THE UNIVERSITY OF HULL

Understanding temporal variability in fish and eel movements to minimise the likelihood of entrainment at water pumping stations

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by

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ABSTRACT

Rivers in the United Kingdom have been subject to extensive modification to meet societal demands for navigation, drinking water, industry, hydropower, drainage, and abstraction. This heavy pressure on river resources has resulted in many constrained rivers becoming vulnerable to flooding and the majority of heavily modified rivers require active flood risk management. Subsequently, there is now a focus on water pumping stations (WPS) that use pumps to control inland water levels. However, these WPS carry a dangerous risk of entrainment (entry into pumps) to riverine fish, and entrainment of fishes through pump intakes is a major cause of mortality in coarse fish populations throughout the UK. Additionally, recruitment of the European eel (*Anguilla Anguilla*) has declined by up to 90% since the 1980s and there is now a legislative requirement to increase eel escapement at WPS. Knowledge of the temporal movements of fish around WPS is required to protect the critically endangered European eel and prevent entrainment of coarse fish. In the present study, an underwater sonar (DIDSON) was utilised to examine temporal (diel and seasonal) patterns in fish activity at Foss WPS, York, England, with an overall aim to determine whether temporal fish movements can be used to minimise fish entrainment at WPS. A five month deployment (N = 153 nights) of a DIDSON successfully imaged thousands of coarse fish and captured downstream movements of European eels (N = 2). Sonar images revealed clear modulated diel patterns in fish movements where activity was highest at dawn and dusk periods, and during the day. But, this was followed by a period of unpredictability throughout winter, and a linear regression model revealed a potentially unpredictable fish population. In all cases, fish activity was significantly different between months, and was highest during the day. These findings suggest that temporal variation in fish movements can be used to inform pump operation such that entrainment of fish is minimised, providing an increased understanding of fish behaviour around WPS, and arguing a demand for more detailed biological assessments to be undertaken at WPS.

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1. INTRODUCTION

1.1 Background

Floodplains in the United Kingdom (UK) have been subject to extensive modification throughout much of the 19th and 20th centuries as human society continued to expand and reclaim wetland habitats for agriculture and the construction of industry and residences. Streams and rivers extending throughout habitable regions have been persistently modified and constrained to meet societal demands for navigation, drinking water, industry, hydropower, drainage, and abstraction (Cowx & Welcomme, 1998). However, as societal demands continue to increase, rivers become more vulnerable to flooding. Subsequently rivers are now heavily modified for flood risk management (Dixon *et al*., 2016). The maintenance and construction of structures that minimise the risk of flooding is essential to meet societal demands for flood protection (Welcomme, 2001). Freshwater ecosystems have become increasingly disconnected through channelisation, dredging and the construction of dams, weirs and other impediments (Nilsson *et al.,* 2005). These modifications have reduced habitat availability for aquatic life, can restrict home ranges and inhabit and prevent the movement of aquatic biota by blocking fish passage between upstream and downstream reaches of a catchment (Nilsson *et al.,* 2005; Katopodis & Williams., 2012; Pennock *et al.,* 2018). Such in-channel structures have contributed to population declines in over 50 threatened fish species throughout Europe (Northcote, 1998; Calles *et al.,* 2012; Liermann *et al.,* 2012).

The concern of fish passage at human mediated riverine structures extends multiple centuries (Katopodis & Williams, 2012). However, the development of a scientifically robust understanding of the problem did not come to fruition until the middle of the 20th century, and has since been followed by the development of essential governing legislation such as the EU Water Framework Directive (2000) (WFD). Although dams and weirs were historically constructed to reduce flood risk in vulnerable areas, there is now a shift in focus to structures that rely on pumps to control inland water levels (Solomon & Wright, 2012; van Esch & Spierts, 2014). These water pumping stations (WPS) also play secondary roles in drinking water usage, wetland drainage, irrigation, and water level control and are undeniably essential for modern society (Buysse *et al.,* 2014). Yet, WPS carry a dangerous risk of entrainment to riverine fish, and entrainment (drawing in) of fishes through pump intakes is a major cause of mortality in fish populations throughout the UK (Environment Agency, 2012; Rytwinski *et al.,* 2017; Figure 1).

In England, there are now over 900 WPS, but little research has been undertaken to assess the impact these structures pose to riverine fish (Solomon & Wright, 2012). Although development on rivers, streams and estuaries is now closely governed in England, the problem of fish entrainment at WPS is complicated as historically constructed WPS vary in location, size and function. Additionally, whilst new build WPS often incorporate 'fish-friendly' practises such as screening (Turnpenny & Keeffe, 2005; Environment Agency, 2013; Zielinski *et al.,* 2015) and/or 'fish-friendly' pump designs (Buysse *et al.,* 2015; Rytwinski *et al.,* 2017), these modifications often fail to integrate an understanding of fish behaviour, and thus their operation is undertaken with little consideration of fish presence (Martins *et al.,* 2014). For WPS to operate 'fish-friendly' practices there must be some compatibility of engineered practises and the predictable temporal movement patterns of fish that potentially interact with them, such that entry into pump intakes is minimised (Coutant & Whitnet, 2000; Martins *et al.,* 2014).

Previous studies on the impacts of WPS on fish populations have largely focused on diadromous fish i.e., salmonids (Brackley *et al.,* 2016) and lamprey (Bracken & Lucas, 2013) The extensive distances covered by these migratory species means they frequently come into contact with WPS during their

Figure 1 Perch following entrainment through a water pumping facility (Angling Trust, 2011).

migrations, and this understanding of fish passage between freshwater and marine environments is widely recognised (Northcote, 1998; Alerstam *et al.,* 2003; Turnpenny & O'Keefe, 2005). However, potadromous fish must also perform coordinated movements within freshwater habitats to facilitate their reproduction, feeding and refuge use (predator, environmental), and unlike long distance migrants, potadromous fish may potentially interact with WPS throughout the year. As of yet, few studies have exclusively shown an understanding as to the importance of WPS management for potadromous fishes, and WPS frequently operate without consideration to movements of these fish populations.

Entrainment of fish is potentially unavoidable in many modern aquatic systems, as water pumping operations have become an integral ecosystem service (Cowx & Portocarrero Aya, 2011). However, the relative risk WPS pose to fishes is expected to be associated with its operational cycle, and it is likely that fish are pre-disposed to negative impacts of WPS on a temporal scale (daily, seasonally). If behaviour makes fish more or less susceptible to entrainment within specific diel periods, then water pumping may be timed to minimise entrainment (Gilligan & Schiller, 2004; Baumgartner *et al.,* 2009). Despite the importance of temporal movements of fish, there is surprisingly little known about how fish use daily movements to exploit habitat heterogeneity (Armstrong *et al.,* 2013). Moreover, there is currently a paucity in the literature surrounding the understanding of fish behaviour around WPS and it is therefore essential that an understanding of how temporal fish movement influences entrainment risk at WPS is developed.

One of the most striking examples of the negative impacts associated with WPS is that of the European eel (*Anguilla Anguilla*). Having previously shown a wide distribution throughout Europe, the European eel has experienced a decline in recruitment up to 90% since the 1980s (Dekker, 2003a), which is likely the result of overfishing (Moriarty & Dekker, 1997; Dekker, 2003b), pollution (Brusle, 1991; Geeraerts & Belpaire, 2010), parasite transfer (Kirk, 2003), changes to climate and ocean current (Kettle *et al.,* 2008) and a high mortality rate when passing through structures that use turbines and pumps (Feunteun, 2002; Piper *et al.,* 2013; Buysse *et al.,* 2014; Besson *et al.,* 2016). This catadromous fish species has a complex life cycle that comprises of a spawning and juvenile phase in the ocean and an adult phase in freshwater on the European continent. However, migration between these two habitats is impaired by interactions with WPS, where eels are particularly vulnerable to entrainment due to their elongated body shape and attraction to flowing water (Miyai *et al.,* 2004). Mortality of eels associated with entrainment at WPS has been recorded as high as 97% (Buysse *et al.,* 2014), and injuries sustained at WPS may otherwise result in poor survival rates if migration is delayed and eels continue to move in unfavourable conditions (Verhelst *et al.,* 2018).

