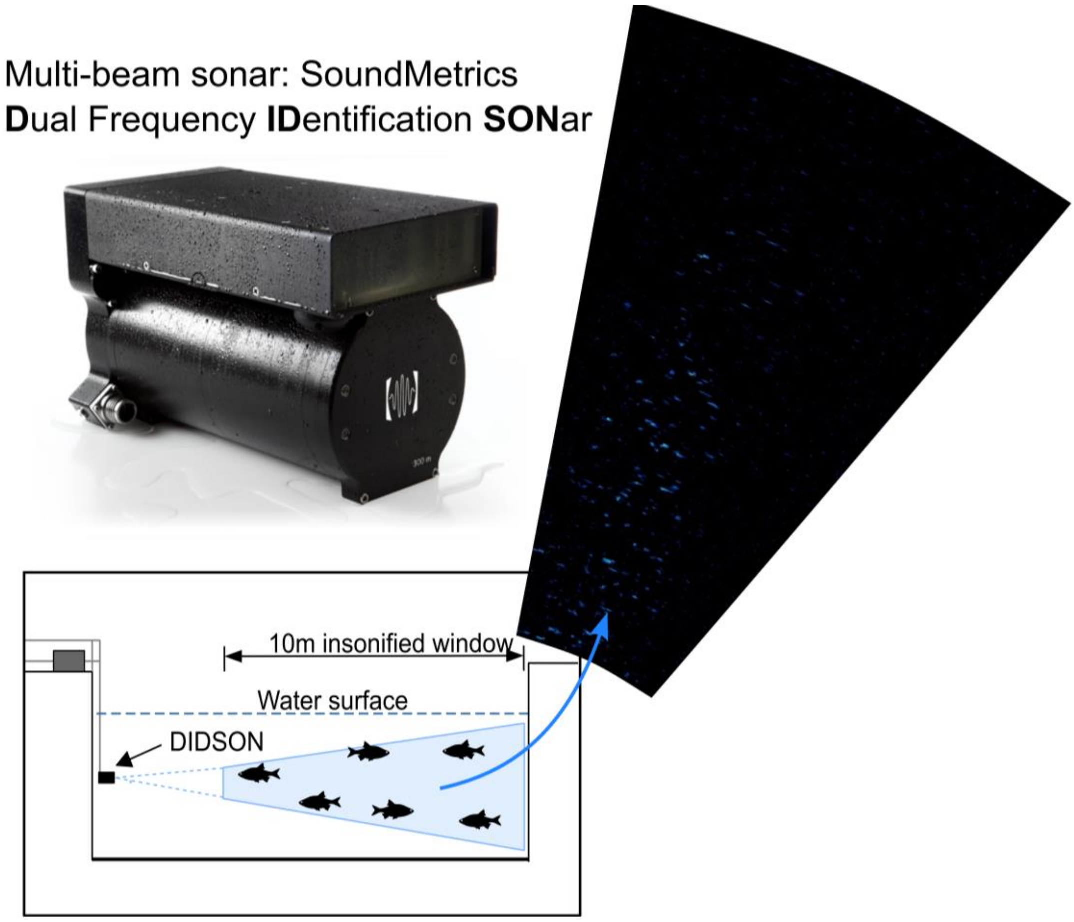


Figure 1.5 The SoundMetrics Dual Frequency Identification Sonar (DIDSON) including a schematic representation of a DIDSON imaging fish across channel and a still image output from the DIDSON. *Image reproduced under Creative Commons licence (CC0 1.0).*

Table 1.1 Summary of data gathered in this thesis using the Dual Frequency Identification Sonar (DIDSON) and the Adaptive Resolution Imaging Sonar (ARIS) multi-beam sonars.

Thesis chapter	Data gathered
Chapter 2 *Using DIDSON*	• Temporal (pluriannual and diel) fish activity • Enumeration of fish targets and abundance estimates • Length-frequency estimation of multi-species community • Lateral movement from main-river to off-channel area • Impact of flood-relief pump operations • Response of fish to modified floodgate operations
Chapter 3 *Using DIDSON*	• Predator-prey interactions and behaviour of predators • Temporal rate of predation • Prey shoal size, areal and density response to predators • Prey shoal behaviour in response to predators: avoidance and flee behaviour • Use of pumping station as refuge and habitat association
Chapter 5 *Using ARIS*	• Assessment of fish distribution in flood-relief drain • Efficacy of artificial fish refuge habitats and habitat type • Impact of duty pump operations • Predator habitat associations • Assessment of fish response to environmental change (flooding) and flood-relief pump operations

This makes hydroacoustic technology ideal for recording fish in highly turbid environments (Artero *et al.,* 2021), such as the pumping station intakes studied throughout this thesis. Single beam echosounders have previously been used to determine spatiotemporal changes in fish assemblages in rivers (DuFour *et al.,* 2018). However, echosounders operate in low frequency and the subsequent image resolution makes it challenging to identify ecological behaviours of fish. Instead, fisheries scientists worldwide have adopted the use of multi-beam sonar, in particular the Soundmetrics Dual Frequency Identification Sonar (DIDSON) and its successor the Adaptive Resolution Imaging Sonar (ARIS) (Martignac *et al.,* 2015) (Figure 1.5). Originally used for military surveillance, high-frequency multi-beam sonars provide high-quality images with near video-like appearance. The DIDSON emits 96 individual beams at a frequency of 1.8 MHz and the returning pings (i.e., sound reflections from objects in the water) can detect fish up to 0.5 - 30 m from the sonar, making it an ideal tool for imaging fish in confined (e.g., individual habitats) and open spaces (e.g., across river channels).

The application of multi-beam sonar for fisheries scientists covers a range of approaches, including monitoring migration of multiple species through fishways (Baumgartner *et al.,* 2006), temporally enumerating fish (Petreman *et al.,* 2014), measuring swimming patterns, fish lengths and population level length-frequency estimations (Zhang *et al.,* 2014), assessing impacts of fishing (Graham *et al.,* 2004), determining seasonal movement patterns (Egg *et al.,* 2018) and habitat occupancy (Baumann *et al.,* 2016) and understanding behaviour around hydropower turbines (Bevelhimer *et al.,* 2017). Accordingly, multi-beam sonar has been used throughout this thesis to develop an understanding of the winter behavioural ecology of river-resident fish (Table 1.1).

1.7 Ethical statement

The research in this thesis forms a doctoral (PhD) study sponsored by the Environment Agency and supervised by the University of Hull. The thesis will be published by the university and may in full or part be published in academic journals. The collection of the data pertaining animal behaviour uses a quantitative methodology which is passive in nature (i.e., no physical interaction with animals), with the exception to chapter 4 that follows an experimental trial using live fish. Accordingly, the experimental design consulted the NC3Rs (2022), and all procedures were conducted in accordance with the United Kingdom Animal (Scientific Procedures) Act 1986 and approved by the University of Hull ethical committee (ethics reference number FEC_2020_47). Field data were collected on non-networked hard drives and later permanently stored on encrypted cloud storage (i.e., Microsoft OneDrive) following the University of Hull's data management policy. At the time of publication, raw data (excluding video footage) and associated data analysis script will be made available online via Zenodo with an indexed DOI. No personally identifiable information was used in this thesis with exception to the named authors and affiliations.

2 UNDERSTANDING THE TEMPORAL DYNAMICS OF A LOWLAND RIVER FISH COMMUNITY AT A HAZARDOUS INTAKE AND FLOODGATE TO INFORM SAFE OPERATION

2.1 Introduction

Anthropogenic modifications to freshwater ecosystems have significantly altered rivers through the construction of dams, weirs, culverts, gates and structures with water intakes, which include hydropower, water abstraction and pumping stations. The human demand for these structures cannot be understated; hydropower, for example, is responsible for almost 20% of all electricity produced worldwide (Moore *et al.,* 2022), and pumping stations form a critical component of managing societal flood risks around the world. Many agricultural, industrial and residential properties in lowland regions are therefore reliant on pumping station operation to prevent inundation of flood water (Baumgartner *et al.,* 2009; Buysse *et al.,* 2014). Yet, these structures can severely impair longitudinal (Baker *et al.,* 2021) and lateral (Tripp *et al.,* 2016) fish migrations and movements. Indeed, there is a lack of information on how multi-species lowland river-resident fish communities interact with pumping stations year-round (but see Martins *et al.,* 2014). The intake of pumping stations (‘hazardous intake’ hereafter) also presents a major hazard to fish where impingement against screens and entrainment through turbines and pumps can lead to injury and mortality of fish (Rytwinski *et al.,* 2017; Bolland *et al.,* 2019).

Legislation exists (e.g., the Eel Regulations 2009; Water Framework Directive; 2000/60/EEC) to protect fish at hazardous intakes and has led to the use of physical (e.g., screens) and behavioural (e.g., sound, light and electricity) deterrents to prevent entrainment of fish (Sheridan *et al.,* 2014; Adam & Schwevers, 2020; Jones *et al.,* 2021). However, much of this work has focused on diadromous fish species of conservation interest, such as the catadromous European eel (*Anguilla anguilla*) (Sheridan *et al.,* 2014; Fjeldstad *et al.,* 2018; Piper *et al.,* 2019) and anadromous Atlantic salmon (*Salmo salar*) (Perry *et al.,* 2014; Tomanova *et al.,* 2021). To date, there is a lack of information on the protection of river-resident fish communities. Physical and behavioural deterrents may be inefficient for multi-species protection because of highly variable species and life stage specific swimming capabilities and behaviours (Poletto *et al.,* 2015). Further, retrofitting engineered fish protection is technically and financially challenging. As such, there is a need to develop cost-effective, non-engineered operational solutions informed by the ecology of the prevailing fish community.

Operational solutions for the protection of migratory fish include using spillway releases to limit fish passage through turbines at dams (Williams, 2008), opening sluice gates to facilitate downstream European eel movement at pumping stations (Egg *et al.,* 2017; Baker *et al.,* 2021) and turbine and pump shutdown during seasonal migrations (Gilligan & Schiller 2003; Trancart *et al.,* 2013). In turn, turbine and pump shutdown could be used during diel movements of river-resident fish (Baumgartner *et al.,* 2009; Reckendorfer *et al.,* 2018). To do so requires knowledge of local multi-species community ecology, as the predictable temporal periods in fish activity at hazardous intakes are intrinsically linked with shifts in day and night light intensity, water temperature and hydrology, and predator avoidance. It is perhaps surprising, then, that the operational management of hazardous intakes rarely includes ecological considerations for river-resident fish (e.g., Harrison *et al.,* 2019). Further, studies investigating the seasonal and diurnal movement patterns of river-resident fish at hazardous intakes are also scarce (but see Knott *et al.,* 2019).

Lateral movements of fish into off-channel and backwater habitats are considered essential for the ecological functioning of fish communities, particularly with regards to temperature and hydrology (Tripp *et al.,* 2016; Thurow, 2016). This is especially true during winter when macrophyte die-off reduces micro-habitat availability, river temperatures drop and main-river flows increase (Lyon *et al.,* 2010). Furthermore, river level management during the winter requires increased pump operations, exacerbating harsh conditions for river-resident fish. Thus, this study took place during winter at the hazardous intake of an off-channel flood control pumping station on a lowland main-river. The connection between the main-river and off-channel pumping station was regulated by a floodgate which is lowered during pump operation, and thus prevents lateral movement of water and fish. Despite the management requirement of flood infrastructure, there are surprisingly few studies that have demonstrated how modifications to operations can successfully incorporate enhanced ecological opportunities for fish (but see Gordos *et al.,* 2007; Seifert & Moore, 2017; Mel *et al.,* 2020). Others have manipulated when floodgates open to improve fish passage (Perry *et al.,* 2015; Wright *et al.,* 2015). Thus, of additional importance in this study was to identify if floodgate operation prevented immigration of fish from the main-river into the off-channel pumping station.

Overall, if behaviour of river-resident fish communities around hazardous intake makes them more or less susceptible to entrainment, then a thorough understanding of fish ecology can be integrated into operational management to aid in fish protection. To do this requires the timing, frequency and abundance of the entire river-resident fish community movements in response to differing operational periods to be quantified. This was achieved here passively and non-invasively using a Dual frequency IDentification SONar (DIDSON) during a pluriannual investigation with highly contrasting inter-annual hydrology and pump operations, and incorporated modifications to floodgate operations.

Therefore, the overall aim of this study was to quantify the temporal dynamics of a lowland multi-species fish community at a hazardous intake, and to identify operational protection measures. In turn, this study addresses the following research questions; (1) What are the prevailing temporal dynamics in the frequency and magnitude of fish counts around a hazardous intake? (2) How does operation of a hazardous intake interact with the ecological functions of local fish communities? (3) How might the knowledge of temporal fish movements be incorporated into management of hazardous intakes and associated river infrastructure? The predictions from these research questions are that (i) the temporal periodicities in fish counts will show diurnal/nocturnal preferences due to movement patterns expected between main-river and lateral refuges i.e., fish will immigrate towards the hazardous intake at dawn and emigrate at dusk, albeit with intra- and inter-annual variability (linked to thermal and hydrological conditions); (ii) operation of the hazardous intake will disrupt the temporal dynamics of the fish counts, i.e., fish counts will be reduced after operations; and (iii) the maximal periodicities in the temporal fish counts will inform when to operate the intake and associated river infrastructure i.e., modify timing of floodgate operation.

2.2 Materials and methods

2.2.1 Study catchment and site

The Yorkshire Ouse is a lowland main-river in North Yorkshire, England, that drains into the Humber Estuary and has a catchment area of at least 3315 km^2 when combined with its tributaries (namely, the Aire, Don, Wharfe, Ure and Foss). The study site was Foss pumping station (‘Foss PS’ hereafter) in York (Lat: 53.952714 N, Long: 1.078850 W) (Figure 2.1a), which is part of the York Flood Alleviation scheme consisting of Castle Mills Lock, Castle Mills Sluice and the Foss flood defence barrier (‘floodgate’ hereafter). Castle Mills Lock and Castle Mills bypass sluice work in conjunction to maintain the upstream stretch of the River Foss at 7.6 meters above ordnance datum (mAOD). The remaining downstream stretch of the river formulates Foss basin and is maintained by Foss PS and the adjacent floodgate. Foss PS consists of eight 6.5 m^{3}s^{-1} pumps, with a total pumping capacity of 52 m^{3}s^{-1} and a 27 m wide intake weedscreen (bar thickness and spacing of 20 mm and 70 mm, respectively). Foss floodgate is positioned across the River Foss at the confluence with the Yorkshire Ouse. When the Yorkshire Ouse reaches 7.6 mAOD, the PS complex becomes operational in two stages:

(1) The floodgate is lowered into the channel from its normal raised position to prevent the movement of water (and fish) from the Yorkshire Ouse into the Foss basin
(2) The PS operates to move water from Foss basin into the Yorkshire Ouse. Pumps operate until flood water in the Yorkshire Ouse subsides (< 7.6 mAOD) and meets the level of Foss basin, at which point the floodgate is raised

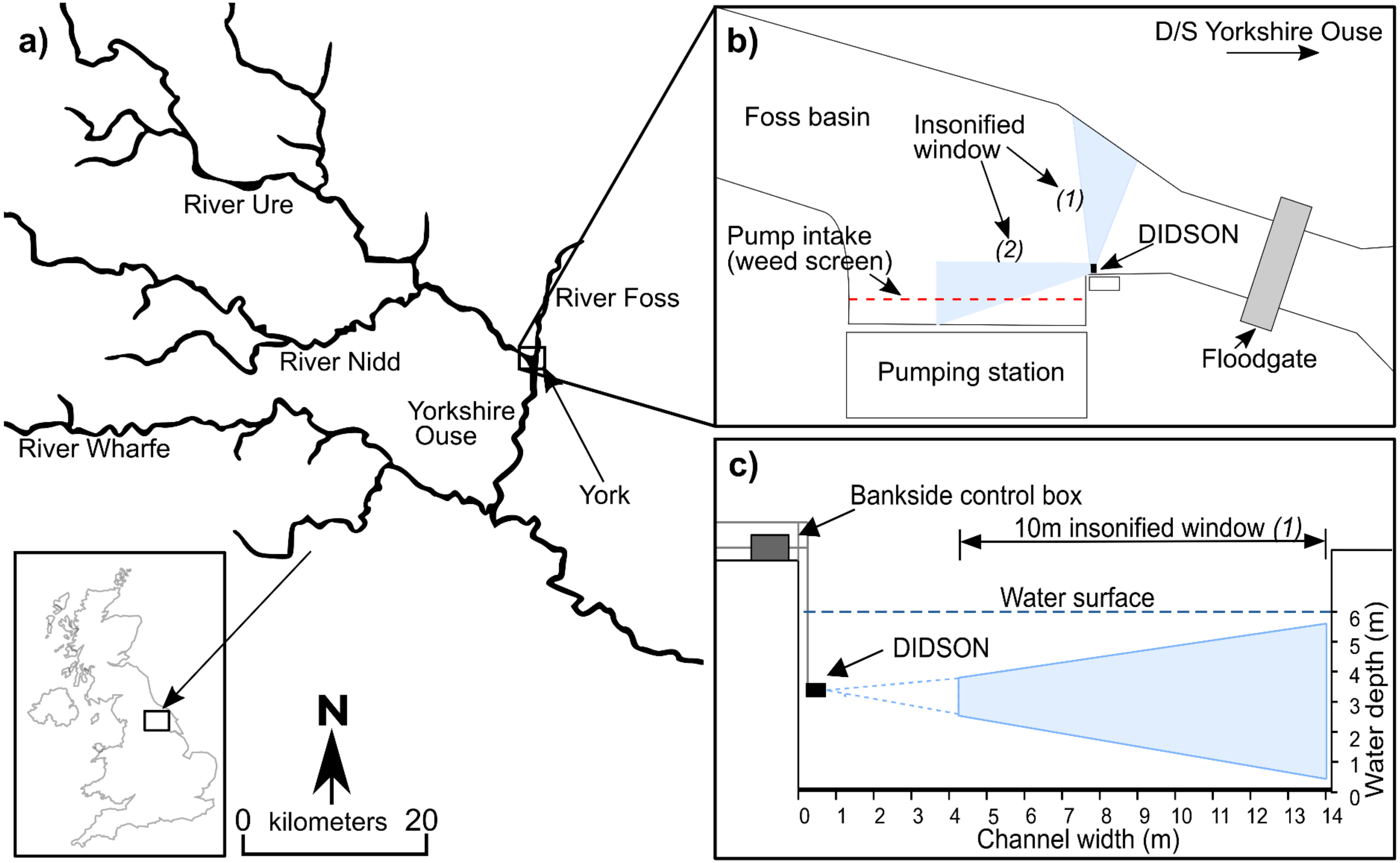


Figure 2.1 a) The location of the Yorkshire Ouse catchment, b) a schematic representation of Foss PS and floodgate, and the DIDSON insonified window across the channel (1) and across the weed screen (2), c) a cross-section representation of (1).

2.2.2 Field methods

2.2.2.1 Multi-beam sonar

It is difficult to non-invasively gather temporal information on fish that is inclusive of 24-hour, multi-seasonal and pluriannual outputs. Here, high-resolution multi-beam sonar (DIDSON, 300m, Sound Metrics, USA. http://www.soundmetrics.com/) addresses this by providing near video-like images of fish in turbid and dark water during the day and night over many months and multiple years. To provide optimal data on the temporal dynamics of lateral fish movements, the DIDSON imaged across the full width of the downstream channel entrance of the River Foss (Figure 2.1b). The DIDSON was installed on a 6 m vertical steel pole, at a submerged depth of 3 m (Figure 2.1c), and the sonar image was aligned with steel pilings on the adjacent river bank to ensure consistent orientation. When pumps operated, the DIDSON was rotated to image across the weed screen to confirm fish presence, but the rate of fish entrainment during pump operation were not assessed due to inadequate coverage of the weed screen.

The data and power cables were routed to a bankside weatherproof box containing a sonar command module and a laptop with remote internet connection (Panasonic TF-19). The DIDSON was operated in high frequency mode (1.8 MHz; 96 0.3°x14° beams, 512 bins) with a window length of 10 m (starting 4 m from point of transducer) at 6 frames s^{-1} (fps), receiver gain at default and focus set to auto to account for changes in fish distance from the transducer (Figure 2.1c). Continuous observations were captured to a 4 TB external HDD which was exchanged throughout the study period. Files were time and date stamped (hh:mm:ss – d/m/y) and stored in 10-minute intervals. All software inputs were performed in SoundMetrics software (DIDSON V5.26.24).

2.2.2.2 Field survey effort

Foss PS was surveyed during the winter for three consecutive years between October and February in 2017/18 (deployment duration of 153 days, 12 days of no sonar operation), 2018/19 (173 days, 25 days) to 2019/20 (147 days, 25 days). The sampling period was selected based on the propensity for river-resident fish to use the backwater for flow and predator refuge and increased likelihood of pump operation. Remote connections were made to the laptop on a daily basis to confirm operation. Pump operation could disturb stabilised sediment in Foss basin and thus weekly site visits were performed to check for and remove silt deposits in the sonar housing. Insufficient data were collected in October in year one, and local flooding prevented data collection in February of year three.

2.2.2.3 In-stream parameters and pump operations

River level data were provided by the Environment Agency using river levels recorded in hourly intervals in the Yorkshire Ouse , downstream of the floodgate at Foss PS (site code: L2404; Lat: 53.952378 N, Long: 1.078385 W) (Figure 2.2a). The commencement of the study in year one was associated with steady river levels (river level min, max, med, IQR: 5.1, 8.1, 5.7, 0.6 mAOD), but there were three pumping events in response to elevated river levels (November; four days, January; three days, two days) and smaller test operations not represented by local river conditions. Year three was similar (river level min, max, med, IQR: 5.1, 8.5, 6.2, 1.1 mAOD), but pumps were operated frequently in response to stochastic river levels, with a total of five events (September; four days, October; two days, one day, two days, December; one day). Year two was characterised as a dry year and river level was lower (river level min, max, med, IQR: 4.9, 7.9, 4.9, 0.5 mAOD); pumps did not operate throughout the sample range allowing for effective baseline data to be gathered. Thus, years one and three were the most hydrologically comparable, with year two serving as a baseline.

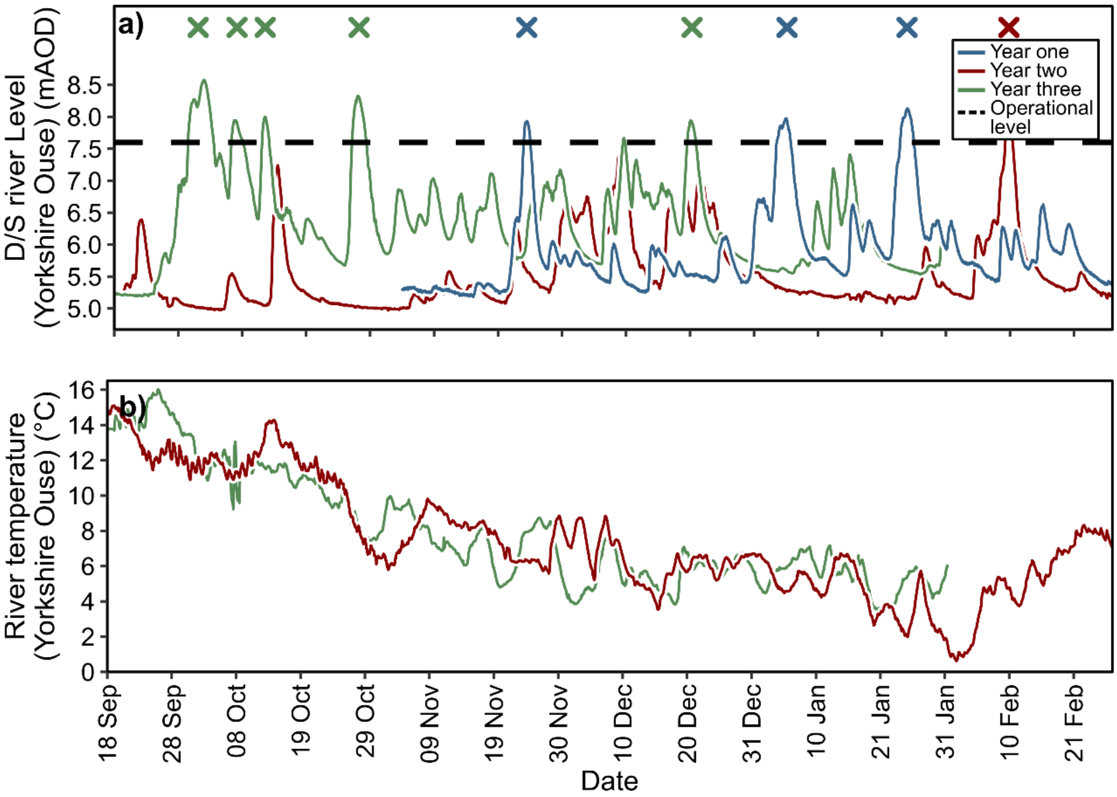


Figure 2.2 a) river level (mAOD) recorded in the Yorkshire Ouse (L2404/SE6057951091). The dashed line measuring 7.6mAOD is indicative of pump operation. The labels X mark pump events. B) river temperature (°C) recorded in the Yorkshire Ouse at the point of sample.

Temperature (°C) data were unavailable in year one, but was recorded in year two and three at hourly intervals using a temperature logger (Tinytag Aquatic 2 tg-4100) attached to the DIDSON mount. A seasonal decline in water temperature was similar in both years two and three (Figure 2.2b).

2.2.3 Analysis of sonar footage

2.2.3.1 Fish counts across the channel during non-operational river levels (Question 1)

To provide accurate fish counts, the recorded files were manually reviewed (Hateley & Gregory, 2006) by an experienced reviewer in the DIDSON software. For each sample month, a 14-day period with no pump operation (floodgate raised) was analysed to assess seasonal variation in fish presence. This allowed the number of consecutive days imaged to be maximised and data loss due to sonar failure to be minimised. Fish counts were taken hourly (individuals·1 frame·h^{-1}, five minutes past the hour ± 5 s^{-1}) from a 2 m^2 field at the centre of the insonified window (presented as individuals·2m^2 h^{-1}). Automated counting was determined to be unsuitable due to a combination of a large insonified window range (Han *et al.,* 2009), dense fish targets vulnerable to pseudoreplication and a concern with identification of non-fish targets, particularly leaf-litter and other floating detritus (Ebner *et al.,* 2009; Doehring *et al.,* 2011). Small (<30 cm) shoaling fish species are challenging to identify in sonar images (Egg *et al.,* 2018) and thus sonar assessments of multi-species communities may be supplemented by historic catch records (Hughes & Hightower, 2015). Previous fish surveys in the Yorkshire Ouse catchment suggest the fish community is comprised of river-resident eurytopic and rheophillic species, such as roach (*Rutilus rutilus*), common bream (*Abramis brama*), dace (*Leuciscus leuciscus*), perch (*Perca fluviatilis*), chub (*Squalius cephalus*) and bleak (*Alburnus alburnus*) (Lucas *et al*., 1998; Bolland *et al*., 2015; Environment Agency, 2022).

Playback speed was adjusted between 5x and 10x by the reviewer to remove non-fish targets. Background subtraction was enabled if floating debris reduced resolution of fish targets. Fish were measured using the DIDSON measurement tool when perpendicular to the sonar beam and grouped into six size classes, 0-10 cm, 11-20 cm, 21-30 cm, 31,40 cm, 41-50 cm and >50 cm total length.

2.2.3.2 Fish counts before and after pump operation (Question 2)

Fish counts were compared before (Pre-PO) and after (Post-PO) two independent pump operations in year three (Operation one: 11/10/19, 36h duration; Operation two: 26/10/19; 56h duration) to determine the effect of pump operation on diel fish counts. To include comparable day and night counts, the sub-sampled fish counts were taken from a fixed 24-hour period (24 samples on the hour; 00:00 – 23:00) and then summed to provide a total daily count. During this period the floodgate was not lowered and the hydrological conditions were comparable (falling).

2.2.3.3 Crepuscular floodgate operation testing (Question 3)

In year three, a five day trial (13 – 17 January 2020) was constructed where the floodgate was strategically lowered 1-hour ahead of dawn for two hours (07:30 – 9:30) to determine whether it prevented fish immigration into Foss basin and thus could be applied prior to pump operation to protect fish in the future. The floodgate trial ran independent of pump operations, but local hydrological conditions were similar, i.e., the downstream river level was rising. Fish counts were sub-sampled at 1 $\text{frame}\cdot15\text{minute}^{-1}$, and also incorporated 30-minutes pre- and post-floodgate closure to ascertain whether fish were deterred by the floodgate entering the water. The median dawn counts were then used for statistical comparison between two other five day periods of normal operation (floodgate raised); (1) immediately after the floodgate trial (20 – 24 January 2020), and (2) a period with comparable magnitude and duration of rising and falling river levels to control for hydrological effects on fish movements (09 - 13 February 2018).

2.2.4 Statistical analysis

The effect of diel phase on hourly fish counts was examined by creating four categories (photoperiod); dawn and dusk (equal to civil twilight ± 1h (i.e., three sample points)), day and night. Similarly, river level was divided into four categories (lvl_stage); rising water level (an increase of ≥ 0.5 m in 12h), falling water level (a decrease of ≥ 0.5 m in 12h), steady (reference) water level (≤ 6.5 m, neither rising or falling), and steady (elevated) water level (> 6.5 m, neither rising or falling).

The fish count data were analysed using R version 4.1.2 (R Core Team, 2022) in R Studio 2022.02.3 (RStudio Team, 2022). All statistical figures presented in the results were created using R packages ‘ggplot2’, ‘ggpubr’, ‘gridextra’ and ‘cowplot’. The fish count data were not normally distributed (Shapiro-Wilk normality tests (R function ‘shapiro.test‘)) and non-parametric testing was used throughout, with descriptive values presented as medians (IQR). For statistical comparison between variables, a combination of Wilcoxon (R function ‘wilcox.test’) and Kruskal-Wallis rank sum tests (R function ‘kruskal.test’) was used (summary statistics generated with R package ‘Rstatix’). Post-hoc testing was performed using Dunn’s test (R function ‘dunn.test’ in package ‘dunn.test’). Correlation testing was performed using Spearman's rank correlation (R function ‘cor.test’).

2.2.4.1 Modelling

The spread of variance in temporal fish count data were unbalanced across the grouping factors hour, lvl_stage, photoperiod, year and month and had a large proportion of zeros (20%). Multicollinearity of the predictor variables was checked by analysis of pairwise scatterplots and the Variance Inflation Factor (VIF ≥ 3) (R function 'vif' in package 'car') and all variables met rejection criteria (max VIF = 2.7). The variance between sample years was a concern due to the confounding effect of unpredictable pump operations. Therefore, a model with annual grouping factors was rejected to avoid overparameterisation and excess model complexity (Bates *et al.,* 2015). Instead, the data were modelled using two approaches; (1) a Generalized Additive Model (GAM) to determine the non-linear effect of diel cycle (hour) and (2) a Generalized Linear Mixed Model (GLMM) to estimate the linear effects of environmental factors on the temporal fish count data within each study year.

The GAM was constructed using R function 'gam' in package 'mgcv', with the smoothing factor hour and subject specific deviation of month (formula = total ~ s(hour, by=month)). Model fit was checked by analysis of the k-index and the deviance explained by the GAM was calculated as 1 – (residual deviance/null deviance). The GLMMs for each study year were specified using the dependant variable fish count and the independent variables river temperature, river level, lvl_stage and photoperiod (fixed effects) (R function glmmTMB in package 'glmmTMB'). Sample month was included as a random effect to account for non-independence present in the response variable (using glmer optimizer 'bobyqa'). The maximal global model was favoured over a stepwise elimination to avoid overestimating the effect size of significant predictors, and Akaike Information Criterion (AIC) was used to assess model performance between Poisson and negative-binomial families (Schmettow, 2021). Overdispersion and zero inflation tests were used to assess the fit of each model (using R function 'testDispersion' and 'testZeroInflation' in package 'DHARMa') (Linden & Mantyniemi, 2011). Model assumptions were verified by plotting residuals versus fitted values in accordance to Zurr & Leno (2016).

Table 2.1 Generalised linear mixed model (GLMM) selection for the effects of river temperature, river level and photo period on the temporal dynamics of fish counts across the channel entrance. The random effect of month was included in all the models. Dispersion factor not calculated for zero inflated models. GLMM constructed with *glmmTMB* package in R 4.0.2.

Model	Model formula	Distribution	Df	Dispersion factor	AIC
mod1_y1_p	(total~lvl+lvl_stage+photo+ (1|month)	Poisson	8	2.23	6875
mod2_y1_nb	(total~lvl+lvl_stage+photo+ (1|month)	Negative binomial	9	0.97	6244
mod3_y1_nb_zi	(total~lvl+lvl_stage+photo+ (1|month)	Negative binomial + zero inflation	10	-	6214
mod1_y2_p	total~temp+lvl+lvl_stage+photo+ (1|month)	Poisson	9	2.25	8915
mod2_y2_nb	(total~temp+lvl+lvl_stage+photo+ (1|month)	Negative binomial	10	1.41	8539
mod3_y2_nb_zi	(total~temp+lvl+lvl_stage+photo+ (1|month)	Negative binomial + zero inflation	11	-	8430
mod1_y3_p	(total~temp+lvl+lvl_stage+photo+ (1|month)	Poisson	10	2.24	5814
mod2_y3_nb	(total~temp+lvl+lvl_stage+photo+ (1|month)	Negative binomial	11	1.21	5454
mod3_y3_nb_zi	(total~temp+lvl+lvl_stage+photo+ (1|month)	Negative binomial + zero inflation	12	-	5456

2.3 Results

2.3.1 Temporal dynamics of fish during non-operational river levels (Q1)

Hourly fish counts showed significant inter-annual differences ($\chi^2{}_2 = 88.517$, *p* = <0.001). The total (hourly) fish count was highest in year two (total, med, min, max, IQR = 7892, 3, 0, 20, 6 individuals·2m^2 h^{-1}) and lowest in year three (total, med, min, max, IQR =4238, 2, 0, 22, 3 individuals·2m^2 h^{-1}). Year one was most similar to year three (total, med, min, max, IQR = 5500, 3, 0, 19, 5 individuals·2m^{-2}) (Table 2.2). Furthermore, the intra-annual (hourly) fish counts were significantly different in all years when grouped by month ($\chi^2{}_5 = 845.71$, *p* = <0.001), and a post-hoc Dunn's test revealed no two months had similar fish counts, except February, which was not significantly different to January (all years combined) (*Z* = 0.59, *p* = 0.277).

Examining the fit of the GAM smoothed lines (hour smoothed by month) revealed a highly contrasting inter-annual relationship in the temporally dynamic fish count data (Figure 2.3). Overall, the maximal daytime fish count (med, IQR: 4, 7 individuals·2m^2 h^{-1}) was significantly higher than night-time (med, IQR: 2, 3 individuals·2m^2 h^{-1}) (*W* = 3407, *p* = <0.001) (Figure 2.4a). Accordingly, a spearman's rho correlation (r_s) was used to determine if daytime fish counts followed daylight hours, of which there was a positive correlation in year one ($r_s = 0.61$, *p* = <0.001), but not year two ($r_s = -0.79$, *p* = <0.001), or three ($r_s = -0.42$, *p* = 0.0011).

Further interpretation revealed the daytime fish counts were typically maximised around the crepuscular period, peaking within 1h of sunrise (adjusted for season) and decreasing throughout the day before peaking a second time within 1h of sunset (Figure 2.3). Thus, when testing for crepuscular fish activity, fish counts were significantly different between all photo periods ($\chi^2{}_3 = 321$, *p* = <0.001) (Figure 2.4a), but fish counts were not significantly different between dawn (N = 3199, med, IQR: 4, 8 individuals·2m^2 h^{-1}) and dusk (N = 2991, med, IQR: 4, 6 individuals·2m^2 h^{-1}) (*Z* = -0.59, *p* = 0.277). Both photoperiods had significantly higher fish counts than during the day (Dawn: *Z* = -2.45, *p* = 0.008, dusk: *Z* = -3.13, *p* = 0.0013) and night (Dawn: *Z* = 12.27, *p* = <0.001, dusk: *Z* = 13.04, *p* = <0.001), confirming the importance of the crepuscular period.

The intra-annual differences in fish counts were further interoperated by including the frequency of pump operation. For example, fish counts in November of year one were clearly modulated by the crepuscular period (Figure 2.3.1c), but the slope of GAM fitted line flattens throughout subsequent sample months as sequential pump operation takes place. Year two, in which pumps did not operate, was in direct contrast to year one where the strength of the crepuscular relationship increased throughout monthly samples. The stochastic pump operation in year three was in turn associated with an inconsistent crepuscular relationship between months.

2.3.1.1 GLMM selection

The GLMMs using Poisson distribution (family = Poisson) were overdispersed (dispersion > 1.2) which was improved (Δ AIC ≥ 400) by using a negative-binomial model (family = nbinom2) (Table 2.1). After zero inflation tests indicated excess zeros in the simulated values (ratioObsSim >1), adding a zero-inflation parameter (ziformula = ~1) to the negative-binomial GLMMs further improved the models. These zero-inflated GLMMs with negative-binomial distributions resulted in the lowest AIC values. In year three an increase in AIC by 2 was accepted to maintain the variance modelling between the three GLMMs. Accordingly, the final three zero-inflated GLMMs with negative-binomial distributions were selected to analyse the effects of environmental variables on the temporal fish count data and model validation indicated no problems (Table 2.3).

Table 2.2 Data summary table containing river level recorded on the Yorkshire Ouse, temperature recorded at the point of sample (DIDSON) and fish count assorted by year, month and light period as derived from visual fish counts of DIDSON sonar captured between November 2017 and January 2020.

									Fish count (individuals·$2m^2$ h^{-1})											
	River level (Ouse) (mAOD)				**Temperature (℃)**				Day					Night					
Year (Month)	*median*	*IQR*	*min*	*max*	*median*	*IQR*	*min*	*max*	*median*	*IQR*	*min*	*max*	*sum*	*Median*	*IQR*	*Min*	*Max*	*sum*	*total*
Year one									6	8	0	19	3239	2	3	0	14	2261	5500
November	5.30	0.50	5.20	7.80	-	-	-	-	11	7	0	19	1495	3	2	0	9	651	
December	5.60	0.30	5.20	6.00	-	-	-	-	6	6	0	18	742	2	5	0	3	661	
January	6.20	0.80	5.50	8.00	-	-	-	-	3	6	0	13	504	2	4	0	14	565	
February	5.70	0.40	5.30	6.50	-	-	-	-	4	5	0	4	498	2	2	0	8	384	
Year two									4	8	0	20	4045	2	4	0	19	3847	7892
September	5.25	0.25	5.00	6.40	12.70	2.10	11.40	15.10	0	2	0	8	173	0	1	0	14	166	
October	5.10	0.20	4.90	7.25	11.54	1.50	6.11	14.30	0	2	0	8	219	0	1	0	8	134	
November	5.30	0.30	4.90	6.70	7.80	2.90	5.50	9.80	5	3	1	13	786	2	2	0	9	513	
December	6.25	0.90	5.30	7.50	6.30	0.80	3.50	8.80	6	5	0	15	630	2	3	0	14	641	
January	5.25	0.10	5.00	5.90	4.60	2.30	1.30	6.70	10	4	0	17	938	6	4	0	17	1648	
February	5.40	0.50	5.10	7.90	5.40	3.00	0.60	8.30	10	4	0	20	1299	3	3	0	19	745	
Year three									3	5	0	22	2698	1	2	0	19	1540	4238
September	5.30	0.80	5.10	8.30	14.50	4.60	13.40	15.00	1	3	0	8	224	0	0	0	4	48	
October	6.70	1.50	5.60	8.60	11.05	2.00	7.30	13.50	3	6	0	22	837	1	4	0	1	387	
November	6.50	0.60	5.70	7.20	7.70	1.60	4.70	10.00	3	3	0	12	511	1	1	0	8	288	
December	6.30	1.00	5.65	7.90	5.70	1.50	3.80	7.60	2	3	1	7	124	1	1	0	7	149	
January	5.70	0.60	5.55	7.40	5.55	1.30	3.50	7.10	10	7	2	19	1002	2	2	0	19	668	

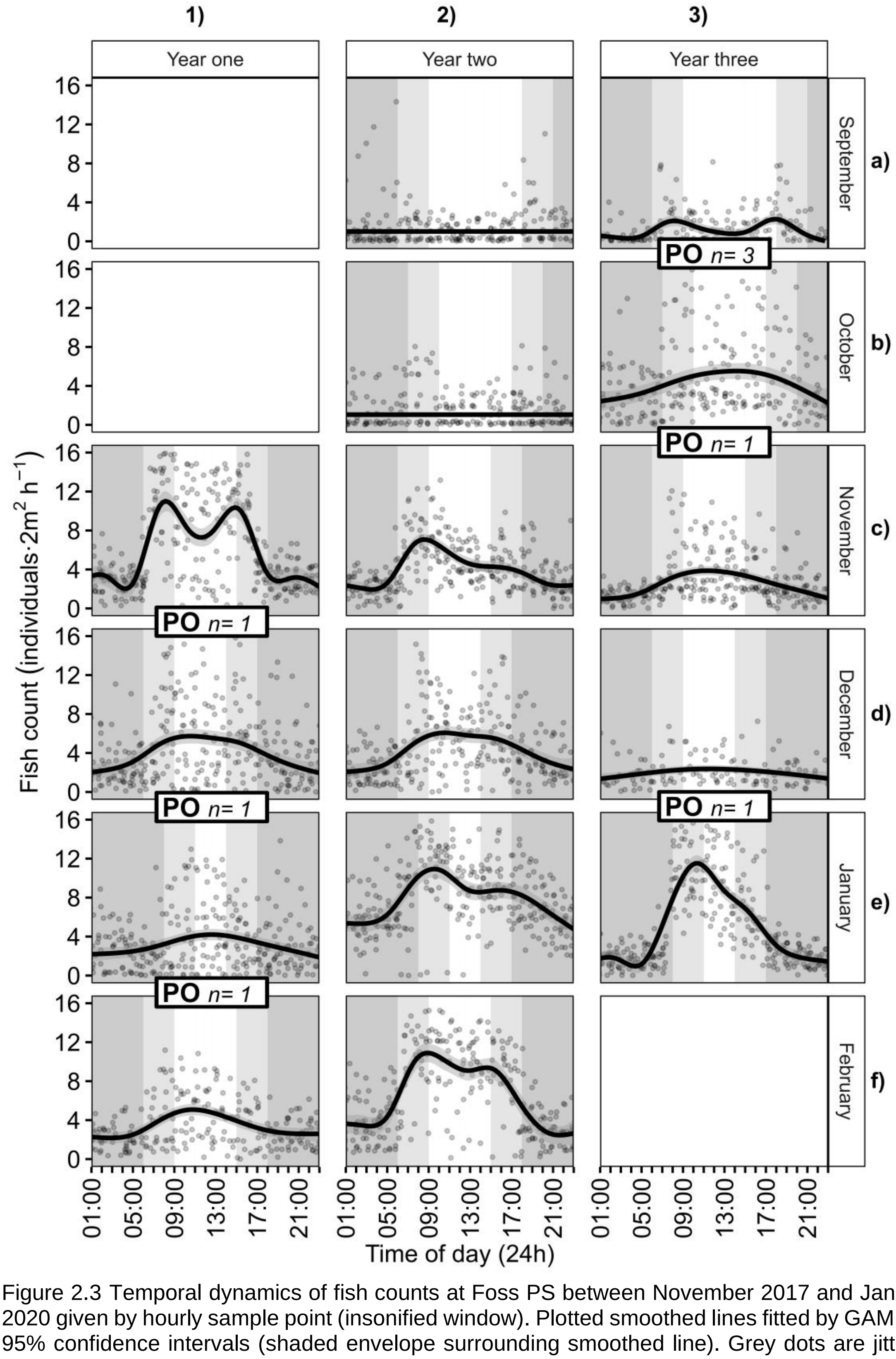


Figure 2.3 Temporal dynamics of fish counts at Foss PS between November 2017 and January 2020 given by hourly sample point (insonified window). Plotted smoothed lines fitted by GAM with 95% confidence intervals (shaded envelope surrounding smoothed line). Grey dots are jittered points to reduce over-plotting. The photo period is represented by shaded bars in the plot area (light grey for crepuscular period). PO = pump operation *between* sample months (*n* = number of operations).

2.3.1.2 Key correlates influencing temporal fish count

The decision to create independent annual models was supported by the differences in among-month variation between the three study years. In year one, falling and stable (reference) river levels were positively correlated with fish counts, but only falling levels were significant. However, the stable (reference) levels were more important as a predictor of fish count during the day (Figure 2.4.1b). The same relationship was observed in year two, except the stable (reference) level was also significant when compared to the intercept of rising levels ($p = 0.001$). In year three, there was no significant relationship with lvl_stage, however the stable (reference) levels showed the same diel relationship as year two and the stable (elevated) levels were also negatively correlated (Figure 2.4.3b). Overall then, the hourly fish counts had a significant negative relationship with river level ($p = <0.001$; Figure 2.5a). Additionally, there was a negative correlation between fish count and river temperature, which was significant in year two ($p = <0.001$), but not year three ($p = 0.105$; Figure 2.5b).

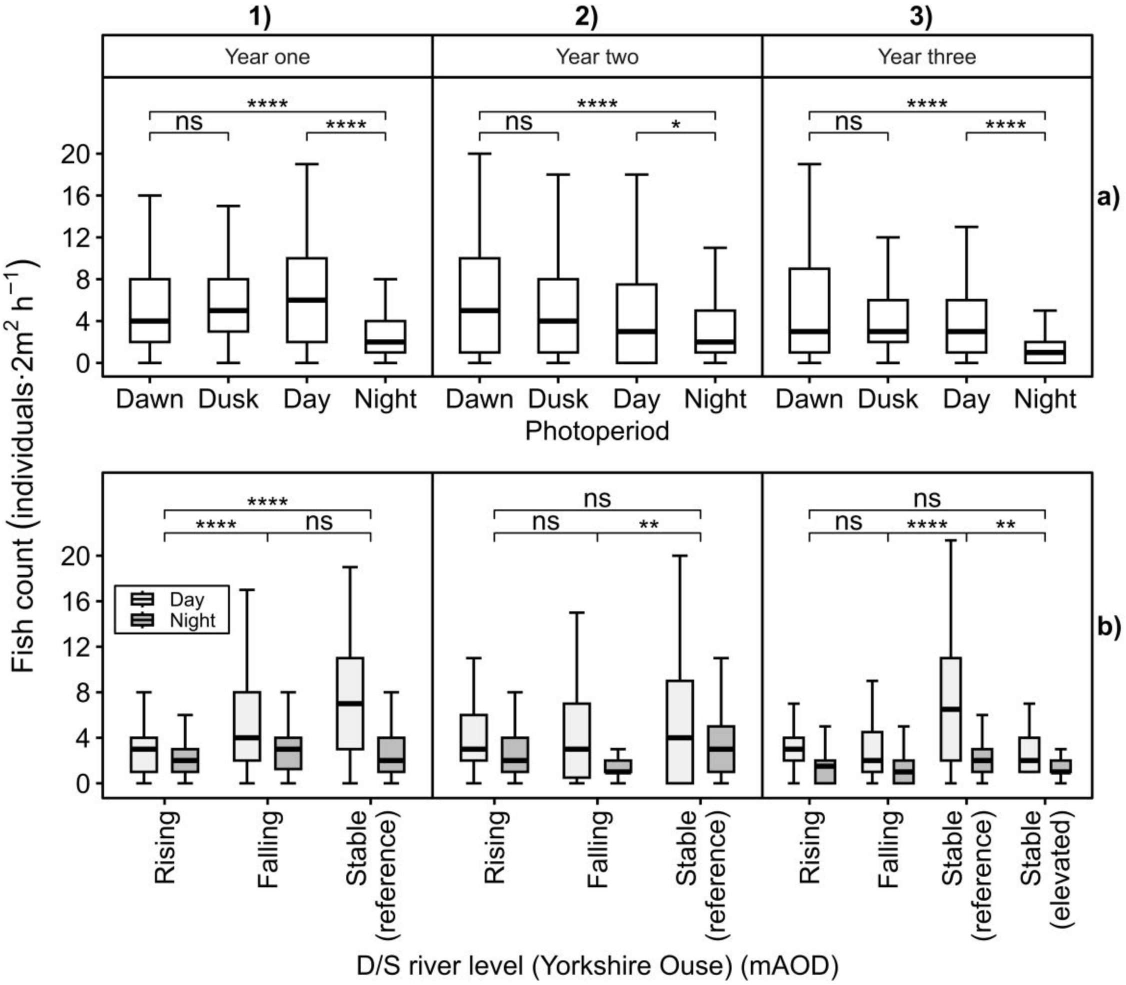


Figure 2.4 Fish count at Foss PS in categories a) photoperiod and b) lvl_stage within day and night light periods. Lines represent quartile 1 to the smallest non-outlier and quartile 3 to the largest non-outlier. Significance between categories indicted by Wilcoxon rank sum (ns = not significant, * = P ≤ 0.05, ** = P ≤ 0.01, *** = P ≤ 0.001, ***** = P ≤ 0.0001). D/S = downstream.

Table 2.3 Results of the fitted GLMM models for years one, two and three of the fish count data. Random effects and fixed effects are given, and the p values also reported for each parameter. GLMM constructed with *glmmTMB* package in R 4.0.2.

Model														
Year one *(mod3_y1_nb_zi)*					Year two *(mod3_y2_nb_zi)*					Year three *(mod3_y3_nb_zi)*				
Random effects					Random effects					Random effects				
Groups	Name	Variance	Std. dev.		Groups	Name	Variance	Std. dev.		Groups	Name	Variance	Std. dev.	
Month	(intercept)	0.002368	0.04866		Month	(intercept)	1.59	1.261		Month	(intercept)	0.2406	0.4905	
Number of obs: 1336, groups: month, 4					Number of obs: 1968, groups: month, 6					Number of obs: 1343, groups: month, 5				
Fixed effects					Fixed effects					Fixed effects				
	Est.	Std. error	Z	Pr(>|z|)		Est.	Std. error	Z	Pr(>|z|)		Est.	Std. error	Z	Pr(>|z|)
(Intercept)	7.4987	0.6475	11.581	<0.001	*(Intercept)*	1.3367	0.70337	1.9	0.057	*(Intercept)*	4.535938	0.608832	7.45	<0.001
lvl	-1.0629	0.1084	-9.801	<0.001	*temp*	-0.1292	0.01809	7.143	<0.001	*temp*	-0.043301	0.026737	-1.62	0.105
lvl_stage Falling	0.389	0.0875	4.447	<0.001	*lvl*	-0.22709	0.06851	-3.315	<0.001	*lvl*	-0.44451	0.088256	-5.037	<0.001
lvl_stage Stable (reference)	0.0326	0.0929	0.352	0.725	*lvl_stage Falling*	0.23001	0.08575	2.682	0.007	*lvl_stage Falling*	-0.104755	0.086211	-1.215	0.224
photoDay	0.2172	0.067	3.241	0.001	*lvl_stage Stable (reference)*	0.34002	0.10418	3.264	0.0011	*lvl_stage Stable (reference)*	0.008203	0.088663	0.093	0.926
photoDusk	0.0866	0.0744	1.163	0.244	*photoDay*	-0.10284	0.04711	-2.183	0.029	*lvl_stage Stable (elevated)*	-0.133706	0.577533	-0.232	0.816
photoNight	-0.6868	0.0618	-11.097	<0.001	*photoDusk*	-0.11672	0.05323	-2.193	0.028	*photoDay*	-0.088639	0.073174	-1.211	0.225
					photoNight	-0.75102	0.04357	-17.238	<0.001	*photoDusk*	-0.145871	0.084269	-1.731	0.083
										photoNight	-1.138237	0.070325	-16.185	<0.001

2.3.1.3 Population size structure

Length-frequency analysis showed that the size distribution of imaged fish had limited temporal fluctuation in size classification. Distribution of fish counts in the three most common size classes (0-10, 11-20, 21-30 cm) suggested the fish count data represents a diverse multi-species community of differing ages. At least 81% of imaged fish were classified as 11-20 cm, which likely represents a younger overall mean population age (Appendix 1). The only exception to this pattern was a recording of fish >50 cm, primarily during the night.

2.3.2 Temporal dynamics of fish during operational levels (Q2)

Total daily fish counts 24 hours before (Pre-PO; total, med, IQR: 323, 6, 8 individuals·$2m^2\ h^{-1}$) and after (Post-PO; total, med, IQR: 55, 1, 2 individuals·$2m^2\ h^{-1}$) two independent pump operations (October 2019) were significantly different (W = 2007, p = <0.001). Fish counts reduced by 85% (W = 478.5, p = <0.001) and 82% (W = 547, p = <0.001) after the two pumping events (Figure 2.6a).

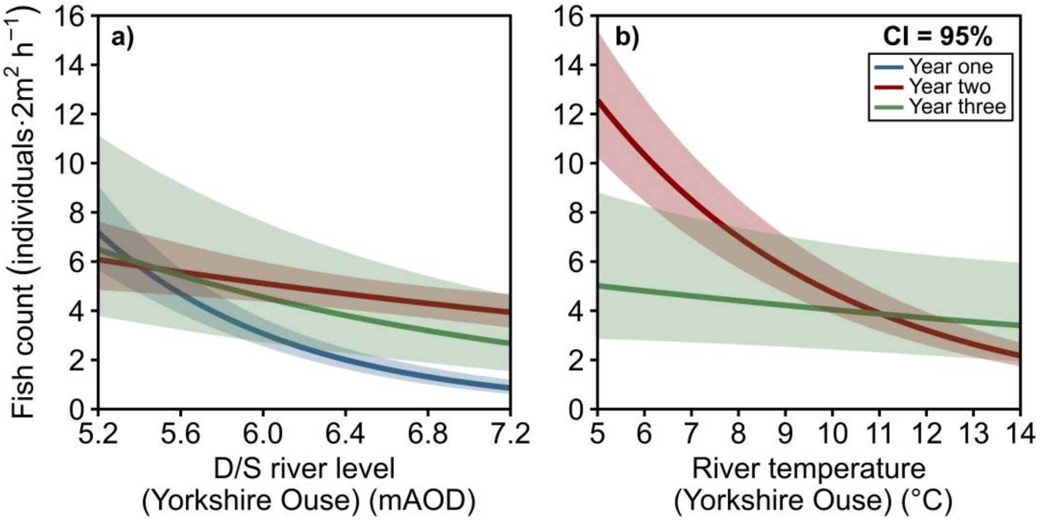


Figure 2.5 The effect of environmental factors on fish counts at Foss PS between November 2017 and January 2020. Negative binomial lines fitted by the GLMMs (Table 2) chosen in the model selection process (Table 2.1). 95% confidence intervals represented by shaded envelope surrounding smoothed line (dotted lines upper and lower bounds). Note the different y scales. D/S = downstream

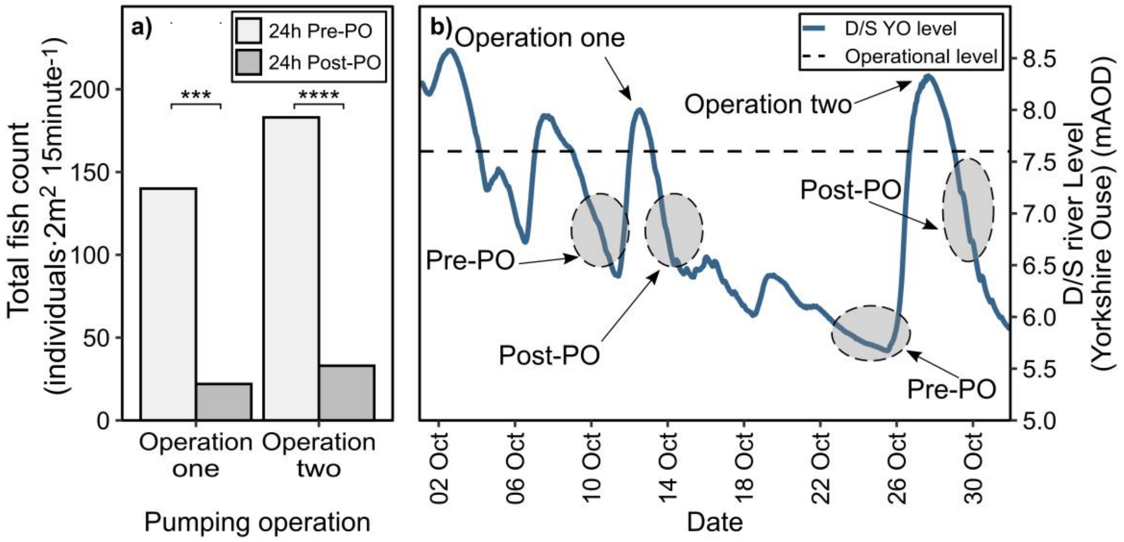


Figure 2.6 a) Total daily fish count at Foss PS observed in a fixed 24h period (00:00 – 00:00) before (24h Pre-PO) and after (24h Post-PO) pump operation and b) annotated hydrograph for October 2019 showing the sonar sample periods (grey circles) during operations one (11/10/19: 36h pumping) and two (26/10/19: 56h pumping). Significance indicted by Wilcoxon rank sum (ns = not significant, * = P ≤ 0.05, ** = P ≤ 0.01, *** = P ≤ 0.001, ***** = P ≤ 0.0001. D/S =downstream.

2.3.3 Dawn floodgate operation testing (Q3)

The fish counts during dawn when the floodgate was lowered (med, IQR: 1, 2 individuals·2m^2 15minute^{-1}) were significantly lower than the following 5-day period of normal operation (med, IQR: 8, 8 individuals·2m^{-2}) (W = 546, p = <0.001) (Figure 2.7.1a & 2.7.2a). The same effect was seen when compared to a hydrologically comparable period in 2018 (med, IQR: 7, 7 individuals·2m^2 15minute^{-1}) (W = 3664, p = <0.001) (Figure 2.7.1a & 2.7.3a), which was similar to the 5-day period of normal operation in 2020 (W = 1693, p = 0.06), although the crepuscular periodicities were stronger in the post floodgate trial comparison (Figure 2.7.2b).

2.4 Discussion

Knowledge on the impacts of hazardous intake operation on temporal (seasonal and diurnal) movements of river-resident lowland fish communities remains underdeveloped. Such knowledge needs to be integrated into operational management to protect fish. This pluriannual study quantified the temporal dynamics and non-spawning movements (Lucas, 2000) of a lowland fish community at an off-channel pumping station in autumn and winter; a period not often considered for conservation and management of river-resident fish. Direct observation of fish movements was achieved using an underwater multi-beam sonar, which allowed for the passive quantification of temporal dynamics of fish movements, without the need for invasive or destructive techniques. This revealed seasonal and inter-annual variations in diel movements, which were strongest during a ‘baseline’ year with no pump operation. Two years of ‘impact’ data revealed pump operations severely disrupted the regular ecological functions (e.g., diel lateral movement between main-river and off-channel area) of the local fish community.

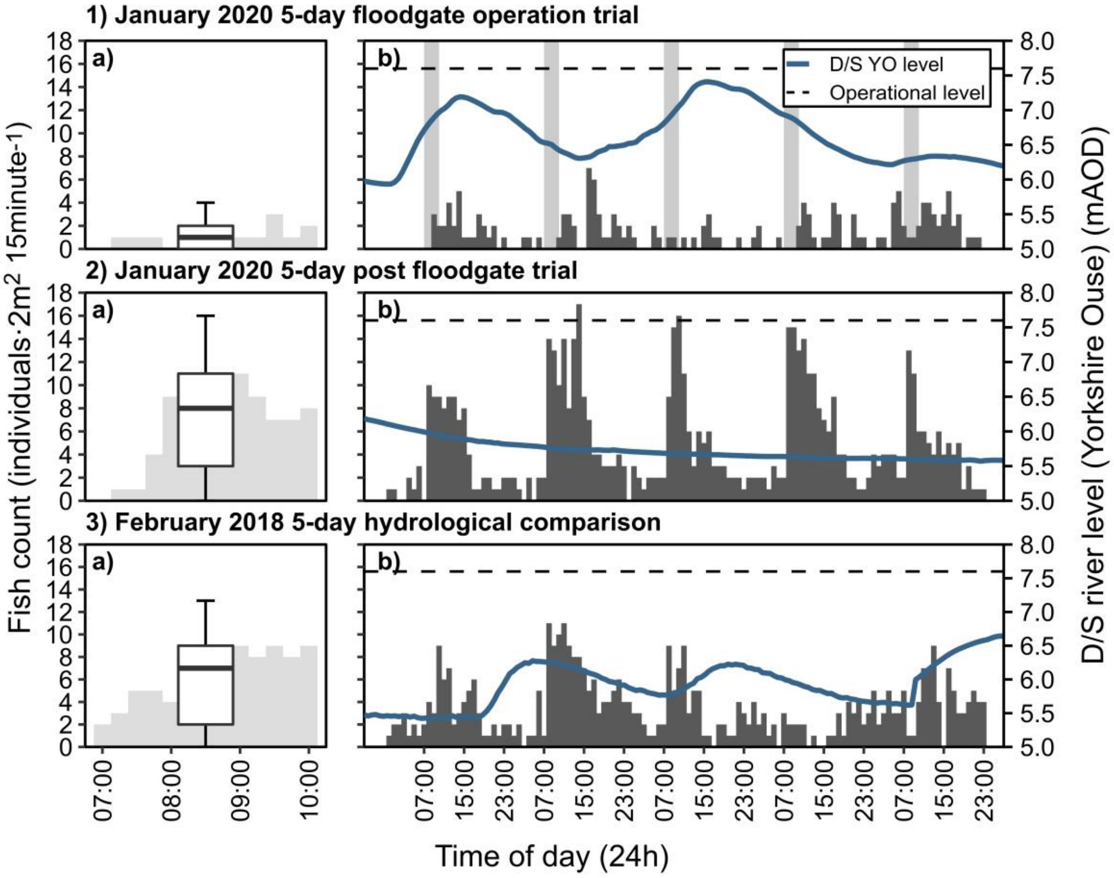


Figure 2.7 The floodgate testing process given as a) boxplot (lines represent quartile 1 to the smallest non-outlier and quartile 3 to the largest non-outlier) and histogram of fish counts measured during the dawn photo period and b) histogram of the observed fish counts with secondary axis overlaying hydrograph of downstream river level. Facet 1 visualises the floodgate testing process, with the period the floodgate was lowered represented by vertical grey shading (07:30 – 09:30am). Facet 2 provides comparison in the period immediately following the trial, and facet 3 provides comparison with a hydrologically comparable period. D/S = downstream.

Modification of floodgate operations, which is seldom considered for the protection of river-resident fish, appeared to be a promising management option for preventing immigration of fish into a hazardous intake area.

2.4.1 Seasonal and diurnal temporal dynamics of fish

The diel light cycle is a fundamental factor when considering the phenomena of fish moving between differential day and night habitats (e.g., Janac & Jurajda, 2013). Here, fish abundance was highest during daylight and lowest at night which agreed with prediction (i). However, fish exhibited strong temporal periodicities in abundance, which included both day- and night-active fishes as well as diel and seasonal variability. These findings are probably a consequence of studying a multi-species fish community that have inter- and intra-species differences in diurnal and nocturnal behaviours. Indeed, Nunn *et al.* (2010) demonstrated that diel movement patterns of lowland fish between a small tributary and the main River Avon was species specific. In Nowak *et al.* (2019), dace (*Leuciscus leuciscus*), bleak (*Alburnus alburnus*) and roach (*Rutilus rutilus*) showed shifts from nocturnal to diurnal behaviour associated with seasonal movements between a small stream and a main-river. Accordingly, the temporal results presented in this study possibly include an undetected diel changeover in fish assemblage. This was also supported by the tendency for more >50 cm fish to be recorded during the night than the day in this study. Any considerable assemblage changeover could then conceivably include species-specific differences in periods of movement and rest (Shukla *et al.,* 2021), and the resulting temporal dynamics would help explain why the fish counts in this study did not always closely align with light periods.

Lateral movements of fish from main-river channels into backwater habitats are particularly important for flow refuge (Hohausova *et al.,* 2003; Lyon *et al.,* 2010), and thus movement is not exclusively mediated by prevailing light levels. During this study, it was not possible to disentangle whether sonar imaged fish were present due to the backwater, or whether infrastructure at the pumping station (sub-aquatic concrete structures, weedscreen and sump chamber) provided cover and refuge from main-river stressors (i.e., flow and predation). Given, maximum fish abundance and activity occurred during the crepuscular light periods, which supported predictions (i) and has also been found for lowland fish movements elsewhere (Barry *et al.,* 2020). Roach, for example, may move laterally throughout the diel period, but maximal movement occurs at dawn and dusk (Hohausova *et al.,* 2003; Heermann & Borcherding, 2006). Similarly, Conallin *et al.* (2011) reported frequent bi-directional movements of fish between a main-river body and perennially connected off-channel habitat, and Bolland *et al.* (2008) observed lowland fish moving towards a marina at dawn and away at dusk. Therefore, the crepuscular movement patterns found here were likely caused by fish moving towards and away from Foss Basin at dawn and dusk, respectively. Undoubtedly, these findings have important considerations for the operational timing of river structures that can interact with lateral fish movements, especially those associated with emigration and immigration of fish between water bodies (see Section 2.4.1.5).

2.4.2 Ecological considerations for temporal dynamics of fish

In year two (no pump operation; baseline year), the GLMM revealed a negative correlation between river temperature and daily fish counts, i.e., the importance of Foss Basin as refuge (during low flow) increased throughout the winter. This finding is in agreement with Allouche *et al.,* (1999), whom suggested low-flow backwaters offer relief from temperature costs (e.g., decreased metabolism, feeding, and swimming performance). That said, diel variations in fish aggregations in Foss Basin were also likely influenced by unquantified ecologically conflicting trade-offs (e.g., Roff & Fairbairn, 2007). One explanation for these movements is a discrete diel shift between foraging phases and predation evasion, particularly from piscivorous birds that feed during the day (Mulder *et al.,* 2019). Notably, in the UK, cormorants (*Phalacrocorax carbo*) migrate inland to forage during the winter (Jepsen *et al.,* 2018), resulting in a seasonal increase in predation pressure that corresponded with the progressively elevated crepuscular periodicities in fish counts observed in year two. Elsewhere, the dispersal of river fish towards isolated winter refuge habitats has also been attributed to evasion of piscivorous winter predators (Nunn *et al.,* 2010; Thurow, 2016). Anthropogenic structures, like the hazardous intake studied here, can also provide refuge for prey fish (e.g., Russell *et al.*, 2008) as vegetation in the main-river dies off during winter. Furthermore, avian predators are deterred by the associated human activity (Lemmens *et al.,* 2016). Accordingly, the stochastic diel fish count data here may have been influenced by temporally variable predator-prey interactions (Brodersen *et al.,* 2008).

Year one and three were characterised by rising river levels and intermittent pump operations, which resulted in periods of contrasting river level criteria to year two. Movements of lowland fish are intrinsically linked with large-scale river hydrology (Poff *et al.,* 1997), and lateral movement into floodplains (Tripp *et al.,* 2016; Koster *et al.,* 2020), backwaters (Hohausova *et al.,* 2003; Coulter *et al.,* 2017) and off-channel areas (Lyon *et al.,* 2010; Pusey *et al.,* 2020) is common during elevated river levels and floods, particularly over winter. Such movements are considered to be a behavioural adaptation to avoid adverse environmental conditions in main-river bodies. Hence, it was perhaps surprising to see that the temporal fish count data here was negatively correlated with river level in the GLMM; overall fish counts were highest during stable (reference) levels, and lowest during rising and stable (elevated) river levels (all years). A common conclusion from other studies which have assessed lateral movements of fish into off-channel habitats during non-flood periods (e.g., Conallin *et al.,* 2011; Chesire *et al.,* 2016; Magoulick *et al.,* 2021), is that intermittence in the availability of these habitats provides stimulus for lateral (seasonal) movements of fish. However, the prevalence of increased lateral fish movements into Foss basin during stable river levels suggests that hydrological stability was important for this lowland fish community. The potential reasons for reduced fish counts in Foss Basin during rising river levels could be that elevated levels in the Yorkshire Ouse and differing water velocities at the River Foss confluence mean fish either avoided this area during flood (Togaki *et al.,* 2021), sought flow refuge in the main-river (Bolland *et al.,* 2015), or did not exclusively use lateral movements as a strategy to manage harsh ecological conditions. The increase in fish counts during falling levels possibly then represents the gradual repopulation of the backwater once high flows subsided (Lucas & Baras, 2001).

2.4.3 Impact of pump operations

When Foss PS operated three independent conditions changed, all with potentially negative implications for fish in Foss Basin; the lateral connection to the main-river was blocked by the floodgate, hydrological conditions in the basin changed (Franklin & Hodges, 2015) and fish in the basin were at risk of entrainment (Martins *et al.,* 2014). It was beyond the scope of this investigation to gather direct evidence of the scale and impact of entrainment (e.g., netting the outfall during pump operation). Nonetheless, in support of prediction (ii), the total daily fish count reduced by 85% following two independent pump operations. Furthermore, the confounding difference in the seasonally progressive crepuscular fish counts between a year with no pump operation (year two) and two years with intermittent operation (year one and three) suggests that these operations disrupted the regular ecological behaviour of this fish community. Indeed, the temporal dynamics in year one were not related to temperature, and the GLMM correlation in year three was insignificant. Ultimately, these results have provided new evidence that hazardous intake operation potentially endangers river-resident fish populations and can severely impair ecological function.

2.4.4 Impact of floodgate operations (independent of pump operation)

Normal floodgate operation at Foss PS is in direct contrast to floodgates which form a perennial barrier, from which studies on these structures typically recommend more frequent opening to improve fish passage (Doehring *et al.,* 2011; Wright *et al.,* 2015). That said, given that closing floodgates prevents passage of fish, optimising their operation could provide a quick and cheap non-engineered solution for reducing lateral movements of fish into hazardous areas. Using fish movement knowledge gathered in year one and two (e.g., lateral, crepuscular movement), floodgate operation was modified in year three to assess whether immigration of fish from the main river into the backwater was prevented. As predicted (iii), lowering the floodgate ahead of dawn significantly reduced immigration of fish into Foss Basin, independent of hydrological conditions. Coupled with the finding that fish returned to their normal movement pattern immediately after the trial period, the modified floodgate operation could be advantageous for fish protection if implemented at dawn ahead of pump operation.

2.4.5 Directions for future research

Development of modified floodgate operations to reduce entrainment of fish (e.g., Perry *et al.,* 2015) requires further investigation and studies at different hazardous intakes are recommended to compliment this work. In particular, monitoring downstream of the floodgate would have provided an enhanced understanding of whether fish approached the basin when the floodgate was lowered. It is important to iterate that even though fish counts were lowest during rising river levels, extrapolating these numbers suggests the potential for thousands of fish to be occupying the backwater during pump operation. Understanding the requirement for the protection of fish residing in Foss basin after the floodgate was lowered for pump operation was beyond the scope of this study. In this case, one option would be to install artificial habitat for flow refuge without interrupting flow conveyance and elevating flood risk. Thus, future studies should aim to quantify both natural flow velocities (no operation) and those generated by pump operation, possibly informed by Computational Fluid Dynamics (e.g., Mulligan *et al.,* 2017).

Considering the prevalence of hazardous intakes (including pumping stations) on lowland rivers around the world, understanding river-resident fish movement around these structures clearly warrants further investigation. Using DIDSON provides a suitable method for moving away from monitoring singular species and enables the entire fish community to be studied. Given the dynamic findings presented here, perhaps future work, including telemetry investigations, need incorporate multi-species analysis. Additionally, in systems without heavy macrophyte growth, which limited this investigation to winter months, it would be beneficial to perform similar investigations during the summer to fully establish seasonal movements.

2.4.6 Conclusions and management implications

Although there is a growing body of literature which has proposed operational changes to hazardous intakes based on ecological considerations for diadromous fish (Egg *et al.,* 2017; Bolland *et al.,* 2019; Baker *et al.,*2021), river-resident fish are currently underrepresented in management plans for hazardous intakes globally. During this study, many thousands of river-resident fish across a multi-species community were passively and non-invasively quantified (using multi-beam sonar) during autumn and winter over three years with highly contrasting hydrology, including a year without pump operation. The latter enabled an unprecedented understanding of the ecologically sensitive temporal activity patterns of lateral fish movements between the main-river and backwater, the impact of pump operation to be quantified and the formulation of low-cost non-engineered operational changes for fish protection. Specifically, crepuscular movements into the backwater were predicted by the photoperiod and cool temperatures, and were presumably influenced by trade-offs between feeding and predation costs, but were disrupted by intermittent changes to water level. Prolonged periods of pump in-operation in year two led to large aggregations of fish in the basin which, paradoxically, potentially elevates entrainment risk when pumps do start-up. Collectively, the findings in this paper highlight the positive outcomes that can be gained from having a thorough understanding of the temporal movement of fish in the immediate vicinity of hazardous intakes. Indeed, this knowledge has led to the identification of the following management recommendations:

(1) Overall, fish abundance was highest during daylight and lowest at night, which was in agreement with predictions (i); pumps should not be started during the day to protect the most fish.

(2) Given fish tended to immigrate into Foss Basin at dawn and lowering the floodgate during a trial temporarily interrupted this movement, which was in agreement with predictions (i, iii), the floodgate should be lowered prior to dawn ahead of predicted pump operation due to elevated river levels.

The need to balance these operational changes based on ecological fish considerations, i.e., start pumps at night and lowering the floodgate at dawn, whilst maintaining flood protection, cannot be understated. It is hoped these recommendations can be successfully incorporated into management whilst not increasing societal flood risks if they are carefully timed towards predicted hydrological conditions. Manipulating operations of existing infrastructure will be more cost-effective than retrofitting alternative protection measures (e.g., fine-mesh screening). While the findings from this study should readily transfer to management of similar structures, there may be locally specific ecological and hydrological considerations. Ultimately, human-mediated river use is rarely synchronised with the ecological needs of fish, and compromises between both elements are essential to ensure long-term sustainability of riverine ecosystems. Here, this study has uniquely shown how long-term knowledge of the river-resident fish community at a hazardous intake across a wide range of hydrological conditions led to the development of non-engineered protection strategies.

3 ANTHROPOGENIC WATER LEVEL MANAGEMENT INFRASTRUCTURE INFLUENCES NON-CONSUMPTIVE PREDATOR EFFECTS: AN INSIGHT INTO PREDATOR-PREY INTERACTIONS IN A HEAVILY MODIFIED LOWLAND RIVER

3.1 Introduction

The interaction between piscivorous predators and prey fishes is a fundamental process which influences the ecological dynamics of fish communities (Beauchamp *et al.,* 2007). Understanding ecological implications of predation, for example, the trophic direction of predator-prey interactions (Beauchamp *et al.,* 2007) and density-dependant predation (Lannin & Hovel, 2011) is partially achieved by measuring consumptive effects (i.e., mortality); methods for which include detection of prey tags in predators (Kallo *et al.,* 2020) and analysing stomach contents of predators (Hall & Kingsford, 2016). However, studying only the consumptive effects of predation fails to quantify the temporal rate of non-consumptive interactions (e.g., non-mortal) and the resulting behaviours of prey. These non-consumptive effects (NCEs) include alterations to activity, habitat use, foraging and morphology of fish (Orrock *et al.,* 2013), although their effects are rarely quantified.

Several behavioural mechanisms contribute to the evasive responses of prey fish exposed to predation risks. Fundamentally, shoaling (group aggregation), is important for predator risk detection, dilution, and confusion (Pitcher, 1998). Management of predation risk then includes the movement of fish shoals into safer refuge habitats (Orrock *et al.,* 2013). Prey refuges, including space under boulders and trees in freshwater streams (Conallin *et al.,* 2014), and undercut banks, marginal vegetation and anthropogenic structures in rivers (Copp, 1997), provide direct benefits for prey by reducing the likelihood of being consumed and are essential for prey to persist in the same environments as their predators (Nunes *et al.,* 2019). The successful evasion of predators is therefore expected to be dependent on the local distribution and availability of refuge habitat (Heithaus *et al.,* 2009). Paradoxically, the increased safety refuge offers can be costly to prey fish by concentrating resources (space, light) and reducing foraging opportunities, a phenomenon which strengthens the NCEs of predation (Donelan *et al.,* 2017). In turn, schooling (coordinated directional movement) occurs when prey fish move between low risk (refuge) and high risk (open water) habitats (Campanella *et al.,* 2019). Temporal variation (seasonal, diel) in prey activity and refuge use then reflects a trade-off between metabolic costs and avoiding the active period of predators (Basille *et al.,* 2015).

Despite the importance of understanding the ecological implications of non-consumptive predation it remains largely unknown due to the methodological challenges of studying such interactions in the wild. The use of underwater high-resolution sonar appears to be a promising method for improving this understanding (Price *et al.,* 2013; Becker *et al.,* 2014; Campanella *et al.,* 2019; Smith *et al.,* 2020), although simultaneous observation of predators and prey remain rare. Such work has demonstrated the potential for this application in several ecosystems. For example, Becker *et al.* (2014) observed dynamic schooling of estuarine fish in response to diurnal differences in the rate of predator attacks. Campanela *et al.* (2019) then show crepuscular anti-predator movements of prey fish into refuge on a marine reef system. Smith *et al.* (2020) expanded on this, finding crepuscular directional movements of prey fish to be concentrated around an anthropogenic intake in a freshwater lake. However, to-date there is a paucity in the ecological information on predator-prey interactions in lowland rivers, with existing examples being limited to traditional invasive methods (e.g., Grant & Harrington, 2015; Kallo *et al.,* 2020).

Lowland rivers are important for migration, spawning, and provide foraging resources and refuges for fish (Oglecki *et al.,* 2021) but are becoming increasingly vulnerable to anthropogenic modifications. The negative impact on lowland river ecology is typically described by modifications to ecohydrological processes including increased nutrient run off (Kupiec *et al.,* 2021), water quality pollution (dos ReisOliveira *et al.,* 2019) and creation of unnatural hydrological conditions (Davis *et al.,* 2015). Additionally, the implementation of river maintenance measures (RMMs) including the installation and operation of anthropogenic water level management infrastructure (pumping stations), is required for Flood Risk Management (FRM) (Gardner *et al.,* 2013; Angelopoulos *et al.,* 2018).

RMMs prioritise water conveyance and are ignorant to lowland river ecology; for example, channelisation and dredging homogenise river structure (Harrison *et al.,* 2004), and the seasonal removal of riparian vegetation and natural in-stream features (e.g., fallen trees) can exacerbate winter die-off of natural habitat (Singh *et al.,* 2021). These factors modify the distribution of macrophytes and remove macroinvertebrates (Dar *et al.,* 2014), and can lead to overall declines in fish abundance (Baczyk *et al.,* 2018). Elsewhere, Gardner *et al.* (2013) show the potential for FRM practices to modify ecological behaviour of lowland fish. Loss of refuge habitat is particularly problematic for prey fish as piscivorous birds are known to frequently overwinter on lowland rivers (Jepsen *et al.,* 2018). Thus, reducing the diversity and spatial distribution of aquatic habitats is also expected to modify ecological interactions between predators and prey. It is surprising then that the impact of anthropogenic activities on lowland river ecology rarely includes considerations for predation effects, and exactly how predators and prey interact in these anthropogenic settings is understudied.

Interestingly, non-operational pumping stations may inadvertently provide refuge for prey fish behind bar racks (weed screens) that prevent entrainment of debris. This structurally complex environment offers protection to prey fish from large aquatic and avian predators which are seldom able to fit through the bar apertures, and once passed the screen, the pump chamber is sheltered and able to hold thousands of fish. Additionally, many of these structures operate infrequently (e.g., once in five years), meaning large aggregations of fish accumulate over time. However, these refuges come with several caveats; when pumps operate, they become hazardous to prey fish, with mortality a high likelihood (Rytwinski *et al.,* 2017) and because they are often situated at terminal points (e.g., confluences), they can concentrate and confine fish (e.g., Smith *et al.,* 2020). The latter exacerbates density-dependant predation effects (Lannin & Hovel, 2011), and may counterintuitively enhance the NCEs of predators (e.g., Donelan *et al.,* 2017).

RMMs in lowland rivers could lead to previously unquantified changes to natural ecological interactions of predator and prey. Additionally, knowledge of the temporal distribution of predators and prey in lowland rivers, particularly their rate of interactions and the evasive responses of prey fish is lacking. Therefore, this study aimed to identify the behavioural interactions between predators and prey fish at a pumping station intake by measuring the temporal periodicities in the rate of predator-prey interactions and quantifying the attack behaviour of predators and the anti-predator response of prey fish. Accordingly, developing this understanding could provide enhanced knowledge of species-specific predation factors, inform conservation of lowland fish and direct management of anthropogenic structures.

3.2 Materials and methods

3.2.1 Study catchment and site

The Welland catchment is in the east Midlands of England and forms a catchment area of at least 1656 km^2 (Figure 3.1a). At its sources, water flows through pasture-dominated hills before reaching the floodplains in the lower Welland. The major tributaries of the West Glen and East Glen Rivers flow easterly into the Rivers Glen and Welland and a series of drainage channels. The River Welland then flows through Market Harborough, Stamford and Spalding, before becoming tidal and discharging into the sea. Common lowland river-resident fish expected in this catchment include roach (*Rutilus rutilus*), dace (*Leuciscus leuciscus*), perch (*Perca fluviatilis*) and chub (*Leuciscus cephalus*) (Environment Agency, 2022). Localised piscivorous predators include the northern pike (*Esoc Lucius*) and great cormorant (*Phalarcrocorax carbo*). This study was performed at Bourne Eau PS, located at the confluence between the Bourne Eau and the River Glen (Lat: 52.754185 N Long: -0.289369 W) (Figure 3.1b).