The European eel is now critically endangered and a series of legislative instruments are now in place that aim to aid its recovery, namely the Eel Recovery Plan (Council Regulation No 1100/2007) and The Eels (England and Wales) Regulations 2009 (Eels Regulations) Statutory Instrument, which requires pump operators to screen water intakes that abstract more than $20m^3s^{-1}$ of water a day (20 cubic metres per second (cumecs)), unless exempted by the Environment Agency (EA). European member states must also develop Eel Management Plans (EMPs) that target 40% escapement of silver eels from freshwater habitats. Despite 11 EMPs being in place throughout England and Wales, there is a paucity in eel monitoring data at WPS and knowledge on their impact on downstream migration of silver eels is limited. Therefore, it is essential to gather more and better-targeted information on eel behaviour at WPS to meet EC 1100/2007 regulations and improve escapement.

Foss WPS, located on the River Foss immediately upstream of its confluence with the Yorkshire Ouse in York, UK was constructed in 1988 in response to a series of large flooding events and currently offers flood protection to thousands of properties surrounding the Yorkshire Ouse and Foss. The WPS has eight pumps, a large floodgate barrier, and is located in a large isolated off-channel area (Foss basin). The barrier is operated in response to flood events and when lowered the River Foss is drained through pumping. Following a large-scale flooding event in December 2015, Foss WPS underwent redevelopment in 2016 to increase pumping capacity from 30 m^3s^{-1} to 52 m^3s^{-1} (Figure 2). Because Foss WPS is off-channel and operates in cooperation with a floodgate barrier, fish and eels in Foss basin are unable to move downstream without entering pumps. Fish protection is currently limited to a slow start-up procedure that aims to disperse fish. However, there are currently no further protection measures,

Figure 2 Foss WPS, York, UK. Photo taken during its reconstruction in 2016.

such as fish deterrents, bypass channels and physical or behavioural screening at Foss WPS to prevent entrainment of fish and eels and/or delays to migration. It is therefore critical to determine the risk to fishes and eels at Foss WPS and identify cost-beneficial solutions where possible.

1.2 Aims and objectives

Foss WPS provides a good opportunity to monitor fish behaviour as it operates with an adjacent flood defence barrier, much like gravity bypass sluices at many inland WPS. Secondly, Foss WPS currently has limited fish-friendly pumping practices and it is therefore critical to identify remedial measures that minimise the likelihood of entrainment. This research aims to ascertain passage of European eels at Foss WPS, identify temporal patterns in fish presence and identify where operational changes may be made that are favourable for escapement of downstream migrant European eels and instream movements of coarse fish. The overall aim is to provide an increased understanding of how fish behaviour can be used to inform remediation measures at WPS and demonstrate the function for biological fish assessments. To achieve this the following specific objectives were identified.

- Perform a literature review that identifies key impacts of WPS, the life cycle and migration stimuli of European eels, the key motivators behind riverine fish behaviour and provide a summarised review of remediation measures suitable for WPS.
- Construct an understanding of historical pumping at Foss WPS to identify interannual and seasonal patterns of water pumping that may influence the likelihood of entrainment for fish and eels.

- Quantify temporal (diel, seasonal) patterns in fish presence and identify environmental stimuli that may increase or decrease fish movements at WPS.
- Monitor Foss WPS for the presence of European eel at key migratory periods.
- Determine entrainment risk to fish and eels during pump operation.
- Identify suitable remedial options and/or operational changes which may be applied to Foss WPS to mitigate fish entrainment.

1.3 Structure and content of thesis

Sections 2 - 5 provides a review on the current understanding of entrainment and impingement of fish at WPS, summarises the life cycle, ecology and decline of the European eel, provides an overview of key motivators behind riverine fish behaviour and identifies the current remediation measures that have been employed at structures that utilise water pumping.

Section 6 establishes the study catchment and site and methods for data collection in the field are described, with information on fish monitoring technique and data analysis.

Section 7 presents the results of historical findings at Foss WPS, the number of recorded eels and provides a detailed review of diel activity of fishes monitored at Foss WPS, a monitored pumping event and a concluding statistical analysis.

Section 8 discuses the results in the context of objectives and provides reasoning as to the results observed. Temporal variations in fish activity are discussed in specific reference to refuge use and pump operation at Foss WPS. The discussion moves on to suggest possible remediation measures for Foss WPS and provides an overview of how the present study increased understanding of fish behaviour at WPS generally. The discussion is closed by key conclusions with suggestions for future investigations.

2. INLAND WATER PUMPING STATIONS

2.1 Introduction

Globally, there is a reliance on pumping stations to maintain and manage freshwater systems. WPS are key structural river modifications, and throughout England, they are now critically important for flood risk management (van Esch & Spierts, 2014). Flood defence WPS are essential tools used to maintain water at an acceptable level to reduce the risk of flooding in flood prone catchments. However, WPS construction usually involves significant alterations to natural riverine function including the addition of moving parts that move water often, without consideration to fish passage (Krakers *et al.,* 2015). WPS regulate river flow, and potentially disrupt flow-dependent life-history characteristics of fish, including spawning and recruitment events (Humphries *et al.,* 2002). Additionally, these riverine structures serve as major physical barriers to fish populations and reduce habitat availability for aquatic life (Cowx & Welcomme, 1998).

There is now a growing body of evidence that suggest WPS carry a dangerous risk of impingement and entrainment to fish (Kock *et al.,* 2009; Simpson & Ostrand, 2012; Piper *et al.,* 2013; Van Esch & Spierts, 2014), and WPS are recognised as a major cause of fish mortality across England (Environment Agency, 2013; Rytwinski *et al.,* 2017). Impingement refers to the trapping of fish and debris against weed and trash screens (Barnthouse, 2013). Entrainment occurs when a fish travels through the pump intake and is subsequently drawn into pumps (Barnthouse, 2013; Piper *et al.,* 2013).

In the following section, much literature surrounding the impacts of impingement and entrainment is focused on turbines used in hydropower and power station intakes as their economic importance has driven a wealth of research. Whilst their operational function is different to that of WPS, the impacts associated with fish passage of water intakes are comparable to those at WPS. Therefore, studies surrounding fish passage of hydropower and power station intakes are considered an appropriate tool for understanding impacts at WPS.

2.2 Processes that result in fish injury and/or mortality

2.2.1 Impingement of fish at water intakes

In order to protect pumps from damage and minimise the entrainment of debris and fish, WPS have weed screens, trash racks and fish screens installed (Moyle & Israel, 2005; Figure 3). However, this practice carries a risk of impingement against screens to fish that are unable to out swim competing flows. A typical WPS makes functional use of several rows of steel bars located across pump intakes that prevent the entrainment of debris (Figure 3). The size of these structures varies considerably between schemes, which presents a multitude of different aperture widths and approach flows that influence the relative risk of impingement to fish and therefore no one design is applicable to all WPS.

Millions of fish are killed each year through impingement on intakes for water cooling, hydropower, abstraction and at WPS used for inland water control (Langford, 1983; Kennish, 1992: Maes *et al.,* 2004; Patrick *et al.,* 2014). Whilst screening can be designed to prevent entrainment of fish, this often results in injury and/or mortality if fish contact and become impinged on the screens face where modifications are not present (Environment Agency, 2012). Impingement