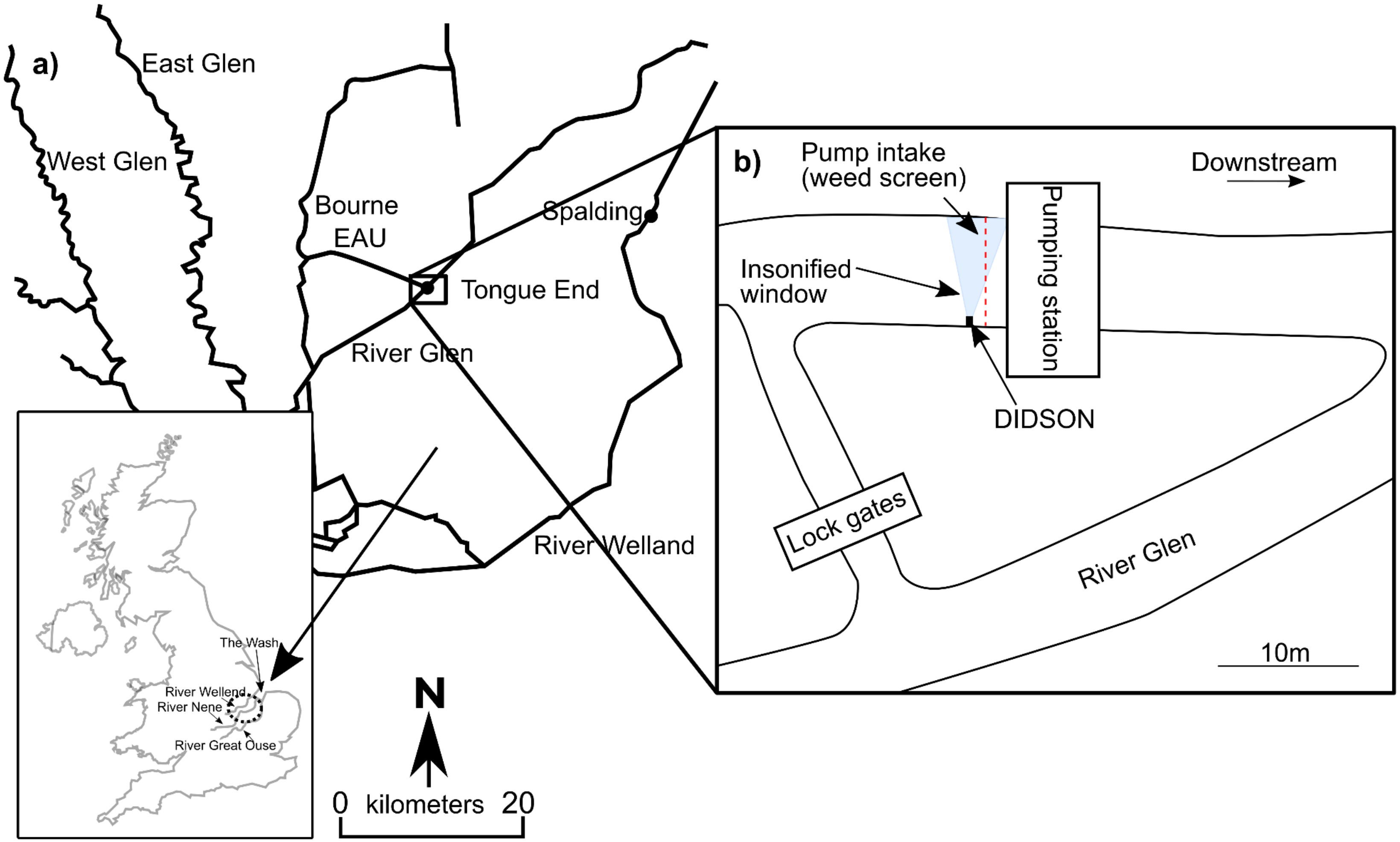


Figure 3.1 a) the location of the study catchment (bottom left) and the lower Welland catchment. b) a schematic representation of the study site showing the position of Bourne Eau PS, adjacent lock gates, and the insonified window.

The Bourne Eau is a short, embanked river which rises in the town of Bourne and flows to join the River Glen at Tongue End. The Bourne Eau typically drains into the River Glen via gravity through a bypass channel with over spill weir and pointing doors adjacent to Bourne Eau PS which operates when the River Glen infrequently floods (Figure 3.1b).

3.2.2 Acoustic imaging (DIDSON)

Dual frequency IDentification SONar (DIDSON 300m, Sound Metrics, USA. http://www.soundmetrics.com/) was used to collect data on predator-prey interactions at Bourne Eau PS. The high-resolution multi-beam sonar allows for the passive collection of natural information on predator and prey in both light and dark, and without the need for invasive monitoring. Additionally, the DIDSON can provide an accurate measurement (m) of the insonified window which provides calibration and standardisation fish shoal measurements.

The DIDSON was installed on a bottom-mounted 2m vertical wooden post via a SoundMetreics X2-rotator. The post was driven into the right-hand riverbank and provided a submerged depth of 0.5m (Figure 3.1b). Data and power cable was routed inside the compound building to a sonar command module and a laptop with remote internet connection (Panasonic TF-19). The DIDSON was operated in high frequency mode (1.8 MHz; 96 0.3°x14° beams, 512 bins) with a window length of 10m (starting 0.42m from point of transducer) at 8 frames s^{-1} (fps), receiver gain at default and focus set to auto to account for changes in fish distance from the transducer.

The position of the DIDSON was aligned with the adjacent bank wall and imaging of the weed screen was used to confirm the correct underwater orientation of the sonar. This provided optimal data collection for this study, where imaging predator-prey interactions in front of the weed screen was a priority. Continuous observations were captured between October and December 2017. Data collection was only interrupted to maintain equipment. Files were time and date stamped (hh:mm:ss – d/m/y) and stored in 10-minute intervals. All software inputs were performed in SoundMetrics software (DIDSON V5.26.24).

3.2.3 Data processing

This study uses a modified methodology first proposed in Price *et al.* (2013). To identify the temporal periodicities in predator-prey interactions, a 7-day sample period at the start of each month was selected to enable a representation of the full study duration (e.g., 7 days per sample month). Of this, the data were further sub-sampled into four two-hour discrete sample periods over a 24-hour day.

These were dawn, daytime, dusk and night-time. Day- and night-time samples were taken at midday and midnight respectively (11:30am – 13:30pm, 11:30pm – 01:30am). The crepuscular sample period was equal to civil twilight ± 1h to best capture fish behaviour around sunrise and sunset when fish were most likely to be active. The overall duration of sonar footage analysed included 168 hours of DIDSON images. The recorded files provided by the sonar were processed minute-for-minute by an experienced reviewer using an adjusted playback speed between 5x and 10x. This allowed quick backward and forward navigation and accounted for differences in fish activity.

3.2.3.1 Predation Related Event (PRE)

Verifying prey consumption in sonar images was difficult, ambiguous and unreliable and instead predator presence in the sonar window was used to determine if a Predation Related Event (PRE) had occurred, which allowed for discrete predation events to be used as sample points for detailed analysis. Both predator and prey needed to be present in the insonified window for a PRE to be recorded. The duration of a PRE was recorded from the first point when a predator entered the sonar window until the end point of prey shoal response after a predator left the sonar window. To prevent over-recording of PREs in scenarios where predators briefly left the insonified window, the recording of a PRE was continued if a predator re-entered the sonar window within 30s. A total of 168 hours of DIDSON footage was analysed in which 147 PREs were identified. Based on initial exploratory observations, eight measures of predators and nine measures of prey were selected to include in the analysis (Table 3.1).

3.2.4 Measurements of predators

The species and number of predators present in the PRE was recorded. Predator size (±1 cm) was measured within the DIDSON software using the fish measurement tool. To quantify differences between attacked and unattacked prey, the attack status of the predator was recorded including number of attacks and attack duration. Diving behaviour is indicative of foraging in cormorants (White *et al.,* 2008). A predator attack was determined by rapid acceleration of a predator towards a prey shoal. Acceleration and deceleration of both predator and prey was associated with frame-by-frame differences in body shape and measurable change in spatial position of individuals in the insonified window. In all instances it was possible to visually confirm predator species and attack status from body shape, swimming characteristics and dynamics of predator attack behaviour in sonar images, of which two predator species were identified; northern pike (med, IQR: 118, 17.25 cm) and great cormorant (med, IQR: 84, 18.5 cm) (Figure 3.2).

Table 3.1 A list of metrics and descriptive terms used to describe predator-prey interactions.

Term	Description	Data type
Duration of PRE	Duration of a PRE from the point when a predator enters the sonar window until the end point of prey shoal response.	Continuous
Predator metrics taken during a single PRE		
Number of predators present	Number of predators present	Discrete
Predator species	(1) Great Cormorant (*Phalacrocorax carbo*) (2) Northern pike (*Esox lucius*).	Discrete, categorical
Predator size	Length of predator (cm)	Continuous
Predator attack	(0) no attack (1) attack.	Discrete, categorical
Number of attacks	Number of predator attacks	Discrete
Duration of attack	Duration of predator attack	Continuous
Time until attack	Time from when predator enters sonar window until first attack	Continuous
Predator foraging rate	Number of attacks per minute (*n attacks·minute*$^{-1}$)	Continuous
Prey shoal metrics taken during a single PRE		
Prey shoal size	Number of prey in a shoal (ImageJ)	Discrete
Prey shoal area	Area in m^2 of a prey shoal (ImageJ)	Continuous
Prey shoal density	Prey shoal size divided by prey shoal area ($n \cdot m^2$)	Continuous
Prey shoal density response	Extent of prey density response to a predator (change in density pre- and post-behavioural reaction)	Continuous
Prey shoal areal response	Extent of prey areal response of a prey shoal to predator (change in area pre- and post-behavioural reaction)	Continuous
Prey shoal behavioural response to predator	(0) no response (1) flee (2) flee (into weed screen) (3) flee (away from weed screen) (4) avoid (5) avoid (into weed screen) (6) avoid (away from weed screen)	Discrete, categorical
Duration of prey shoal behavioural response	Duration of a behavioural response	Continuous
Number of prey shoal behavioural responses	Number of behavioural responses	Discrete
Weed screen switching rate	Number of times prey switch sides at the weed screen (*n switches·minute*$^{-1}$)	Continuous

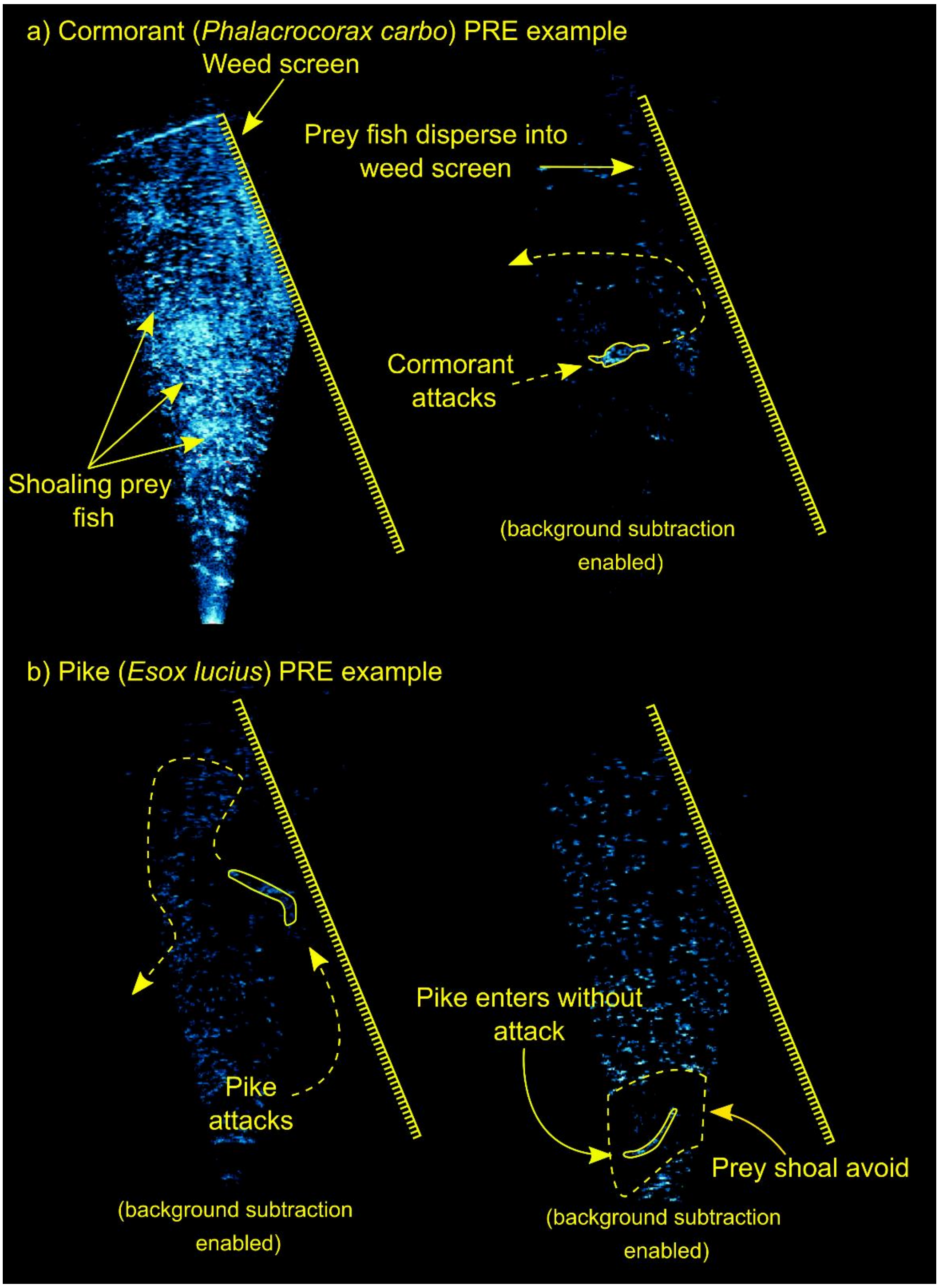


Figure 3.2 A schematic representation of a) cormorant PRE showing prey shoal and cormorant attack, b) pike PRE showing an attack, and no attack with prey avoidance.

Attack duration was based on the rate of predator trajectory towards prey fish, with attacks being timed from the point of rapid acceleration until deceleration and interaction with prey shoal. As PREs typically met or exceeded one minute in length, the foraging rate of predators was defined by the number of attacks per minute during a single PRE.

3.2.5 Measurements of prey

A prey shoal was defined by an aggregation of fish which included synchronised movements and close inter-individual distances (e.g., one body length apart) within the insonified window. Prey response to predators was evident by a rapid change in prey trajectory and areal response. The end point of prey response was considered when prey had aggregated and slowed movements relative to previous swimming behaviour prior to predator interaction. To provide a quantification of anti-predator prey responses, sonar images from discrete PREs required preparation. Firstly, a background subtraction algorithm was applied in DIDSON software to discard static background noise and acoustic detections smaller than 5 cm^2 (i.e., waterborne particles). Secondly, the image parameters intensity and threshold were adjusted to 25 and 10 respectively. This process also removed the static weed screen of the pumping station from the image to facilitate frame analysis. To measure prey shoal size, area, density and to detect the areal and density response of prey to predators, two frames for every PRE were prepared for export to JPEG images. These were (1) 1s prior to the PRE (PRE_1) and (2) at the onset of prey reaction to predator (PRE_2) (e.g., when individual aggregations in the prey shoal rapidly change trajectories).

Exported frames were processed in ImageJ (Schneider *et al.,* 2012). DIDSON images were first converted to 8-bit JPEGS and image threshold set to 30/255 to allow for contrast between foreground and background fish shapes. To ensure accurate shoal measurements a fixed length (2 m) was acquired from the DIDSON images and calibrated to 169 ± 1 pixels. Once calibrated, the region of interest (ROI) was set to the boundary of the prey shoal and measured using the area measurement tool. All fish present in the ROI were counted using the particle counting tool to provide a measurement of shoal size. Density was then calculated as shoal size divided by area. The difference in areal and density measurements between PRE_1 and PRE_2 was used to determine the extent of prey areal and density response to predators.

3.2.5.1 Behaviour of prey at the weed screen

The extent to which prey switch sides at the weed screen was measured to determine the rate at which prey fish interact with the weed screen structure for refuge during predator interactions. Switching sides was determined by prey schooling and collectively crossing the centre line of the weed screen from left to right, or right to left. For comparison with the foraging rate of predators, the weed screen switching rate was defined as the number of switches per minute during a single PRE. To enhance this level of analysis, the behavioural response of prey fish, including the direction of school movement towards and away from the weed screen was measured using seven discrete behavioural identifiers (Table 3.1).

The behavioural categories were chosen to reduce labour intensive data processing and best represent the clearest observation of different prey behaviours. Prey schools were defined as fleeing if there was an obvious rapid change in shoals trajectory (e.g., the shoal ‘bursts’) away from a predator attack. Conversely, fish were defined as avoiding predators if fish aggregated and avoided the predator by swimming away slowly without rapid acceleration or burst activity. When there was no obvious directionality to prey movements (e.g., when a shoal bursts), behaviour was recorded as (0) no response, (1) flee or (4) avoid. When directional movement (schooling) was observed this was categorised as (2) flee (into weed screen), (3) flee (away from weed screen), (5) avoid (into weed screen), (6) avoid (away from weed screen). Because PREs could include more than one predator interaction (e.g., multiple attacks), changes in prey behaviour were recorded and the duration of each behaviour was measured from the start of the reaction until the end of the reaction. Because of the unbalanced distributions of behavioural responses, it was not possible to determine the relationship between the directional response recorded and the weed screen switch rate.

3.2.6 Statistical methods

The data derived from predator-prey interactions at Bourne Eau PS was analysed using R version 4.0.2 (R Core Team, 2022) in RStudio 1.4.11 (RStudio Team, 2022). All statistical figures presented in the results were created using R packages ‘ggplot2’, ‘ggpubr’, ‘gridextra’ and ‘cowplot’. Data was checked for normality of variance using Shapiro-Wilk normality tests (R function ‘shapiro.test‘). The distribution of data from predator-prey interactions were not normally distributed and non-parametric testing was used throughout with descriptive values presented as medians (IQR). For statistical comparison between variables, a combination of Wilcox rank sum tests (R function ‘wilcox.test’) and Kruskal-Wallis rank sum tests (R function ‘kruskal.test’) was used. Post-hoc testing was performed using Dunn’s test (R function ‘dunn.test’ in package ‘dunn.test’) to determine which levels of the independent variable differed from each other across the categorically variable. Proportional differences between species-specific predation factors were compared using a test of equal proportions (R function ‘prop.test’). Correlation testing was performed using Spearman's rank correlation (R function ‘cor.test’).

To investigate if PRE duration and foraging rate (continuous independent variables) and predator species (discrete independent variables) influenced weed screen switching rate (continuous dependant variable) a pair of Generalized Linear Models (GLMs) were constructed (R function ‘glm’). Given that the data were nonnormal (right-skewed) and nonnegative, the model was first fitted using Gamma distribution. However, this was dropped in favour of using Gaussian distribution and a log link function, which in this application reduced the Akaike's Information Criterion (AIC) and provided more accurate predicted values (compared to fitted values), than a Gamma model. Additionally, a combination of a concern for multicollinearity and unbalanced variance across the independent variables led to the decision to create two independent univariate models with an interaction term for species, as opposed to a global model containing all terms and interactions. To remove zeros (n = 5) and allow the log-linked models to run, 1×10^{-9} was added to the dependant variable weed screen switching rate.

3.3 Results

3.3.1 Temporal dynamics and predator behaviour

Pike were the most frequent predator observed, making up 81% of PREs. There was a positive linear trend in the count of pike PREs between October and December 2017 (Figure 3.3.1). There was no clear trend in cormorant PREs, which were highest in October and December but lowest in November (Figure 3.3.2). The duration of pike PREs was significantly longer (med, IQR: 85, 125 s^{-1}) than cormorant PREs (med, IQR: 35, 51 s^{-1}) (Wilcox rank-sum: $W = 847$, $p = <0.001$), and showed a positive linear trend between October and December where increased PRE duration was associated with night-time pike presence (Figure 3.3.1c). Differences in pike PRE duration were then attributable to sample period (Kruskal-wallis: $\chi^2{}_2 = 14.16$ $p = <0.001$) and attack dynamics ($W = 1946$, $p = 0.04$) as pike events were shorter when foraging at dawn and dusk, and longest during night-time with no observed attacks (Dunn’s test: $Z = -3.6$, $p = <0.001$). Conversely, cormorant PRE duration was longest at dusk (51 s^{-1}), but overall there was no significant effect of sample period ($\chi^2{}_2 = 0.59$ $p = 0.74$).

A total of 98 behaviours defined as attacks were captured throughout the duration of the study; 32% of pike PREs featured predator attacks (48 attacks in 120 PREs), from which the foraging rate was highest during the crepuscular periods (med, IQR: 1.6, 2.1 attack·min^{-1}) with no daytime and night-time foraging observed ($\chi^2{}_2 = 13.66$ p = 0.003; Table 3.2). In contrast, 100% of cormorant PREs featured attacks (50 attacks in 27 PREs), for which the foraging rate (med, IQR: 3.3, 1.7 attack·min^{-1}) was significantly higher than pike ($W = 2916$, $p = <0.001$).

Cormorants, like pike, followed a crepuscular foraging dynamic, except foraging was maximised at dusk, and daytime, but no night-time foraging was observed (Table 3.2). The foraging rate of both predator species was maintained throughout the duration of the study (Spearmans rank: pike $r_s = -0.35$, $p = 0.76$; cormorant: $r_s = 0.06$, $p = 0.76$), although the increase in pike PREs without attacks would suggest that foraging was reduced from October to December.

Shoal density was significantly higher in cormorant PREs ($W = 1672$, $p = 0.012$). Density-dependant predation was evidenced in pike PREs where pike attacked shoals that were denser than unattacked shoals ($W = 548$, $p = <0.001$). It was not possible to measure time until attack in cormorant PREs as their diving behaviour resulted in recording of instantaneous attack from the point of entry into the insonified window. Similarly, there was little variation in time until attack in pike PREs (med, IQR, 0, 28 s^{-1}), except in instances where pike attacked after a period of 'sit and wait' (max = 294 s^{-1}) (Table 3.2). However, the duration of attacks by cormorants (med, IQR: 3, 2 s^{-1}) was significantly longer than pike (med, IQR: 2, 2 s^{-1}) ($W = 1599$, $p = 0.007$).

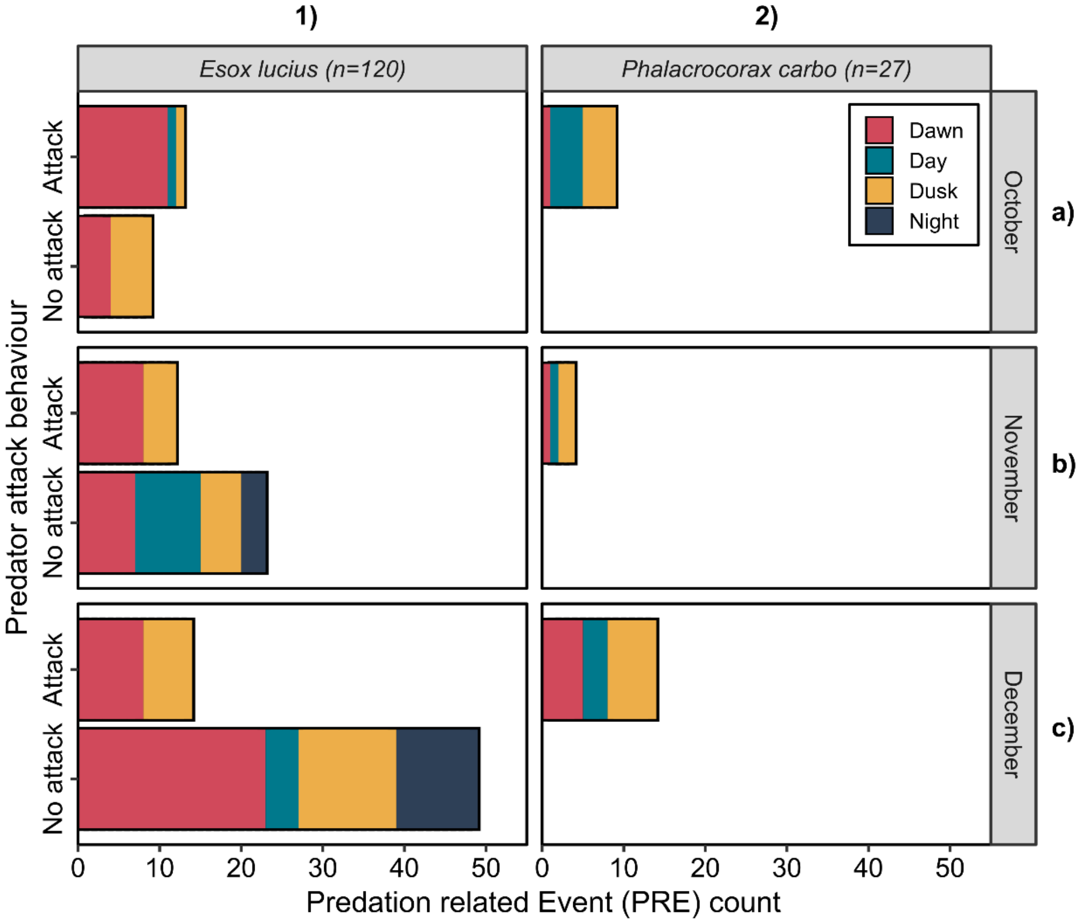


Figure 3.3 The overall number of PREs observed using DIDSON between October and December 2017 for 1) *Esox Lucius* and 2) *Phalacrocorax carbo* PREs. Counts are secondarily facetted month (a - c) and the observed PRE count is given by sample period (coloured bars) and whether a predator attack was recorded during the PRE.

Table 3.2 Attack dynamics of two predator species observed in DIDSON video.

	Predator species									
	Northern Pike *(Esox lucius)*					Cormorant *(Phalacrocorax carbo)*				
	Sample period									
	Dawn	Day	Dusk	Night	**All**	Dawn	Day	Dusk	Night	**All**
Attack (n)										
Total	18	12	18	0	**48**	16	6	28	0	**50**
Attack duration (s^{-1})										
Median	3	4	1	0	**2**	3	3	3	0	**3**
Min	0	4	1	0	0	1	0	1	0	0
Max	15	4	3	0	15	8	6	13	0	13
IQR	3	0	1	0	2	3	0.5	3	0	2
Time until attack (s^{-1})										
Median	1	0	27	0	**0**	0	0	0	0	**0**
Min	0	0	0	0	0	0	0	0	0	0
Max	243	0	294	0	294	198	0	0	0	198
IQR	21.5	0	41	0	28	0	0	0	0	0
Foraging rate (attack min^{-1})*****										
Median	1.6	1.6	1.6	0	**1.6**	1.6	2.5	3.3	0	**3.3**
Min	1.6	1.6	1.6	0	0	1.6	1.6	1.6	0	1.6
Max	5	1.6	5	0	5	5	8.3	8.3	0	8.3
IQR	1.7	2.1	2.1	0	2.1	0.7	1.1	1.1	0	1.7
Predator Size (mm)										
Median	118	124	112	121	**118**	98	85	79	0	**84**
Min	58	73	75	102	58	72	69	65	0	5
Max	132	153	140	131	153	110	109	120	0	120
IQR	20	29	21	14	18	17	12	12.5	0	8.5

****** foraging rate calculated without inclusion of unattacked shoals*

3.3.2 Prey fish behaviour

3.3.2.1 Shoal size, areal and density response of prey

Overall, prey fish aggregated and used shoaling as their primary anti-predator response. From the frames used for analysis, an estimated 33000 prey fish were counted (using a particle counting tool; ImageJ). There was no significant difference in shoal size between sample months ($\chi^{2}{}_{2} = 4.46$ $p = 0.1$). Although, prey shoal size exhibited a strong diel trend where individual counts were lowest at day and night and highest during the crepuscular period (dawn and dusk), which coincided with the maximal predator activity ($\chi^{2}{}_{2} = 46.69$, $p = <0.001$).

Concerning the measurable areal response of prey fish to predator interactions, prey responded to pike attacks by rapidly forming a tighter shoal (med, IQR Δ area = -2.82, 2.64 m^2) with a significantly smaller response recorded for unattacked shoals (med, IQR Δ area = -0.63, 2.28 m^2) ($W = 1403$, $p = <0.001$; Figure 3.4a). Similarly, pike attacks resulted in shoals becoming denser (med, IQR Δ density = 2.4, 13.6) although this was not significantly different to unattacked shoals (med, IQR Δ density = 1.00, 7.12) ($W = 792$, $p = 0.30$; Figure 3.4b). Likewise, although not statistically different, the areal response to cormorant attacks was smaller than to pike (med, IQR Δ area = -1.94, 2.79 m^2) ($W = 510$, $p = 0.16$; Figure 3.4a). The density response was particularly interesting as prey shoals lost individuals when attacked by cormorants (med, IQR Δ density = -2.3, 19.2), which was significantly different to the density response of prey when attacked by pike ($W = 290$, $p = 0.04$; Figure 3.4b).

3.3.2.2 Directional schooling behaviour and refuge use

In the presence of predators, observations of uni-directional prey fish movements from the river into the pumping station through the weed screen and vice versa (weed screen switching) confirmed the importance of this structure and provided a basis for inferential prey refuge use. Weed screen switching rate by prey fish was not significantly different when attacked by either cormorants (med, IQR: 3.3, 3.4 switches$\cdot$min^{-1}) or pike (med, IQR: 3.3, 3.8 switches$\cdot$min^{-1}) ($W = 277$, $p = 0.77$; Figure 3.4c). Although, foraging rate was a significant predictor of weed screen switching rate when attacked by cormorants ($\text{GLM}_{\text{(intercept)}} = 0.54 \pm 0.26$, $p = 0.02$; r_s=0.78 p =<0.001), but no significant relationship was found when attacked by pike ($\text{GLM}_{\text{(foraging\_rate + foraging\_rate:}E\_lucius\text{)}} = 0.21 \pm 0.12$, $p = 0.79$; $r_s = 0.26$, $p = 0.29$; Figure 3.5a). PRE duration was then a significant predictor of weed screen switching rate when attacked by cormorants ($\text{GLM}_{\text{(interecept)}} = 0.88 \pm 0.21$, $p = <0.001$), and was close to significance when attacked by pike ($\text{GLM}_{\text{(pre\_dur + pre\_dur:E\_lucius)}} = 0.018 \pm 0.004$, $p = 0.06$).

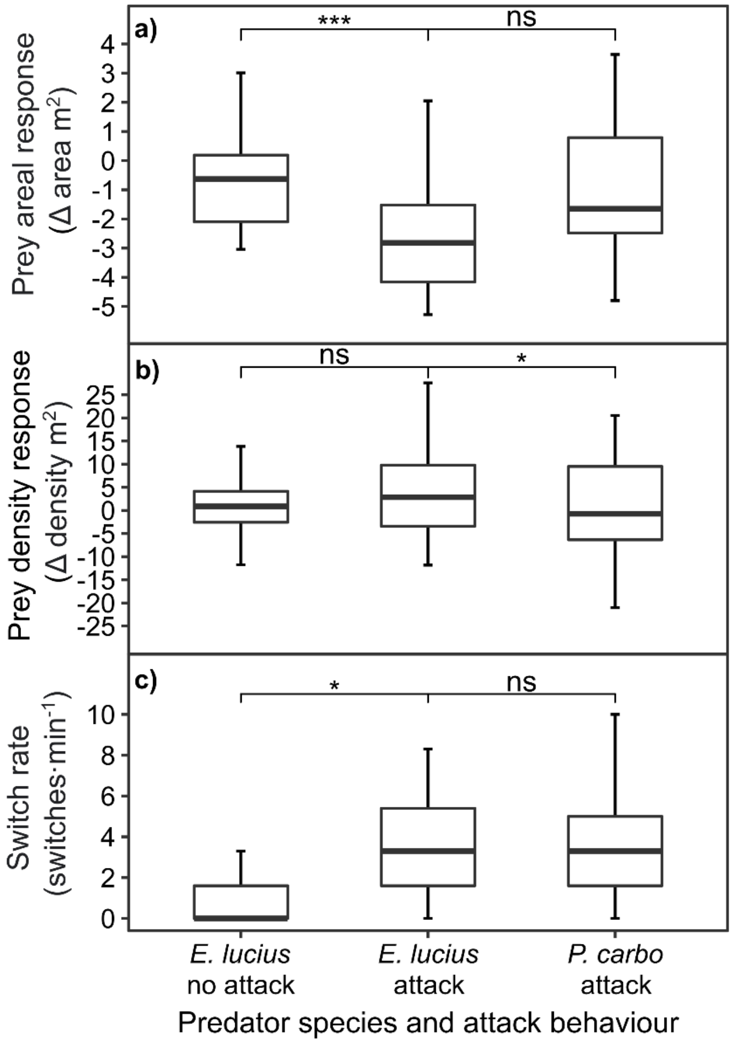


Figure 3.4 The response of prey fish to predator interactions given by a) prey areal response b) prey density response and c) the weed screen switching rate. Plots represent measured prey responses to the *first* interaction in a PRE and does not include repeat attack behaviours. Error bars represent quartile 1 to the smallest non-outlier and quartile 3 to the largest non-outlier. Significance indicted by Wilcoxon rank sum (ns = not significant, * = P ≤ 0.05, ** = P ≤ 0.01, *** = P ≤ 0.001, ***** = P ≤ 0.0001).

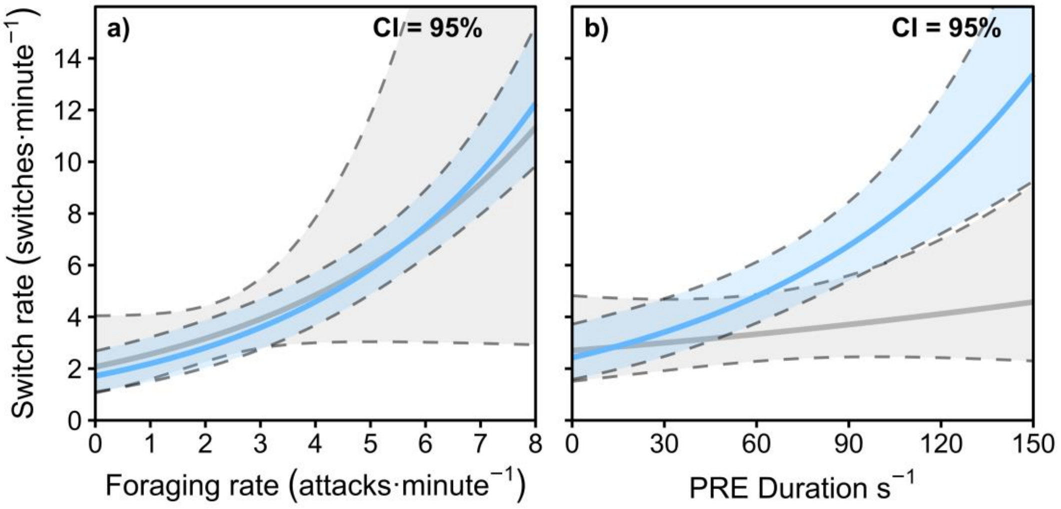


Figure 3.5 The predicted effect of a) foraging rate of predators and b) PRE duration on the weed screen switching rate of prey fish. Guassian (link = log) lines plotted by a minimal GLM including predator species interaction *((a) switch_rate ~ pre_dur*sp_pred; (b): switch_rate ~ foraging_rate*sp_pred).* 95% confidence intervals represented by shaded envelope surrounding smoothed line (dotted lines upper and lower bounds). Blue line = cormorants, grey line = pike.

Overall, the correlation between PRE duration and weed screen switching rate was stronger in cormorant PREs ($r_s = 0.58$, $p = 0.001$) compared to pike PREs ($r_s = 0.48$, $p = 0.03$) (Figure 3.5b), which would suggest that when accounting for overall shorter duration of cormorant PREs, prey fish used the pumping station as refuge more than in pike PREs. Additionally, there was a significant difference in the weed screen switching rate between attacked and unattacked (med, IQR: 0.8, 2.87 switches·min^{-1}) shoals in pike PREs ($W = 290$ $p = 0.004$; Figure 3.4c).

Prey shoal behaviour at the weed screen was further described by movement in response to predator interactions; a total of 223 of which were observed with 48% fleeing and 52% avoiding (Table 3.3; Figure 3.6). The difference between response duration and response category was significant ($\chi^2{}_6 = 116.75$, $p = <0.001$) where flee responses were shorter (med, IQR: 11, 18.5s^{-1}) in duration than avoid responses (med, IQR: 90, 72s^{-1}) ($Z = 6.49$, $p = <0.001$) (Table 3.3). Prey fish mainly responded to cormorant attacks by fleeing towards the weed screen (56%) (17% flee away, 25% flee, 2% no response) (test of equal proportions: $\chi^2{}_2 = 17.48$, $p = <0.001$; Figure 3.6b). Conversely, prey fish fled away from the weed screen when attacked by pike (45%) (33% flee away, 22% flee) ($\chi^2{}_2 = 6.67$, $p = 0.03$; Figure 3.6a). Unattacked shoals did not flee, and the majority of their movements were described as avoiding (63%) with limited directionality towards (7%) or away from the weed screen (14%) (16% no response) ($\chi^2{}_2 = 125.4$, $p = <0.001$).

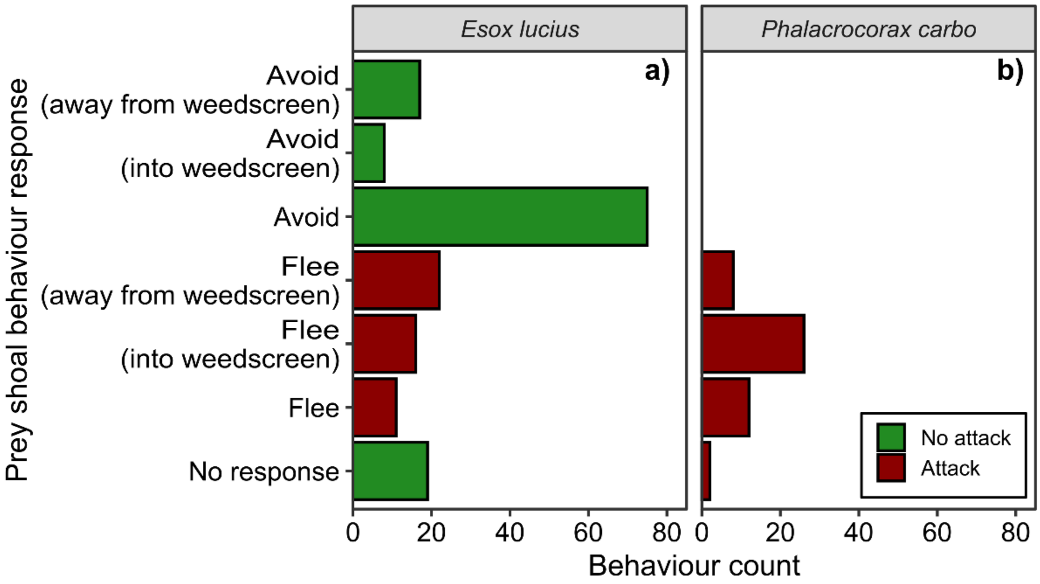


Figure 3.6 Count of observed prey behavioural responses resulting from interactions with a) *Esox lucius* and b) *Phalacrocorax carbo* given by attack status. Plot represents all behavioural responses recorded during a PRE. Note: All *Phalacrocorax carbo* PREs were considered to be attacks.

Table 3.3 Number of behavioural responses by prey shoals in observed PREs.

	Shoal behaviour						
	No response	Flee	Flee (into weed screen)	Flee (away from weed	Avoid	Avoid (into weed screen)	Avoid (away from weed
	Sample period (n)						
Total	25	20	43	30	79	9	17
Dawn	3	10	13	20	45	4	5
Day	7	2	10	2	5	2	4
Dusk	8	8	19	8	24	3	8
Night	7	0	1	0	5	0	0
	Behaviour duration (s^{-1})						
Median	0	11	12	15	90	66	75
Min	0	0	3	2	11	8	15
Max	312	34	66	51	478	181	229
IQR	0	18.5	10	114	72	64	69

3.4 Discussion

The adapted sonar methodology (Price *et al.,* 2013) provided a suitable framework for non-invasively quantifying predator prey interactions, which was enhanced by identifying multiple prey response effects with a specific, and novel focus in the context of an anthropogenic structure (pumping station) in a heavily modified lowland river. The results, gathered with multi-beam sonar (DIDSON), demonstrated that the lowland prey fish community experience temporally dynamic species-specific predation risks from two dissimilar predators (i.e., aquatic vs aerial), pike and cormorant. The overall predation rates presented in this study should be considered minimum estimates; the real-world predation rate is presumably higher since the PREs were subsampled from four discrete time periods, and data was limited by the width of the DIDSON field-of-view. Non-consumptive predation effects were evidenced by quantified changes to shoal structure (density, area) and both shoaling (group aggregation) and schooling (coordinated directional movement), including diurnal migrations and use of a pumping station intake as refuge, were the primary ways in which prey managed predation risk. Although the use of refuge habitat to manage predation is well established in the literature (Berryman & Hawkins, 2006), these findings provide the first quantified evidence for the use of an anthropogenic structure as prey refuge in lowland rivers (but see Chester & Robson, 2013). In turn, this study proposes important considerations for how FRM, including RMMs on lowland rivers can influence the ecological interactions between piscivorous predators and their prey.

Three winter months were chosen for the study period as this was after RMMs (seasonal macrophyte removal) were performed. Correspondingly, the study area was associated with heavily degraded riverbanks and depleted instream habitat, which created a high risk from predators. The results show no temporal (monthly) relationship in the rate of PREs (with attacks) for either predator, although there was a positive linear trend in the number of pike PREs (without attack) during winter. Measuring avian predation on fish is challenging and potential bird encounters (i.e., did not enter water) were not recorded, whereas instream predator presence was. Additionally, decreasing water temperature promotes more sessile behaviours in pike (Kobler *et al.,* 2008) and can reduce frequency and speed of attacks (Ohlund *et al.,* 2015), which would explain why pike PREs increased throughout winter, but the number of attacks did not. Why cormorant PREs were reduced in November is unclear; the prey fish were still numerous and pike predation was not reduced. Amongst the possible reasons then include deterrence from agricultural practices (Lemmens *et al.,* 2016), turbidity conditions (Dodrill *et al.,* 2016) and movement to alternative foraging sites (Gremillet & Wilson, 1999).

The diel distribution of both predator and prey fish within four light periods (dawn, day, dusk, night) was analysed. Piscivorous birds rely on sight to hunt and require good visibility to locate prey fish (Becker *et al.,* 2014), so it was not surprising that cormorant predation in this study included daytime hunting. However, whilst overall pike presence was diurnal, there was no evidence for daytime foraging by pike, as seen elsewhere (Jacobsen & Perrow, 1998). The daytime foraging differences possibly result from contrasting avian (pursuit-dive) and instream (sit and wait) hunting strategies of cormorant and pike. Maximal activity and interactions of both predators and prey fish occurred during the transitional (crepuscular) period; similar to what has been described elsewhere for cormorants (Russel *et al.,* 2003; White *et al.,* 2008), pike (Kobler *et al.,* 2008) and prey fish (Helfman, 1986; Campanella *et al.,* 2019). During this low-light period, predators may have a visual advantage over prey (“twighlight hypothesis” Pitcher & Turner, 1986) because the ability for prey to detect predators is lowered. Thus, the crepuscular period made for a favourable hunting time in this study.

The temporal recurrence of this diel pattern suggests that prey fish in this lowland system experience long periods of predator risk. It is likely that prey have learnt to assess this temporal predation risk (Bosiger *et al.,* 2012) and diel activity of prey fish in this study was timed to avoid maximal predator activity (e.g., Ory *et al.,* 2014). Accordingly, prey fish shoal size at the pumping station varied within the diel period, ranging from small (<30 individuals) dispersed and infrequent shoals at night, to medium (≤ 200 individuals) shoals during the daytime and large (> 300 individuals) dense shoals during the crepuscular period. The reduced fish counts during the day certainly suggests daytime cormorant predation has a major influence on prey activity (Bosiger & McCormick, 2014). In brief, predictable predation risk stimulated prey to seek refuge at the pumping station during the day, which was associated with recurring diel movement of prey towards reduced-risk refuge at dawn, and movement towards high-risk foraging sites at dusk (e.g., Orrock *et al.,* 2013). Therefore, diurnal movement behaviour was carefully timed to facilitate trade-offs between foraging out of refuge and predator evasion (Fu *et al.,* 2015), with prey presumably foraging nocturnally (Metcalfe *et al.,* 1999). Elsewhere, this has been reported for lowland fish including brown trout (*Salmo trutta*) (Conallin *et al.,* 2014), but observations in multi-species communities like the studied here, are scarce.

Recordings of singular predators throughout this study suggest that predator activity, rather than predator abundance, influenced the diel behavioural pattern of prey. The results here show that cormorants were very active hunters with at least 50 attacks recorded in 125 hours of DIDSON footage (dawn, day, dusk), although this was not comparable to other studies due to methodological disparities. Despite having over 4x as many PREs as cormorants, there was 48 attacks by pike during the same period, which was similar to pike attack rates recorded elsewhere (Turesson & Bronmark, 2004). Accordingly, when hunting, the foraging rate of cormorants was twice that of pike. This is in line with previous suggestions that cormorants have a high foraging rate, in part because of limited underwater vision and a tendency for multiple short-distance pursuits once underwater (White *et al.,* 2007).

On the other hand, pike in this constrained lowland setting were frequently observed to ‘sit and wait’, especially at night where they selected nocturnal resting sites close to the pumping station. This was followed by morning periods of active pursuit and attack on nocturnal prey fish returning from the upstream river, which was exemplified by maximal foraging at dawn. Conversely, cormorant foraging was maximised at dusk; probably because they were able to exploit high densities of prey leaving shelter in contrasting light. Indeed, the results show that whilst predation by both species was density-dependant, cormorants selected denser shoals than pike for hunting, similar to other studies (e.g., Lemmens *et al.,* 2016). Given, pike consistently attacked denser shoals than those where attacks did not occur, contrasting previous findings which found prey density was less important for determining when pike attacks occur (Turesson & Bronmark, 2004). These finding suggests that not only did predator shape prey behaviour, but the opposite is also true.

The extent of prey shoal response to both predator presence and attacks included changes to area and density, which followed typical descriptions of shoal structure (Pitcher, 1986; but see Romenskyy *et al.,* 2020), and was accompanied by directional movement behaviours associated with refuge use. In encounters where pike did not attack, the primary anti-predator response was avoidance and shoal contraction, which was associated with small reduction to shoal area and marginal increases in density, but no apparent refuge use. The fact that prey were able to avoid pike without fleeing proposes some level of active risk assessment, and that pike presence may not be a threat alone (Ferrari *et al.,* 2010). Increased shoal density as an anti-predator strategy agrees with findings form others (e.g., Meuthen *et al.,* 2016), and the tendency for shoal density to increase when pike were present suggests a sit-and-wait strategy could invoke significant NCEs over time (Preisser *et al.,* 2007).

This study found significant differences in the way prey responded to dissimilar predator strategies. The initial shoal response to attacks by both predators was a ‘burst’ i.e., expansion from the point where the predator entered the shoal, followed by contraction. Prey shoals then responded to attacks from pike by fleeing and rapidly forming a smaller and denser shoal. Conversely, when attacked by cormorants, the areal response was reduced and the density response suggested shoals lost fish i.e., cormorant attacks had a more immediate negative impact on shoal structure. Multiple successive attacks (i.e., a high foraging rate) by cormorants was probably a combination of both predator behaviour (i.e., maximising number of attacks with limited dive duration) and prey behaviour (i.e., exploiting dense aggregations of prey) (e.g., Rieucau *et al.,* 2015). The fact that prey were able to aggregate faster under pike predation suggests that they were able to respond more predictably to cues from instream predators, whereas they were unable to prepare a robust shoal response to cormorants without information on distance or trajectory (Hemmi & Pfeil, 2010). This pattern closely follows the risk allocation hypothesis (Lima & Bednekoff, 1999) i.e., prey responded strongly to predators that are usually absent (Supekar & Gramapurohit, 2020).

Other studies have shown that structurally complex habitats reduce predation risk for prey (e.g., Ory *et al.,* 2014). Here, the weed screen used to protect the pumping station intake structure appeared to function as a refuge habitat and quantifying the weed screen switching rate provided evidence for species-specific predator-mediated habitat use (Mittelbach, 1986). During periods of high predator activity, the prey shoals increased the number of transitions between open water and refuge, i.e., inside the pumping station, behind the weed screen. When attacked by pike, prey fish fled but directional movement towards and away from the refuge was unbiased. But, when attacked by cormorants, prey fish primarily fled into refuge. Hence, prey fish were probably only protected from cormorants during the day when they could hide in the pumping station. Although there was no significant difference in refuge use when attacked by pike or cormorants. Indeed, the high proportion of flee response into refuge in cormorant events, but not pike events, combined with a significant GLM prediction for increased refuge use under cormorant predation, but not pike predation, suggests the pumping station intake was most important as a refuge from cormorant predation. Therefore, cormorants perhaps evoke stronger NCEs on this fish population than pike.

The reduced refuge use during pike predation may suggest prey are more habituated to this predator due to their persistence in shared space (Ferrari *et al.,* 2010). In turn, when prey occupy the transitionary zone between refuge and open water, it allows them to swim into cover when fleeing from predators (Fu *et al.,* 2015). Likewise, anti-predator decisions of prey in this study depended on the hunting mode used by their predator and suggest prey may not always use structured habitat for protection (Martin *et al.,* 2010). Shoaling thus appears to be more appropriate for managing pike predation, but may be ineffective for cormorant predation. These findings add real-world, non-experimental evidence to previous suggestions that enclosed and sheltered habitats are more important to protect prey from cormorants than pike (Lemmens *et al.,* 2016). Given, understanding this problem is confounded, in part, by the potential for multiple predator effects (MPE: Griffin *et al.,* 2013). In this study pike were more likely to concentrate and confine fish, resulting in evasive behaviour of prey and denser shoals, which may increase encounters with cormorants. On the other hand, unpredictable attacks by cormorants could overwhelm and distract prey, potentially increasing the success of ambush predators. Thus, these dissimilar predators can inadvertently facilitate each other's hunting success if the response of prey to one predator increases the risk to the other predator (Ford & Swearer, 2013; Palacios *et al.,* 2018).

3.4.1 Conclusions and implications

Human land use is recognised as a major threat to freshwater biodiversity in lowland rivers (Dudgeon *et al.,* 2006). Similarly, FRM infrastructure degrades freshwater ecosystems by removing essential fish habitat (Angelopoulos *et al.,* 2018). The findings in this paper highlight a previously unconsidered impact anthropogenic infrastructure on predator and prey ecology in lowland rivers with direct observation of predator prey interactions. The majority of studies which have aimed to determine the non-consumptive, ecological dynamics of predator and prey interactions have relied on studying isolated effects i.e., activity (Orrrock *et al.,* 2013) and foraging (Catano *et al.,* 2015), but this study is amongst the first to simultaneously quantify behaviour of predator and prey in an aquatic setting. Multi-beam sonar has proved to be an effective tool for generating this understanding by quantifying unprovoked behaviours and interactions of predators and prey in a real-world setting. The outcomes of this study highlight the need for land users implementing FRM practices and RMMs to include ecological considerations for river-resident fish.

The impact of anthropogenic practices that modify winter refuge for prey fish communities in lowland river ecosystems is arguably underappreciated. Suitable winter habitats are lacking, and fish in these heavily modified ecosystems have increasingly fewer places to evade predators. Whilst fish in healthy ecosystems move between refuges to avoid predators, prey fish in this modified lowland setting are confined to living with predators in hazardous habitats. The resulting effect demonstrated here is that prey fish were paradoxically dependant on hazardous anthropogenic structure for refuge, and lowland piscivores have learnt to exploit this, similar to that proposed by Smith *et al.* (2020). This refuge provided the greatest level of protection for prey, but it is likely that resource quality is low i.e., access to food, space and light (Donelan *et al.,* 2017), which could counterintuitively enhance NCEs of predators (Orrock *et al.,* 2013), potentially imposing individual (growth, foraging) and population level (reproduction) fitness costs. Additionally, the specific implication for the structure in this study is that fish may be exposed to hazardous water management strategies, i.e., pump start-up for flood protection purposes, which could remove thousands of fish from the upstream catchment.

With continuous anthropogenic growth the resulting pressures on ecological processes in lowland catchments are expected to increase. The future of lowland river rehabilitation for ecosystem enhancement and protection of river-resident fish should diverge from past practices which focus on physical modifications (e.g., restoring floodplains), and instead consider modifying RMMs so that ecological interactions can occur more naturally. Primarily, decreasing the length of maintained river stretches could provide prey with increased refuge habitat, in turn reducing predator concentrations (Baczyk *et al.,* 2018). Alternatively, providing artificial refuge in the form of enclosed cages with overhead cover appears to be a promising option for protecting lowland fish from cormorants, even in systems with multiple predators (Lemmens *et al.,* 2016). Whilst the findings from this study propose universal ecological considerations, which are expected to transfer to similar anthropogenic lowland rivers with seasonal FRM, they may not be directly transferable to all lowland river systems. The physical construct of lowland systems can vary considerably and whether FRM may in fact restrict prey to activity at anthropogenic structures thus requires further investigation. Development of pluriannual monitoring programs is required as the effect of inter-annual RMMs on lowland predator prey ecology is still unknown. Ultimately, this study is the first to establish the temporal rate of interactions between multiple predators, a prey fish community and anthropogenic refuge in a heavily modified lowland setting.

4 EXPERIMENTAL MANIPULATION TO DETERMINE HABITAT PREFERENCE OF ROACH (*RUTILUS RUTILUS*): UNDERSTANDING IF INTRODUCED ARTIFICIAL HABITAT CAN PROVIDE A SAFE ALTERNATIVE TO SHELTER IN HAZARDOUS ANTHROPOGENIC STRUCTURES

4.1 Introduction

Lowland rivers are essential ecosystems which support much of the world's freshwater fish diversity (Huckstorf *et al.,* 2008) and are critical for the day-to-day foraging and refuge movements and seasonal spawning migrations of river-resident fish (Oglecki *et al.,* 2021). Still, lowland rivers are threatened globally by anthropogenic land use activities (Dudgeon *et al.,* 2006), especially Flood Risk Management (FRM) during winter (Angelopoulos *et al.,* 2008). FRM strategies frequently require River Maintenance Measures (RMMs) (see review Baczyk *et al.,* 2018) including the installation and operation of hazardous anthropogenic water level management infrastructure (e.g., pumping stations) to regulate flow and water level. The resulting effect of RMMs is that channelization, dredging and the winter removal of riparian vegetation dramatically reduce the available habitat for river-resident fish. Habitat degradation is now considered a major cause of global biodiversity loss and requires restoration in freshwater ecosystems (Maxwell *et al.,* 2016; Cowan *et al.,* 2021).

The presence of physical habitat is fundamental for anti-predator behaviours used by prey, as shade allows for inconspicuousness whilst assessing predators (Helfman, 1981) and structures provided by submerged habitats limit predator access to prey fish (Ellner *et al.,* 2001; Nunes *et al.,* 2019). The ecological demand for suitable habitats may lead to river-resident fish in modified lowland rivers to occupy pumping stations for refuge from predators, i.e., pike (*Esox lucius*) and cormorant (*Phalacocorax carbo*), throughout winter (see Chester & Robson, 2013; Sousa *et al.,* 2019). These structures concentrate and confine fish, have poor resources for fish (i.e., space, food, light) and when pumps operate mortality risk is high (Rytwinski *et al.,* 2017). Attempts to reduce the risks associated with pumping stations have previously included physical and behavioural deterrents which reduce entrainment (Turnpenny & O'Keeffe, 2005), opening gravity drainage channels to restore passage of migratory fish (Baker *et al.,* 2021) and pump shutdown during diel movements of river-resident fish (Reckendorfer *et al.,* 2018), but these remediation measures fail to address predator-prey interactions. Cormorants are protected by the European Community Directive on the Conservation of Wild Birds (EEC/79/409) and therefore lethal methods are undesired for ecological management. Alternatively, cormorant predation at pumping stations could be managed by addressing habitat loss. Simply reducing RMMs would be ineffective for this purpose due to the requirement for physical structures during winter. Accordingly, the provision of suitable alternative refuge habitats that reduce vulnerability to predators (e.g., Orpwood *et al.,* 2010) could help mitigate the undesired occupation of hazardous anthropogenic structures by river-resident fish.

Ideally, ecological restoration should aim to re-establish natural processes to alleviate the impacts of aquatic habitat degradation (Cowan *et al.,* 2021). Except, restoration is challenging in lowland rivers as reintroduction of natural refuge features is prevented by anthropogenic activities (i.e., RMMs). Accordingly, the installation of artificial habitat has received increasing attention as an approach to mitigate ecological degradation (see reviews Cowan *et al.,* 2021; Watchorn *et al.,* 2022). artificial habitats, which in aquatic ecosystems include pipes and felled trees (Frehse *et al.,* 2021), caged rocks (Mercader *et al.,* 2019) and PVC structures with interstitial spaces (Baumann *et al.,* 2016) have wide application. For example, in Allen *et al.* (2014), artificial habitat was used to supplement degraded natural habitat and improve angling success in reservoirs. Similar work has shown artificial habitat increased the local abundance and biodiversity of fish in reservoirs (Frehse *et al.,* 2021). Elsewhere, Lemmens *et al.* (2016) suggested artificial habitat can facilitate the coexistence of lowland prey fish, such as rudd (*Scardinius erythrophthalmus*) and roach (*Rutilus rutilus*), with cormorants, in lakes and ponds which lacked natural predator refuge. So far, this work has been promising, but no study has yet explored the potential for artificial habitat restoration to be used as a safe alternative for lowland river-resident fish which shelter from predators in hazardous anthropogenic structures.

Currently a major problem with habitat restoration programmes is the tendency for artificial habitat installation to lack robust planning (Hale *et al.,* 2017) and accompanying monitoring (Lindenmayer *et al.,* 2017). Thus, their ecological functioning and relative fish occupation are often unknown. Fish use settlement cues (e.g., enclosed space & shade) to select habitats which maximise their fitness (i.e., adaptive habitat selection; Orians & Wittenberger, 1991). But maladaptive habitat preferences may occur in anthropised rivers with degraded habitat (Hale & Swearer, 2016). Paradoxically then, fish may be attracted to and prefer habitats where their fitness is reduced (i.e., ecological trap; Robertson & Hutto, 2006). This is true of pumping stations which in degraded lowland rivers offer shelter and winter predator refuge and thus have become attractive daytime habitat. Indeed, previous work has shown habitat restoration can, unfortunately, be a major cause of traps (Robertson *et al.,* 2013). Providing alternative artificial habitat should increase in-channel habitat heterogeneity and provide prey fish with predator refuge that is preferred to the PS. However, maladaptive habitat selection can limit perception of available habitat meaning fish may avoid restored habitats and poor habitat counterintuitively becomes even more attractive (i.e., a perceptual trap; Pattern & Kelly, 2010).

Generating a robust understanding of fish habitat selection behaviour whilst planning habitat restoration work is required to prevent restoration failures (Hale *et al.,* 2020). A major concern for the provision of artificial habitat for river-resident fish which occupy hazardous anthropogenic structures is ensuring artificial habitat is attractive. Elsewhere, Lemmens *et al.* (2016) demonstrated the importance of artificial habitat design, and found sheltered habitats were preferred by roach over unsheltered habitats. A further method to help ensure fish occupy artificial habitat would be to physically exclude fish from the poor habitat, although this must be performed with caution in the real-world as fish not attracted to artificial habitat would be highly vulnerable to predation during the day. Hazardous intakes are often permanently screened to prevent entry of protected migratory fish, such as European eel (*Anguilla Anguilla*; Turnpenny & O'Keeffe, 2005), but such methods are expensive and logistically challenging, and thus would not be recommended for river-resident fish unless necessary. Instead, it may be possible to temporarily exclude fish from hazardous intakes (e.g., a net across the entrance) provided artificial habitat occupancy initially increased and persisted once exclusion ceased, especially as this could be more cheaply, easily and quickly implemented in the real-world. Subsequently, in accordance with the framework presented in Hale *et al.* (2015), direct testing of fish habitat preference both with and without habitat management activities (i.e., physical exclusion) is required to determine if fish will occupy artificial habitat naturally in systems where ecological traps may occur.

Studying fish behaviour and artificial habitat installations in the natural environment is preferred, but is difficult to exclude confounding factors, especially when studying anthropogenic structures which may become operational. Accordingly, tank-based experiments are initially required to test fish habitat preferences and likelihood of artificial habitat success in a controlled environment and in the absence of predators, prior to a pilot study in the real-world and then full-scale restoration to provide safe alternative fish refuge. Using roach, a cyprinid ubiquitous to lowland rivers and lakes in Europe, and simulated habitat designs, the overall aim of this study was to quantify habitat preference between open water, a simulated pumping station and artificial habitat, once provided. This was achieved by manipulating habitat choice and measuring habitat preference of a fish shoal over four experimental interventions. Roach are described as nocturnal (Fu et al., 2015); maximal movement activity occurs during the crepuscular period (Heermann & Borcherding, 2006) and feeding during the night (Metcalfe et al., 1999*)* Thus, the main hypothesis of this study were evaluated in consideration of daytime habitat use, which were (i) roach will prefer simulated pumping station over open water, (ii) when artificial habitat is introduced roach will prefer artificial habitat over pumping station and open water (iii) when entry to simulated pumping station is prevented roach will prefer artificial habitat over open water, (iv) when the pumping station is provided again after a period of exclusion roach will prefer artificial habitat over pumping station and open water, and (v) roach will prefer sheltered artificial habitat over unsheltered artificial habitat. The findings from this study are important to further our understanding of river-resident fish habitat selection and improve the success of artificial habitat installation in degraded lowland rivers with hazardous intakes.

4.2 Materials and methods

4.2.1 Fish collection and housing

A total of 186 (mortality = 14) wild roach (mean fork length ± SD; 116 ± 12cm) were caught (rod and line) from a lake (Lat: 53.716473N Long:-0.555654W) with known cormorant predation pressure on 16 and 29 September 2019. Captured roach were transported to the experimental facility (Environment Agency, Calverton Fish Farm, England) in two aerated (O^2 0.1L min^{-1}) transportation tanks (200L) pre-dosed with Virkon (1g), Vidalife (20ml) and Protex (2ml). Upon arrival at the experimental facility, roach were first treated for external parasites in a partially salinated (0.1% salinity) water bath before being transferred to a sheltered holding tank supplied (in parallel) with biologically filtered ground water (temperature = 9.8 ± 0.3 °C). All roach received a 14-day acclimation period (no feeding) with no human interaction to allow recovery from capture and transportation.

4.2.2 Experimental design

The experimental trials were conducted in six ~780L gravity drained (0.1L s^{-1} inflow and 4% gradient) opaque fiberglass tanks (2800 $_{x}$ 600 $_{x}$ 440mm, length $_{x}$ width $_{x}$ height), which were again supplied (in parallel) with biologically filtered ground water and were divided into three compartments using opaque Perspex dividers (Figure 4.1a). Two compartments at each end of the tank (600 x 600mm) were simulated habitats and the centre compartment (1600 x 600mm) was open water, and thus simulated a lowland river where fish could swim between a pumping station and adjacent artificial habitat. The bottom of the tanks was covered with self-adhesive white film to provide maximum contrast between fish shapes and the background in video images. Photoperiod was controlled with a 25W 100cm LED unit (NiCrew N13274B) above each tank with a 30-minute transition during the crepuscular period (8:16h L:D; 06:30 – 15:30).

4.2.2.1 Simulated habitat designs

To determine roach habitat preference, three habitat designs were simulated, i.e., a pumping station, a reed bed (unsheltered; treatment A) and a sheltered reed bed (treatment B). To simulate a pumping station, the habitat compartment was covered and a Perspex panel with 20mm bars and 50mm apertures was placed at the entrance to the compartment to simulate a weed screen (Figure 4.1b, right). This could be exchanged with an opaque Perspex screen to prevent access during intervention two. The simulated reed bed (artificial habitat) was constructed using a light-gauge steel mesh (50mm aperture) secured to a plywood board (600 x 600mm) and approximately 100 cable ties (10 x 400mm) hung vertically from the mesh. For treatment A (unsheltered), a large aperture (500x500mm) was cut in the plywood board (Figure 4.1b, left), which conversely provided the cover in treatment B (sheltered).

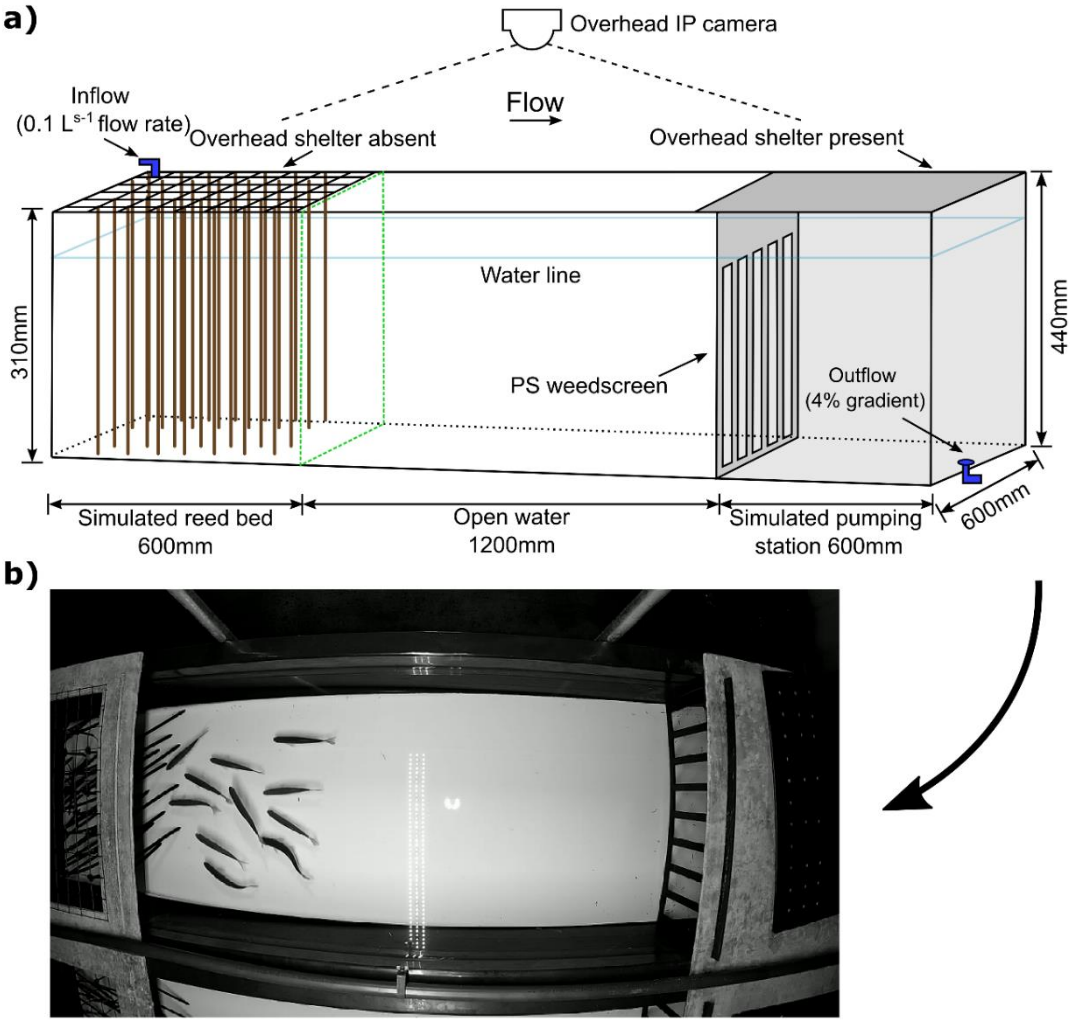


Figure 4.1 a) a schematic diagram (not to scale) representing the experimental tank used to test roach habitat preference. The diagram represents treatment A. Green dashed line indicates position for opaque Perspex screen installed when preventing access to habitat. Grey shading indicates cover. b) a screen capture from the IP camera showing the overhead view with simulated reed bed (left) and simulated pumping station (right).

The artificial habitat was mounted on top of the experimental tank and the simulated reed bed (i.e., cable ties) extended throughout the entire water column. During baseline measurements, an opaque Perspex screen was fitted at the entrance to the habitat compartment to prevent access.

4.2.3 Video system

Six infra-red IP cameras (Hikvision 5MP IP POE H265 30m IR 2.8mm D150H) were mounted above the experimental tanks and the field of view (FOV) covered of all three habitats (Figure 4.1b). The cameras were networked to a desktop computer with a dedicated graphics adapter (Windows 10) using an 8-way PoE switch (YaunLey YS082G-P). To provide maximum contrast with the experimental tank and consistency between day and night recordings, the cameras were always operated in infra-red and greyscale. A freeware video client (iSpy v7.2.1.0) provided continuous recording of all cameras to a 4tb external HDD at 1280x720p, 12 frames s^{-1} (fps) using an MPEG-4 codec. This allowed for unencrypted access to video files post-experiment. Files were time and date stamped (hh:mm:ss – d/m/y) and stored in 10-minute intervals. The raw video files did not require any processing prior to examining fish habitat use.

4.2.4 Experimental process

The effect of introducing artificial habitat on roach habitat preference between simulated pumping station, artificial habitat and open water was examined over four 12-day experimental runs (R1 – R4). Each treatment (A, B) received 12 replicates (three replicates per run) forming 24 discrete trials. During the four runs, the position of the simulated pumping station (left, right), and the tank number to receive each treatment (one to six) was alternated to control for tank-end effects. On the first day of each run a dose of Protex (5ml) was added to the holding tank to minimise handling-induced stress. After 1h exposure, 72 roach were selected at random from the holding tank; 12 roach were added to the open water compartment of each experimental tank. This group size was deemed sufficient for roach to aggregate and shoal; previous experimental work on roach habitat occupancy found no significant difference at densities of 10, 50 or 100 (Orpwood *et al.,* 2010). Roach were allowed to acclimate overnight before observations began the next day. To best represent a real-world scenario (described in 4.2.4.1), this iterative experiment had four interventions (Figure 4.2), each with a 3-day observation period to allow for temporal variation in roach movements. All interventions were performed 1h post-dawn (i.e., 08:00) to allow for fish to first select daytime habitat. Fish were also fed (cubes of frozen blood worm) to minimise human interaction effects. Trial fish were returned to a second holding tank when each experimental run was completed. All fish were studied no more than twice, in accordance with NC3Rs (2022).

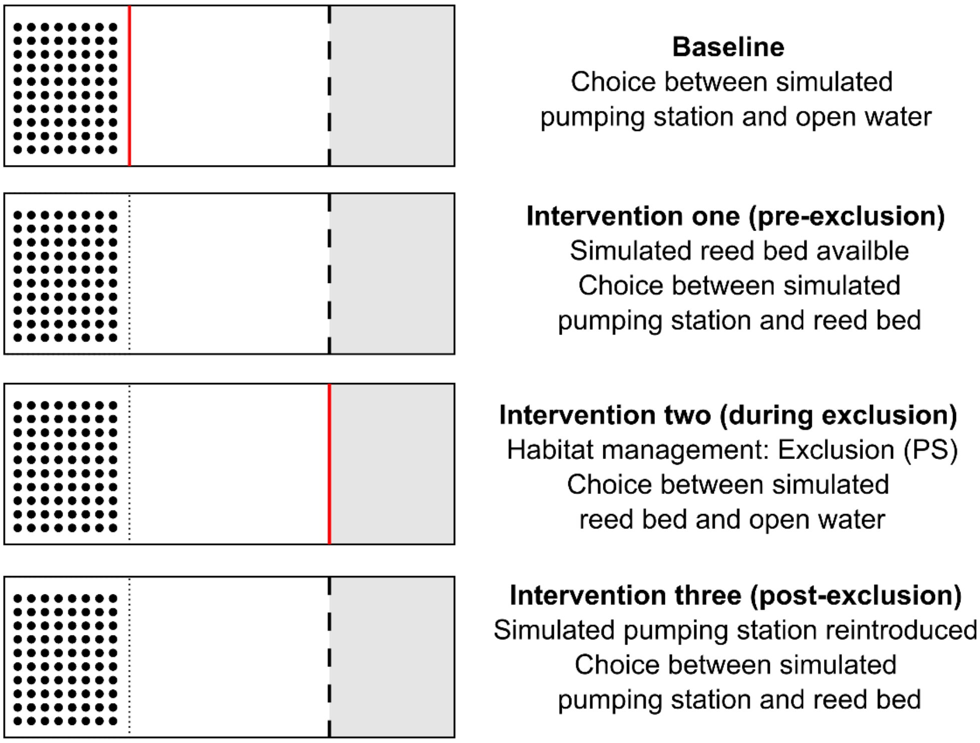


Figure 4.2 Representation of the iterative experimental design used to test roach habitat preference. Red line indicates opaque Perspex screen installed to prevent habitat access. Dashed line represents weed screen. Dotted line indicates threshold for simulated reed bed compartment.

4.2.4.1 Experimental interventions

Experimental interventions were iterative changes to habitat availability rather than bespoke treatments to test habitat preference under specific combinations (e.g., open water + pumping station or open water + artificial habitat), and thus repeated measures enabled change in fish habitat preference to be quantified. In accordance to Figure 4.2, the experiment was performed as follows.

- Baseline. To best represent a real-world application, i.e., artificial habitats being introduced to an existing fish population occupying a pumping station, roach were initially exposed to a baseline measurement with access to open water and simulated pumping station, and without access to artificial habitat (opaque Perspex screen installed at entrance).
- Intervention one. To determine if provision of artificial habitat changed the fish habitat preference, access to the artificial habitat was provided (opaque Perspex screen removed), and thus roach had a choice between occupying artificial habitat, open water and simulated pumping station.

- Intervention two. To determine if habitat management (i.e., physical exclusion) from the simulated pumping station increased roach occupancy of the artificial habitat, access to the simulated pumping station was prevented (simulated weed screen removed and (opaque Perspex screen installed), and thus roach a choice between occupying artificial habitat and open water.
- Intervention three. To determine whether habitat preference had changed, in comparison to intervention one, access to the simulated pumping station was re-introduced (opaque Perspex screen removed and simulated weed screen reinstalled), and thus roach had a choice between occupying artificial habitat, open water and simulated pumping station again.

4.2.5 Data analysis

4.2.5.1 Video observations

Habitat preference was analysed using data collected from a total of 6,912 hours of video footage; a multi-video streaming client (IVSDesktopPlayer 1.0.0.4) was used to playback six 10-minute video files at once. A systematic hourly sub-sample of fish counts (number of individuals occupying each habitat compartment) was chosen to provide (1) a suitable sample frequency that captures habitat preference, (2) an accurate representation of diel activity and (3) an appropriate cost-benefit sub-sample frequency vs gain in accuracy. The effect of diel phase was examined by creating day and night categories.

4.2.5.2 Statistical analysis

Data was analysed in context of R1 and R2, and R3 and R4 due to between run differences. The fish count data was analysed using R version 4.1.2 (R Core Team, 2022) in R Studio 2022.02.3 (RStudio Team, 2022). All statistical figures presented in the results were created using R packages ‘ggplot2’, ‘ggpubr’, ‘gridextra’ and ‘cowplot’. Data was checked for normality of variance using Shapiro-Wilk normality tests (R function ‘shapiro.test‘), which was non-normal; thus, descriptive values presented as medians (IQR) and non-parametric statistical analysis were performed. The count data in each habitat category were described as simulated reed bed (c_reed), simulated pumping station (c_ps), both simulated reed bed and pumping station (c_both) and open water (c_open)

Differences in habitat occupancy across treatments (A and B) and intervention periods were compared using a combination of Wilcox Rank-sum test (R function ‘wilcox.test’) and Kruskal-Wallis rank sum tests (R function ‘kruskal.test’). The analysis considered each trial to be independent of each other, and the fish group was treated as an individual. For all tests, the significance threshold was fixed at p = 0.05.

4.3 Results

4.3.1 Baseline: Choice between open water and simulated pumping station

In the absence of artificial habitat, roach in all experimental runs preferred to occupy the simulated pumping station rather than open water during the day (med, IQR (c_ps): 12, 10 individuals, Wilcox rank-sum *W* = 422405, *p* = <0.001) (Figure 4.3a; Figure 4.3c). There were between-run differences at night-time, during which roach in R1 and R2 rarely left the pumping station to enter open water (med, IQR (c_open): 0, 0 individuals; Figure 4.3b), but roach in R3 and R4 a preference for open water at night-time (med, IQR (c_open): 11, 4 individuals, *W* = 63928, *p* = <0.001; Figure 4.3d).

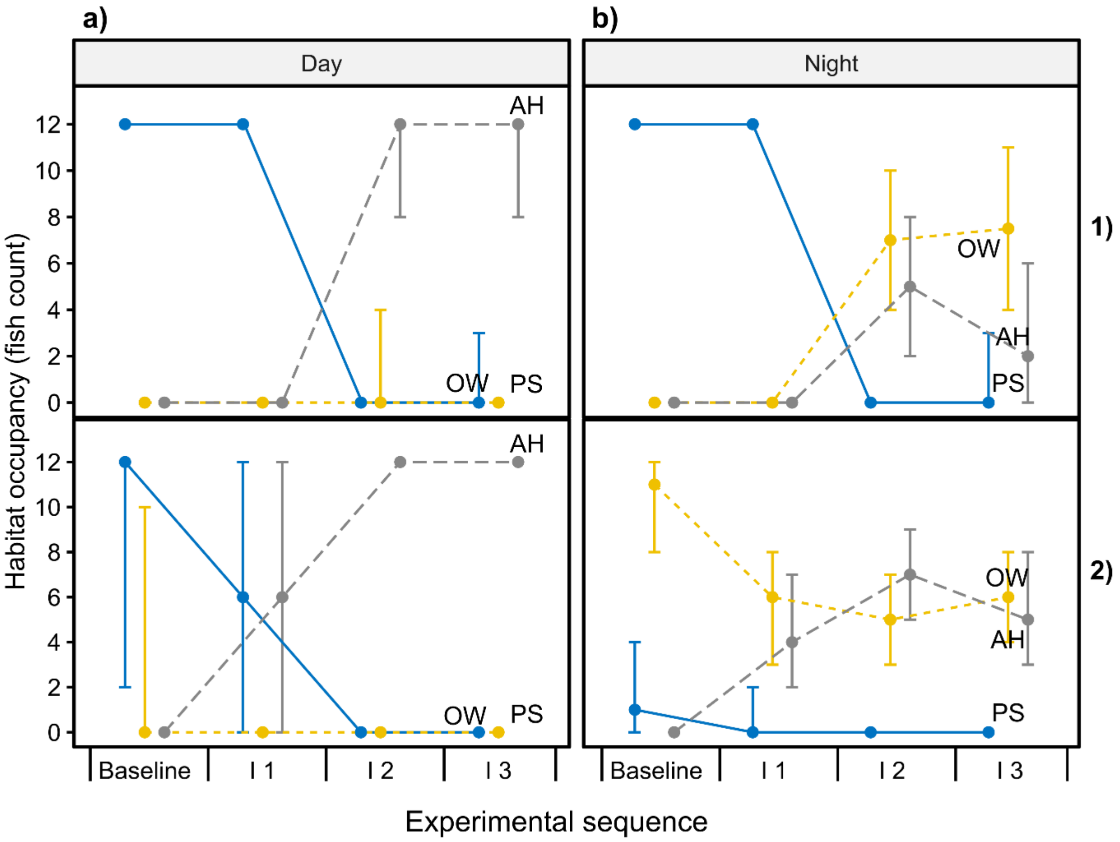


Figure 4.3 Habitat occupancy across the three habitat options (AH = Artificial habitat (grey dashed line), OW = Open water (yellow dashed line), PS = Pumping station (solid blue line)). Light period given by a) day and b) night. 1) represent runs R1 and R2 and 2) R3 and R4, respectively. Error bars represent median to quartile 1 to median to quartile 3. The experimental sequence shows the process from baseline to interventions one, two and three (I1 – I3).

4.3.2 Intervention one: Choice between open water, simulated pumping station and artificial habitat (pre-exclusion)

Habitat preference in R1 and R2 was unchanged when access to the artificial habitat was provided (c_ps baseline vs intervention one: W = 56052, p = 0.17); roach rarely left the simulated pumping station during both day (med, IQR (c_open): 0, 0 individuals; Figure 4.3a), and night (med, IQR (c_open): 0, 0 individuals; Figure 4.3b). In contrast, half the roach in R3 and R4 occupied the simulated pumping station during the day (med, IQR (c_ps): 6, 12 individuals) when offered artificial habitat (med, IQR (c_reed): 6,12 individuals) (c_ps baseline vs intervention one: W = 71318, p = <0.001; Figure 4.3c). At night, roach in R3 and R4 were distributed across all three habitats but showed an overall preference for open water (med, IQR (c_open): 6, 5 individuals; $\chi^2{}_2$ = 365.21 p = <0.001) (Figure 4.3d). When roach selected a night-time habitat, they preferred the artificial habitat (med, IQR (c_reed): 4, 5 individuals) over the pumping station (med, IQR (c_ps): 0, 2 individuals, W = 67884, p = <0.001).

4.3.3 Intervention two: Choice between open water and artificial habitat (during physical exclusion from simulated pumping station)

When roach were excluded from the simulated pumping station, daytime occupation of artificial habitat increased significantly in all runs (med, IQR (c_reed): 12, 2 individuals, c_reed intervention one vs intervention two: W = 60569, p = <0.001) (Figure 4.3a, Figure 4.3c). Roach in R1 and R2 began to occupy open water at night (med, IQR (c_open): 7, 6 individuals). Night-time occupancy of open water in R3 and R4 was reduced compared to intervention one (med, IQR (c_open): 5, 4 individuals; intervention one vs intervention two: W = 161699, p = 0.001) (Figure 4.3b, Figure 4.3d).

4.3.4 Intervention three: Choice between open water, simulated pumping station and artificial habitat (post-exclusion)

Roach in R1 and R2 did not leave the simulated pumping station in the day during baseline and intervention one (pre-exclusion), but showed a change in habitat occupancy towards the artificial habitat (med, IQR (c_reed): 12, 4 individuals) when the simulated pumping station was re-introduced (W = 3078, p = <0.001; Figure 4.3a). Similarly, roach in R3 and R4 switched their preference for simulated pumping station during the baseline and equal preference for pumping station and artificial habitat during intervention one, to occupying artificial habitat during the day in intervention three, despite the simulated pumping station being re-introduced (med, IQR (c_reed): 12, 0 individuals, baseline vs intervention three W = 23513, p = <0.001) (Figure 4.3c). The night-time preference for open water was unchanged in R1 and R2 compared to intervention two (med, IQR (c_open): 7.5, 7 individuals; W= 136461, p = 0.06; Figure 4.3b), although there was a significant increase in R3 and R4 (med, IQR (c_open): 6, 4 individuals; W = 124590, p = < 0.001; Figure 4.3d).