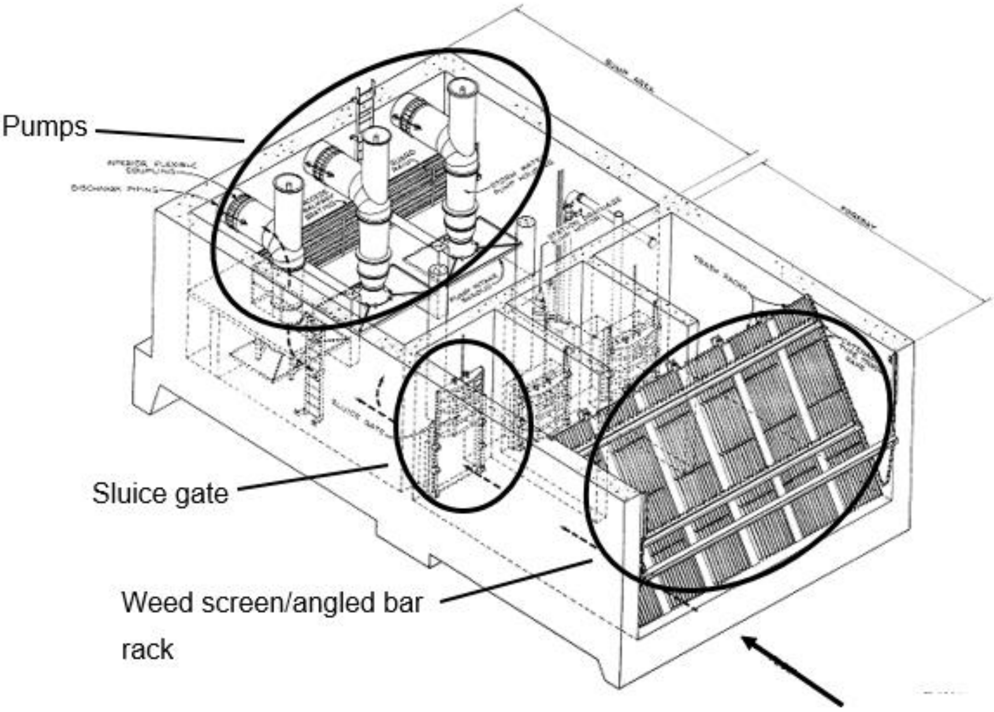


Figure 3 A typical open forebay type water pumping station structure. Water enters the facility through a weed screen, passes through an open sluice door and is then pumped through the facility and expelled in the outfall reach.

can function on an extreme scale, and Bryhn *et al*. (2013) found over 31 million fish were impinged at the intake point of a nuclear power plant in Sweden over one year. Many of the fish impinged were small species such as sticklebacks which presents an issue for the recruitment of larger predatory fish such as pike (*Esox Lucius*) and perch (*Perca fluviatilis*) if prey species become scarce.

Susceptibility to impingement is not uniform in its effect across fish species. Salmonids are good swimmers and have strong behavioural avoidance techniques when encountering apposing flows and thus are less susceptible to impingement (Kemp *et al.,* 2005). But, fish with elongated body shapes such as the European eel have poor reactions as their slender bodies are vulnerable to prolonged changes in flow and Calles *et al.* (2010) demonstrated 41% rate of mortality in tagged eels that became impinged on a 20 mm trash rack at the intake of a hydropower dam. The relative risk of impingement tends to increase with fish body size and flow velocity (Baumgartmner *et al.,* 2009; Halls & Kshatrya, 2009). Thus, high flows usually yield an increase in impingement of fish, and in Satpathy *et al.* (2015), a total of 79 species were identified on the cooling intake of a power plant during a coastal upwelling event in India. This presents a scenario where hydrological features used by fish for orientation may subsequently attract them towards pump intakes, particularly so in migrant species that move on high flows.

Although there are examples where pumping events show significant losses to impingement (Ehrler *et al.,* 2003), other large scale population assessments have revealed population-level reductions of fish ≤ 5% (Newbold & Iovanna, 2007). Thus, whilst impingement at pumping intakes is clearly problematic for fishes that encounter such structures, it is perhaps unlikely to present long-term detrimental effects on fish populations alone, and instead probably contributes to a wider problem of entrainment (Henderson *et al.,* 1984).

2.2.2 Entrainment of fish through turbines and pumps

Fish mortality associated with entrainment at turbine mediated structures has received considerable attention (Pracheli *et al.,* 2016), and although direct studies on WPS are limited (i.e., van Esch, 2012; Buysse *et al.,* 2014; 2015), examples at hydropower intakes provide a good basis for developing an understanding of the issue (Greenwood, 2008). When fish pass through structures that use pumps, they are subject to pressure changes, shear forces and blade strikes that can lead to injury and death (Barntouse, 2013; Brown *et al.,* 2014). The extent to which fish receive damage is dependent on the species, size and life stage of the fish. Coarse fish species (i.e., non-salmonids) in English rivers usually show a similar vulnerability to entrainment. For example, Buysse *et al*. (2014) found common roach (*Rutilus rutilus*), common bream (*Abramis brama*) and perch had similar mortality rates, with around 50% of all individuals being killed following entrainment. This problem is exacerbated in larger and longer fish, with European eels and pike showing mortality rates between 88% and 100%. Thus, assessments on WPS in England need to be undertaken with multi-fish species considerations.

2.2.2.1 Blade strikes, abrasion and grinding

Many WPS do not have adequate deterrents to prevent fish entry into pumps, and entrained fish become vulnerable to contact with moving blades and abrasion against pump housing. Contact with pump structures can vary from high speed collisions (strikes), to low speed abrasion or grinding with blades and pump housings (Krakers *et al.,* 2015). Fish that come into contact with blades are vulnerable to bruising of body tissues, cuts and slices, major bleeding and amputation including decapitation (Krakers *et al.,* 2015; Pracheli *et al.,* 2016).

Form and function of pump design has a considerable impact on the likeliness of injury and death to fish. Although low flows reduce impingement, the relative risk of entrainment tends to be higher as fish readily swim into intake housings, subsequently becoming overwhelmed by intake velocities closer to the pump housing. Additionally, blade design is important in determining the severity of injuries, and pumps with more blades are more likely to strike fish. Pumps that use thin blades easily slice delicate flesh of fish and increase mortality when compared to pumps with thicker blade edges (Krakers *et al.,* 2015). Larger and longer fish are more vulnerable to blade strikes (Halls & Kshatriya, 2009; Deng *et al.,* 2011; Figure 4). For example, the long slender body of the European eel and its undulating swimming behaviour tends to draw them towards the side of pump housing (Cada, 2001). This behaviour can result in the eel being trapped

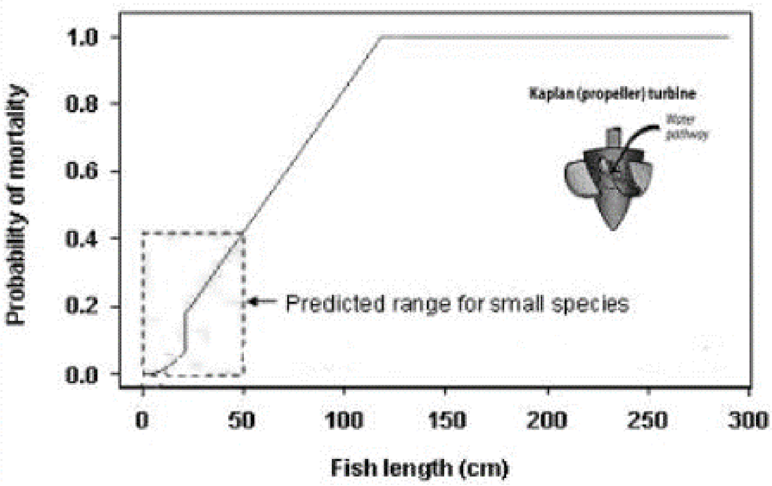


Figure 4 Probability of mortality due to blade strike and relative fish size (Halls & Kshatriya, 2009)

against the wall of the pump housing where they become subject to prolonged grinding and contact with blades (Cada *et al.,* 2007; Figure 5). The risks associated with entrainment are exacerbated as European eels are not only vulnerable to blade strikes but have a high risk of abrasion and grinding. Subsequently, swimming behaviour of eels could make them more vulnerable to mortality via entrainment than other fishes. A similar relationship between size and life stage is found in the majority of fish, and the probability of mortality associated with entrainment is often much higher for adults than juveniles (Ferguson *et al.,* 2008). Although, mortality via blade contact can occur at all life stages and it is likely that where smaller fish are less vulnerable to contact with blades, they remain predisposed to abrasion and grinding (Deng *et al.,* 2011).

2.2.2.2 Shear stress

When fish enter pump intakes they are vulnerable to shear stresses caused by opposing water flows generated by pumping (Cada *et al.,* 2007). Differences in water velocity create flow boundaries in which fish can become trapped. The forces exerted by opposing water results in shear stress being applied to the body of fishes (Cada *et al.,* 2007). These fluid forces can bruise body tissues, remove scales, cause bleeding of the gills and often result in disorientation and loss of equilibrium which presents prolonged swimming impairment (Cada, 2001; Deng *et al.,* 2005; 2010). There are anecdotal estimations that shear stress accounts for approximately 15% contribution to overall mortality through

Figure 5 European eels following entrainment through an axial flow pump, a) Injuries from blade strikes, b) external blood loss, c) haematomas (HIFI, unpublished data).

entrainment (Mathur *et al.,* 2000). The degree to which to fish experience shear stress is dependent on velocity of water and the swimming capability of the fish. For slow swimming fish, fast water scenarios are likely to present increasing injury and mortality risk with increasing water velocity (Neitzel *et al.,* 2004). Fish that have increased swimming capabilities in turn have a higher velocity threshold and thus are less prone to injury from shear stress (Deng *et al.,* 2010).

2.2.2.3 Rapid pressure change

As fish enter pumping facilities they are exposed to slow compression in the intake followed by a decompression once they pass the runner blades (Brown *et al.,* 2014; Richmond *et al.,* 2014; Fu *et al.,* 2016).This rapid change in barometric pressure (barotrauma) causes injury and mortality to fishes that pass through pumps by rupturing the swim bladder (Rummer & Bennett, 2005), damaging the eyes (Brown *et al.,* 2009) and causing internal bleeding (Stephenson *et al.,* 2010). When fish pass through pockets of low pressure in pumps, body fluids may become saturated with gas bubbles formed during decompression (Brown *et al.,* 2014). Once embolisms occur in their blood, gills and other organs fish are vulnerable to rupturing and bleeding.

The risk of injury and death caused by barotrauma is not uniform across species. For example, in the lamprey, a fish species without a swim bladder, the risk of injury when passing through pumps is significantly lower than that of salmon (Colotelo *et al.,* 2012). However, it is unknown whether pressure changes affect different metabolic pathways and the lamprey's vulnerability to pressure changes is likely to shift throughout their life cycle.

2.3 Post passage of fish

Fish that are drawn into pumps are subsequently discharged through culverts where they may be subjected to further hazards. For example, fish that survive the entrainment process often have limited success in returning to the main river system and this process may contribute to mortality indirectly (Baumgartner *et al.,* 2009). There have been reports of birds aggregating at pump outfalls awaiting fish that pass through and disorientation following passage through WPS is likely to increase predation risk in fish (Cada, 2001; Becker, 2003; Buysse *et al.,* 2014). For fish that survive entrainment, physiological stress caused by passage can impair regular behaviours such as habitat use and feeding which leads to choices that reduce survival, and subsequently, entrainment can indirectly contribute to mortality through changes made to regular behaviours (Hecker *et al.,* 2005).

2.4 Comparisons of pumps

For most WPS, the probability that a fish will be killed is determined by the function and structure of pumps used. In England, there are four primary types of pumps, namely Archimedes screw, axial flow, mixed flow and radial flow (Environment Agency, 2012). Many WPS in the UK use axial flow pumps (Figure 6), which vary in size, number of blades, and volume of water they are able to pump and therefore present different levels of risk for fishes attempting passage. Unfortunately, little research has looked to directly asses WPS with regards to pump type and the relative fish mortality risk they present. Although, some early conclusions suggest that number of blades and fish mortality are synonymous (Environment Agency, 2012). For example, Francis turbines used at hydropower facilities have up to 24 blades and typically carry a much higher mortality rate than Kaplan turbines which have between four and eight blades (Pracheli *et al.,* 2016). Cross-flow turbines, which have low head pressure but high number of blades, also carry a high mortality rate. Similarly, turbines where

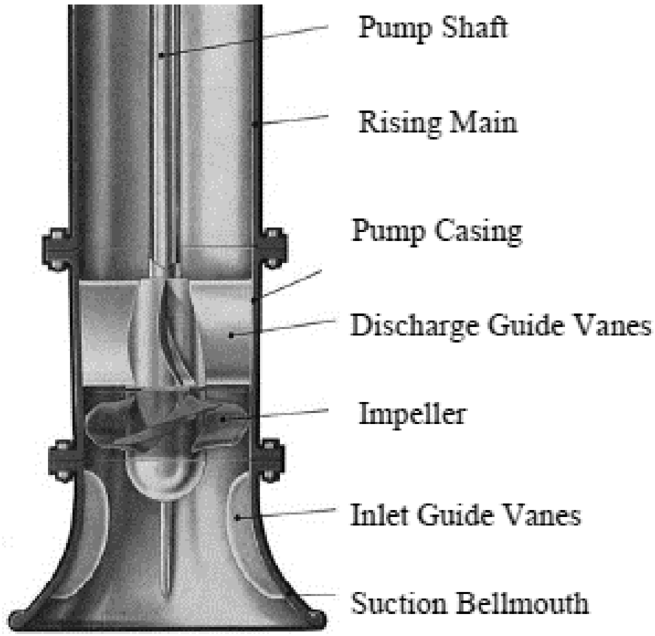


Figure 6 An example of a traditional axial flow pump design (Jackson, 2014).

blades are closer together tend to yield higher mortality rates than those with dispersed blades (Deng *et al.,* 2007).

2.4.1 Fish friendly pumps

There has been a growing effort to improve water pumping devices in order to make them ‘fish-friendly’ (Environment Agency, 2013). These improvements have primarily focused on targeting the main impacts associated with entrainment. Manufactures have aimed to reduce the number of blades, increase the radius of blade edges, and reduce critical flows to minimise shear stress and maintain pressures within pumps (Odeh, 1999). Many early fish-friendly designs were used for transporting fish in the aquaculture industry but have now been transferred to water pumping applications. There are three primary designs for fish-friendly pumping: Archimedes, centrifugal pumps and modified axial flow pumps.

Centrifugal pumps developed by Hidrostal are suggested as the industry-leading standard for fish-friendly pumping and utilise a single spiral vane which reduces blade strikes and prevents rapid fluctuations in pressure (Spierts & Vis, 2012). Axial flow pumps have also been modified with rounded edges and increased blade widths to allow fish to follow flows through the pumps safely. In a limited number of studies, these pumps have been shown to have great success in reducing fish mortality and now widely applied to suitable WPS (i.e., Vis & Kemper, 2012).

Archimedes screw pumps have been shown to greatly reduce mortality in eels where eel mortality was as high as 97% in a traditional propeller pump and between 17% and 30% for Archimedes screw pumps (Buysse *et al.,* 2014). However, the authors were unable to reduce eel mortality at a WPS by installing an Archimedes screw pump, perhaps suggesting a dependence on site specific conditions (Buysse *et al.,* 2015). Given this, eels still remain vulnerable to blade strikes due to abrasion with pump housing during passage and thus their application as fish-friendly pumps may be species specific (Buysse *et al.,* 2015).

Whilst fish-friendly pump designs can improve fish passage, they are limited in scope and where they may be beneficial to one species they in turn become detrimental to the passage of others. This is often materialised as a size-specific bias, where new-build ‘fish-friendly’ pumps significantly increase survival of small (≤10 cm) fish but do little to reduce mortality in larger fish (Hecker *et al.,* 2005). Such fish-friendly practises must also make compromises to allow for power extraction efficiency and therefore pumping structures may require more pumps in order to meet output requirements. This does question whether the overall result will be much more fish-friendly than traditional pumps if extra devices need to be installed. Developing ‘fish-friendly’ pumps is unlikely to function as a solution to fish entrainment alone, and instead is probably a best case solution if fish are unable to be deterred from pump entry.

3. THE EUROPEAN EEL

3.1 Life history of the European eel

European eels are an extraordinary example of a catadromous fish, and their life history has become of much interest to science due to their fascinating migrations between the ocean and European continent. Little was known about the life cycle of the European eel until early research by Schmidt (1922) began to suggest that they undertake significant migrations from continent to ocean. Whilst there are at least eighteen *Anguillid* species recognised worldwide (Aoyama, 2009), larvae of European eels travel east across the Gulf Stream and colonise much of Western Europe and adjacent land masses (Schmidt, 1922; Figure 7). The spawning location of European eels is thought to be located in the Sargasso Sea in the Western North Atlantic Ocean (Schmidt, 1922; Tesch, 2003; Aoyama, 2009). When eels reach the Eastern Atlantic coast, they metamorphose into glass eels. Glass eels then begin to migrate upstream through transitional waters and rivers where they grow to partial maturity as yellow eels (Tesch, 2003). A second metamorphosis takes place as yellow eels mature and transition to silver eels, where they then begin their migration from the continent towards the Sargasso Sea, before spawning and presumably dying.