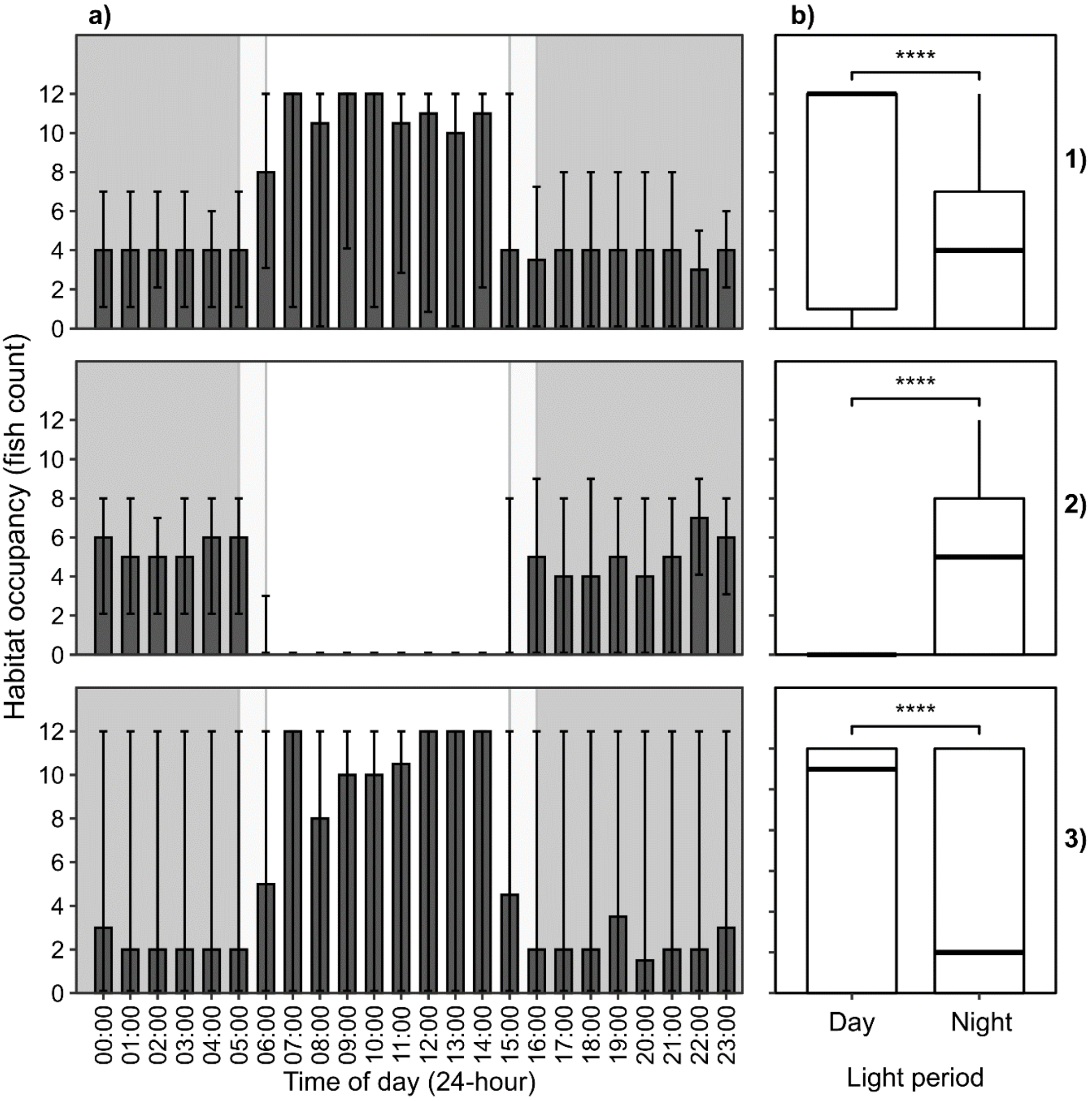


Figure 4.4 Habitat occupancy across the three habitat options given by 1) artificial habitat (simulated reed bed) 2) open water and 3) simulated pumping station. a) The diel relationship (24-hour) in habitat occupancy of roach shown as the median hourly fish count. Background shading represents light period with grey (night), light grey (crepuscular period) and white (day). b) Box plots for day and night light periods. Error bars represent quartile 1 to the smallest non-outlier and quartile 3 to the largest non-outlier. Significance indicted by Wilcoxon rank sum (ns = not significant, * = P ≤ 0.05, ** = P ≤ 0.01, *** = P ≤ 0.001, ***** = P ≤ 0.0001).

4.3.5 Temporal trends

Roach were predominately nocturnal, with daytime counts in artificial habitat or pumping station habitat (med, IQR (c_both): 12, 0 individuals) significantly higher than at night in all runs (med, IQR (c_both): 7, 9 individuals, *W* = 8486796, *p* = <0.001; Figure 4.4b). In all runs, movements between open water and preferred daytime habitat occurred during sunrise (Figure 4.4.1a; Figure 4.4.3a) and movement between open water and night-time habitat occurred during sunset (Figure 4.4.2a). In R3 and R4 during intervention one (performed 1h after dawn; 08:00), the number of roach that occupied artificial habitat peaked the following morning when roach selected daytime habitat (i.e., 24 hours after intervention artificial habitat occupancy increased to 9.5 (med, IQR (c_reed): 9.5, 9.75 individuals). Daytime artificial habitat occupancy did not change from one day to another (Figure 4.5), except in R3 and R4 where it was reduced by two fish across the 3-day period in intervention one (Figure 4.5.2a) and increased by two fish during intervention three in R1 and R2 (Figure 4.5.1c).

4.3.6 Treatment effects: unsheltered (treatment A) and sheltered (treatment B) artificial habitat

Overall, roach occupancy of artificial habitat was significantly higher in sheltered treatments (med, IQR: 10, 12 individuals) when compared to unsheltered treatments (med, IQR: 12, 8 individuals (*W* = 432182, *p* = 0.005; Figure 4.6d). This effect was significant during intervention one in R3 and R4 (but not R1 and R2) (med, IQR (c_reed treatment A): 4, 12 individuals; med, IQR (c_reed treatment B): 7, 11 individuals; *W* = 10602, *p* = 0.001; Figure 4.6.2a)), during R1 and R2 (but not R3 and R4) in intervention two (med, IQR (c_reed treatment A): 10, 4 individuals; med, IQR (c_reed treatment B): 12, 3 individuals; *W* = 48029, *p* = 0.01; Figure 4.6.1b), and during R1 and R2 (but not R3 and R4) in intervention three (med, IQR (c_reed treatment A): 10, 5 individuals; med, IQR (c_reed treatment B): 12, 3 individuals; *W* = 9926, *p* = 0.002; Figure 4.6.1c).

4.3.7 Tank effects

Roach did not leave the simulated pumping station in R1 and R2 (right-hand) during daytime baseline measurements (med, IQR (c_ow right-hand): 0, 0 individuals) but did enter open water in R3 and R4 (left-hand) (med, IQR (c_ow left-hand): 0, 10 individuals) (*W* = 127034, *p* = <0.001). Similarly, roach did not leave the simulated pumping station in R1 and R2 at night (med, IQR (c_ow right-hand): 0, 0 individuals) but did enter open water at night in R3 and R4 (left-hand) (med, IQR (c_ow left-hand): 11, 4 individuals) (*W* = 23010, *p* = <0.001), possibly because the pumping station was the opposite end of the experimental tank.

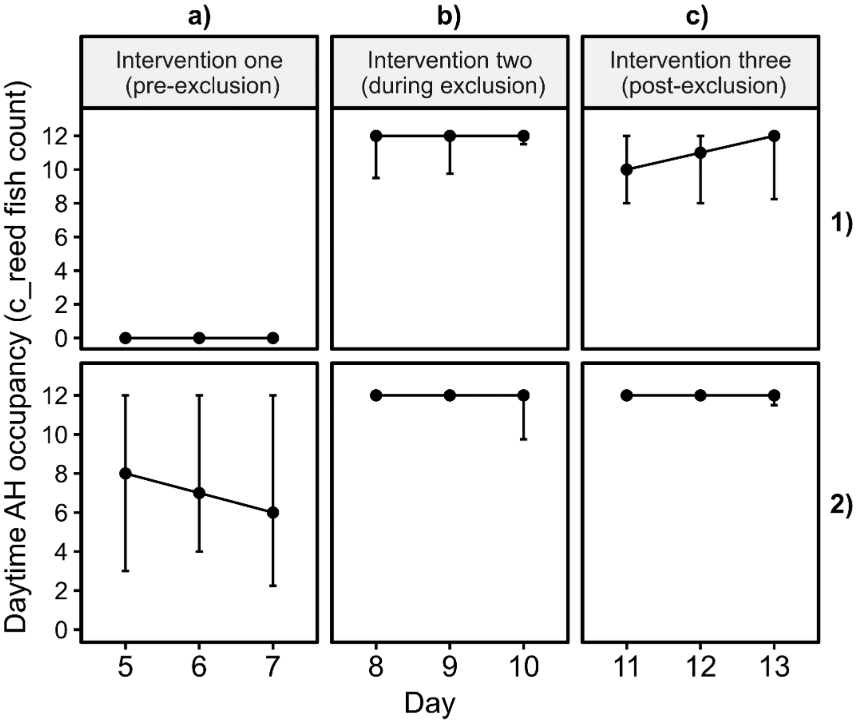


Figure 4.5 Daytime AH (artificial habitat) occupancy during a) intervention one, b) intervention two and c) intervention three. 1) represents R1 and R2 and 2) R3 and R4 respectively. Error bars represent median to quartile 1 and median to quartile 3.

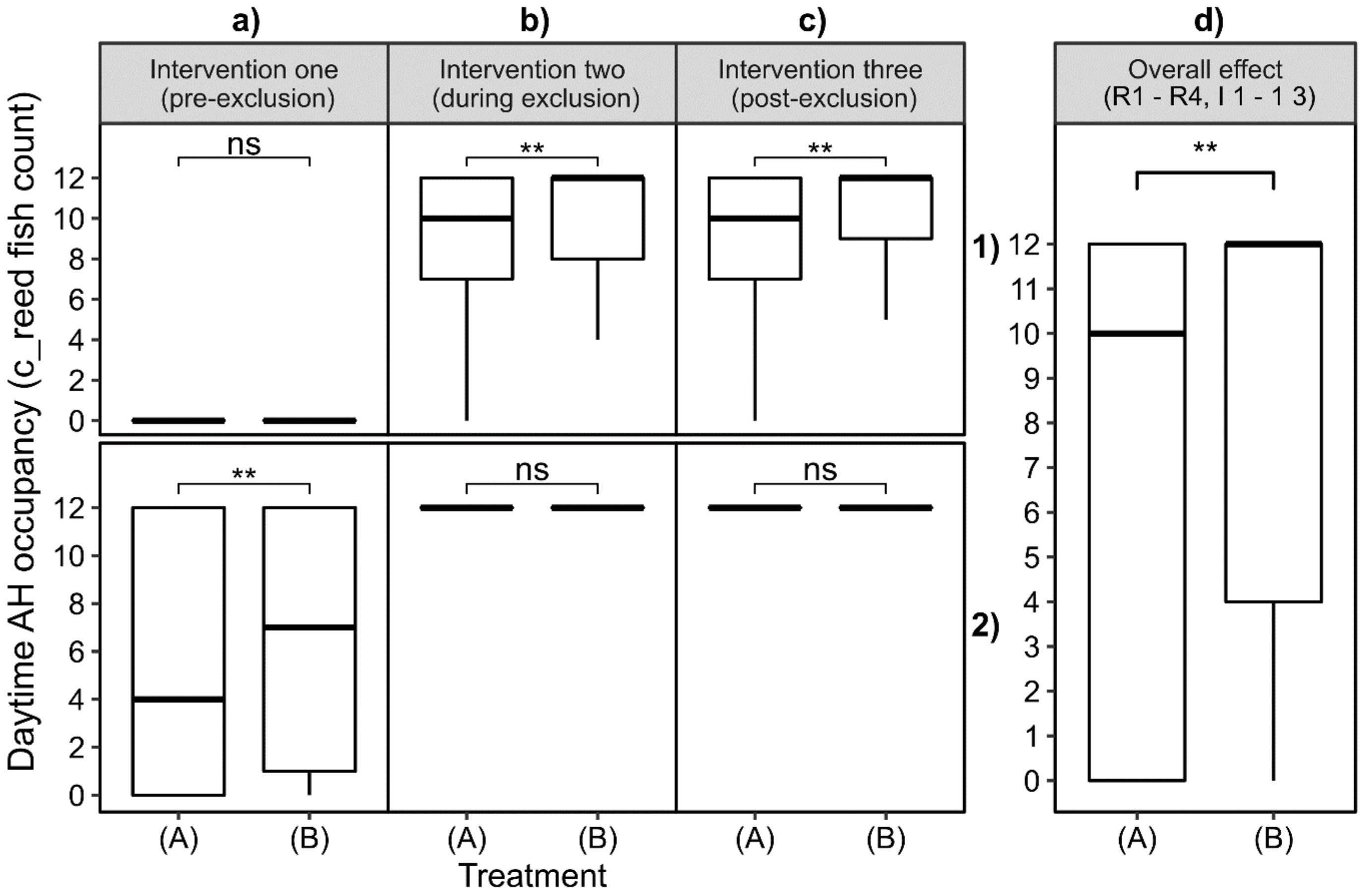


Figure 4.6 Daytime AH (artificial habitat) occupancy in unsheltered (A) and sheltered (B) treatments across 1) R1 and R2, 2) R3 and R4 during a) intervention one, b) intervention two c) intervention three and d) interventions one – three for all runs combined. Error bars represent quartile 1 to the smallest non-outlier and quartile 3 to the largest non-outlier. Significance indicted by Wilcoxon rank sum (ns = not significant, * = P ≤ 0.05, ** = P ≤ 0.01, *** = P ≤ 0.001, ***** = P ≤ 0.0001).

This was also observed at night during intervention one (med, IQR (c_ow right-hand): 0, 0 individuals; med, IQR (c_ow left-hand): 6, 5 individuals; W = 29931, p = <0.001). When roach were excluded from the pumping station during intervention two, daytime artificial habitat occupancy was significantly different between R1 and R2 (med, IQR (c_reed): 12, 4 individuals) and R3 and R4 (med, IQR (c_reed): 12, 0 individuals; W = 302408, p = <0.001) trials. This was also observed during intervention three (med, IQR (c_reed right-hand): 12 4 individuals; med, IQR (c_reed left-hand): 12, 4 individuals; W = 275790, p = <0.001).

4.4 Discussion

The variation in fish habitat choice during this experimental manipulation emphasises the necessity of rigorous assessment and experimental testing to understand and predict how fish will respond to the introduction of artificial habitat in the real-world. This studied aimed to provide safe artificial habitat for river-resident fish (i.e., roach) that occupy hazardous anthropogenic structures (e.g., pumping stations) in heavily degraded lowland rivers. Direct observation of habitat selection and occupancy was monitored during the day, night and crepuscular period using overhead infrared cameras. All roach occupied a simulated pumping station rather than open water during baseline observation. Half of the fish did not respond to the provision of artificial habitat (intervention one) and occupancy of artificial habitat was influenced by overhead shelter. After habitat management, i.e., physical exclusion from pumping station (intervention two), roach preferred artificial habitat rather than pumping station and this persisted once access to the pumping station was reintroduced (intervention three). Therefore, these findings suggest appropriate habitat management is required to accompany habitat restoration plans for fish that occupy hazardous anthropogenic structures.

4.4.1 Baseline observation effects

Roach in the baseline period preferred the pumping station as daytime habitat compared to open water and roach aggregations in open water increased at night. This supported hypothesis (i) and confirmed wild caught roach in this experimental setting behaved in line with previous observations of river-resident fish at pumping stations (authors unpublished findings) and was consistent with previous findings (Orpwood *et al.,* 2010). Although predation was not studied here, diurnal habitat use and nocturnal activity in open water is regarded as an important anti-predator strategy for fish vulnerable to avian predation pressure during the day (Bosiger *et al.,* 2012). The phenomenon of anti-predator behaviour in the absence of predation is described by the ghost of predation past hypothesis (see Gliwicz & Jachner 1992; Sheriff *et al.* 2010), and suggests previous avian predation threats to the study fish maintained anti-predator behaviour throughout the experiment. That said, not all roach aggregated in open water at night, exemplifying potential for inter-individual differences in diel habitat choice (e.g., Camacho & Hendry, 2020). It was also observed, although unquantified, that night-time aggregations of roach were looser than during the day and thus fish may have followed an ideal free distribution (IFD) to maximise resource access at night (Fretwell & Lucas, 1970).

4.4.2 The effect of introducing artificial habitat (Intervention one – pre-exclusion)

In agreement with previous research into roach artificial habitat occupancy under avian predation (Lemmens *et al.,* 2016), and in partial support for hypothesis (ii), roach in R3 and R4 had a positive reaction to the addition of artificial habitat, evident by daytime occupancy. Similarly, following behaviours demonstrated in the wild (e.g., Hohausova *et al.,* 2003), occupancy of artificial habitat was maximised during the sunrise period where fish selected daytime habitat. Even though roach occupied artificial habitat, overall occupancy counts suggest the shoal split evenly and did not show preference for either the pumping station or artificial habitat. As they were not preferentially selecting the artificial habitat, the implementation of artificial habitat without additional habitat management could then represent the formation of an “equal-preference trap” (Robertson & Hutto, 2006). Further studies are needed to determine how this effect would translate to the wild, but it is possible that the introduction of artificial habitat without deliberately providing stimulus cues could mean artificial habitat ends up with overall the same attractiveness as existing structures (i.e., pumping stations).

Roach in R1 and R2 continued to occupy the pumping station once artificial habitat was introduced. Exactly why these roach did not respond is unclear, but among the possible reasons include (1) fish in R1 and R2 were more neophobic and thus avoided isolation in open water or lacked neophillic individuals to disperse and encounter artificial habitat (Cote *et al.,* 2010), and (2) the experimental design was vulnerable to tank-end influence, with the simulated pumping station in R1 and R2 located at the downstream and thus deeper end of the tank. Further work is needed to fully determine these effects, for example individual fish boldness assessments could be incorporated, provided fish can be identified during observations (White *et al.,* 2013), although this was beyond the scope of this study.

4.4.3 The effect of habitat management (Intervention two – during exclusion)

Artificial habitat choice was significantly influenced by habitat management, which in this study was physically excluding fish from the pumping station. When excluded from the pumping station, roach in all runs occupied artificial habitat during the day, suggesting exclusion from poor habitat enhanced settlement cues of artificial habitat (Hale *et al.* 2018). In agreement with the hypothesis (iii), roach preferred artificial habitat to open water when the pumping station was unavailable, even for roach which were reluctant to leave the pumping station during intervention one. Further, in contrast to observations during intervention one, the preference for artificial habitat over open water was observed for both sheltered and unsheltered treatments. Thus, when habitat choice was restricted, open water becomes less attractive regardless of whether artificial habitat is sheltered. Although, exclusion of roach from the pumping station was accompanied by an increase in diurnal movements between open water and artificial habitat during the day, which could suggest artificial habitat may have been perceived as sub-optimal habitat, even when it is their only choice. Whether this process is considered maladaptive habitat selection is unclear, but other experiments studying habitat choice of roach also found that they do not always occupy structured habitat during the day (Martin *et al.,* 2014). Physical exclusion during intervention two also had an apparent effect on nocturnal behaviour; roach that did not leave the pumping station at night in R1 and R2 switched to an IFD at night (occupying open water and artificial habitat), and roach in R3 and R4 again followed the IFD found in baseline observations.

4.4.4 The effect of shelter over unsheltered artificial habitat

artificial habitat occupancy was significantly higher in the sheltered artificial habitat treatments compared to the unsheltered artificial habitat treatments. These observations supported hypothesis (v) and are consistent with the findings of others (Orpwood *et al.,* 2010) which proposed unsheltered habitats to be poor quality for roach. Further, roach in the unsheltered treatments spent more time in open water and increased visits to the pumping station during the day. This result agreed with the adaptive habitat selection hypothesis (Orians & Wittenberger, 1991) and may suggest these roach considered the threat of predation in open water less costly than competing for space in poor quality habitat. Overall, the seemingly lower quality unsheltered artificial habitats presented an increased tendency for maladaptive habitat selection, increasing the likelihood of ecological traps (Hale *et al.* 2016). These findings show that roach and potentially similar-sized prey which occupy the same ecological roles, like rudd (see Lemmens *et al.,* 2016), should benefit from artificial habitat presence, but providing cover will likely be critical for the success of habitat restoration.

4.4.5 The effect of reintroducing the pumping station (Intervention three – post-exclusion)

Observations during Intervention three provided evidence in agreement with the hypothesis (iv) i.e., following a period of physical exclusion from the pumping station, habitat preference for most roach (≥ 9 individuals) switched to artificial habitat once access to the pumping station was reintroduced. That said, small numbers (≤ 3 individuals) were neophobic and returned to known habitat, i.e., the pumping station, rather being part of a larger shoal in artificial habitat. Roach that switched to artificial habitat were likely attracted to the complex internal structure, which is known to have a profound effect on habitat choice and directly influences prey detectability (Ferrari *et al.,* 2017). The artificial habitats were designed to simulate the inside of a reed bed and was more complex than the simulated pumping station. The tendency for roach to occupy artificial habitat with small interstitial spaces was similar to studies which used vertical pipes and rocks to provide predator protection (Santos *et al.,* 2008; Frehse *et al.,* 2021). That said, the small numbers of roach that returned to the pumping station might have preferred more open structures, as reported by Baumann *et al.* (2016). Consequently, it is likely that phenotypic variation in habitat choice behaviours will occur during habitat restoration and efficacy of any artificial habitat is unlikely to permanently attract 100% of fish as some fish will always prefer the hazardous intake if its accessible.

Overall, daytime occupancy of the complexly structured artificial habitat increased after three different interventions, i.e., artificial habitat introduction, physical exclusion from pumping station and reintroduction of pumping station, whereas occupancy of the comparatively uncomplex pumping station decreased. Indeed, these findings suggest artificial habitat should be valuable for enhancing river-resident fish refuge opportunities at hazardous intakes during winter when natural instream vegetation is absent (Lemmens *et al.,* 2016). In turn, this study has shown that habitat selection behaviours of roach changed when exposed to different habitat choices during restoration. If tank-end influenced pumping station occupancy for roach in R1 and R2 during baseline observations and intervention one, then the effect of physical exclusion (intervention two) appeared to alleviate this as the preference switched to artificial habitat and persisted once the pumping station was reintroduced (intervention three), regardless of tank-end. The implication of this is that ecologists and managers should set realistic expectations for artificial habitat performance given habitat preference of fish will be inherently variable between hazardous intakes in the real world (Hale *et al.,* 2020), but physical exclusion should change habitat selection behaviours of wild roach.

The Field of Dreams hypothesis for habitat restoration states that ‘if you build it, they will come’ (Hilderbrand *et al.,* 2005). Yet, roach which occupied the pumping station in a baseline measurement only partially occupied artificial habitat when it was added (intervention one). Habitat management (intervention two; physical exclusion) enhanced the attractiveness of artificial habitat. Thus, the results in this study follow previous suggestions (e.g., Walsh & Breen, 2001; Bond & Lake, 2003; Sudduth *et al.,* 2011) and challenge the Field of Dreams hypothesis by suggesting ‘if you build it, they might come’. Fundamentally, by showing physical exclusion can successfully manipulate settlement cues used by fish when occupying new habitats, the findings here demonstrate the importance of rigorous planning for habitat restoration projects (i.e., Hale *et al.,* 2017). The increased attractiveness of artificial habitat provided by physical exclusion avoids the creation of a perceptual trap when restoring habitat and as a result prevents the more serious consequence of ecological entrapment if occupancy of pumping stations was to become reinforced (Robertson *et al.,* 2013). Hence, this study proposes that artificial habitats correctly built and installed with associated habitat management activities (i.e., physical exclusion) will provide an attractive and suitable alternative for fish that occupy hazardous anthropogenic water infrastructure.

4.4.6 Future research and implications for management

Scaling up this experiment to a real-world setting will be challenging. artificial habitat structures need to installed at a spatial-scale consistent with how fish use existing landscape features to ensure restored habitat is within the perceptual range of fish (Hale *et al.,* 2019). Whilst physical exclusion was simple to implement in this experimental setting a net or similar will need to be temporarily installed upstream of the pumping station intake prior to dawn to disperse fish towards artificial habitat. Long-term monitoring of the pumping station and introduced artificial habitat will also be required to first establish occupancy and then because fish habitat preferences are likely to be temporally variable, especially in combination with anthropogenic in-river activities (i.e., RMMs), potentially leading to annual (or more frequent) exclusion from intakes. In conclusion, the effectiveness of artificial habitats as a safe alternative for lowland river-resident fish which shelter from predators in hazardous anthropogenic structures (i.e., pumping stations) in modified lowland rivers is dependent on physical exclusion to prevent formation of an ecological trap. The restoration of habitat lost during river maintenance measures should favour artificial structures which also provide overhead shelter. Given variability in fish behaviour observed during controlled tank-based experiments, managers that implement artificial habitat during restoration work at anthropogenic structures should attempt to quantify the location and movement of the prevailing fish community to confirm effectiveness. Thus, restoration of heavily modified lowland rivers requires artificial habitat to be developed and tested in collaboration with structure managers and ecologists to prevent restoration failures.

5 THE IMPACT OF EXTREME FLOOD RELIEF PUMP OPERATIONS ON RIVER-RESIDENT FISH AND THE EFFECTIVENESS OF ARTIFICIAL HABITAT FOR PREDATOR AND FLOW REFUGE

5.1 Introduction

Understanding the distribution, abundance and habitat use of freshwater fish is fundamental for the correct ecological management, conservation and restoration of riverine ecosystems (Kruk, 2007; Methot & Wetzel, 2013). Furthermore, demonstrating how environmental changes can affect distribution of fish in riverine ecosystems is a major challenge facing ecologists (Poff, 1997; Knouft & Anthony, 2016). Flooding is a profound example of environmental change regularly witnessed in rivers worldwide. In unmodified lowland rivers with heterogeneous natural hydro-geomorphological features (i.e., meanders, floodplains and unaltered flow), fish have evolved to live with floods (Peirson *et al.,* 2008). They respond to episodic and seasonal flooding by longitudinal movement (David & Closs, 2002) and lateral dispersal into inundated floodplains (Manfrin *et al.,* 2020), or occupy habitats which provide flow refuge (e.g., behind boulders, fallen trees and dense vegetation; Lake *et al.,* 2006). However, human society needs flood protection and thus fluvial morphology has been severely affected by anthropogenic modifications (Dudgeon *et al.,* 2006; dos Reis Oliveira *et al.,* 2020). Flood Risk Management (FRM) in lowland regions includes channelization, dredging and construction of raised riverbanks to protect surrounding land from floods has homogenised longitudinal river habitats and isolated modified rivers from floodplains (Kruk, 2007), although the effects on prevailing fish communities are rarely quantified.

FRM can also include the operation of hazardous water level management infrastructure (pumping stations) that regulate flow and prevent flooding. Traditional assessments on the deleterious impacts of pumping stations have focused on assessing individual fish, for example the processes that lead to entrainment into hazardous intakes (Barnthouse, 2013), post-entrainment health assessments (Bierschenk *et al.,* 2019) and passage of migratory fish (Bolland *et al.,* 2019). Yet, these studies lack information on the collective impact of FRM on overall fish community distribution and abundance in pumped catchments. Namely, the loss of aquatic vegetation from winter FRM practices has a profound impact on the distribution of refuge habitats for fish (see Baczyk *et al.,* 2018). Habitat degradation in these systems is especially concerning for river-resident fish, such as roach (*Rutilus rutilus*), which occupy pelagic zones but also require temporally variable access to refuge from flow and predation. Homogenised drainage channels upstream of flood-relief pumping stations may also concentrate large aggregations of fish at pumping stations during winter when upstream habitat is void (Morat *et al.,* 2017). Furthermore, when these systems flood, fish are unable to respond naturally (i.e., longitudinal, lateral and refuge movements) and are vulnerable to being displaced downstream (Jurajda *et al.,* 2006). Consequently, high flows in heavily channelised and pump managed flood-relief channels could disperse fish downstream and may be entrained in pumps, although this is poorly understood (but see Harrison *et al.,* 2019).

The applicability of commonly used sampling techniques for generating an understanding of the impact of flood events on river resident-fish communities in deep and turbid lowland drains is challenging. Boat electric fishing surveys can be used to examine fish distribution and abundance (Lyon *et al.,* 2014) and netting has been used to examine the habitat use of juvenile fish in constrained lowland rivers during floods in slackwaters (Bolland *et al.,* 2015), but both lack the spatial extent and resolution required here. Electronic tagging would provide movement information before, during and after floods for a limited number of individuals (e.g., cost limitations), provided fish were tagged prior to an unpredictable flood event (Thorstad *et al.,* 2014). Alternatively, mobile horizontal echosounding using high-frequency side-scan sonar (SSS) is a non-invasive method for quantifying the distribution and abundance of fish populations in large rivers (Lawson *et al.,* 2019; Papastamatiou *et al.,* 2020). SSS surveys are routinely used in England to assess fish distribution, but quantified enumerations of fish are rarely performed. In this study, SSS data from before and after an extreme flood-relief pump operation (six pumps) in December 2020, when 131mm rain fell (150% of the 1981 – 2010 long-term average; Environment Agency, 2021), were analysed to assess the distribution and abundance of fish upstream of a pumping station and corroborated with anecdotal angler reports.

Artificial habitats can be used to supplement degraded natural habitats (Allen *et al.,* 2014) and increase the local abundance of fish (Frehse *et al.,* 2021), but their effectiveness is yet to be quantified in heavily managed lowland drains. When pumps do not operate, and thus there is no flow, artificial habitats could provide protection from instream and avian predators (Lemmens *et al.,* 2016). Given, structural design may affect occupancy of artificial habitats; for example, structurally complex designs with interstitial spacing may be necessary in predator-crowded communities, but sheltered open space may also be needed to avoid prey-crowding (Bolding *et al.,* 2010). Additionally, artificial habitats could also provide flow refuge during flood-relief operations. Accordingly, as a pilot study, fish abundance in the vicinity of three artificial habitat designs were uniquely evaluated during no flow and duty pump operation scenarios using multi-beam sonar, as has been performed in reservoirs (Baumann *et al.,* 2016). Such knowledge will help overcome the lack of robust monitoring to determine the ecological function of artificial habitat and relative fish occupancy (Lindenmayer *et al.,* 2017), especially under real-world circumstances (Hale *et al.,* 2015).

Overall, this study integrated inter-annual SSS and multi-beam sonar surveys with an aim to assess the impact of anthropogenic activities, i.e., pump operation and artificial habitat introduction, on a river-resident fish community in a pumped catchment. The specific objectives were to quantify (1) fish distribution and abundance pre- (2017, 2019) and post-flood (2021) to assess the impact of extreme flood-relief pump operations (six pumps), and (2) the influence of artificial habitat structure type, diel cycle and duty pump operation on fish abundance at artificial habitats. These findings will inform future habitat improvement work according to the Water Framework Directive (WFD; 2000/60/EC) and help inform pump intake managers and ecologists how to manage local fish populations in channelised flood-relief drains.

5.2 Materials and methods

5.2.1 Study catchment and site

The River Nene is a lowland main-river in the east of England that drains into The Wash and has a catchment area of at least 2363 km^2, of which 830 km^2 comprises the Lower Nene catchment. The North Level Drain (NLD) catchment (340 km^2) is a tributary of the River Nene, regulated by Tydd PS (20.17 cumecs) (Lat: 52.738804 N Long: 0.162728 W) (Figure 5.1a). The fish population in NLD is typical of lowland rivers including roach, pike (*Esox lucius*), bream (*Abramis brama*), tench (*Tinca tinca*), perch (*Perca fluviatilis*) and rudd (*Scardinius erythrophthalmus*) (Environment Agency, 2022). This study was performed on the 12km reach of the NLD upstream of Tydd PS (Figure 5.1a), which is void of habitat during the winter and previous fisheries monitoring (author's unpublished findings) have revealed large aggregations of river-resident fish at Tydd PS. Subsequently, early mitigation efforts to protect fish from predators and entrainment into pumps during start-up have included the installation of artificial habitats upstream of the PS (Figure 5.1c). River level (mAOD) was monitored using the nearest (~20 km from Tydd PS) river gauge in the River Welland catchment (Lat: 52.720221 N Long: -0.141261 W) to represent river conditions in NLD (Figure 5.2).

5.2.2 Artificial habitat

Three artificial fish habitat designs (partial refuge (A), partial refuge (B) and complete refuge (C)) were constructed using steel gabion baskets (3 mm thickness 1000 $_x$ 1000 $_x$ 1000 mm length $_x$ width $_x$ height) with 76.2 x 76.2 mm apertures. Four one-and-a-half sized apertures (i.e., 152.4 x 76.2 mm) were created on the front-facing side of each basket. Six baskets were joined (5000 x 2000 x 1000 mm) to encompass a volume of approximately 10 m^3 per habitat (Figure 5.1c; Figure 5.3) and best represent patches of marginal reeds present in NLD throughout summer, whilst ensuring water conveyance was not impeded in the drain channel.

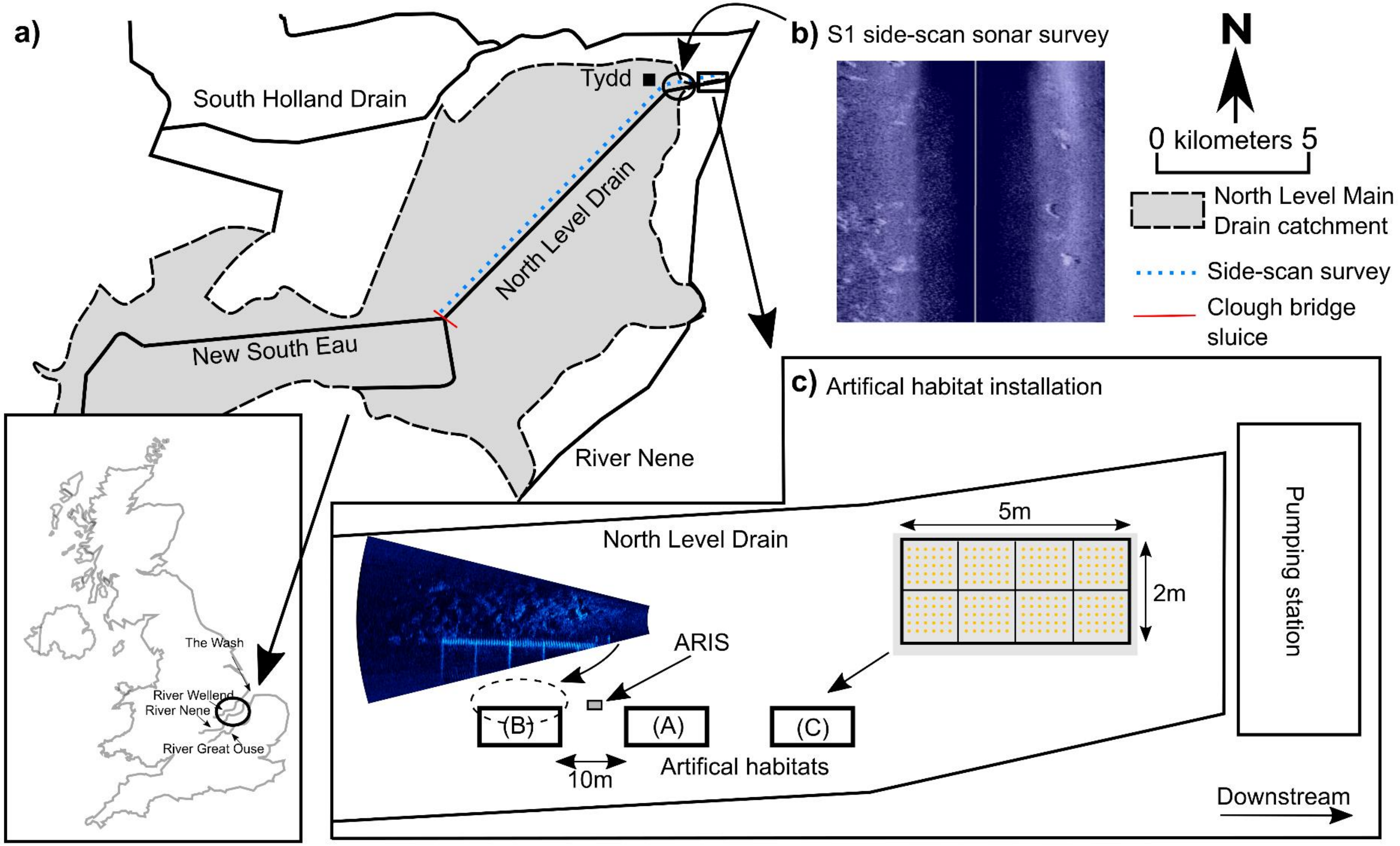


Figure 5.1 a) the location of the study catchment (bottom left) and the North Level Drain catchment including survey reach (blue dotted line). b) representative image of S1 side-scan sonar survey (52.737735N,0.148511W). c) a schematic representation (not to scale) of the artificial habitat installation, showing the position (52.738804N, 0.162728W) of the structures partial refuge (A), partial refuge (B) and complete refuge (C) with a diagram of habitat structure (grey shading represents cover, orange circles represent bamboo canes), representation of ARIS insonified window and the downstream pumping station.

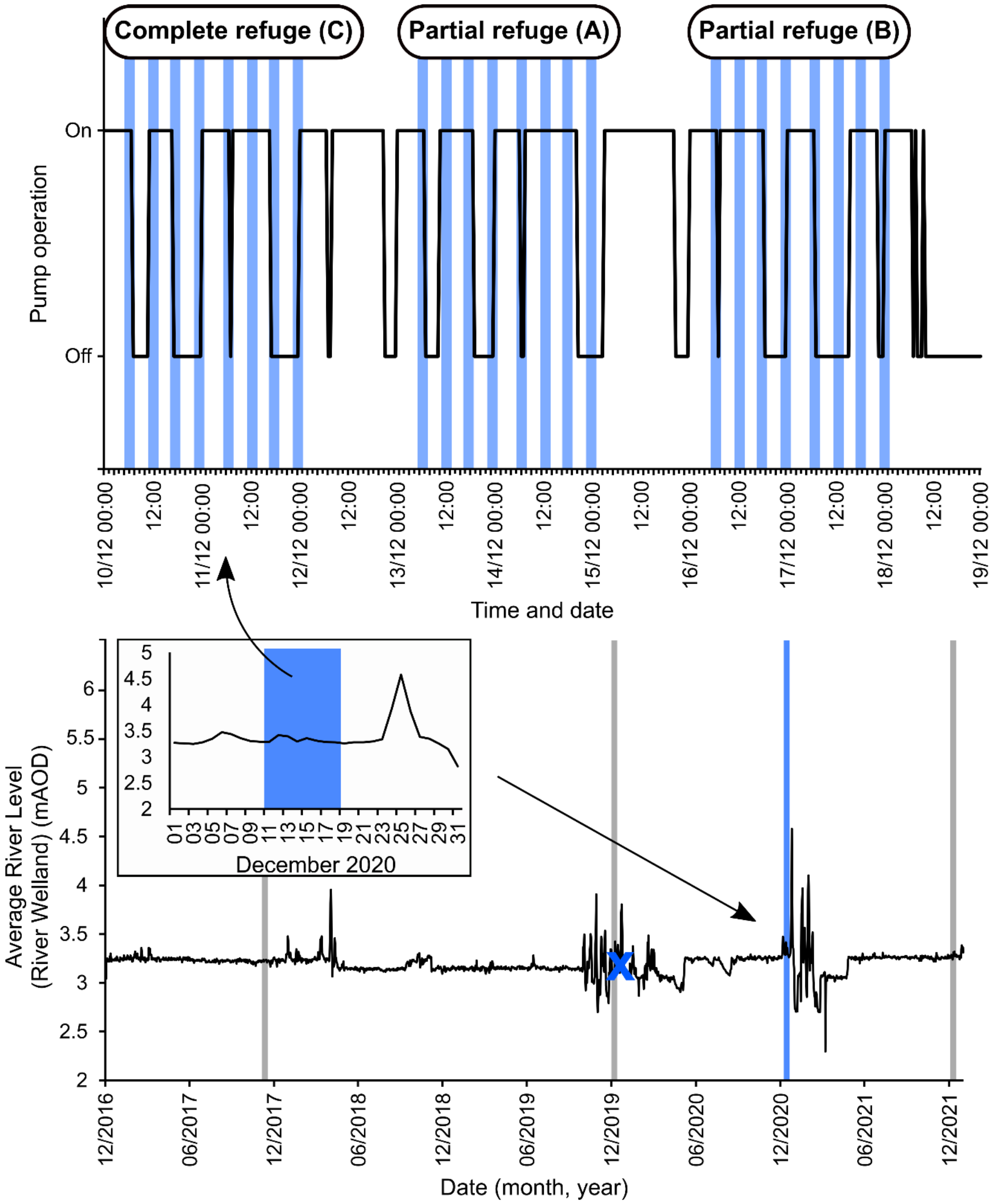


Figure 5.2 (top) pump operations at Tydd pumping station on 10 – 18 December 2020 and (bottom) average daily river level (mAOD) recorded in the River Welland (52.720221 N,-0.141261 W) adjacent to North Level Drain catchment between December 2016 and December 2021. Vertical grey bars indicate date of side-scan surveys. The blue cross indicates when artificial habitats were installed upstream of Tydd pumping station and the vertical blue lines indicate when the ARIS sonar surveys were performed (inset figure for clarity).