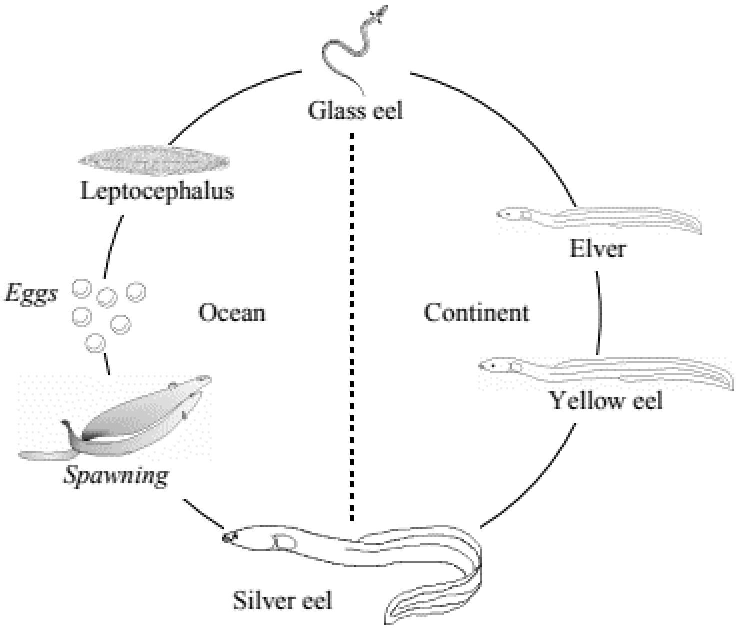


Figure 7 A schematic diagram of the European eel life cycle. In the interest of simplicity, the Preleptocephalus stage is not shown (from Dekker, 2002).

3.1.1 Larval stage (Leptocephali)

The life history of anguillids is unlike many other catadromous fish, because the development of their transparent leaf-like larvae (Leptocephali) is lengthy, and once spawning occurs, their larvae become widely distributed throughout the ocean (Miller & Tsukamoto, 2017). Leptocephali live exclusively in the ocean and are thought to be highly adapted to planktonic life (Miller & Tsukamoto 2004). The planktonic nature of eel Leptocephali larvae allows them to be transported along the Gulf Stream and North-Atlantic Drift for up to nine months before they reach the continent. Upon reaching the continent, they begin to metamorphosis into glass eels and their leaf shaped body elongates, becoming rounded and increasing their swimming capabilities for movements into tidal waters (Otake 2003; Tesch 2003).

3.1.2 Glass eels

Once larvae complete their metamorphosis into glass eels, their osmoregulatory function shifts as they prepare for migration upstream into freshwater habitats. Immigration into the continent is usually associated with the circatidal clock (Wippelhauser & Mcleave 1988; Cresci *et al.,* 2017) and successful migrants begin to develop darker pigmentation as part of the metamorphosis process (Tesch, 2003). These pigmentation stages are thought to increase proportionally as glass eels immigrate into freshwaters in preparation for transition to yellow eels (Dekker, 2002). This immigration process can be monitored, and classification of pigmentation stages have been constructed by several authors over a century (Schmidt 1906; Boetius 1976; Elie *et al.,* 1982; Fukuda *et al.,* 2013).

3.1.3 Elvers and yellow eels

Upstream habitat availability is often limited by obstructions in rivers such as dams, weirs and hydropower schemes and thus many coastal regions may be inaccessible to juvenile eel where obstructions are close to the tidal limit. Therefore, depending upon behaviour of the individual eel, and the availability of upstream habitat, there may be a decision to remain in coastal, brackish waters or to migrate further upstream and reside as freshwater residents (Tzeng *et al.,* 2000; Daverat & Tomas, 2006). Once taking residence, new recruits enter their growth phase and may be considered elvers. Whilst various classification schemes have been proposed (Elie *et al.,* 1982; Tesch, 2003), there is still considerable confusion as to when the glass eel stage ends and when they become elvers and subsequently yellow eels. However, it is widely considered that elvers are undergoing pigmentation, and yellow eel are those who have finished the pigmentation transition.

The growth phase continues upon settlement in chosen habitat and can last for up to fifty years, although it can be as little as two years (ICES, 2006). This growth period is vulnerable to fluctuations in environmental conditions. For example, high exploitation (human, natural) of yellow eel will naturally increase growth rate within the population as remaining eel have increased food resources (Moriarty, 2003). Similarly this often leads to a decrease in the age-at-maturity population wide as younger eels accumulate sufficient body reservoirs (Jessop *et al.,* 2004). Additionally, male and female eels are sexually dimorphic, and their sexual characteristics seem to determine the rate of growth, with females typically being longer when entering silvering than males (Olivera & McCleave, 2002).

3.1.4 Adults (silver eels)

Following the completion of their growth phase, eels undergo their second stage of metamorphosis called silvering, where they make the transition from juveniles and prepare for migration from the continent to the Sargasso sea (Durif *et al.,* 2005). Immediately prior to metamorphosis, growth increases significantly, which is thought to allow eels to accumulate sufficient body fat stores before the transatlantic migration (Vollestad, 1992; Durif *et al.,* 2005). The digestive tract begins to reduce in size, and transitioning eels cease to feed throughout the remaining silvering process (Sbaihi *et al.,* 2001). This may suggest that energy content of an eel is a strong precursor to silvering, and may dictate the rate of sexual maturity (Larsson *et al.,* 1990; Vollestad, 1992).

When the optimum size-at-maturity is reached, the body of the yellow eel undergoes several physiological and morphological changes to prepare for migration into sea. This includes changes to eye size (Pankhurst & Lythgoe, 1983), gonad weight (Vollestad, 1992; Han *et al.,* 2003), increases to size of pectoral fins (Durif *et al.,* 2005), silvering of body pigmentation (Pankhurst &

Lythgoe, 1982; Acou *et al.,* 2005; Durif *et al.,* 2005) and lateral line differentiation (Acou *et al.,* 2005).

3.1.4.1 Morphological discrimination of silvering stages

Durif *et al.* (2009) developed a silvering index to explain the silvering process of mature eels. Using this index, eels are classified by body length, body weight pectoral fin length, and eye size. The silvering index has proven extremely useful for determining the migratory stages of eel and subsequently identifying if a particular individual is ready to spawn or not.

1. The eye diameter increases (Pankhurst & Lythgoe, 1983), retinas transition from green-sensitive to blue-sensitive (Archer *et al.,* 1995) and the density of cones decreases to facilitate vision at depth (Acou *et al.,* 2005).
2. Gastrointestinal tract reduces in size to allow for gonad growth and energy preservation (Sbaihi *et al.,* 2001; Han *et al.,* 2002).
3. Gonad size and weight increase as sperm and eggs develop (Han *et al.,* 2002).
4. Pigmentation cells differentiate as the ventral becomes silvery-white, and the dorsal darkens, becoming brownish-black (Durif *et al.,* 2005).
5. The lateral line system develops, which further contrasts the dorsal and ventral body colours (Acou *et al.,* 2005).
6. Clearly defined corpuscles with nueuromasts populate the lateral line, allowing eels to orientate themselves with apposing water flows (Voigt *et al.,* 2000).