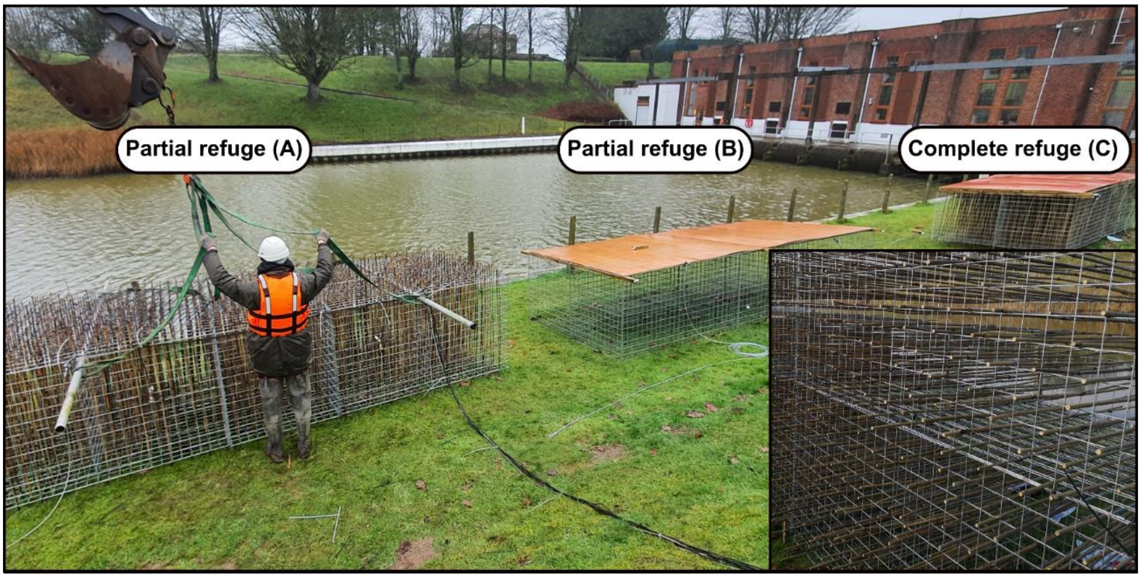


Figure 5.3 Photographs of the three artificial habitats installed upstream of Tydd PS (52.738804N, 0.162728W). From left to right, partial refuge (A), partial refuge (B) and complete refuge (C). Inset photo shows bamboo canes installed through apertures in steel cages. Positions of artificial habitats differ in this photo from the final installed positions (Figure 5.1c).

The complete refuge (C) used marine plywood boards (16mm thickness) attached to wooden framing to create overhead shelter, and bamboo canes (6 – 8 mm thickness, 1200 mm length) inserted in every other aperture in the gabion baskets (secured with cable ties) to create interstitial spaces with approximately 150 mm spacing. The size and number of interstitial spaces was selected to target both juvenile and adult roach and similar sized silver fish, whilst also excluding larger bodied predator species like pike. Partial refuge (A) was created with bamboo canes, but without overhead shelter, and partial refuge (B) was created with overhead shelter, but without bamboo canes. artificial habitat were installed in NLD in December 2019 (Lat: 52.738804N Long: 0.162728W) (Figure 5.2). Bank-side access (personnel and crane equipment) and distance from power source (Tydd PS) determined the final placement of artificial habitats.

5.2.3 Field study methods

5.2.3.1 Side-scan sonar

SSS surveys were performed with a commercially available Humminbird® Solix 15 CHIRP MEGA SI (Johnson Outdoors Inc., Racine, WI) using a frequency range of 1150 - 1275 MHz (2017, 2019 scans) and 780 – 850 MHz (2021 scans) powered by a 12v battery. The frequency range allowed for detection of target fish using a total swath width of 30 m (15 m either side of the boat) to cover varying channel widths between 20 – 30 m. The transducer was attached to a pole at the front end of a small workboat with an outboard engine, fixed at a depth of 30 cm and towed upstream following the centre of NLD at an optimal speed of 2 – 5 km $^{h-1}$. The SSS tracks were converted to a 2d image in real-time on the sonars console, which allowed for observations of fish targets to be made during sampling. The final outputs were processed as a ‘New Sonar Mosaic’ using Reefmaster® (ReefMaster Software Ltd, West Sussex, UK).

SSS surveys were performed during normal and steady river levels over one morning (09:00 – 12:00) on 27 November 2017, 10 December 2019 and 17 December 2021. The latter was in response to extreme flood-relief pump operation at Tydd PS on 23–27 December 2020 (six pumps, 96 hours). The sampling day was selected to detect winter shoaling behaviour of river-resident fish.

5.2.3.2 Multi-beam sonar

Monitoring fish abundance at the artificial habitats post-installation was first attempted in January 2020 using underwater light-based cameras but was ineffective due to fluctuating turbidity. Fish abundances at artificial habitats were monitored using Adaptive Resolution Imaging Sonar (ARIS Explorer 3000, Sound Metrics®, USA. http://www.soundmetrics.com/) on 10–18 December 2020. The ARIS was installed on an L-shape steel pole (2 x 1 m) via a SoundMetrics AR3-rotator at a depth of ~ 2 m. Data and power cable was routed to a bankside weatherproof box containing sonar command module and a laptop with remote internet connection (Panasonic TF-19). To image refuge (A) and (C), the pole was driven into the riverbank between the two structures. After (C) was imaged, the ARIS was rotated to image (A). The ARIS was later moved between refuge (A) and (B) to image refuge (B) (Figure 5.1c). The position was aligned with the leading edge of the artificial habitats, and imaging of the artificial habitat structures was used to confirm correct orientation of the sonar.

The ARIS was operated in high frequency mode (1.8 MHz, 96 0.3° x 14° beams, 512 bins) with a window length of 8.4 m (starting 3 m from point of transducer) at 9.7 frames s^{-1} (fps), receiver gain at default and focus set to auto to account for changes in fish distance from the transducer. Continuous observations were captured except when data collection was only interrupted to maintain equipment and reposition the ARIS. Files were time and date stamped (hh:mm:ss – dd/mm/yyyy) and stored in 10-minute intervals. All software inputs were performed in SoundMetrics software (ARIScope V2.6.3.1559).

5.2.4 Analysis of sonar outputs

5.2.4.1 Fish distribution in North Level Drain

To measure distribution of fish in the NLD, SSS surveys started at the downstream extent (i.e., Tydd PS, including artificial habitats in 2021 scans) and were conducted in an upstream direction to Clough Bridge Sluice (Figure 5.1a); a total range and area of ~12 km and ~30 km^2, respectively. The reach upstream of Clough Bridge Sluice was narrow, shallow and unable to support adult roach populations. During SSS surveys in NLD, all fish were aggregated approximately near the A1101 road bridge, 1 km upstream of Tydd PS; 70 m river length x 25 m river width x 2.4 – 2.7 m deep (S1; Figure 5.1b).

5.2.4.2 Fish abundance in North Level Drain

The SSS survey data (S1) was analysed for fish abundance by enumerating fish targets in the final image produced by Reefmaster. The data was processed in ImageJ v1.53e (Schneider *et al.,* 2012), which has previously been demonstrated as an effective tool for enumerating fish targets in SSS data (Bollinger & Kline, 2017; Lawson *et al.,* 2019). To provide a standardised measure of area, a transect was drawn across the river width (25 m) and calibrated to 758 ± 1 pixels. Once calibrated, approximate fish measurements were taken and individual region of interest (ROI) were applied to light and dark backgrounds to identify acoustic shadows cast by fish shapes, and acoustic reflections of fish (Figure 5.4). Fish counts were then quantified by applying the findMaxima tool and adjusting background (light, dark) and detection tolerance (0 – 45) to ensure over- and under-plotting of fish targets was minimised. The points plotted by findMaxima were scrutinised by applying a ‘within tolerance’ threshold and ensuring plotted points corresponded with fish targets. The total area analysed was 840 m^2 and 990 m^2 in the 2017 and 2019 samples, respectively (Table 5.1). The estimated fish abundance (10 m^2) was then calculated to provide a standardised comparison to estimates from multi-beam artificial habitat surveys.

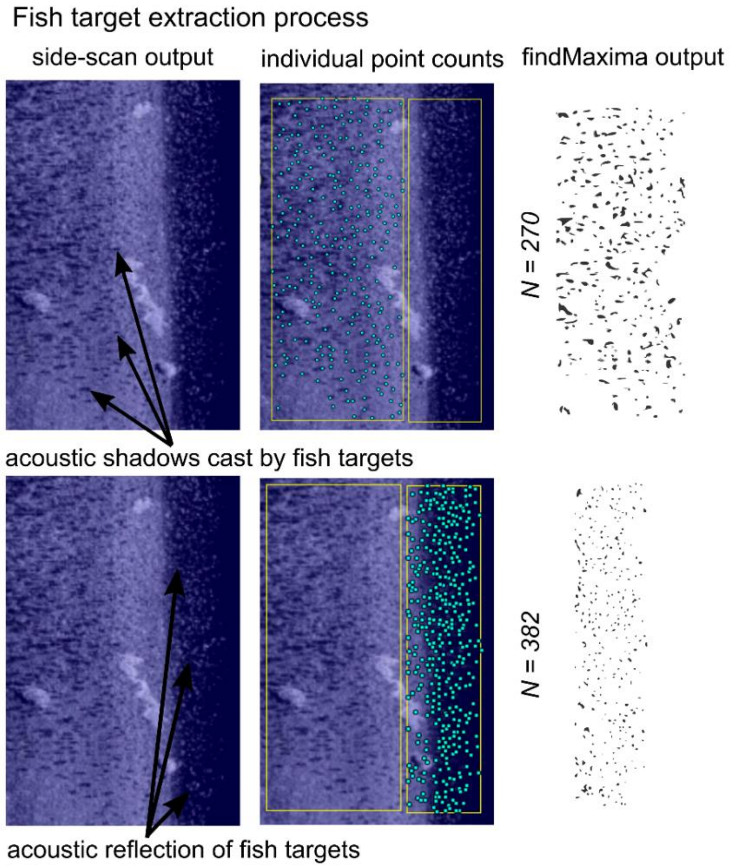


Figure 5.4 A representation of the fish target extraction method used for enumerating fish in the side-scan images. The findMaxima outputs and counts are generated from ImageJ.

Table 5.1 Side-scan sonar survey results throughout the study period. Region of Interest (ROI) specifies where counts were taken on light and dark backgrounds. Total fish count given by findMaxima outputs (ImageJ).

	Total area (m^2)		*n* ROIs		Fish count	
Sample year	Surveyed (S1)	Analysed	Light	Dark	Total	Estimated fish abundance (10 m^2)
November 2017	1600	840	6	6	5213	63
December 2019	1600	990	8	4	1474	15.4
December 2021						
(main drain)	1600	0	-	-	0	0
(artificial habitats)	900	0	-	-	0	0

5.2.4.3 Fish abundance at artificial habitat

Two days of sonar footage from each artificial habitat structure were selected to determine the relationship between artificial habitat structure type and fish abundance, which also mitigated data gaps due to no sonar operation and installation adjustments. To determine temporal variability the data were sub-sampled into four two-hour discrete sample periods over a 24-hour day (dawn = civil twilight ± 1h 06:30 – 08:30, daytime = 11:30 – 13:30, dusk = civil twilight ± 1h 15:30 – 17:30, night-time = 23:30 – 01:30). Multi-beam sonar surveys of artificial habitat were performed during duty pump operation (one pump, 30 hours) for 64%, 35%, 85%, 83% and 52% for the total sample range, dawn, dusk, and midday and midnight samples, respectively (Figure 5.2). Flow velocity was 0.25 m s^{-1}, calculated by measuring the speed of floating debris in multi-beam images. The overall duration of sonar footage analysed included 24 hours of ARIS images. Counts of fish occupying the space immediately adjacent to the artificial habitat structures (approximately 14 m^2; Figure 5.5) were taken by an experienced reviewer every 15 minutes (individuals·1 frame·15min^{-1} ± 5 s^{-1}) and calculated as fish abundance (10 m^2). Background subtraction was applied if floating debris reduced resolution of fish targets. Playback speeds were adjusted as necessary and quick backward and forward navigation allowed for observation of fish interacting with artificial habitats. Fish were measured using the ARIS measurement tool when perpendicular to the sonar beam.

5.2.5 Statistical analysis

The data derived from side-scan and multi-beam sonar surveys was analysed using R version 4.0.2 (R Core Team, 2022) in RStudio 1.4.11 (RStudio Team, 2022). All statistical figures presented in the results were created using R packages ‘ggplot2’, ‘ggpubr’, ‘gridextra’ and ‘cowplot’. Data was checked for normality of variance using Shapiro-Wilk normality tests (R function ‘shapiro.test‘). The data from SSS and multi-beam surveys were not normally distributed, and non-parametric testing was used throughout with descriptive values presented as medians (IQR). For statistical comparison between variables, a combination of Wilcox rank sum tests (R function ‘wilcox.test’) and Kruskal-Wallis rank sum tests (R function ‘kruskal.test’) was used. Post-hoc testing was performed using Dunn’s test (R function ‘dunn.test’ in package ‘dunn.test’).

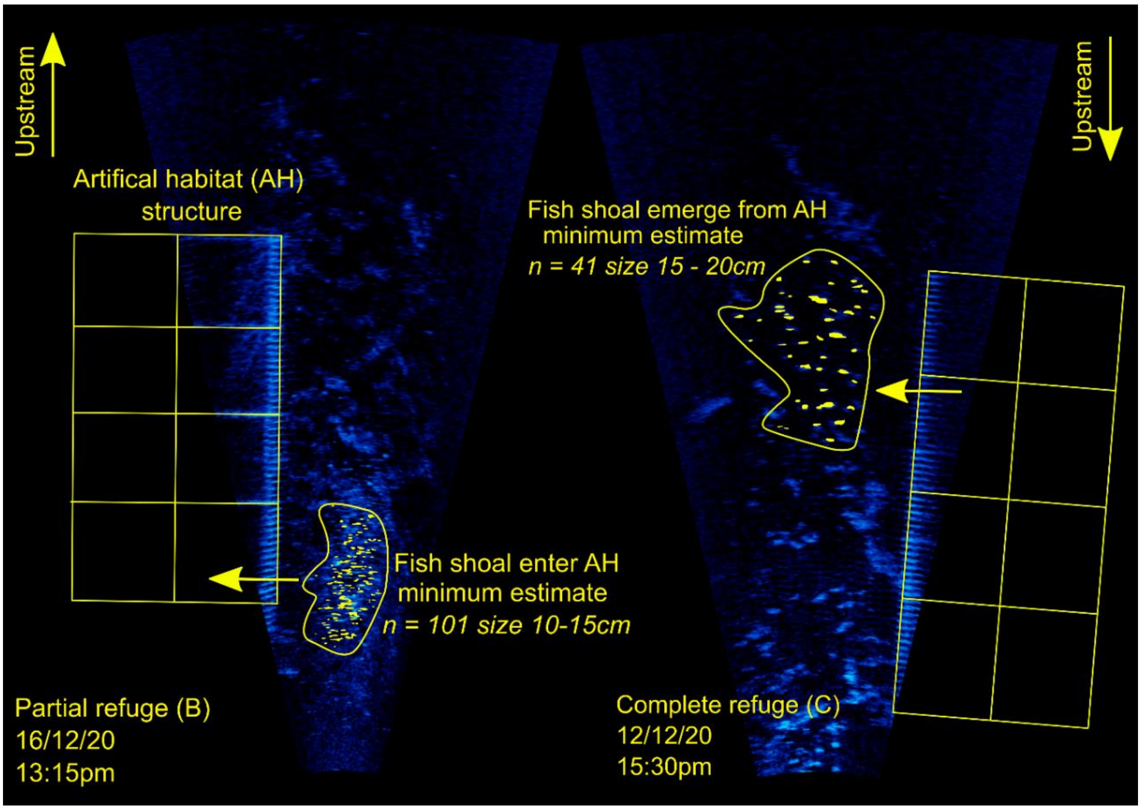


Figure 5.5 A schematic representation of the artificial habitat structures overlaid on raw ARIS outputs. Fish counted in frame, including estimated size indicated by circled yellow marks.

5.3 Results

5.3.1 Fish abundance in North Level Drain

A total of 5,213 and 1,474 fish (10 – 20 cm size class) were identified in pre-flood SSS surveys in November 2017 and December 2019, respectively (Table 5.1; Figure 5.6a; Figure 5.6b; Appendix 2; Appendix 3). Abundance was significantly higher in 2017 (med, IQR: 63, 15.5 fish·10 m^2) than 2019 (med, IQR: 15.4, 6.95 fish·10 m^2; $W = 144$ $p = <0.001$) (Figure 5.7). The post-flood SSS survey in December 2021 was void of fish targets and contained only clearly defined riverbanks (Figure 5.6c; Appendix 4).

5.3.2 Fish abundance at artificial habitats

A total of 881 fish were identified at refuge (A) (med, IQR: 4.29, 5.89 fish·10 m^2), 786 at refuge (B) (med, IQR: 3.57, 8.04 fish·10 m^2) and 556 at refuge (C) (med, IQR: 3.21, 8.21 fish·10 m^2), although the median abundance was not significantly different between artificial habitat structure type ($\chi^2_2 = 0.82$, $p = 0.66$) (Table 5.2; Figure 5.8a). Significant differences in fish counts were attributed to photoperiod ($\chi^2_{23} = 50.87$, $p = <0.001$), with highest abundance during the crepuscular period (med, IQR dawn: 9.29, 17.7; dusk: 5, 6.79 fish·10 m^2) and lowest during the day (med, IQR: 1.07, 2.86 fish·10 m^2) and night (med, IQR: 2.14, 4.82 fish·10 m^2) (Table 5.2; Figure 5.8b); post-hoc Dunn's test showed no photo periods had similar fish abundances. Fish abundances at all artificial habitats were significantly higher when the duty pump at Tydd PS was off (med, IQR: 7.86, 9.64 fish·10 m^2), compared to when one duty pump was on (med, IQR: 2.14, 5.71 fish·10 m^2; $W = 2667$, $p = <0.0001$) (Figure 5.8c). The population size-class was consistent with the SSS survey (10 – 20cm), and five large-bodied fish (120 – 135 cm) were imaged and identified as pike. The subsequent SSS survey at the artificial habitat installation post-extreme pump operation (17 December 2021) was void of fish, but artificial habitat structures were easily identified (Figure 5.6d).

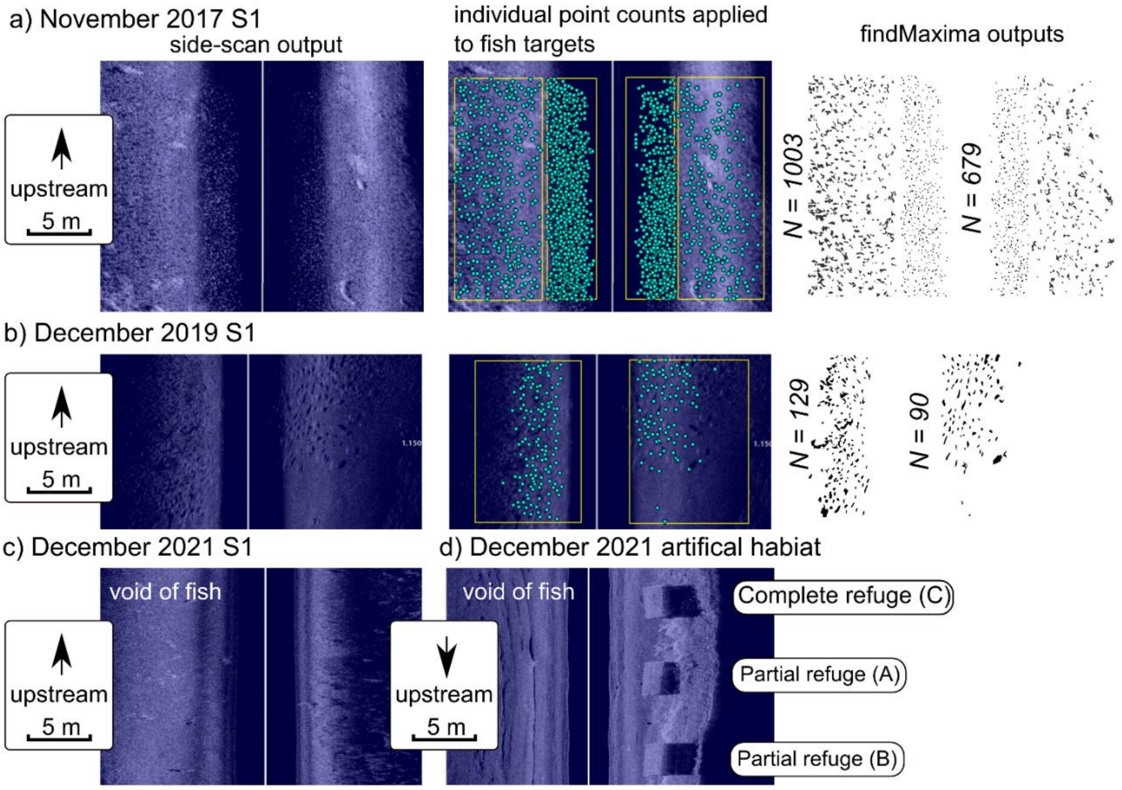


Figure 5.6 Composite image from North Level Drain (52.737735N,0.148511W) with a representation of the side-scan survey S1 (downstream to upstream) for a) 27 November 2017, b) 10 December 2019, c) 17 December 2021 and d) 17 December 2021 at artificial habitats upstream of Tydd pumping station (52.738804N, 0.162728W) (Figure 5.1c). findMaxima output presented from ImageJ.

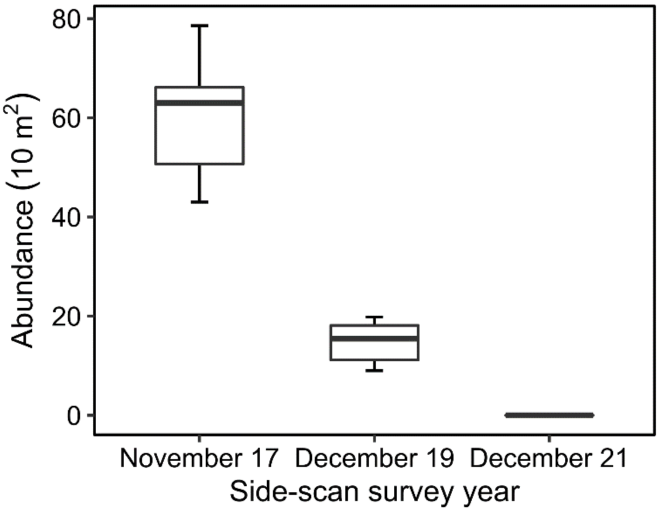


Figure 5.7 Median abundance derived from fish counts in side-scan sonar images of North Level Drain (52.737735N,0.148511W) taken on 27 November 2017, 10 December 2019 and 17 December 2021. Lines represent quartile 1 to the smallest non-outlier and quartile 3 to the largest non-outlier.

Table 5.2 Multi-beam survey results from artifical habitat sampled on 10 – 18 December 2020.

Artificial habitat (photo period)	Estimated fish abundance (10 m^2) Median	Min	Max	IQR	Hours pumped during sample (%)	
Complete refuge	3.21	0	30	8.21	9	(75%)
Dawn	6.78	0.71	18.57	8.21	1.50	(37.50%)
Day	0.71	0	2.85	1.42	4	(100%)
Dusk	10	2.14	30	4.64	2	(50%)
Night	1.78	0	12.85	6.07	1.50	(37.50%)
Partial refuge (A)	4.29	0	80.70	5.89	10.75	(89.50%)
Dawn	19.2	0	80.74	22.50	1.25	(31.25%)
Day	1.48	0	12.14	5.17	4	(100%)
Dusk	4.64	0	12.85	3.57	4	(100%)
Night	3.21	0	7.14	3.92	1.50	(37.50%)
Partial refuge (B)	3.57	0	72.10	8.04	10.50	(87.50%)
Dawn	13.21	0	47.14	21.25	1.50	(37.50%)
Day	0	0	72.14	7.32	2	(50%)
Dusk	3.21	0	18.57	3.75	4	(100%)
Night	2.14	0	12.85	3.57	3	(75%)

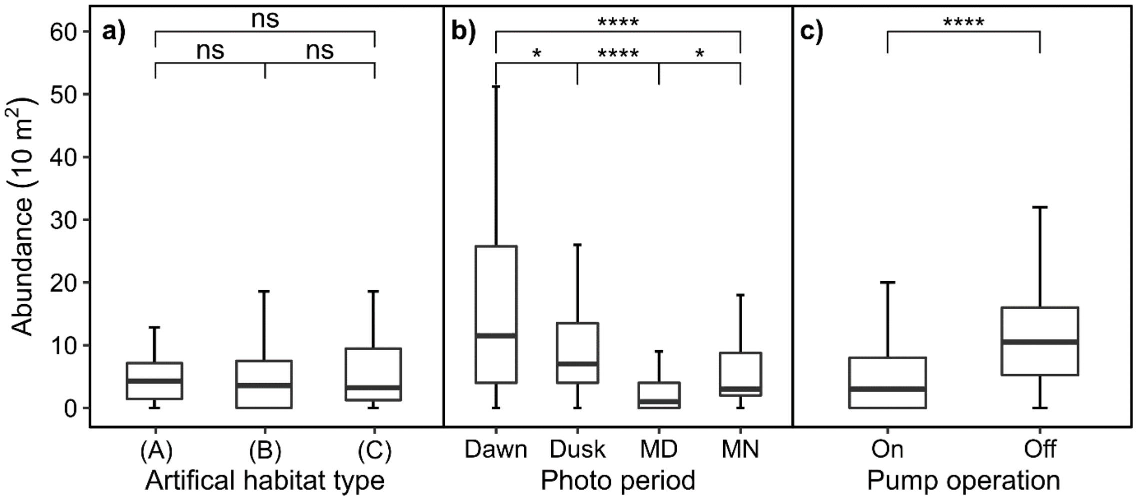


Figure 5.8 Median fish count represented by a) artificial habitat structures with partial refuge (A), partial refuge (B) and complete refuge (C). b) photo period MD = midday, MN = midnight and c) pump operation. Lines represent quartile 1 to the smallest non-outlier and quartile 3 to the largest non-outlier. Significance between categories indicted by Wilcoxon rank sum (ns = not significant, * = P ≤ 0.05, ** = P ≤ 0.01, *** = P ≤ 0.001, ***** = P ≤ 0.0001).

5.4 Discussion

The results presented here are the first to provide a quantitative estimate of distribution and abundance of river-resident fish in a flood relief lowland drainage system with a pumping station, before and after extreme flood-relief operation and at artificial fish habitats using side-scan and multi-beam sonar, respectively. SSS surveys pre-flood (2017, 2019) found highly abundant aggregations of river-resident fish (approximately 1 km upstream of the pumping station) but the entire drain was void of fish post-flood (2021). When artificial habitats (installed for predator refuge) were monitored pre-flood (2020) using multi-beam sonar, fish abundance followed a crepuscular pattern and was comparable between three different artificial habitat structures, but the effectiveness as flow refuge was unclear (largely due to methodological limitations). artificial habitats monitored with SSS post-flood were void of fish. Overall, these findings suggest that flood relief pump operations significantly alter the abundance of river-resident fish upstream of pumping stations and artificial habitat introduction has the potential to be effective predator refuge.

Following exceptionally high rainfall during December 2020 (Environment Agency, 2021), Tydd PS operated at full capacity (six pumps) for four days. Anglers consistently reported reduced catch-returns of adult river-resident fish from NLD throughout 2021 (unpublished data), which was later corroborated by SSS surveys in December 2021. Fish have evolved to live in lowland rivers with in-channel habitat heterogeneity and laterally connected floodplains, which provide flow refuge during elevated river levels and floods (Peirson *et al.,* 2008). Pumped catchments, however, have homogenised (e.g., dredged and in-stream habitat removed) and straightened channels isolated from their floodplains. Furthermore, pumping stations tightly regulate river levels by operating more pumps to increase the volume of water discharged; in-channel flow velocity (here ~ 1.5 m s^{-1} with six pumps operating) can greatly exceed those of natural rivers (Lake *et al.,* 2006; Filkweert & Worth, 2012) and the swimming capability of fish (Baumgartner *et al.,* 2009). Roach, for example, have slender body-morphology poorly adapted for living in fast-flowing conditions with an estimated sustained swimming capability of two minutes at 0.7 m s^{-1} flow velocity (Clough & Turnpenny, 2001). Thus, while no direct evidence, all these factors combine to speculate that the highly abundant fish aggregations pre-flood (2017, 2019) were displaced downstream (e.g., Poff & Zimmerman, 2010) and removed from NLD by entrainment through flood relief pump operations during December 2020 (e.g., Harrison *et al.,* 2019). Elsewhere, Barnthouse (2013) also reported that thousands of fish were potentially killed by entrainment through pumps during a single flood event. The long-term impacts remain to be seen but recovery from extreme floods in channelised rivers can occur when only few adults survive (Juradjda *et al.,* 2006), although the catchment studied here was relatively small and the pumping station would prevent re-colonisation from further downstream, something which can occur in natural rivers with good longitudinal connectivity (Tummers *et al.,* 2016; Benitez *et al.,* 2018).

During the multi-beam surveys, fish aggregated around the artificial habitats and followed a crepuscular pattern commonly described for pelagic fish communities vulnerable to predation (Pitcher & Turner, 1986). Maximal abundances at dawn and dusk may be associated with movements towards or away from artificial habitats, as is commonly seen with diel movements to and from refuge habitats (e.g., Hohausova *et al.,* 2003). In contrast to previous findings (Bolding *et al.,* 2010; Daugherty *et al.,* 2014; Baumann *et al.,* 2016), this study found no significant difference in fish abundance between habitat structure type. Contrary to expectations, fish abundances were significantly reduced during routine river level management, i.e., single ‘duty’ pump operating, possibly attributed to fish seeking flow refuge inside artificial habitat (e.g., Costa *et al.,* 2019) and thus could not be imaged by the multi-beam sonar. Overall, these findings highlight the importance of monitoring artificial habitats under real-world conditions (i.e., Hale *et al.,* 2015) to understand the influence of diurnal processes, artificial habitat structure and flow on effectiveness as both predator and flow refuge.

5.4.1 Future research

The fortunate coincidence of an extreme flood event occurring mid-investigation cannot be planned for or implemented into an empirical study design due to unpredictability of such events. But, if an opportunity arose to study these conditions again, this work would benefit from an increased temporal rate of SSS surveys, i.e., immediately before and after an extreme pumping event. Although not be possible at Tydd PS due to the volumes of water pumped presenting a risk to people, equipment and fish in nets, the collection of entrained fish from pump outlets would directly quantify the number of fish entrained (e.g., Baumgartner *et al.,* 2009). Alternatively, incorporating telemetry data and tracking fish would be advantageous to confirm downstream displacement of fish and pumping station entrainment time (Thorstad *et al.,* 2013), although this would need considerable foresight to ensure tagged fish were not released immediately prior to an extreme flow event. Future artificial habitat research needs to understand the effectiveness of full-scale habitat restoration efforts for predator and flow refuge; poorly placed artificial habitats are ineffective (Hale *et al.,* 2015). Telemetry techniques (e.g., passive integrated transponder tags) would be required to quantify the number of fish inside artificial habitat during floods (e.g., Teixeira & Cortes, 2007), although vast numbers of fish may need to be tagged in a large river and it is unlikely all artificial habitat installations could be studied.

5.4.2 Conclusions and management implications

Populations of river-resident fish in lowland flood relief drain systems are highly abundant and thus river mangers and ecologists have a responsibility to understand the impact of FRM activities (e.g., in-channel habitat removal) and pump operations on the distribution, abundance and behaviour of fish. During the course of this investigation at a flood relief pumping station (total capacity = 20.17 cumecs), a coincidental major rainfall event (131mm over 31 days; 150% of the 1981 – 2010 average) caused all six pumps to operate for four days. This study uniquely demonstrated that thousands of fish were potentially removed from the channelised and homogenised upstream river. In future years, climate change will drive an increased necessity for flood relief pump operations (Chang *et al.,* 2013; Hannaford, 2015), and thus exacerbate the problem demonstrated here and increase the necessity for management actions. While safer operations of pumping stations tend to focus on fish-friendly pumps for diadromous fish (Bierschenk *et al.,* 2019), this study has demonstrated a requirement for FRM to be more ecological sensitive by providing sources of flow refuge in homogenised systems to prevent population-scale impacts on river-resident fish. Further, this study also demonstrates the potential of artificial habitat for predator refuge (when pumps were not operational), but further investigation is required to understand effectiveness of catchment-scale installations and the potential as flow refuge. The novel findings presented here, and the proposed management actions are critical for ensuring long-term survival of river-resident fish communities in pumped catchments around the world.

6 GENERAL DISCUSSION

6.1 Introduction

Lowland river-resident fish thrive in unmodified rivers with longitudinal and lateral connectivity and heterogeneous habitats that provide refuge from predation and flow, and facilitate ecologically conflicting abiotic-biotic trade-offs (Hudie & Dill, 1994; Basille *et al.,* 2015; Wolf *et al.,* 2017). However, anthropogenic modifications for Flood Risk Management (FRM) have homogenised river systems by altering the spatiotemporal distribution of habitats for fish. The demand for flood risk management necessitates the use of pumping stations to control water levels and provide flood-relief, which also requires seasonal River Maintenance Measures (RMM) including the removal of riparian, marginal and in-channel vegetation (Baczyk *et al.,* 2018). In pumped catchments, this has led to fish occupying pumping stations, which present a major risk of mortality (Rytwinski *et al.,* 2017), but the physical structure and weed screened intake, counterintuitively provides fish with protection from predators in habitat void catchments. Bespoke legislation (i.e., Eels Regulations 2009) exists for the protection of conservation-status diadromous fish at pumping stations (Bolland *et al.,* 2019). Given, the Water Framework Directive (WFD) also suggests operational managers should provide protection for river-resident fish, but ecological considerations are rarely implemented into management and the literature concerning protection of river-resident fish at hazardous intakes is rare (Baumgartner *et al.,* 2009; Kühne & Schwevers, 2016; Reckendorfer *et al.,* 2018; Knott *et al.,* 2019). Understanding the ecological behaviours of river-resident fish in modified pumped catchments could be used to improve protection at pumping stations by informing safe operation and determining remedial measures.

The overall aim of this thesis was to develop an understanding of the behavioural ecology of lowland river-resident fish species at pumping stations and to inform safe operation and identify suitable remedial solutions. Initially, a pluriannual study was performed at an off-channel flood-relief pumping station where the focus was on passively quantifying (using multi-beam sonar) temporal fish presence across the channel entrance of the pumping station in context of lateral diel movements, refuge from predation and under three different hydrological scenarios, including a year without pump operation (Chapter 2). Then, understanding the temporal rate of predator-prey interactions, the attack behaviour of predators, and the refuge seeking behaviour of prey occupying a pumping station in a heavily modified, single-thread lowland river was achieved using multi-beam sonar (Chapter 3). To investigate the potential for habitat restoration in pumped catchments using artificial habitat, two designs were tested in controlled conditions with a unique iterative experimental design (Chapter 4). Finally, catchment-wide distribution and abundance of river-resident fish in a pumped flood-relief lowland drain and at artificial habitat designed to provide predator and flow refuge for river-resident fish occupying a pumping station intake was examined before and after a major flood event using state-of-the-art side-scan sonar (Chapter 5). In this chapter, the knowledge gained from chapters 2 to 5 are discussed with reference to existing literature and key conclusions and recommendations for management and future studies are presented.

6.2 Understanding behavioural ecology of river-resident fish at pumping stations

Chapter 1 provided an overview of the key ecological factors considered for habitat selection and habitat use of river-resident fish. Specifically, this was presented in the context of selecting high-quality habitats which facilitate trade-offs between foraging and predation, and refuge from abiotic factors such as flooding and temperature associated costs. In unmodified rivers, river-resident fish have adapted to such conditions by moving between habitats which offer different resources i.e., foraging sites and predator refuges. How exactly these processes occur in rivers which have been modified for flood risk management, including the operation of pumping stations and use of river maintenance measures, and thus how the regular ecological behaviours of river-resident fish interact with pumping stations was unclear and has been developed throughout this thesis.

Non-invasive multi-beam sonar recordings of thousands of river-resident fish moving laterally from a main-river to an off-channel pumping station has provided fundamental evidence for demonstrating the need to protect these species from hazardous intake operations (Chapter 2). This research provided an unprecedented insight into the ecologically sensitive temporal activity patterns of river-resident fish at a pumping station. Specifically, crepuscular movements towards the pumping station were predicted by the photoperiod and cool temperatures and were representative of ecological trade-offs between feeding and predation costs (e.g., Basille *et al.,* 2015; Fu *et al.,* 2015). When the intake area is safe (i.e., no operation during winter), huge aggregations of fish occur and settle to overwinter, which counterintuitively elevate entrainment risk for subsequent flood-relief pump operations. Further, diel movements were disrupted by intermittent changes to water level, but in contrast to previous findings (e.g., Hohausova *et al.,* 2003; Lyon *et al.,* 2010; Tripp *et al.,* 2016) hydrologically stable conditions were a predictor of fish movement towards the pumping station, suggesting fish did not move laterally during high river levels (Chapter 2). When river levels reached 7.6 mAOD a floodgate was lowered, trapping thousands of fish upstream and increasing vulnerability to entrainment during pump. Additionally, fish counts taken upstream of the floodgate 24h before and 24h after two pump operations suggested up to 85% of fish could be entrained in a single pump event. This work significantly moves forward previous anecdotal suggestions that river-resident fish overwinter in pump intake chambers (Turnpenny & O'Keeffe, 2005; Reeds, 2019), and has provided fundamental evidence for demonstrating a need to protect river-resident fish at pumping stations.

Seasonal RMMs in pumped catchments have adverse effects on the distribution of essential winter predator refuge habitats for river-resident fish and is thought to be a primary driver for fish aggregations at pumping stations, although not directly quantified. In Chapter 3, a methodology using multi-beam sonar was developed based on Price *et al.* (2013) and provided a unique insight into the ecological behaviours of river-resident fish at pumping stations by simultaneously quantifying predator-prey interactions. In support of diel movements found in Chapter 2, prey fish occupied the pumping station during the day for refuge from predators and left at night to forage, similar to diel schooling movements associated with predation risk described in Campenella *et al.* (2019). Cormorant attacks were density-dependant and occurred during the crepuscular period and daytime and pike were present in all temporal periods (including night), but only attacked during the crepuscular period. River-resident prey fish managed predation-risk by fleeing towards a pumping station and seeking refuge behind the weed screen, a finding which has been uniquely quantified here for the first time and moves forward previous suggestions towards the use of anthropogenic structures for prey refuge (Chester & Robson, 2013). These findings support the maladaptive habitat selection process described in Hale *et al.,* (2015), but present it in a new context by demonstrating how river-resident fish in habitat-void pumped catchments have paradoxically become attracted to hazardous pumping stations for refuge from predators (Chapter 2 - 5). Accordingly, this study captured a previously unconsidered non-consumptive effect of predation by determining predator mediated use of a hazardous refuge in the absence of upstream habitat (Donelan *et al.,* 2017). Future considerations for the impacts of river maintenance measures (e.g., Baczyk *et al.,* 2018) therefore need to include the maladaptive occupation of pumping stations for predator refuge, and ultimately the concentration of predator-prey interactions and potential for strengthened non-consumptive predation effects at these structures.

The use of experimental testing in a laboratory-controlled environment enabled identification of the ecological responses of river-resident fish to the addition and removal of habitat in a scenario designed to mimic a pumped catchment i.e., a downstream pumping station, open water and alternative habitat choice (Chapter 4). Fundamentally, this research has helped understand the habitat selection behaviours of a ubiquitous river-resident fish (common roach). All roach preferred a pumping station when no alternative habitat was provided, adding further evidence that fish are attracted to these structures in habitat-void rivers (Chapter 2 - 5). Half of all study fish remained in the pumping station when an alternative habitat was added and only half of the remaining fish located and occupied the introduced habitat (Chapter 4). Accordingly, this experiment was able to demonstrate the potential for an equal preference trap (i.e., habitats are equally favourable; Robertson & Hutto, 2006), a perceptual trap (i.e., addition of habitat reinforces selection of poor habitat; Pattern & Kelly, 2010) and an ecological trap (i.e., fish select a poor-quality habitat over a high-quality habitat; Hale *et al.* 2016). Such response of fish to the provision of alternative habitat has shown how maladaptive attraction to pumping stations (Chapter 3) can alter refuge seeking behaviours, and thus prevent fish occupying novel habitats in pumped catchments with degraded habitat (Chapter 4) (Hale *et al.,* 2015). Accordingly, this research contests the Field of Dreams hypothesis (Hilderbrand *et al.,* 2005) and suggests 'if you build it, they might come' (e.g., Sudduth *et al.,* 2011). Thus, adding alternative habitats without thorough consideration towards the ecological behaviours of river-resident fish will likely lead to restoration failures in pumped catchments (Hale *et al.,* 2017). Overall, this research increased knowledge of river-resident fish habitat selection behaviour.

Side-scan sonar provided an unrivalled spatial quantification of river-resident fish distribution in a pumped flood-relief drain with heavily degraded river habitats (Chapter 5). This novel method shows great promise for mapping spatiotemporal distribution and abundance of fish with potential for identifying habitat selection processes which occur on spatial scales not considered by fixed deployments (i.e., multi-beam sonar). River-resident fish were highly abundant, but distribution of fish was limited to a single location (under a bridge) upstream of a pumping station (Chapter 5). The limited distribution of fish was associated with a high degree of RMMs and the subsequent homogenisation and degradation of refuge habitat required for prey to manage predation risk. Following an extreme rainfall event and a major flood-relief pump operation, thousands of fish were seemingly displaced downstream and entrained through pumps (Chapter 5). Thus, this research has demonstrated that floods in pumped catchments can have catastrophic effects of river-resident fish populations, potentially far exceeding the effects of floods on fish in natural systems (Peirson *et al.,* 2008). The demand for appropriate mitigation to protect river-resident fish in these conditions will rise in future years as climate change increases the necessity for flood relief pump operations (Chang *et al.,* 2013; Hannaford, 2015). Accordingly, FRM needs to become more ecologically sensitive by providing alternative habitat options for river-resident fish in pumped catchments.

6.3 Providing protection for river-resident fish at pumping stations

6.3.1 Fish-friendly operational management

Changes made to operational management of pumping stations have received little attention in the literature. Although previous authors have alluded to the possibility of operational changes at hazardous intakes (Chapter 1, section 1.4.3), as yet no study has explored the possibility with the interrogation given here (Chapter 2). A pluriannual quantification of river-resident fish presence was achieved using multi-beam sonar (DIDSON) and revealed that the overall temporal frequency in diel presence of fish was similar that established in the literature (e.g., Nunn *et al.,* 2010; Nowak *et al.,* 2019), but the operational regime of the pumping station significantly interrupted diel movement patterns. Further, similar diel movements between a pumping station (without pump operation) and upstream river were observed in a different catchment and revealed a concentration of predator-prey interactions during the crepuscular period (Chapter 3). Arguably these findings have highlighted the use of pumping stations as refuge to be considered as one of the primary drivers behind diel movements of river-resident fish in pumped catchments, especially in single-thread channels (Chapter 3 & 5). Understanding these movements will be fundamental to modifying operation of pumping stations.

In addition to changing when pumps operate, modifying floodgate operations so that the floodgate was lowered ahead of predicted diel river-resident fish movements successfully reduced immigration into the off-channel area immediately before pumps operated, reducing the number of fish vulnerable to entrainment (Chapter 2). Given that closing the floodgate prevented passage of fish, optimising the timing of their operation will provide a quick and cheap non-engineered solution for reducing lateral movements of fish into hazardous areas. These previously unconsidered interactions between pumping station operation and diel movement behaviour of river-resident fish will be effective for incorporating fish-friendly practices into operational management and reducing entrainment. Accordingly, the quantified maximal periods of fish presence presented here provide new evidence and move forward the concept of timing operation of hazardous intakes towards movements of the prevailing fish community (Baumgartner *et al.,* 2009; Kühne & Schwevers, 2016; Reckendorfer *et al.,* 2018; Knott *et al.,* 2019), a finding which has global ramifications.

6.3.2 Provision of alternative artificial fish habitat

Pumped catchments are largely composed of heavily channelised, single-thread rivers with homogenised riverbanks and heavily degraded fish habitats. Providing protection for river-resident fish in these systems is challenging as traditional methods such as physical screening and behavioural guidance systems are ineffective (see Chapter 1.4). Given that fish in these systems are now expected to occupy pumping stations for refuge (Chapters 2 – 5), fish which are prevented entry or removed from pumping stations require suitable alternative habitat or face increased vulnerability to high flows and predation. In Chapter 2, changes to when pumps operate and modification of floodgate operations to prevent entry of fish before pumps operate are recommended as protection measures for river-resident fish, but neither of these options address habitat provisions. Chapter 3 exemplified the concentration of predator-prey interactions at a pumping station, in turn presenting a need for alternative habitats to be installed upstream of pumping stations to provide safe predator refuges away from hazardous intakes.

It is shown in Chapters 4 and 5 that installing artificial habitats in pumped catchments will provide a cheap solution for protecting river-resident fish at pumping stations, if suitable planning and monitoring is performed. An iterative experimental process intended to simulate a real-world artificial habitat installation revealed artificial habitats designed to mimic marginal reed beds can provide attractive alternative habitat, which roach preferred compared to a simulated pumping station design (Chapter 4). Similar to findings by Russell *et al.* (2008) and Orpwood *et al.* (2010), artificial habitats with overhead cover were preferred by roach and will be required to protect river-resident fish from avian predators (Chapter 4). Stimulating occupancy of artificial habitat and ensuring fish switched from selecting pumping station habitat to selecting artificial habitat required habitat management i.e., a period of physical exclusion from the pumping station; a finding which will be fundamental to the success of installing artificial habitats in pumped catchments.

A pilot installation of three different artificial habitat designs upstream of a pumping station in a pumped flood-relief lowland drain was conducted in Chapter 5 and was able to demonstrate the potential for artificial habitat as predator refuge. Importantly, reasonable abundances of river-resident fish were quantified (using multi-beam sonar) at the artificial habitats, but data collection was limited by pump operation in real-world conditions and thus further study is required to determine the true effectiveness of artificial habitat in this scenario. Hence, this research highlights the importance of rigorous experimental testing and the creation of a pilot study before implementing full-scale restoration using artificial habitats (Hale *et al.,* 2017). Collectively, these findings show great promise for the use of artificial habitats to protect river-resident fish in pumped catchments; in Chapter 2 artificial habitat could be provided in the off-channel area for low-flow refuge during pump operation and in Chapter 3 artificial habitat could be provided upstream of the pumping station to provide alternative predator refuge.

6.4 Recommendations for management and future research

River-resident fish performed regular diel movements between a main-river and an off-channel area with a pumping station over three years. **It is recommended that knowledge of habitat selection and diel movement behaviour of river-resident fish is incorporated into operational management of pumping stations to provide fish-friendly operational practices.** Operating pumps when fish presence is low will reduce entrainment and provide ecological benefits for river-resident fish communities. Further, changing when pumps operate will be considerably more cost-effective than retrofitting alternative protection measures (e.g., fine-mesh screening), which are also undesired for pumping station operation.

Operational changes for fish protection are broadly applicable to pumping stations globally, although this will require bespoke ecological assessments for different pumping station installations and the local prevailing fish community. In this study (Chapter 2), fish abundance at the pumping station was highest during daylight and lowest at night. **It is recommended that pumps are not started during the day to protect the most fish.** Similar recommendations have been suggested by previous authors who have studied hydropower and power station intakes but is yet to be incorporated into pumping station operational management. **It is recommended that further research is conducted on the integration of fish-friendly operational management at pumping stations and the response of river-resident fish to operational changes.** Such research will address concerns for how effective operational changes will be for reducing river-resident fish entrainment.

When integrating ecological considerations for river-resident fish into operational management plans it is important to fully understand the relationship between prevailing river conditions (i.e., river levels) and when pumps operate, along with associated operational infrastructure. In this study (Chapter 2), lateral movement of river-resident fish into an off-channel area with a pumping station were associated with the crepuscular period and thus were prevented by lowering a flood gate prior to dawn. **It is recommended that the operation of infrastructure (i.e., flood gates and lock gates) associated with pumping stations elsewhere is monitored to determine whether operation can be timed to prevent river-resident fish interacting with hazardous intakes ahead of predicted pump operations.** By doing so, entrainment of fish will be reduced, but further investigation is required to determine the effects of isolating fish from predator refuge areas at the pumping station, both used when pumps are and are not operational, i.e., do fish find adequate flow and predator refuge, respectively. Future research could utilise multi-beam sonar (DIDSON or ARIS) installed downstream and upstream of flood gates to simultaneously quantify behavioural responses of fish to flood gate operation.

Chapter 2 provided a temporal understanding of river-resident fish presence before and after pump operations and showed that fish presence was reduced by 85% following pump operation. This provided insight into the potential negative impacts on fish populations associated with pump operation. Although it has been presumed here that fish were entrained, it is not clear if they were injured or deterred from using the off-channel area. **It is recommended that future research on river-resident fish protection at pumping stations validates fish entrainment during pump operation.** This could be achieved by quantifying the number of fish entrained during pump operation using multi-beam sonar (DIDSON or ARIS) and installing nets across pump outfalls to quantify and validate numbers of fish retrieved following entrainment.

Multi-beam sonar (DIDSON) proved to be an invaluable tool for passively quantify the ecological interactions of predators and river-resident prey fish, a phenomenon which has previously only been observed in rivers using baited predation recorders. **It is recommended that future studies on predator-prey interactions of fish specifically incorporate multi-beam technology to quantify behaviours of predators and prey.** Such efforts will provide a far greater understanding of the behavioural processes and ramifications of predator-prey ecology than previously achieved with invasive methods (e.g., stomach content analysis) or from manufactured observations. Given, the methodology used here was limited to quantifying predator-prey interactions in the insonified window and thus it was not possible to determine interactions out of view. **It is recommended that future studies using multi-beam spatially deploy sonar over suitable temporal scales to gather more inclusive knowledge on distribution of predation events.** This could be achieved by attempting to quantify predation events away from the pumping station to determine the rate of predation which occurs upstream.

Predator-prey interactions which occur at pumping stations are complex, within which temporal variations in predator presence, attack rate, refuge use by prey and other behavioural considerations exist. Further, lowland rivers in pumped catchments exist in many physical constructs, ranging from large main-rivers with off-channel areas to single-thread channels with degraded habitats, both of which can have contrasting operational regimes. **It is recommended that similar investigations to the predator-prey analysis presented here are performed in pumped catchments with different physical constructs and operational regimes in an attempt to fully determine whether FRM and RMM causes aggregations of predators and river-resident prey fish at pumping stations.** Additionally, this study was limited to one winter season (Chapter 3). **It is recommended that a pluriannual study is developed to determine**

the interannual relationship and long-term trends in predator-prey interactions at pumping stations. By doing so, a thorough understanding of the effects of seasonality in predator-prey interactions at pumping stations will be gained. If monitoring was to be attempted throughout the year then an improved understanding of the effect of RMMs on river-resident fish distribution in pumped rivers will also be gained.

Chapters 2 and 3 have focused on generating a broad understanding of river-resident fish behavioural ecology at pumping stations and **it is recommended that future studies are designed to cover individual ecological components in more detail.** For example, quantifying longitudinal and lateral directional movement, including the regular nocturnal upstream foraging movements. This will be advantageous for understanding dispersal of river-resident fish away from pumping stations and could be achieved by using electronic tags (e.g., Passive Integrated Transponder (PIT) or acoustic) tags in fish and positioning monitoring equipment throughout the river.

The impact of anthropogenic practices, including the seasonal removal of macrophytes, which modify winter refuge for prey fish communities and concentrate them at pumping stations (Chapter 3) is arguably underappreciated by pumping station operators and flood risk management stakeholders. Fundamentally, the homogenised nature of these ecosystems do not meet the requirements for fish habitats under the Water Framework Directive (2000/60/EEC) and Habitat Directive (92/43/EEC). Initially, where possible, **it is recommended that the length of maintained riverbanks is decreased so ecological interactions can occur more naturally**. When river maintenance measures cannot be altered **it is recommended that artificial refuge in the form of enclosed cages with overhead cover are installed upstream of pumping stations.** Providing river-resident fish with safe alternative habitat will help prevent occupancy of pumping stations and reduce predator concentrations.

The successful manipulation of habitat selection and overall habitat preference over the duration of the laboratory experiment emphasised the promise for using alternative artificial habitats to provide protection from predators for river-resident fish when they are (temporarily) prevented from entering pumping stations (Chapter 4). Providing artificial habitat in the presence of a simulated pumping station was partially successful, but habitat management (physical exclusion from pumping station) successfully altered habitat preference of roach even when pumping station was provided again. **It is recommended that future installations of artificial habitats upstream of pumping stations incorporate habitat management to manipulate existing habitat preferences of river-resident fish.** Using knowledge of diel movements of river-resident fish to and from pumping stations (Chapter 2 & 3), this could be achieved by pulling a net across pump intakes to prevent fish entering. Fish exposed in open water will then locate nearby habitat. **It is recommended that long-term, pluriannual monitoring and quantification of fish occupancy accompanies future artificial habit installations.** This could be achieved by using electronic tags (e.g., Passive Integrated Transponder (PIT)) tags in fish and positioning within the artificial habitats to detect fish. By doing so, knowledge on the effectiveness of artificial habitats will be improved and the temporal frequency of habitat management activities required for fish to occupy artificial habitats can be determined.

During the habitat selection laboratory experiment individual roach were not marked or tagged and thus it was not possible to identify movements and behaviours of individuals. **It is recommended that future habitat selection laboratory experiments incorporate tagged fish in an attempt to elucidate the behaviours of individuals.** Visible Implant Elastomer tags are ineffective for this due to issues tracking them in video images. Alternatively, this could be achieved by scaling-up the experiment to a larger aquaria facility and using Passive Integrated Transponder tags in fish with antennas added to the entrance of specific habitat options. Additionally, individual fish may display differing neophillic or neophobic habitat selection behaviours. **It is recommended that individual boldness assessments are performed prior to performing experiments.** By doing so, this knowledge will help inform how artificial habitats are expected to perform in real-world conditions.

Artificial habitats designed for predator and low-flow refuge were installed as a pilot study 50m upstream of a flood-relief pumping station and provided protection for river-resident fish during duty pump operation (Chapter 5). The next step in this research is to incorporate knowledge from restoration planning (Chapter 4) and the pilot installation (Chapter 5) to design a full-scale implementation of artificial habitats to correctly determine if the real-world application provides long-term protection for river-resident fish in pumped catchments. Further, it was unclear whether fish were able to locate and occupy the artificial habitats for flow refuge during a flood, and thus future research is required to specifically identify the use of artificial habitats as flow refuge. Initially, **it is recommended that reaches upstream of a pumping station where artificial habitats can be installed are identified, with reference to locations where fish are abundant and vulnerable to predation and flow displacement.** Further, the size, number and spatial distribution of habitats required to support river-resident populations must be fully determined. Given the distribution of river-resident fish identified with side-scan sonar (Chapter 5), **it is recommended that artificial habitats are installed in marginal locations between 0.1 and 1km upstream of a pumping station.** Granted, the further away fish can be deterred from a pumping station the greater the benefit for reducing entrainment likeliness. Understanding how river-resident fish disperse between these habitats will be essential for determining their positioning and effectiveness as refuge in future installations.

Pumping stations which do not operate for long periods (as little as one event in five years) paradoxically offer safe refuge for river-resident fish but could have catastrophic fish kills when pumps operate. However, there is currently a paucity in understanding how fish respond to unexpected events and the severity of impacts on the prevailing fish community. Pluriannual side-scan sonar surveys showed fish populations in a pumped flood-relief drain were numerous before a flood, but the drain was later completely void of fish after a major flood-relief pump operation (Chapter 5). **It is recommended that, when possible (i.e., a predictable operation), the abundance of river-resident fish occupying pumping stations is directly quantified before and after pump operation.** With reasonable foresight a combination of side-scan and multi-beam sonar surveys could be used to achieve this in combination recommendations for post-entrainment validation.

Side-scan sonar provided an unprecedented insight into the catchment-wide distribution of river-resident fish in a pumped flood-relief drain with degraded habitats (Chapter 5), where netting and electric fishing were not possible. This novel method has unrivalled potential for providing a low-cost, low-labour and high accuracy approach to determine distribution of river-resident fish over large spatial scales. **It is recommended that future investigations of river-resident fish distribution in pumped catchments utilise side-scan sonar.** Further, this study was able to determine the impact of a major flood on a population of river-resident fish residing upstream of a pumping station using annual side-scan surveys but would greatly benefit from an increased temporal sample rate. **It is recommended that future side-scan surveys are performed at regular temporal periods (e.g., once a month) to continually assess the distribution of river-resident fish.** Such efforts will provide enhanced knowledge on the distribution of river-resident fish in heavily degraded pumped catchments and will be imperative for informing where to install artificial habitats.

6.5 Conclusion

In recognizing the ecological value and importance of river-resident fish to biodiversity and ecosystem function, operational management of pumping stations and other hazardous intakes should shift towards a more inclusive management regime that considers conservation of non-diadromous fish species. River-resident fish performed regular and predictable diel movements between a pumping station and main-river or upstream habitats in two different catchments in response to abiotic factors (temperature, hydrology and pump operation) and biotic factors (predator-prey interactions). Integrating ecological considerations for river-resident fish into operational management is currently challenging due to contrasting objectives of pumping station stakeholders and operators and the desires for fish protection from ecologists and conservationists. This research has identified that changes to pumping station operations, i.e., night-time start-up, and associated infrastructure, i.e., close floodgates prior to dawn, could simply and cheaply remediate the likelihood of significant fish entrainment during start-up. However, further efforts are needed to prevent river-resident fish occupying pumping stations in the first instance, which will also dissipate intense predator aggregations. The provision of alternative artificial habitat holds promise to provide river-resident fish with a safe habitat once temporarily excluded from pumping stations. However, further research is needed to quantify the applicability of this measure in-situ and on a pluriannual basis, to determine long-term responses of river-resident fish. Overall, the findings presented in this thesis have provided a fundamental insight into understanding the ecological requirements of river-resident fish in an effort to improve ecological function of flood-relief pumped catchments by informing operational changes and providing protection with alternative artificial habitats.

REFERENCES

Abecasis, D., Steckenreuter, A., Reubens, J., Aarestrup, K., Alós, J., Badalamenti, F., Bajona, L., Boylan, P., Deneudt, K., Greenberg, L., Brevé, N., Hernández, F., Humphries, N., Meyer, C., Sims, D., Thorstad, E. B., Walker, A. M., Whoriskey, F., Afonso, P. (2018) A review of acoustic telemetry in Europe and the need for a regional aquatic telemetry network. *Animal Biotelemetry*, 6(1).

Adam, B., Bosse, R., Dumont, U., Hadderingh, R. H., Joergensen, L., Kalusa, B., Lehmann, G., Pischel, R. & Schwevers, U. (2006) *Fish Protection Technologies and Downstream Fishways*. Germany: DWA.

Adam, B. & Schwevers, U. (2020) *Fish Protection Technologies and Fish Ways for Downstream Migration*. Switzerland: Springer.

Allen, M. J., Bush, S. C., Vining, I. & Siepker, M. J. (2014) Black Bass and Crappie Use of Installed Habitat Structures in Table Rock Lake, Missouri. *North American Journal of Fisheries Management*, 34(2), 223-231.

Allouche, S., Thevenet, A. & Gaudin, P. (1999) Habitat use by chub (*Leuciscus cephalus L. 1766*) in a large river, the French Upper Rhone, as determined by radiotelemetry. *Archiv Fur Hydrobiologie*, 145(2), 219-236.

Amaral, S. D. (2003) Evaluation of Angled Bar Racks and Louvers for Guiding Silver Phase American Eels. *American Fisheries Society Symposium*.

Angelopoulos, N. V., Harvey, J. P., Bolland, J. D., Nunn, A. D., Noble, R. A. A., Smith, M. A., Taylor, M. J., Masters, J. E. G., Moxon, J. & Cowx, I. G. (2018) Overcoming the dichotomy of implementing societal flood risk management while conserving instream fish habitat - A long-term study from a highly modified urban river. *Journal of Environmental Management*, 224, 69-76.

Artero, C., Marchetti, S., Bauer, E., Viala, C., Noël, C., Koenig, C., Berzins, R. & Lampert, L. (2021) High-Resolution Acoustic Cameras Provide Direct and Efficient Assessments of Large Demersal Fish Populations in Extremely Turbid Waters. *Applied Sciences*, 11(4).

Baczyk, A., Wagner, M., Okruszko, T. & Grygoruk, M. (2018) Influence of technical maintenance measures on ecological status of agricultural lowland rivers - Systematic review and implications for river management. *Science of the Total Environment*, 627, 189-199.

Baker, N. J., Wright, R. M., Cowx, I. G., Murphy, L. A. & Bolland, J. D. (2021) Downstream passage of silver European eel (Anguilla anguilla) at a pumping station with a gravity sluice. *Ecological Engineering*, 159.

Barnthouse, L. W. (2013) Impacts of entrainment and impingement on fish populations: A review of the scientific evidence. *Environmental Science & Policy*, 31, 149-156.

Barry, J., McLoone, P., Fitzgerald, C. J. & King, J. J. (2020) The spatial ecology of brown trout (*Salmo trutta*) and dace (*Leuciscus leuciscus*) in an artificially impounded riverine habitat: results from an acoustic telemetry study. *Aquatic Sciences*, 82(3).

Basille, M., Fortin, D., Dussault, C., Bastille-Rousseau, G., Ouellet, J. P. & Courtois, R. (2015) Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. *Ecology*, 96(10), 2622-31.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting Linear Mixed-Effects Models Usinglme4. *Journal of Statistical Software*, 67(1).

Baumann, J. R., Oakley, N. C. & McRae, B. J. (2016) Evaluating the Effectiveness of Artificial Fish Habitat Designs in Turbid Reservoirs Using Sonar Imagery. *North American Journal of Fisheries Management*, 36(6), 1437-1444.

Baumgartner, L. J., Reynoldson, N. K., Cameron, L. & Stanger, J. G. (2006) Assessment of a Dual-frequency Identification Sonar (DIDSON) for application in fish migration studies. *NSW fisheries annual report*, 84.

Baumgartner, L. J., Reynoldson, N. K., Cameron, L. & Stanger, J. G. (2009) Effects of irrigation pumps on riverine fish. *Fisheries Management and Ecology*, 16(6), 429-437.

Beauchamp, D. A., Wahl, D. H. & Johnson, B. M. (2007) Predator–Prey Interactions, *Analysis and interpretation of inland fisheries data*.

Becker, A. & Suthers, I. M. (2014) Predator driven diel variation in abundance and behaviour of fish in deep and shallow habitats of an estuary. *Estuarine, Coastal and Shelf Science*, 144, 82-88.

Belcher, E. & Lynn, D. C. (2000) Acoustic, Near-Video-Quality Images For Work In Turbid Water. *The Proceedings of Underwater Intervention 2000 Conference.*

Belletti, B., Garcia de Leaniz, C., Jones, J., Bizzi, S., Borger, L., Segura, G., Castelletti, A., van de Bund, W., Aarestrup, K., Barry, J., Belka, K., Berkhuysen, A., Birnie-Gauvin, K., Bussettini, M., Carolli, M., Consuegra, S., Dopico, E., Feierfeil, T., Fernandez, S., Fernandez Garrido, P., Garcia-Vazquez, E., Garrido, S., Giannico, G., Gough, P., Jepsen, N., Jones, P. E., Kemp, P., Kerr, J., King, J., Lapinska, M., Lazaro, 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. & Zalewski, M. (2020) More than one million barriers fragment Europe's rivers. *Nature*, 588(7838), 436-441.

Benitez, J. P., Dierckx, A., Matondo, B. N., Rollin, X. & Ovidio, M. (2018) Movement behaviours of potamodromous fish within a large anthropised river after the reestablishment of the longitudinal connectivity. *Fisheries Research*, 207, 140-149.

Berryman, A. A. & Hawkins, B. A. (2006) The refuge as an integrating concept in ecology and evolution. *Oikos*, 115(1), 192-196.

Bevelhimer, M., Scherelis, C., Colby, J. & Adonizio, M. A. (2017) Hydroacoustic Assessment of Behavioral Responses by Fish Passing Near an Operating Tidal Turbine in the East River, New York. *Transactions of the American Fisheries Society,* 146(5), 1028-1042.

Bierschenk, B. M., Pander, J., Mueller, M. & Geist, J. (2019) Fish injury and mortality at pumping stations: a comparison of conventional and fish-friendly pumps. *Marine and Freshwater Research*, 70(3).

Bolding, B., Bonar, S. & Divens, M. (2010) Use of Artificial Structure to Enhance Angler Benefits in Lakes, Ponds, and Reservoirs: A Literature Review. *Reviews in Fisheries Science*, 12(1), 75-96.

Bolland, J. D., Cowx, I. G. & Lucas, M. (2008) Factors affecting the dispersal of coarse fish *Environment Agency Technincal report*. Available online: https://consult.environment-agency.gov.uk/east-anglia-c-e/hoveton-great-broad-temporary-fish-barriers/supporting_documents/factorsaffectingcoarsefishdispersalreprtee.pdf

Bolland, J. D., Murphy, L. A., Stanford, R. J., Angelopoulos, N. V., Baker, N. J., Wright, R. M., Reeds, J. D. & Cowx, I. G. (2019) Direct and indirect impacts of pumping station operation on downstream migration of critically endangered European eel. *Fisheries Management and Ecology*, 26(1), 76-85.

Bolland, J. D., Nunn, A. D., Lucas, M. C. & 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, 434-440.

Bollinger, M. A. & Kline, R. J. (2017) Validating Sidescan Sonar as a Fish Survey Tool over Artificial Reefs. *Journal of Coastal Research*, 336, 1397-1407.

Bond, N. R. & Lake, P. S. (2003) Local habitat restoration in streams: Constraints on the effectiveness of restoration for stream biota.

Bosiger, Y. J., Lonnstedt, O. M., McCormick, M. I. & Ferrari, M. C. (2012) Learning temporal patterns of risk in a predator-diverse environment. *PLoS One*, 7(4), e34535.

Bosiger, Y. J. & McCormick, M. I. (2014) Temporal links in daily activity patterns between coral reef predators and their prey. *PLoS One*, 9(10), e111723.

Brodersen, J., Nilsson, P. A., Hansson, L. A., Skov, C. & Bronmark, C. (2008) Condition-dependent individual decision-making determines cyprinid partial migration. *Ecology*, 89(5), 1195-1200.

Brönmark, C., Hulthén, K., Nilsson, P. A., Skov, C., Hansson, L. A., Brodersen, J. & Chapman, B. B. (2014) There and back again: migration in freshwater fishes. *Canadian Journal of Zoology*, 92(6), 467-479.

Brooker, R. M., Feeney, W. E., White, J. R., Manassa, R. P., Johansen, J. L. & Dixson, D. L. (2016) Using insights from animal behaviour and behavioural ecology to inform marine conservation initiatives. *Animal Behaviour*, 120, 211-221.

Buysse, D., Mouton, A. M., Stevens, M., Van den Neucker, T. & Coeck, J. (2014) Mortality of European eel after downstream migration through two types of pumping stations. *Fisheries Management and Ecology*, 21(1), 13-21.

Campanella, F., Auster, P. J., Taylor, J. C. & Munoz, R. C. (2019) Dynamics of predator-prey habitat use and behavioral interactions over diel periods at sub-tropical reefs. *PLoS One*, 14(2), e0211886.

Catano, L. B., Rojas, M. C., Malossi, R. J., Peters, J. R., Heithaus, M. R., Fourqurean, J. W. & Burkepile, D. E. (2016) Reefscapes of fear: predation risk and reef hetero-geneity interact to shape herbivore foraging behaviour. *Journal of Animal Ecology*, 85(1), 146-56.

Chang, H.-K., Tan, Y.-C., Lai, J.-S., Pan, T.-Y., Liu, T.-M. & Tung, C.-P. (2013) Improvement of a drainage system for flood management with assessment of the potential effects of climate change. *Hydrological Sciences Journal*, 58(8), 1581-1597.

Cheshire, K. J. M., Ye, Q., Gillanders, B. M. & King, A. (2016) Annual Variation in Larval Fish Assemblages in a Heavily Regulated River During Differing Hydrological Conditions. *River Research and Applications*, 32(6), 1207-1219.

Chester, E. T. & Robson, B. J. (2013) Anthropogenic refuges for freshwater biodiversity: Their ecological characteristics and management. *Biological Conservation*, 166, 64-75.

Clough, S. & Turnpenny, A. W. H. (2001) Swimming Speeds in fish: Phase 1. Available online: https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/290589/sw2-026-tr1-e-e.pdf

Conallin, A. J., Hillyard, K. A., Walker, K. F., Gillanders, B. M. & Smith, B. B. (2011) Offstream movements of fish during drought in a regulated lowland river. *River Research and Applications*, 27(10), 1237-1252.

Conallin, J., Boegh, E., Olsen, M., Pedersen, S., Dunbar, M. J. & Jensen, J. K. (2014) Daytime habitat selection for juvenile parr brown trout (Salmo trutta) in small lowland streams. *Knowledge and Management of Aquatic Ecosystems*(413).

Cooke, S. J., Blumstein, D. T., Buchholz, R., Caro, T., Fernandez-Juricic, E., Franklin, C. E., Metcalfe, J., O'Connor, C. M., St Clair, C. C., Sutherland, W. J. & Wikelski, M. (2014) Physiology, behavior, and conservation. *Physiological and Biochemical Zoology*, 87(1), 1-14.

Copp, G. H. (1997) Importance of marinas and off-channel water bodies as refuges for young fishes in a regulated lowland river. *Regulated Rivers-Research & Management*, 13(3), 303-307.

Costa, M. J., Pinheiro, A. N. & Boavida, I. (2019) Habitat Enhancement Solutions for Iberian Cyprinids Affected by Hydropeaking: Insights from Flume Research. *Sustainability*, 11(24).

Cote, J., Clobert, J., Brodin, T., Fogarty, S. & Sih, A. (2010) Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B*, 365(1560), 4065-76.

Coulter, A. A., Schultz, D., Tristano, E., Brey, M. K. & Garvey, J. E. (2017) Restoration Versus Invasive Species: Bigheaded Carps' Use of A Rehabilitated Backwater. *River Research and Applications*, 33(5), 662-669.

Coutant, C. C. & Whitney, R. R. (2000) Fish behavior in relation to passage through hydropower turbines: A review. *Transactions of the American Fisheries Society*, 129(2), 351-380.

Cowan, M. A., Callan, M. N., Watson, M. J., Watson, D. M., Doherty, T. S., Michael, D. R., Dunlop, J. A., Turner, J. M., Moore, H. A., Watchorn, D. J. & Nimmo, D. G. (2021) Artificial refuges for wildlife conservation: what is the state of the science? *Biological Reviews of the Cambridge Philosophical Society*, 96(6), 2735-2754.

Cowx, I. G., Noble, R. A. A., Nunn, A. D., Harvey, J. P., Welcomme, R. L. & Halls, A. (2004) Flow and level criteria for coarse fish and conservation species. *Environment Agency Science Report SC020112/SR*. Available online: https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/291545/scho1204bilg-e-e.pdf

Cowx, I. G. & Welcomme, R. L. (1998) *Rehabilitation of Rivers for Fish*. Oxford, UK: Fishing News Books.

Craig, K. & Crowder, L. B. (2002) Factors Influencing Habitat Selection in Fishes with a Review of Marsh Ecosystems, in Weinstein, P. M. (ed), *Concepts and Controversies in Tidal Marsh Ecology*.

Darr, N. A., Pandit, A. K. & Ganai, B. A. (2014) Factors affecting the distribution patterns of aquatic macrophytes. *Limnological Review*. 14(20), 75 – 81.

Daugherty, D. J., Driscoll, M. T., Ashe, D. E. & Schlechte, J. W. (2014) Effects of Structural and Spatiotemporal Factors on Fish Use of Artificial Habitat in a Texas Reservoir. *North American Journal of Fisheries Management*, 34(2), 453-462.

David, B. O. & Closs, G. P. (2002) Behavior of a stream-dwelling fish before, during, and after high-discharge events. *Transactions of the American Fisheries Society*, 131(4), 762-771.

Davis, J., O'Grady, A. P., Dale, A., Arthington, A. H., Gell, P. A., Driver, P. D., Bond, N., Casanova, M., Finlayson, M., Watts, R. J., Capon, S. J., Nagelkerken, I., Tingley, R., Fry, B., Page, T. J. & Specht, A. (2015) When trends intersect: The challenge of protecting freshwater ecosystems under multiple land use and hydrological intensification scenarios. *Science of the Total Environment*, 534, 65-78.

Dodrill, M. J., Yard, M. D. & Pine, W. E. (2016) Assessing Predation Risks for Small Fish in a Large River Ecosystem between Contrasting Habitats and Turbidity Conditions. *The American Midland Naturalist*, 175(2), 206-221.

Doehring, K., Young, R. G., Hay, J. & Quarterman, A. J. (2011) Suitability of Dual-frequency Identification Sonar (DIDSON) to monitor juvenile fish movement at floodgates. *New Zealand Journal of Marine and Freshwater Research*, 45(3), 413-422.

Donelan, S. C., Grabowski, J. H. & Trussell, G. C. (2017) Refuge quality impacts the strength of nonconsumptive effects on prey. *Ecology*, 98(2), 403-411.

Dos Reis Oliveira, P. C., van der Geest, H. G., Kraak, M. H. S. & Verdonschot, P. F. M. (2019) Land use affects lowland stream ecosystems through dissolved oxygen regimes. *Scientific Reports – Nature,* 9(1), 19685.

Dos Reis Oliveira, P. C., van der Geest, H. G., Kraak, M. H. S., Westveer, J. J., Verdonschot, R. C. M. & Verdonschot, P. F. M. (2020) Over forty years of lowland stream restoration: Lessons learned? *Journal of Environmental Management*, 264, 110417.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z., Knowler, D. J., Leveque, C., Naiman, R. J., Prieur-Richard, A. H., Soto, D., Stiassny, M. L. & Sullivan, C. A. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews of the Cambridge Philosophical Society*, 81(2), 163-82.

DuFour, M. R., Mayer, C. M., Qian, S. S., Vandergoot, C. S., Kraus, R. T., Kocovsky, P. M. & Warner, D. M. (2018) Inferred fish behavior its implications for hydroacoustic surveys in nearshore habitats*. Fisheries Research*, 199, 63-75.

Dugatkin, L. A. & Druen, M. (2004) The social implications of winner and loser effects. *Proceedings of the Royal Society B: Biological Sciences*, 271 Supplement 6, S488-9.

Ebner, B., Clear, R., Godschalx, S. & Beitzel, M. (2009) In-stream behaviour of threatened fishes and their food organisms based on remote video monitoring. *Aquatic Ecology*, 43(2), 569-576.

Egg, L., Mueller, M., Pander, J., Knott, J. & Geist, J. (2017) Improving European Silver Eel (*Anguilla anguilla*) downstream migration by undershot sluice gate management at a small-scale hydropower plant. *Ecological Engineering*, 106, 349-357.

Egg, L., Pander, J., Mueller, M. & Geist, J. (2018) Comparison of sonar-, camera- and net-based methods in detecting riverine fish-movement patterns. *Marine and Freshwater Research*, 69(12), 1905-1912.

Ellner, S. P., McCauley, E., Kendall, B. E., Briggs, C. J., Hosseini, P. R., Wood, S. N., Janssen, A., Sabelis, M. W., Turchin, P., Nisbet, R. M. & Murdoch, W. W. (2001) Habitat structure and population persistence in an experimental community. *Nature*, 412(6846), 538-43.

Environment Agency (2021) Water situation report December 2020. Available online: https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/952056/Water_situation_report_December_2020.pdf

Environment Agency (2022) *EA Ecology & Fish Data Explorer.* Available online: https://environment.data.gov.uk/ecology/explorer/

Ferrari, M. C. O., Elvidge, C. K., Jackson, C. D., Chivers, D. P. & Brown, G. E. (2010) The responses of prey fish to temporal variation in predation risk: sensory habituation or risk assessment? *Behavioral Ecology*, 21(3), 532-536.

Ferrari, R., Malcolm, H. A., Byrne, M., Friedman, A., Williams, S. B., Schultz, A., Jordan, A. R. & Figueira, W. F. (2017) Habitat structural complexity metrics improve predictions of fish abundance and distribution. *Ecography*, 41(7), 1077-1091.

Fjeldstad, H.-P., Pulg, U. & Forseth, T. (2018) Safe two-way migration for salmonids and eel past hydropower structures in Europe: a review and recommendations for best-practice solutions. *Marine and Freshwater Research*, 69(12).

Flikweert, J. & Worth, D. (2012) Pumped catchments Guide for hydrology and hydraulics.

Ford, J. R. & Swearer, S. E. (2013) Shoaling behaviour enhances risk of predation from multiple predator guilds in a marine fish. *Oecologia*, 172(2), 387-97.

Franklin, P. A. & Hodges, M. (2015) Modified tide gate management for enhancing instream habitat for native fish upstream of the saline limit. *Ecological Engineering*, 81, 233-242.

Frehse, F. d. A., Weyl, O. L. F. & Vitule, J. R. S. (2021) Differential use of artificial habitats by native and non-native fish species in Neotropical reservoirs. *Hydrobiologia*, 848(9), 2355-2367.

Fretwell, S. & Lucas, H. (1970) On territorial behavior and other factors influencing habitat distribution in birds.

Fretwell, S. D. (1972) Populations in a seasonal environment. *Monographs in Population Biology*, 5, 1-217.

Fu, C., Fu, S.-J., Cao, Z.-D. & Yuan, X.-Z. (2015) Habitat-specific anti-predator behavior variation among pale chub *(Zacco platypus*) along a river. *Marine and Freshwater Behaviour and Physiology*, 48(4), 267-278.

Gardner, C. J., Deeming, D. C. & Eady, P. E. (2013) Seasonal movements with shifts in lateral and longitudinal habitat use by common bream,Abramis brama, in a heavily modified lowland river. *Fisheries Management and Ecology*, 20(4), 315-325.

Gilligan, D. & Schiller, C. (2003) Downstream transport of larval and juvenile fish in the Murray River. Available online: https://www.dpi.nsw.gov.au/__data/assets/pdf_file/0009/545634/FFRS-50_Gilligan-and-Schiller-2003.pdf

Gliwicz, Z. M. & Jachner, A. (1992) Diel Migrations of Juvenile Fish - a Ghost of Predation Past or Present. *Archiv Fur Hydrobiologie*, 124(4), 385-410.

Gordos, M. (2007) Audit and remediation of fish passage barriers in coastal NSW. Available online: https://cdn.csu.edu.au/__data/assets/pdf_file/0011/748325/Gordos_Matthew_109.pdf

Graham, N., Jones, E. G. & Reid, D. G. (2004) Review of technological advances for the study of fish behaviour in relation to demersal fishing trawls. *ICES Journal of Marine Science,* 61(7), 1036-1043.

Grant, K. R. & Harrington, L. A. (2015) Fish selection by riverine Eurasian otters in lowland England. *Mammal Research*, 60(3), 217-231.

Gremillet, D. & Wilson, R. P. (1999) A life in the fast lane: energetics and foraging strategies of the great cormorant. *Behavioral Ecology*, 10(5), 516-524.

Griffin, J. N., Byrnes, J. E. & Cardinale, B. J. (2013) Effects of predator richness on prey suppression: a meta-analysis. *Ecology*, 94(10), 2180-7.

Hale, R., Blumstein, D. T., Mac Nally, R. & Swearer, S. E. (2020) Harnessing knowledge of animal behavior to improve habitat restoration outcomes. *Ecosphere*, 11(4).

Hale, R., Coleman, R., Pettigrove, V., Swearer, S. E. & Strecker, A. (2015) REVIEW: Identifying, preventing and mitigating ecological traps to improve the management of urban aquatic ecosystems. *Journal of Applied Ecology*, 52(4), 928-939.

Hale, R., Coleman, R., Sievers, M., Brown, T. R. & Swearer, S. E. (2018) Using conservation behavior to manage ecological traps for a threatened freshwater fish. *Ecosphere*, 9(8).

Hale, R., Colton, M. A., Peng, P. & Swearer, S. E. (2019) Do spatial scale and life history affect fish-habitat relationships? *Journal of Animal Ecology*, 88(3), 439-449.

Hale, R. & Swearer, S. E. (2016) Ecological traps: current evidence and future directions. *Proceedings of the Royal Society B: Biological Sciences,* 283(1824).

Hale, R. & Swearer, S. E. (2017) When good animals love bad restored habitats: how maladaptive habitat selection can constrain restoration. *Journal of Applied Ecology*, 54(5), 1478-1486.

Hall, A. & Kingsford, M. (2016) Predators Exacerbate Competitive Interactions and Dominance Hierarchies between Two Coral Reef Fishes. *PLoS One*, 11(3)

Han, J., Honda, N., Asada, A. & Shibata, K. (2009) Automated acoustic method for counting and sizing farmed fish during transfer using DIDSON. *Fisheries Science*, 75(6), 1359-1367.

Hannaford, J. (2015) Climate-driven changes in UK river flows: A review of the evidence. *Progress in Physical Geography-Earth and Environment*, 39(1), 29-48.

Harrison, P. M., Martins, E. G., Algera, D. A., Rytwinski, T., Mossop, B., Leake, A. J., Power, M. & Cooke, S. J. (2019) Turbine entrainment and passage of potadromous fish through hydropower dams: Developing conceptual frameworks and metrics for moving beyond turbine passage mortality. *Fish and Fisheries*, 20(3), 403-418.

Harrison, S. S. C., Pretty, J. L., Shepherd, D., Hildrew, A. G., Smith, C. & Hey, R. D. (2004) The effect of instream rehabilitation structures on macroinvertebrates in lowland rivers. *Journal of Applied Ecology*, 41(6), 1140-1154.

Hateley, J. & Gregory, J. (2006) Evaluation of a multi-beam imaging sonar system (DIDSON) as Fisheries Monitoring Tool: Exploiting the Acoustic Advantage. Available online: http://www.soundmetrics.com/getmedia/0acd2abb-356c-4d2d-8986-9241ab309d52/UKEA_DIDSON_Report.pdf.aspx

Heermann, L. & Borcherding, J. (2006) Winter short-distance migration of juvenile fish between two floodplain water bodies of the Lower River Rhine. *Ecology of Freshwater Fish*, 15(2), 161-168.

Heithaus, M. R., Wirsing, A. J., Burkholder, D., Thomson, J. & Dill, L. M. (2009) Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. *Journal of Animal Ecology*, 78(3), 556-62.

Helfman, G. S. (1981) The Advantage to Fishes of Hovering in Shade. *Copeia*(2), 392-400.

Helfman, G. S. (1986) Fish Behaviour by Day, Night and Twilight, *The Behaviour of Teleost Fishes*, 366 - 387.

Hemmi, J. M. & Pfeil, A. (2010) A multi-stage anti-predator response increases information on predation risk. *Journal of Experimental Biology*, 213(Pt 9), 1484-9.

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

Hohausova, E., Copp, G. H. & Jankovsky, P. (2003) Movement of fish between a river and its backwater: diel activity and relation to environmental gradients. *Ecology of Freshwater Fish*, 12(2), 107-117.

Huckstorf, V., Lewin, W. C. & Wolter, C. (2008) Environmental flow methodologies to protect fisheries resources in human-modified large lowland rivers. *River Research and Applications*, 24(5), 519-527.

Hughes, N. F. (1998) A model of habitat selection by drift-feeding stream salmonids at different scales. *Ecology*, 79(1), 281-294.

Hughes, N. F. (2000) Testing the ability of habitat selection theory to predict interannual movement patterns of a drift-feeding salmonid. *Ecology of Freshwater Fish*, 9(1-2).