3.1.5 Spawning of the European eel

The location of spawning grounds means mature European eels must migrate thousands of kilometres across the Atlantic Ocean and display amongst the longest one-way migrations for any fish species (Alerstam *et al.,* 2003). To facilitate such long distance migration, European eels must be competent swimmers and have several adaptations suitable for such long distance migrations (van den Thillart *et al.,* 2004). This is at least in part facilitated by adaptations to sensory systems, including vision, hearing, chemoreception, electroreception and magnetoreception (Tesch, 2003; Nishi *et al.,* 2004; Tsukamoto 2009; Durif *et al.,* 2013). It is likely that a combination of migratory functions such as following odour cues, compass orientation (i.e., lunar phase, geomagnetic compass) and sensitivity to hydrographic features (temperature, salinity, light, depth) are used by European eels to locate spawning grounds in the Sargasso Sea (Papi, 2006). For example, sensory cells present throughout the gills, nares and oral cavity may allow eels to perceive strong horizontal and vertical salinity gradients associated with large oceanic currents (Kultz, 2012), odours released by conspecifics could be used to determine the location of mates (Huertas *et al.,* 2008), and magnetoreception may allow eels to orientate themselves in accordance to the earth's magnetic field (Durief *et al.,* 2013).

3.2 Migration stimuli of European eels

Seaward migration is often obligatory or facultative for catadromous fish, and the downstream migration of mature European eels has become time-dependant, which presents predictability in the timing of arrival at river structures (Jansen *et al.,* 2007). The onset of migration is usually stimulated by instabilities that arise from physiological and morphological changes that prepare eels for the marine environment whilst they are still in freshwater (Acou *et al.,* 2008). Eel catches during April – July are typically all yellow eels, and those in August are usually a mixture of yellow and silver eels, with September and November catches all being silver eels (Netherlands) (van Ginneken *et al.,* 2007). Thus, it is usually suggested that eels begin their migration from freshwater towards the Sargasso Sea during late autumn and winter (September-December) (Vollestad *et al.,* 1986; Hansen *et al.,* 1995; Cullen & McCarthy, 2003; Jensen *et al.,* 2007). However, the exact timing of migration is largely underpinned by variations in individuals and localities (Hansen *et al.,* 1995; Durif *et al.,* 2003; Jansen *et al.,* 2007). It is likely that silver eels move under a series of 'optimum' environmental patterns, including seasonal (i.e., temperature), monthly (i.e., lunar cycle) and daily (i.e., atmospheric pressure, light and water flow) factors (Hansen *et al.,* 1995). Thus, migration may either be early or late depending on internal factors (i.e., genetics, growth, metabolism, sexual maturity) and external factors (i.e., photoperiod, temperature, water discharge) (Vollestad *et al.,* 1994; Hansen *et al.,* 1995; Jansen *et al.,* 2007). Consequently, variations in stimuli may trigger early or late migration and it is perhaps more sensible to expected eel migration with an expected window of August to December.

Whilst there appears to be no exact temperature threshold that triggers migration in European eels, there is some indication that a reduction in water temperature can trigger downstream movements. For example, Vollestad *et al.* (1986) found that more than 90% of variation in the timing of downstream migration could be explained by variation in summer water temperature and water discharge. Decreasing water temperatures may drive silver eels downstream in search of warmer waters (Boubee *et al.,* 2001). These findings have been supported by several authors (i.e., Todd, 1981; Haraldstad *et al.,* 1985; Boubee *et al.,* 2001; Miyai *et al.,* 2004), pointing to a general assumption that migrational movements in most eels will be stimulated by a mean decline in water temperature between summer and winter (Figure 8).

Flow in rivers has a controlling influence on the movements of fish, and European eels may be expected to move downstream in periods of flood (Todd, 1981; Boubee *et al.,* 2001; Miyai *et al.,* 2004; Figure 8). This is probably associated with current velocity, as studies on rivers with modified flow regimes where flow is high found that eels move earlier in the season than eels in rivers with natural flow (Boubee *et al.,* 2001). Downstream movements of European eels are often observed during heavy rainfall and high winds throughout stormy weather where eels are able to move in the direction of wind and river flow with

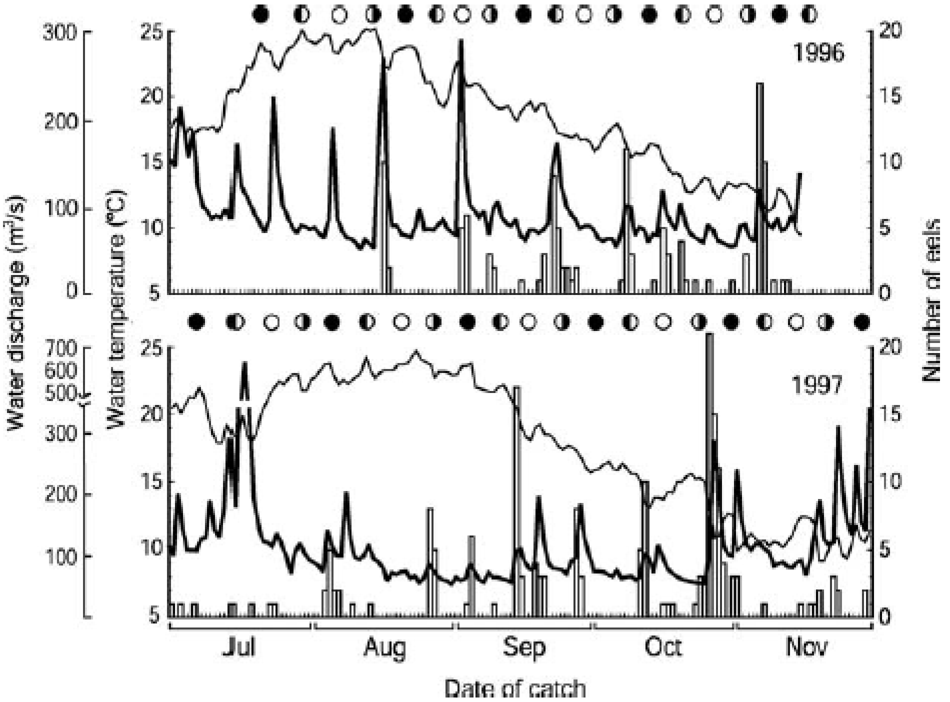


Figure 8 In accordance with Miyai *et al.* (2004), total number of eels caught between July and November 1996 (top) and 1997 (bottom). Temperature (top line) and water discharge (bottom, bold line), and lunar phase (circles).

reduced energy expenditure (Boubee *et al.,* 2001; Cullen & McCarthy, 2003). This is probably also correlated with atmospheric depressions typical of stormy weather patterns (Okamura *et al.,* 2002).

Variation in photoperiod is known to affect fish physiology and metabolism, and the length of photoperiod has been shown to alter the spawning and migration times of a wide range of seasonal spawning fish species (Bromage *et al.,* 2001). European eels exhibit negative phototactic feeding behaviours, (Dou & Tsukamoto 2003; Rodriguez *et al.,* 2009) and increase the rate of movement as daylight decreases throughout seasons and is thus considered to be nocturnal (Vollestad *et al.,* 1994; Durif *et al.,* 2005; Parmeggiani *et al.,* 2015). As demonstrated in Vollestad *et al.* (1994), shortening of daylight hours during winter could activate the last stages of silvering process and function as a migrational cue (Durif *et al.,* 2005).

The theory that downstream movements of European eels are synchronised meteorologically to the lunar cycle has been explored for over fifty years (Lowe, 1952; Boetius, 1967; Deelder, 1984; Tesch, 2003). The lunar cycle follows a predictable pattern of visible moonlight, whereby a full moon is brightest, and a new moon is darkest. In between this, there are varying phases of progressive moonlight as the cycle rotates. According to Lowe (1952), mature silver eels migrate downstream between the final quarter moon and the first quarter moon following a new moon. Trends in catches by fishermen are typically high during the last quarter and new moon phases where moonlight falls early in the evening suggesting movement to be stimulated by the lack of moonlight (Deelder, 1954; Deelder, 1984; Miyai *et al.,* 2004; Figure 8). Unpredictable eel runs even occur where the moon is obscured by heavy cloud coverage (Deelder, 1970), perhaps suggesting that eels have an ‘internal rhythm’ associated with the lunar cycle (Boetius, 1967; Cullen & McCarthy, 2003; Bruijis & Durif, 2009).

The function of an endogenous lunar cycle has been supported by more recent studies (Cairns & Hooley, 2003; Haro, 2003; Durif *et al.,* 2005), which suggest it is likely linked to light sensitivity and nocturnal behaviour. Similarly, ‘’New Moon Hypothesis’’ suggests that eels spawn periodically once a month during a new moon phase (Tsukamoto *et al.,* 2003). Others (Okamura *et al.,* 2002; Miyai *et al.,* 2004) have also shown eel catches to peak during the new moon and decrease at the full moon. Although, several authors have cited other environmental cues as more important where migration movements have not coincided with the lunar phase (Acou *et al.,* 2005, Acou *et al.,* 2008; Reckordt *et al.,* 2014). It is likely that the observed variation in a lunar relationship is caused by complex interactions between several environmental factors (daylight, weather and temperature), and given the variation in timing and silver development, the predictability of the lunar cycle remains a key tool in determining likelihood of mature eel movements.

3.3 The decline of the European eel

Freshwater eels, notably the American, Japanese and European eels have all seen notable declines in recruitment since the 1970s (Arai, 2014). Freshwater eels are perhaps the most important eel family as they have considerably complex catadromous life cycles and in many countries are an important food source. In the past four decades, the stocks of these eels have declined dramatically, and juvenile abundance has deceased by up to 99% in the European eel, 80% in the Japanese eel and recruitment in American eels is virtually unheard of (Figure 9; Dekker *et al.,* 2003a).

As a result of a complex life cycle with larval dispersal in the ocean, a prolonged juvenile phase on the continent and seaward migration as adults, the European eel is vulnerable to natural and anthropogenic threats at all stages of its life and

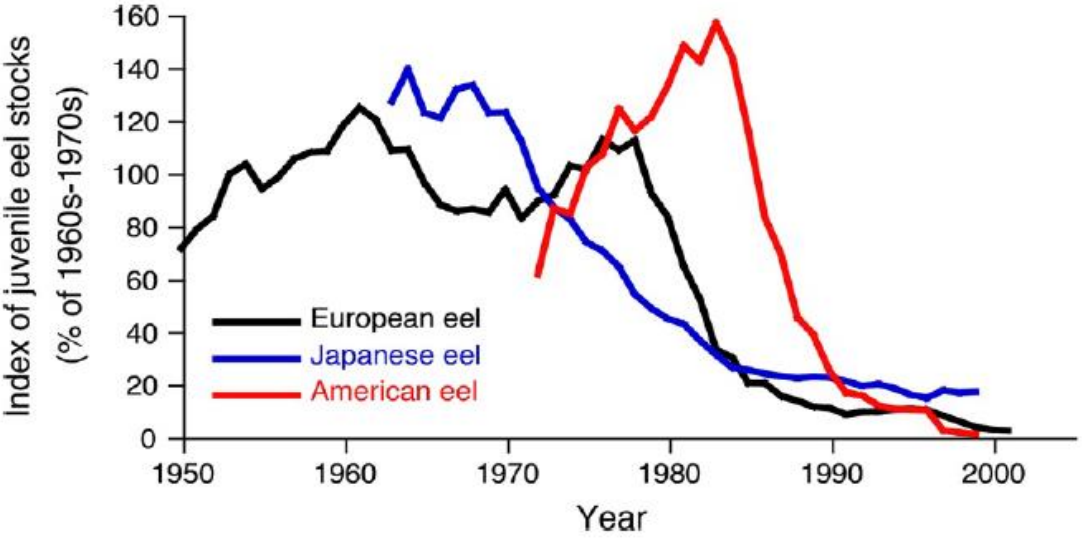


Figure 9 The decline of three anguillid eel stocks from 1950 – 2004. Data for Japanese and European eel were taken from landings of juvenile eels by local angler. American eel numbers were taken from Lake Ontario (Figure from Arai, 2014, data supplied by Dekker)

thus faces the potential for prolonged declines in recruitment. Moreover, given the relative longevity of European eels, declining recruitment tends to have a delayed effect on the densities of eels in freshwaters and subsequent spawning adults seeking escapement from inland catchments (Russell *et al.,* 2003). This leads to a scenario where poor recruitment has seen a continued decline for a number of years.

Since the 1980s, glass eel recruitment in European eels has declined steadily, and it is now widely accepted that recruitment has been falling consistently for the past 30 years with stock status at an all-time low (Dekker, 2003a; Russell *et al.,* 2003; Arai, 2014). This has resulted in a population reduction by a factor of ten in the past decade (Feunteun, 2002), where recruitment has fallen by as much as 90% continent wide across Europe. Such a decline has left the abundance of glass eels to be estimated as <5% of pre-1980 numbers (Figure 9, Dekker, 2003a; ICES, 2006; Bilotta *et al.,* 2011). Due to the continued decline in European eel recruitment and delicate life cycle, the European Union has categorised it as critically endangered in accordance to the IUCN (Jacoby & Gollock, 2014).

3.3.1 Pressure from fishing

A large number of European eel fisheries exist which target different life stages of the eel; seasonal fisheries for glass eels and silver eels, and year-round fisheries for yellow eels (Esteve & Alcaide, 2009). The eels extensive distribution throughout coastal, estuarine and freshwater systems provided an excellent opportunity for many small-scale artisanal eel fisheries to emerge. Large-scale eel fisheries are rare and account for <5% of eels landed for market (Dekker, 2002). As is often with small-scale fisheries, catch data for European eels is unreliable because of the secretiveness of local fishermen and under-reporting of catches (Dekker, 2003b). With so many independent business under-reporting their catches, wide-scale management is challenging (Moriarty & Dekker, 1997).

A decade ago, eel fisheries amounted to around 30,000t a year throughout Europe, of which, glass eels only accounted for around 900t (Ciccotti, 2005). Despite their comparatively small biomass, glass eel catches equate to over two billion recruits, which increases pressure on spawning stock (Feunteun, 2002).

Recently, the focus has shifted towards increasingly intensive eel aquaculture (Ciccotti, 2005; Esteve & Alcaide, 2009); with market supply of cultured eel in excess of 10,000t. This increase in aquaculture moved the focus away from traditional fisheries, but eel farms are heavily reliant on wild-caught seeds i.e., glass eels. Combined with an aquaculture system that relies on wild-caught seeds and poor and illegal reporting of fisheries catches, has led to an wealth of overfishing of European eels throughout Europe (Tzeng, 1997, Dekker, 2003).

3.3.2 Vulnerability to environmental pollution

It has become established that fish response to contaminants is generally dependant on life-history stages and therefore fish with more complex life histories tend to be more susceptible to accumulating pollutants (Feunteun, 2002). Eels can be used as bioindicators for polychlorinated biphenyls (PCBs), pesticides and heavy metals as they accumulate contaminants in their body fat due to specific ecological and physiological traits (Brusle, 1991; Geeraerts & Belpaire, 2010). Because these contaminants bioaccumulate, the toxic effects can occur at different points in the eel life cycle. Though many chemical concentrations found during early life stages are sub-lethal in effect such as changes to lipid metabolism (Hu *et al.,* 2003), decreased body fat stores (Belpaire *et al.,* 2009), and endocrine disruption (Versonnen *et al.,* 2004), they accumulate during growth and may reduce quality of spawning adults (Geeraerts & Belpaire, 2010). Cessation of feeding and a shift to reliance on metabolising of body fats in migrant eels means contaminants stored in the tissues steadily release into the immune system, reproductive system and the nervous system (Geeraerts & Belpaire, 2010). This, combined with reduced body rat reserves, decreases the probability of successful migration and reproduction and therefore reduces the quality of adult spawning stock.

3.3.3 Parasite infection

Anguillicola crassus is a parasite of the swim bladder that was originally endemic to East Asia and only affected the Japanese eel, but the infection rate of European eels began to increase following adoption of the species into Asian aquaculture farms (Feunteun, 2002). The nematode is extremely infectious and severely impairs function of the swim bladder, causing widespread disruptions to migration and in many cases, mortality (Kirk, 2003). A clinical infection of *A.*

crassus will cause severe damage and is likely to affect the entire migratory life of a silver eel due to its longevity.