Hugie, D. M. & Dill, L. M. (1994) Fish and Game - a Game-Theoretic Approach to Habitat Selection by Predators and Prey. *Journal of Fish Biology*, 45, 151-169.

Jacobsen, L. & Perrow, M. R. (1998) Predation risk from piscivorous fish influencing the diel use of macrophytes by planktivorous fish in experimental ponds. *Ecology of Freshwater Fish*, 7(2), 78-86.

Janáč, M. & Jurajda, P. (2013) Diel Differences in 0+ Fish Samples: Effect of River Size and Habitat. *River Research and Applications*, 29(1), 90-98.

Jepsen, N., Ravn, H. D. & Pedersen, S. (2018) Change of foraging behavior of cormorants and the effect on river fish. *Hydrobiologia*, 820(1), 189-199.

Jones, P. E., Tummers, J. S., Galib, S. M., Woodford, D. J., Hume, J. B., Silva, L. G. M., Braga, R. R., Garcia de Leaniz, C., Vitule, J. R. S., Herder, J. E. & Lucas, M. C. (2021) The Use of Barriers to Limit the Spread of Aquatic Invasive Animal Species: A Global Review. *Frontiers in Ecology and Evolution*, 9.

Jurajda, P., Reichard, M. & Smith, C. (2006) Immediate Impact of an Extensive Summer Flood on the Adult Fish Assemblage of a Channelized Lowland River. *Journal of Freshwater Ecology*, 21(3), 493-501.

Källo, K., Baktoft, H., Jepsen, N. & Aarestrup, K. (2020) Great cormorant (Phalacrocorax carbo sinensis) predation on juvenile down-migrating trout (*Salmo trutta*) in a lowland stream. *ICES Journal of Marine Science*, 77(2), 721-729.

Katopodis, C. & Williams, J. G. (2012) The development of fish passage research in a historical context. *Ecological Engineering*, 48, 8-18.

Knott, J., Mueller, M., Pander, J. & Geist, J. (2019) Seasonal and diurnal variation of downstream fish movement at four small-scale hydropower plants. *Ecology of Freshwater Fish*, 29(1), 74-88.

Knouft, J. H. & Anthony, M. M. (2016) Climate and local abundance in freshwater fishes. *Royal Society Open Science,* 3(6), 160093.

Kobler, A., Klefoth, T., Wolter, C., Fredrich, F. & Arlinghaus, R. (2008) Contrasting pike (*Esox lucius L.)* movement and habitat choice between summer and winter in a small lake. *Hydrobiologia*, 601, 17-27.

Komyakova, V., Chamberlain, D. & Swearer, S. E. (2021) A multi-species assessment of artificial reefs as ecological traps. *Ecological Engineering*, 171.

Koster, W. M., Stuart, I., Tonkin, Z., Dawson, D. & Fanson, B. (2020) Environmental influences on migration patterns and pathways of a threatened potamodromous fish in a regulated lowland river network. *Ecohydrology*, 14(2).

Krakers, L. A., Kruyt, N. P., Rutjes, H. A. & Asme (2015) *Full-Scale Validation Of A Comprehensive Criterion To Predict Fish-Friendliness Of Pumps*.

Kruk, A. (2007) Role of habitat degradation in determining fish distribution and abundance along the lowland Warta River, Poland. *Journal of Applied Ichthyology*, 23(1), 9-18.

Kühne, R. & Schwevers, U. (2016) Target species and measurements of fish protection at the pumped storage hydropower plant Geesthacht. *Wasserwirtschaft*, 106.

Kupiec, J. M., Staniszewski, R. & Jusik, S. (2021) Assessment of the impact of land use in an agricultural catchment area on water quality of lowland rivers. *PeerJ*, 9, e10564.

Lake, S., Bond, N. & Reich, P. (2006) Floods Down Rivers: From Damaging to Replenishing Forces, *Floods in an Arid Continent*. Advances in Ecological Research, 41-62.

Lannin, R. & Hovel, K. (2011) Variable prey density modifies the effects of seagrass habitat structure on predator−prey interactions. *Marine Ecology Progress Series*, 442, 59-70.

Lawson, K. M., Ridgway, J. L., Mueller, A. T., Faulkner, J. D. A. & Calfee, R. D. (2019) Semiautomated Process for Enumeration of Fishes from Recreational-Grade Side-Scan Sonar Imagery. *North American Journal of Fisheries Management*, 40(1), 75-83.

Lemmens, P., De Meester, L. & Declerck, S. A. J. (2016) Can underwater refuges protect fish populations against cormorant predation? Evidence from a large-scale multiple pond experiment. *Fisheries Management and Ecology*.

Lima, S. L. & Bednekoff, P. A. (1999) Temporal Variation in Danger Drives Antipredator Behavior: The Predation Risk Allocation Hypothesis. *American Naturalist*, 153(6), 649-659.

Lima, S. L. & Dill, L. M. (1989) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*.

Lindberg, W. J., Frazer, T. K., Portier, K. M., Vose, F., Loftin, J., Murie, D. J., Mason, D. M., Nagy, B. & Hart, M. K. (2006) Density-dependent habitat selection and performance by a large mobile reef fish. *Ecological Applications*, 16(2), 731-46.

Linden, A. & Mantyniemi, S. (2011) Using the negative binomial distribution to model overdispersion in ecological count data. *Ecology*, 92(7), 1414-1421.

Lindenmayer, D. B. & Laurance, W. F. (2017) The ecology, distribution, conservation and management of large old trees. *Biological Reviews of the Cambridge Philosophical Society*, 92(3), 1434-1458.

Lucas, M.C., Mercer, T., Batley, E., Frear, P.A., Peirson, G., Duncan, A. & Kubečka, J. (1998). Spatio-temporal variations in the distribution and abundance of fish in the Yorkshire Ouse system. The Science of the Total Environment 210/211, 437-455.

Lucas, M. & Baras, E. (2001) *Migration of Freshwater Fishes*. Blackwell Science. Oxford Uk.

Lucas, M. C. (2000) The influence of environmental factors on movements of lowland-river fish in the Yorkshire Ouse system. *Science of the Total Environment*, 251-252, 223-32.

Lyon, J., Stuart, I., Ramsey, D. & O'Mahony, J. (2010) The effect of water level on lateral movements of fish between river and off-channel habitats and implications for management. *Marine and Freshwater Research*, 61(3), 271-278.

Lyon, J. P., Bird, T., Nicol, S., Kearns, J., O'Mahony, J., Todd, C. R., Cowx, I. G., Bradshaw, C. J. A. & Jech, J. M. (2014) Efficiency of electrofishing in turbid lowland rivers: implications for measuring temporal change in fish populations. *Canadian Journal of Fisheries and Aquatic Sciences*, 71(6), 878-886.

Maaß, A.-L., Schüttrumpf, H. & Lehmkuhl, F. (2021) Human impact on fluvial systems in Europe with special regard to today's river restorations. *Environmental Sciences Europe*, 33(1).

Magoulick, D. D., Dekar, M. P., Hodges, S. W., Scott, M. K., Rabalais, M. R. & Bare, C. M. (2021) Hydrologic variation influences stream fish assemblage dynamics through flow regime and drought. *Science Report*, 11(1), 10704.

Manfrin, A., Bunzel-Druke, M., Lorenz, A. W., Maire, A., Scharf, M., Zimball, O. & 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, 137169.

Martin, C. W., Fodrie, F. J., Heck, K. L., Jr. & Mattila, J. (2010) Differential habitat use and antipredator response of juvenile roach (Rutilus rutilus) to olfactory and visual cues from multiple predators. *Oecologia*, 162(4), 893-902.

Martins, E. G., Gutowsky, L. F. G., Harrison, P. M., Flemming, J. E., Jonsen, I. D., Zhu, D. Z., Leake, A., Patterson, D. A., Power, M. & Cooke, S. J. (2014) Behavioral attributes of turbine entrainment risk for adult resident fish revealed by acoustic telemetry and state-space modeling. *Animal Biotelemetry*, 2(1).

Martignac, F., Daroux, A., Bagliniere, J. L., Ombredane, D. & Guillard, J. (2015) The use of acoustic cameras in shallow waters: new hydroacoustic tools for monitoring migratory fish population. A review of DIDSON technology. *Fish and Fisheries*, 16(3), 486-510.

Maxwell, S. L., Fuller, R. A., Brooks, T. M. & Watson, J. E. (2016) Biodiversity: The ravages of guns, nets and bulldozers. *Nature*, 536(7615), 143-5.

Mel, R. A., Viero, D. P., Carniello, L. & D'Alpaos, L. (2020) Optimal floodgate operation for river flood management: The case study of Padova (Italy). *Journal of Hydrology: Regional Studies*, 30.

Mercader, M., Blazy, C., Di Pane, J., Devissi, C., Mercière, A., Cheminée, A., Thiriet, P., Pastor, J., Crec'hriou, R., Verdoit-Jarraya, M. & Lenfant, P. (2019) Is artificial habitat diversity a key to restoring nurseries for juvenile coastal fish? Ex situ experiments on habitat selection and survival of juvenile seabreams. *Restoration Ecology*, 27(5), 1155-1165.

Metcalfe, N. B., Fraser, N. H. C. & Burns, M. D. (1999) Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. *Journal of Animal Ecology*, 68(2), 371-381.

Methot, R. D. & Wetzel, C. R. (2013) Stock synthesis: A biological and statistical framework for fish stock assessment and fishery management. *Fisheries Research*, 142, 86-99.

Meuthen, D., Baldauf, S. A., Bakker, T. C. & Thunken, T. (2016) Predator-induced neophobia in juvenile cichlids. *Oecologia*, 181(4), 947-58.

Milinski, M. (1993) Predation risk and feeding behaviour, in Pitcher, T. J. (ed), *Behaviour of Teleost Fishes*.

Mittelbach, G. (1986) Predator-Mediated Habitat Use - Some Consequences for Species Interactions. *Environmental Biology of Fishes*, 16(1-3), 159-169.

Moore, C. (2022) European Electricity Review 2022. Available online: https://ec.europa.eu/info/sites/default/files/energy_climate_change_environment/quarterly_report_on_european_electricity_markets_q1_2022.pdf

Morat, F., Gibert, P., Reynaud, N., Testi, B., Favriou, P., Raymond, V., Carrel, G. & Maire, A. (2018) Spatial distribution, total length frequencies and otolith morphometry as tools to analyse the effects of a flash flood on populations of roach (Rutilus rutilus). *Ecology of Freshwater Fish*, 27(1), 421-432.

Morris, D. W. (2003) Toward an ecological synthesis: a case for habitat selection. *Oecologia*, 136(1), 1-13.

Mulder, I. M., Dempson, J. B., Fleming, I. A. & Power, M. (2019) Diel activity patterns in overwintering Labrador anadromous Arctic charr. *Hydrobiologia*, 840(1), 89-102.

Mulligan, K. B., Towler, B., Haro, A. & Ahlfeld, D. P. (2017) A computational fluid dynamics modeling study of guide walls for downstream fish passage. *Ecological Engineering*, 99, 324-332.

NC3Rs (2022) *3Rs for the public | NC3Rs.* Available online: https://www.nc3rs.org.uk/3rs-public

Nienhuis, P. H. & Leuven, R. S. E. W. (2001) River restoration and flood protection: controversy or synergism? *Hydrobiologia*, 444(1-3), 85-99.

Nilsson, C., Reidy, C. A., Dynesius, M. & Revenga, C. (2005) Fragmentation and flow regulation of the world's large river systems. *Science*, 308(5720), 405-408.

Noatch, M. R. & Suski, C. D. (2012) Non-physical barriers to deter fish movements. *Environmental Reviews*, 20(1), 71-82.

Nowak, M., Klaczak, A., Koščo, J., Szczerbik, P., Fedorčák, J., Hajdú, J. & Popek, W. (2019) Diel changeover of fish assemblages in shallow sandy habitats of lowland rivers of different sizes. *Knowledge & Management of Aquatic Ecosystems*(420).

Nunes, J. A. C. C., Leduc, A., Miranda, R. J., Cipresso, P. H., Alves, J. P., Mariano-Neto, E., Sampaio, C. L. S. & Barros, F. (2019) Refuge choice specificity increases with predation risk in a rocky reef fish. *Journal of Experimental Marine Biology and Ecology*, 520.

Nunn, A. D., Copp, G. H., Vilizzi, L. & Carter, M. G. (2010) Seasonal and diel patterns in the migrations of fishes between a river and a floodplain tributary. *Ecology of Freshwater Fish*, 19(1), 153-162.

Oględki, P., Ostrowski, P. S. & Utratna-Żukowska, M. (2021) Natural and Geomorphological Response of the Small Lowland River Valley for Anthropogenic Transformation. *Resources*, 10(10).

Ohlund, G., Hedstrom, P., Norman, S., Hein, C. L. & Englund, G. (2015) Temperature dependence of predation depends on the relative performance of predators and prey. *Proceedings of the Royal Society B: Biological Sciences* 282(1799), 20142254.

Orians, G. H. & Wittenberger, J. F. (1991) Spatial and Temporal Scales in Habitat Selection. *American Naturalist*, 137, S29-S49.

Orpwood, J. E., Miles, M. S., Russell, I. C. & Armstrong, J. D. (2010) Efficacy of artificial shelters for roach, *Rutilus rutilus*, against predators in the presence of reeds. *Fisheries Management and Ecology*.

Orrock, J. L., Preisser, E. L., Grabowski, J. H. & Trussell, G. C. (2013) The cost of safety: refuges increase the impact of predation risk in aquatic systems. *Ecology*, 94(3), 573-9.

Ory, N. C., Dudgeon, D., Duprey, N. & Thiel, M. (2014) Effects of predation on diel activity and habitat use of the coral-reef shrimp *Cinetorhynchus hendersoni* (*Rhynchocinetidae). Coral Reefs*, 33(3), 639-650.

Palacios, M. M., Malerba, M. E. & McCormick, M. I. (2018) Multiple predator effects on juvenile prey survival. *Oecologia*, 188(2), 417-427.

Pander, J. & Geist, J. (2013) Ecological indicators for stream restoration success. *Ecological Indicators*, 30, 106-118.

Papastamatiou, Y. P., Britton, C. & Burgess, G. H. (2020) Using side-scan sonar to survey critically endangered smalltooth sawfish. *Fisheries Research*, 228.

Patten, M. A. & Kelly, J. F. (2010) Habitat selection and the perceptual trap. *Ecological Applications*, 20(8), 2148-56.

Pavlov, D. S., Mikheev, V. N., Lupandin, A. I. & Skorobogatov, M. A. (2008) Ecological and behavioural influences on juvenile fish migrations in regulated rivers: a review of experimental and field studies. *Hydrobiologia*, 609(1), 125-138.

Paxton, A. B., Steward, D. a. N., Harrison, Z. H. & Taylor, J. C. (2022) Fitting ecological principles of artificial reefs into the ocean planning puzzle. *Ecosphere*, 13(2).

Peirson, G., David Bolland, J. & Cowx, I. (2008) Lateral dispersal and displacement of fish during flood events in lowland river systems in the UK—implications for sustainable floodplain management. *Ecohydrology & Hydrobiology*, 8(2-4), 363-373.

Petreman, I. C., Jones, N. E. & Milne, S. W. (2014) Observer bias and subsampling efficiencies for estimating the number of migrating fish in rivers using Dual-frequency IDentification SONar (DIDSON). *Fisheries Research*, 155, 160-167.

Perry, R. W., Brandes, P. L., Burau, J. R., Sandstrom, P. T. & Skalski, J. R. (2015) Effect of Tides, River Flow, and Gate Operations on Entrainment of Juvenile Salmon into the Interior Sacramento–San Joaquin River Delta. *Transactions of the American Fisheries Society*, 144(3), 445-455.

Perry, R. W., Romine, J. G., Adams, N. S., Blake, A. R., Burau, J. R., Johnston, S. V. & Liedtke, T. L. (2014) Using A Non-Physical Behavioural Barrier To Alter Migration Routing Of Juvenile Chinook Salmon In The Sacramento-San Joaquin River Delta. *River Research and Applications*, 30(2), 192-203.

Piper, A. T., White, P. R., Wright, R. M., Leighton, T. G. & Kemp, P. S. (2019) Response of seaward-migrating European eel (*Anguilla anguilla*) to an infrasound deterrent. *Ecological Engineering*, 127, 480-486.

Piper, A. T., Wright, R. M., Walker, A. M. & Kemp, P. S. (2013) Escapement, route choice, barrier passage and entrainment of seaward migrating European eel, *Anguilla anguilla*, within a highly regulated lowland river. *Ecological Engineering*, 57, 88-96.

Pitcher, T. J. (1998) Shoaling and Schooling in Fishes. In book: Comparative Psychology: a Handbook (*pp.748-760*): Shoaling and Schooling in Fishes. Garland, New York

Pitcher, T. J. & Turner, J. R. (1986) Danger at Dawn - Experimental Support for the Twilight Hypothesis in Shoaling Minnows. *Journal of Fish Biology*, 29, 59-70.

Poff, N. L. (1997) The Natural Flow Regime: A Paradigm for River Conservation and Restoration. *Bioscience*.

Poletto, J. B., Cocherell, D. E., Mussen, T. D., Ercan, A., Bandeh, H., Kavvas, M. L., Cech, J. J., Jr. & Fangue, N. A. (2015) Fish-protection devices at unscreened water diversions can reduce entrainment: evidence from behavioural laboratory investigations. *Conservation Physiology* 3(1), cov040.

Preisser, E. L., Orrock, J. L. & Schmitz, O. J. (2007) Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. *Ecology*, 88(11), 2744-51.

Price, V. E., Auster, P. J. & Kracker, L. (2013) Use of High-Resolution DIDSON Sonar to Quantify Attributes of Predation at Ecologically Relevant Space and Time Scales. *Marine Technology Society Journal*, 47(1), 33-46.

Pusey, B. J., Douglas, M., Olden, J. D., Jackson, S., Allsop, Q. & Kennard, M. J. (2020) Connectivity, habitat, and flow regime influence fish assemblage structure: Implications for environmental water management in a perennial river of the wet–dry tropics of northern Australia. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30(7), 1397-1411.

Reckendorfer, W., Schmalfuß, R., Frik, G., Loy, G., Tezzele, R. & Ratschan, C. (2018) Ecological Measures To Protect Fish Populations. *Wasserwirtschaft*, 108(2-3), 60-64.

Reeds, J. D. (2019) Fish population summary report: Fenn drain *Environment Agency*. Available online: wellandriverstrust.org.uk/wp-content/uploads/2018/01/River-Welland-survey-report-2017.pdf

Rieucau, G., Boswell, K. M., Kimball, M. E., Diaz, G. & Allen, D. M. (2015) Tidal and diel variations in abundance and schooling behavior of estuarine fish within an intertidal salt marsh pool. *Hydrobiologia*, 753(1), 149-162.

Robertson, B. A. & Hutto, R. L. (2006) A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, 87(5), 1075-85.

Robertson, B. A., Rehage, J. S. & Sih, A. (2013) Ecological novelty and the emergence of evolutionary traps. *Trends in Ecology & Evolution*, 28(9), 552-60.

Roff, D. A. & Fairbairn, D. J. (2007) The evolution of trade-offs: where are we? *Journal of Evolutionary Biology*, 20(2), 433-447.

Romenskyy, M., Herbert-Read, J. E., Ioannou, C. C., Szorkovszky, A., Ward, A. J. W. & Sumpter, D. J. T. (2020) Quantifying the structure and dynamics of fish shoals under predation threat in three dimensions. *Behavioral Ecology*, 31(2), 311-321.

Rosenfeld, J. (2003) Assessing the habitat requirements of stream fishes: An overview and evaluation of different approaches. *Transactions of the American Fisheries Society*, 132(5), 953-968.

Russell, I. (2003) The potential for using fish refuges to reduce damage to inland fisheries by Cormorants, Phalacrocorax carbo, in Cowx, I. G. (ed), *Interactions Between Fish and Birds: Implications for Management*, 259–277.

Russell, I., Parrott, D., Ives, M., Goldsmith, D., Fox, S., Clifton-Dey, D., Prickett, A. & Drew, T. (2008) Reducing fish losses to cormorants using artificial fish refuges: an experimental study. *Fisheries Management and Ecology*, 15(3), 189-198.

Russon, I. J., Kemp, P. S. & Calles, O. (2010) Response of downstream migrating adult European eels (*Anguilla anguilla*) to bar racks under experimental conditions. *Ecology of Freshwater Fish*, 19(2), 197-205.

Rytwinski, T., Algera, D. A., Taylor, J. J., Smokorowski, K. E., Bennett, J. R., Harrison, P. M. & Cooke, S. J. (2017) What are the consequences of fish entrainment and impingement associated with hydroelectric dams on fish productivity? A systematic review protocol. *Environmental Evidence*, 6(1).

Santos, J. M., Ferreira, M. T., Pinheiro, A. N. & Bochechas, J. H. (2006) Effects of small hydropower plants on fish assemblages in medium-sized streams in central and northern Portugal. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 16(4), 373-388.

Santos, L. N., Araújo, F. G. & Brotto, D. S. (2008) Artificial structures as tools for fish habitat rehabilitation in a neotropical reservoir. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 18(6), 896-908.

Schmettow, M. (2021) New Statistics for Design Researchers A Bayesian Workflow in Tidy R. Available online: https://www.google.co.uk/books/edition/New_Statistics_for_Design_Researchers/Xlw4EAAAQBAJ?hl=en&gbpv=1&printsec=frontcover

Schneider, C. A., Rasband, W. S. & Eliceiri, K. W. (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9(7), 671-5.

Seifert, R. E. & Moore, J. W. (2017) Floodgate Operations and Fish Communities in Tidal Creeks of the Lower Fraser River (British Columbia, Canada). *Estuaries and Coasts*, 41(4), 1206-1221.

Sheridan, S., Turnpenny, A. W. H., Horsfield, R., Solomon, D., Bamford, D., Bayliss, B., Coates, S., Dolben, I., Fear, P., Hazard, E., Tavner, I., Trudgill, N. & Wright, R. M. (2014) Screening at intakes and outfalls: measures to protect eels (*Anguilla anguilla*). *In: Turnpeny, A.W.H. & Horsfield, International Fish Screening Techniques. Southampton: WIT Press, 17 - 30.*

Sheriff, M. J., Krebs, C. J. & Boonstra, R. (2010) The ghosts of predators past: population cycles and the role of maternal programming under fluctuating predation risk. *Ecology*, 91(10), 2983-94.

Shukla, I., Kilpatrick, A. M. & Beltran, R. S. (2021) Variation in resting strategies across trophic levels and habitats in mammals. *Ecology and Evolution*, 11(21), 14405-14415.

Singh, R., Tiwari, A. K. & Singh, G. S. (2021) Managing riparian zones for river health improvement: an integrated approach. *Landscape and Ecological Engineering*, 17(2), 195-223.

Smith, C. D., Plumb, J. M., Adams, N. S. & Wyatt, G. J. (2020) Predator and prey events at the entrance of a surface-oriented fish collector at North Fork Dam, Oregon. *Fisheries Management and Ecology*, 28(2), 172-182.

Solomon, D. J. & Wright, R. M. (2012) Prioritising pumping stations for facilities for the passage of eels and other fish: Final report version 1.1. *Environment Agency, Kelvedon, Essex*. Available online: https://www.ada.org.uk/downloads/other/downloads_page/eels_pumping_station_report_anglian_v1_2.pdf

Song, M., Wang, J., Nie, Z., Wang, L., Wang, J., Zhang, J., Wang, Y., Guo, Z., Jiang, Z. & Liang, Z. (2022) Evaluation of artificial reef habitats as reconstruction or enhancement tools of benthic fish communities in northern Yellow Sea. *Marine Pollution Bulletin*, 182, 113968.

Sousa, R., Nogueira, J. G., Lopes-Lima, M., Varandas, S. & Teixeira, A. (2019) Water mill canals as habitat for *Margaritifera margaritifera*: Stable refuge or an ecological trap? *Ecological Indicators*, 106.

Sudduth, E. B., Hassett, B. A., Cada, P. & Bernhardt, E. S. (2011) Testing the field of dreams hypothesis: functional responses to urbanization and restoration in stream ecosystems. *Ecological Applications*, 21(6), 1972-88.

Supekar, S. C. & Gramapurohit, N. P. (2020) Does temporal variation in predation risk affect antipredator responses of larval Indian Skipper Frogs (*Euphlyctis cyanophlyctis*)? *Canadian Journal of Zoology*, 98(3), 202-209.

Team R. (2022) *RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA.* Available online: http://www.rstudio.com/

Team R. (2021) *R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.* Available online: https://www.R-project.org

Teixeira, A. & Cortes, R. M. V. (2007) PIT telemetry as a method to study the habitat requirements of fish populations: application to native and stocked trout movements. *Hydrobiologia*, 582, 171-185.

Thorp, J. H. & Delong, M. D. (1994) The Riverine Productivity Model - an Heuristic View of Carbon-Sources and Organic-Processing in Large River Ecosystems. *Oikos*, 70(2), 305-308.

Thorp, J. H., Thoms, M. C. & Delong, M. D. (2006) The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Research and Applications*, 22(2), 123-147.

Thorstad, E. B., Rikardsen, A. H., Alp, A. & Okland, F. (2014) The Use of Electronic Tags in Fish Research – An Overview of Fish Telemetry Methods. *Turkish Journal of Fisheries and Aquatic Sciences*, 13(5).

Thurow, R. F. (2016) *Life Histories of Potamodromous Fishes*. In book: Morais, Pedro; Daverat, Franchise, eds. An introduction to fish migration. Boca Raton, FL: CRC Press. p. 29-54.

Togaki, D., Inoue, M., Shiota, Y., Fujimi, Y. & Kawanishi, R. (2021) Route selection by fish during post-spate movement in a braided river: a potential effect on local assemblages. *Limnology*, 23(1), 127-136.

Tomanova, S., Courret, D., Richard, S., Tedesco, P. A., Mataix, V., Frey, A., Lagarrigue, T., Chatellier, L. & Tetard, S. (2021) Protecting the downstream migration of salmon smolts from hydroelectric power plants with inclined racks and optimized bypass water discharge. *Journal of Environmental Management*, 284, 112012.

Tomczyk, P. & Wiatkowski, M. (2020) Challenges in the Development of Hydropower in Selected European Countries. *Water*, 12(12).

Trancart, T., Acou, A., De Oliveira, E. & Feunteun, E. (2013) Forecasting animal migration using SARIMAX: an efficient means of reducing silver eel mortality caused by turbines. *Endangered Species Research*, 21(2), 181-190.

Tripp, S., Jack Killgore, K. & Garvey, J. E. (2016) Fish Movements and Passage Through a Water Control Structure: River Stage and Floodplain Connectivity. *River Research and Applications*, 32(4), 812-819.

Tummers, J. S., Hudson, S. & Lucas, M. C. (2016) Evaluating the effectiveness of restoring longitudinal connectivity for stream fish communities: towards a more holistic approach. *Science of the Total Environment*, 569-570, 850-860.

Turesson, H. & Bronmark, C. (2004) Foraging behaviour and capture success in perch, pikeperch and pike and the effects of prey density. *Journal of Fish Biology*, 65(2), 363-375.

Turnpenny, A. W. H. & O' Keeffe, N. (2005) Screening for intake and outfalls. *Environment Agency*. Available online: https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/291568/scho0205bioc-e-e.pdf

van Esch, B. P. M. (2012) Fish Injury and Mortality During Passage Through Pumping Stations. *Journal of Fluids Engineering*, 134(7).

Vannote, R. L. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37(130-137).

Villéger, S., Brosse, S., Mouchet, M., Mouillot, D. & Vanni, M. J. (2017) Functional ecology of fish: current approaches and future challenges. *Aquatic Sciences*, 79(4), 783-801.

Walsh, C. J. & Breen, P. F. (2017) A biological approach to assessing the potential success of habitat restoration in urban streams. *SIL Proceedings, 1922-2010*, 27(6), 3654-3658.

Watchorn, D. J., Cowan, M. A., Driscoll, D. A., Nimmo, D. G., Ashman, K. R., Garkaklis, M. J., Wilson, B. A. & Doherty, T. S. (2022) Artificial habitat structures for animal conservation: design and implementation, risks and opportunities. *Frontiers in Ecology and the Environment*.

White, C. R., Butler, P. J., GrÉMillet, D. & Martin, G. R. (2008) Behavioural strategies of cormorants (*Phalacrocoracidae*) foraging under challenging light conditions. *Ibis*, 150, 231-239.

White, C. R., Day, N., Butler, P. J. & Martin, G. R. (2007) Vision and foraging in cormorants: more like herons than hawks? *PLoS One*, 2(7), e639.

White, J. R., Meekan, M. G., McCormick, M. I. & Ferrari, M. C. O. (2013) A Comparison of Measures of Boldness and Their Relationships to Survival in Young Fish. *Plos One*, 8(7).

Williams, J. G. (2008) Mitigating the effects of high-head dams on the Columbia River, USA: experience from the trenches. *Hydrobiologia*, 609(1), 241-251.

Wright, G. V., Wright, R. M. & Kemp, P. S. (2015) Impact of Tide Gates on the Migration of Adult European Eels*, Anguilla anguilla*. *Estuaries and Coasts*, 38(6), 2031-2043.

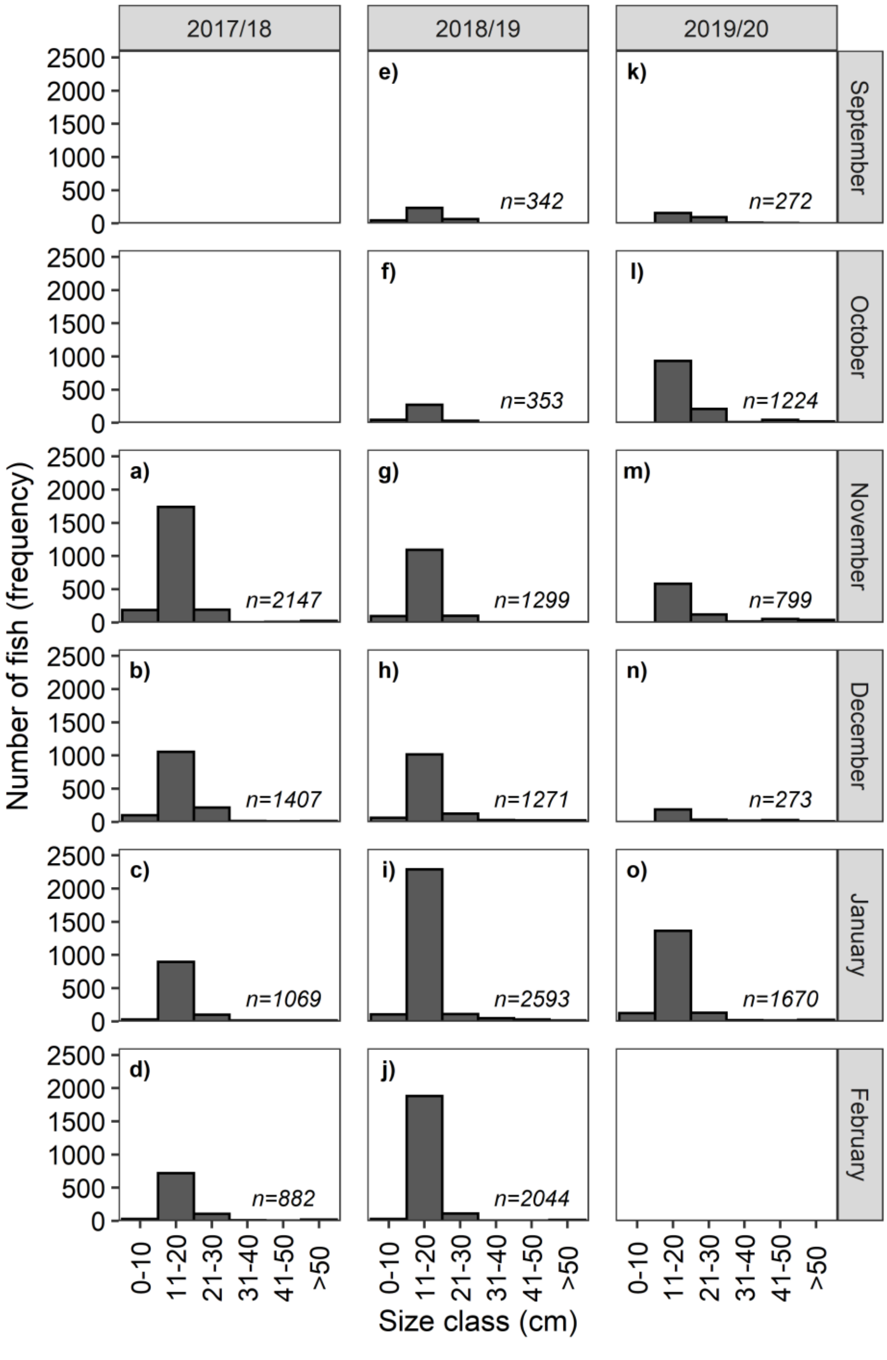
Zhang, H., Wei, Q. & Kang, M. (2014) Measurement of swimming pattern and body length of cultured Chinese sturgeon by use of imaging sonar*. Aquaculture*, 434, 184-187.

Zuur, A. F., Ieno, E. N. & Elphick, C. S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1(1), 3-14.

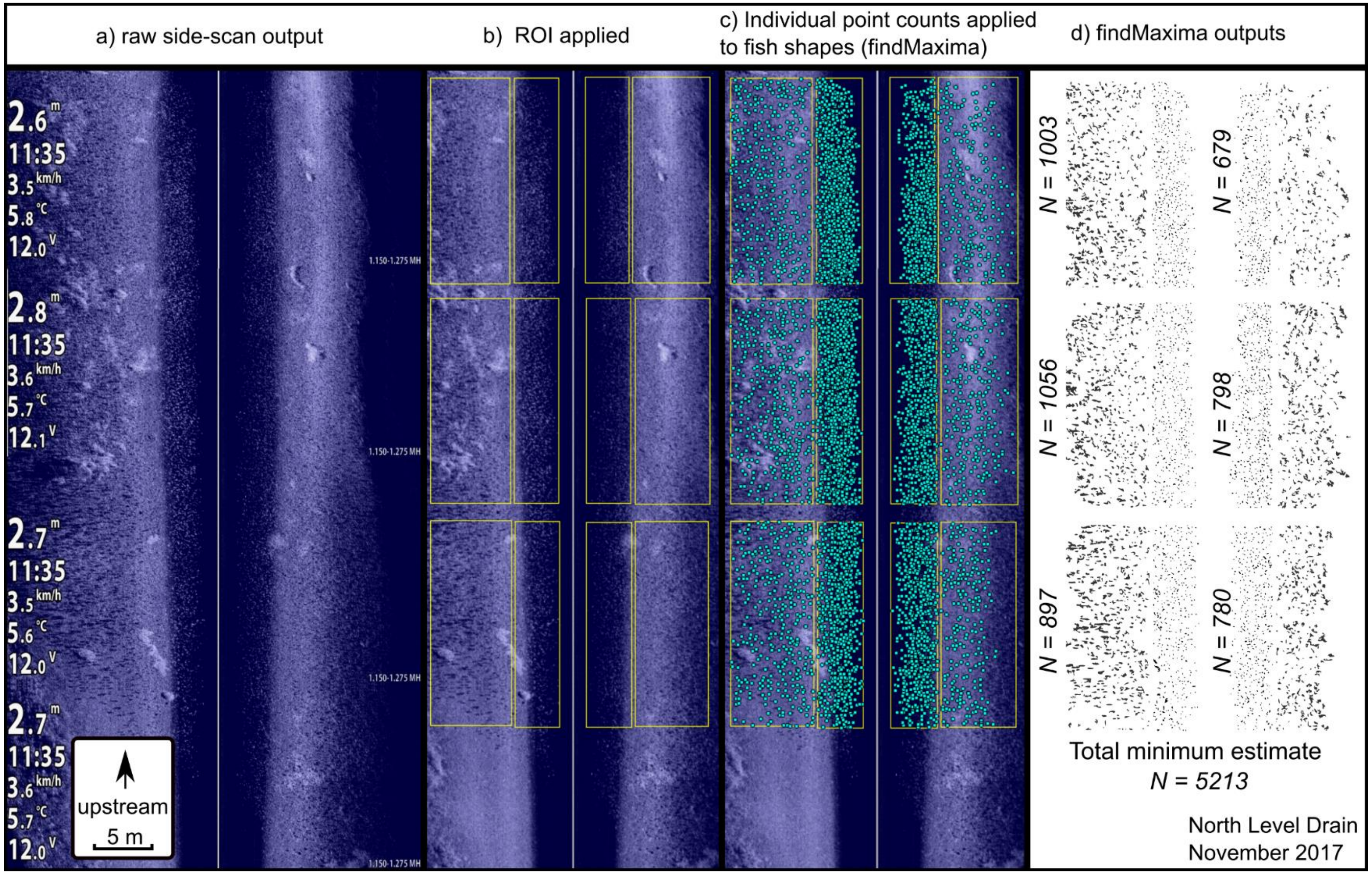
Zuur, A. F. & Leno, E. N. (2016) A protocol for conducting and presenting results of regression-type analyses. *Methods in Ecology and Evolution*, 7(6), 636-645.

APPENDICIES

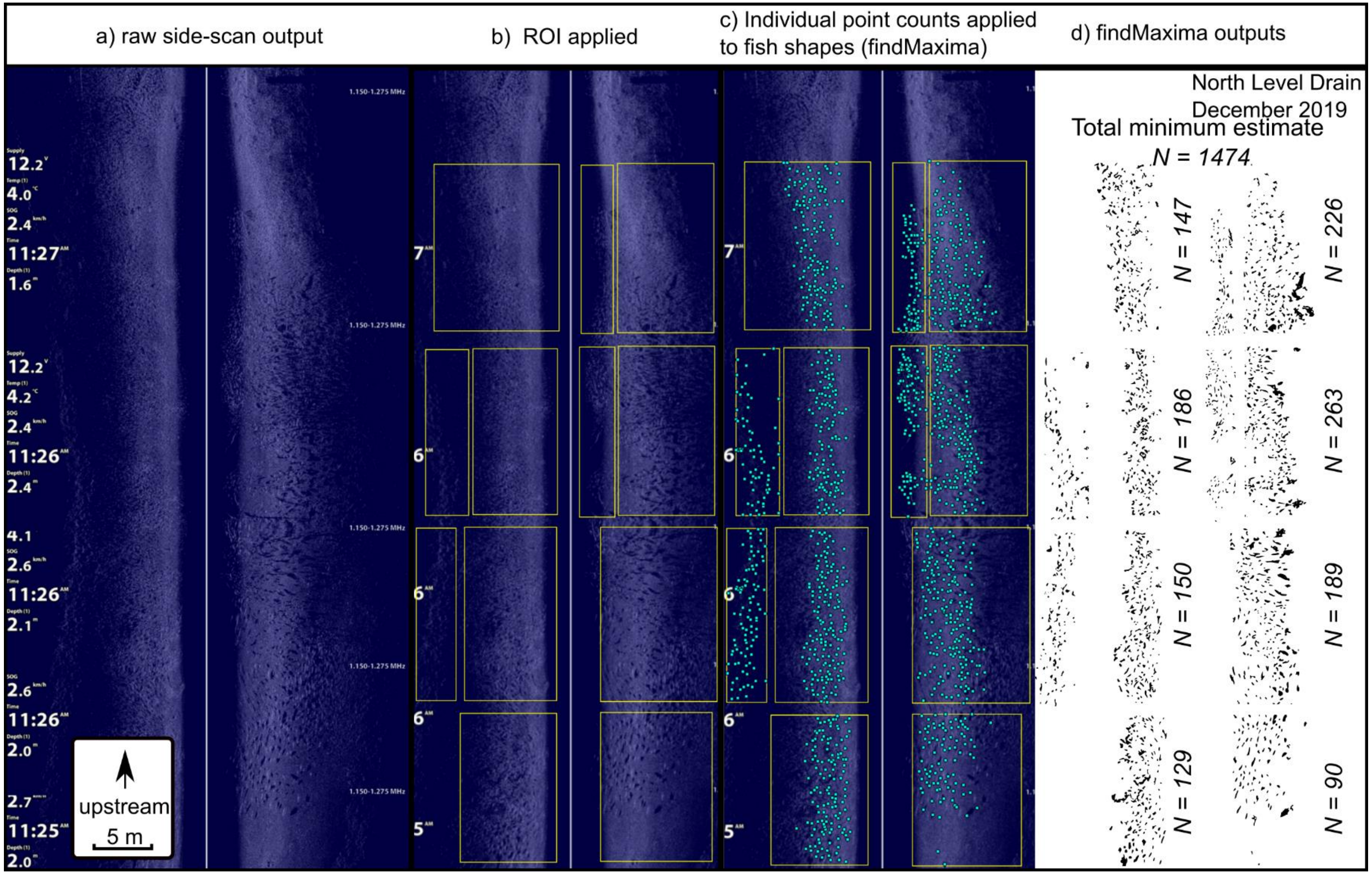
Appendix 1. Length frequency histograms of fish imaged with DIDSON at Foss PS.



Appendix 2. Composite image from North Level Drain (52.737735N,0.148511W) with a representation of the side-scan survey S1 (downstream to upstream) for 27th November 2017. The enumeration process is shown as a) – d).



Appendix 3. Composite image from North Level Drain (52.737735N,0.148511W) with a representation of the side-scan survey S1 (downstream to upstream) for 10th December 2019. The enumeration process is shown as a) – d).



Appendix 3. Composite image from North Level Drain (52.737735N,0.148511W) with a representation of the side-scan survey S1 (downstream to upstream) for 17th December 2021. Inset image shows artificial habitat scans.