3.3.4 Changes to climate and oceanic conditions

There are several suggestions that changes in ocean-climate conditions have had considerable impact on production of eels throughout Europe (Kettle et al. 2008; Miller *et al.,* 2009; Parcariz *et al.,* 2014). Kettle *et al*. (2008) show a significant relationship between the North Atlantic Oscillation (NAO) and European eel recruitment. They suggest that oceanic temperature and salinity changes associated with the NAO produce interanual fluctuations in eel recruitment and significantly reduce the number of successfully spawning silver eels. Moreover, changes in oceanic frontal features may have shifted spawning location and therefore potentially reduced transport to recruitment areas on the continent (Miller *et al.,* 2009). Moreover, as global temperatures have risen and the climate has gradually become drier, eel habitats have become increasingly fragmented where wetlands have dried out (Kettle *et al.,* 2011). In addition, where ecosystem function has changed throughout the ocean, the availability and quality of food for drifting eel larvae is likely to have changed (Pacariz *et al.,* 2014). Combined with potentially increased predation risk, this may lead to a scenario where drifting leptocephali have access to fewer resources and thus reduces survival and feeding success.

3.3.5 Barriers to migration

Construction on floodplains and wetlands has contributed considerably to habitat loss as they often make well-suited habitats for eels (Feunteun, 2002). Much of the available freshwater systems have become increasingly disconnected due to the loss of hydrological continuity (Piper *et al.,* 2015). Construction of barriers including dams, weirs, and hydropower and WPS limit both upstream juvenile movements and downstream silver eel escapement. This undoubtedly has a profound effect on the standing stock of European eel because migration is blocked at two critical life-stages. Trends in dam construction worldwide closely follow the decline in freshwater eel recruitment through Asia, America and Europe suggesting this to be a global risk to eels (Miller *et al.,* 2017). There are an estimated 28,000 river barriers throughout

England, many of which are impassable to European eels (Figure 10; Environment Agency, 2010).

River infrastructure can delay and otherwise prevent downstream migration of silver eels (Acou *et al.,* 2008; Piper *et al.,* 2013; 2015). These obstructions have often been described as responsible for decreasing populations of eels throughout Europe (Moriarty & Dekker, 1997; Besson *et al.,* 2016). At hydropower and WPS, eel mortality may be as high as 100% where eels interact directly with turbine blades (Bruijs & Durif, 2009). Additionally, nonphysical features associated with riverine structures can inhibit normal behaviour in fish (Vowles *et al.,* 2015). Particularly, artificial lighting can confuse nocturnal fish such as in eels, and function as a behavioural barrier to migration, which often leads to fragmentation of populations.

3.3.6 Mitigation measures

The European Union (EU) requires member states to implement an Eel Management Plan (EMP) enforcing a target for at least 40% escapement of

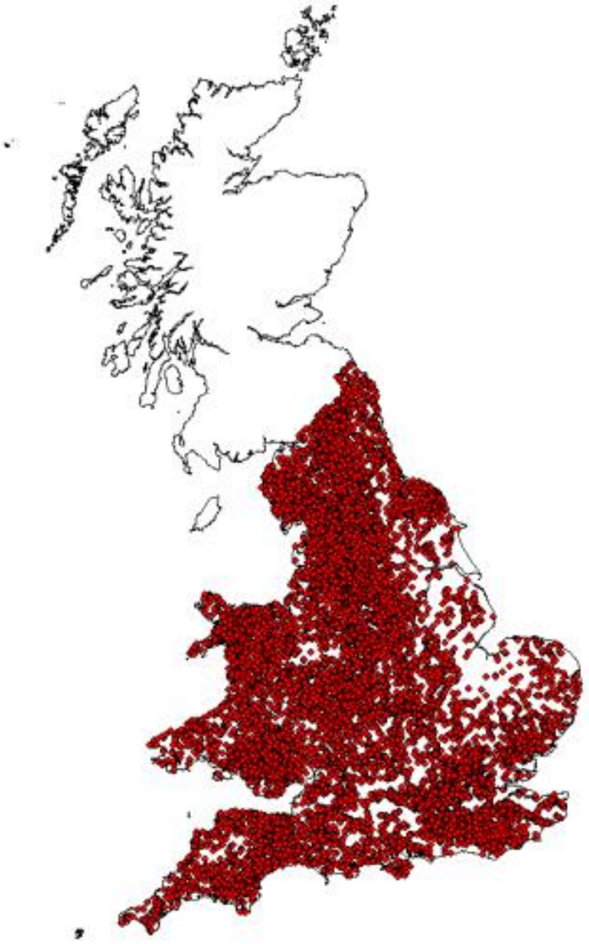


Figure 10 A schematic representation of the number of river barriers in England & Wales using GIS analysis (Environment Agency, 2010).

silver eels (produced under conditions with no anthropogenic disturbance) from inland freshwater systems and actively managing eel fisheries (DEFRA, 2010). First efforts were directed towards improving the upstream passage over riverine structures for inland migration of elvers (Miller *et al.,* 2009). Much of this effort was towards identifying impassable structures and attempting to restore ecological continuity through the construction of structures that would enable fish passage (i.e., elver passes). However, it has become increasingly clear that effort needs to also be directed towards enabling successful downstream migration of mature silver eels (Piper *et al.,* 2013; Reckordt *et al.,* 2013; Piper *et al.,* 2015; Besson *et al.,* 2016; Vehelst *et al.,* 2017).

The European eel was listed in Appendix II of the Convention on International Trade in Endangered Species (CITES) in 2007 (ICES, 2016). Since its implementation, any trade or sale of this species needs to be done under a permit. As of 2016, all trade of eels in and out of the EU has been banned. The International Union for the Conservation of Nature (IUCN) listed the European eel as critical endangered and it was added to the Red list in 2009. This is currently due for review in 2019 where it is hoped current remediation measures will have improved eel stocks significantly.

4. KEY FACTORS INFLUENCING COARSE FISH MOVEMENTS IN UK RIVERS

4.1 Introduction

Coarse fish (i.e., non-salmonids) are present throughout rivers in the UK and are an essential component of the aquatic ecosystem. These ubiquitous fish species provide critical ecosystem services including nutrient recycling, maintenance of sediments, regulation of food web dynamics and maintenance ecosystem biodiversity (Holmlund & Hammer, 1999). Consequently, coarse fish presence, activity and movement in freshwater habitats underpins a biological consideration for humans who manage inland water systems.

Although mass movements from one section of a river to another are a common adaptation in fish, why fish choose to move between habitats is a question with large scope as there are a multitude of factors that influence fish behaviour. Abiotic factors, such as water temperature, river flow, depth, physical barriers and availability of refuge habitat influence how and when fish utilise rivers (Lucas & Baras, 2000; Lapointe *et al.,* 2013; Alexandre *et al.,* 2016). Additionally, biotic factors and process such as predation and feeding (Binner *et al.,* 2008) have a similar influence and, collectively these factors contribute to a system whereby community structure and population density are closely governed by the availability of habitat.

In a broad sense, habitat defines where a fish species lives but does little to describe how this influences fish behaviour. It is however more applicable, that the availability of key habitat features such as flow refuge, feeding and spawning areas, can determine behaviour, presence and activity of coarse fish. Accordingly, habitat functions as the foundation for productive and healthy ecosystems for fishes, and the stochasticity of environmental factors such as flow and refuge cover influences the distribution of fish in rivers (Lapointe *et al.,* 2013). Yet, in many river systems, the spatial and temporal patterns of hydrological conditions have been altered through modification of floodplains, river banks and the addition of WPS that regulate flow (Pringle, 2003). Indeed, heterogeneity of riverine systems has been reduced by construction of anthropogenic structures such as dams, weirs, and WPS. Therefore fish must adapt to heavily constrained river systems, and their behaviours are likely to be influenced by the presence of riverine structures.

4.2 Habitat requirement of coarse fish

Habitat availability is a critical component in controlling fish community and structure in rivers. Riverine fish communities usually show longitudinal patterns in their structure as habitat preference closely follows species-specific tolerances (Table 1; Cowx, 2001). These habitat preferences have previously been used to construct an early understanding of quantifying river habitats by species (i.e., Huet, 1959 - ‘trout’, ‘grayling’ ‘barbel’ and ‘bream’ zones). It has now been recognised that such habitat preference closely follow abiotic and biotic conditions, which is explained by the abiotic-biotic continuum concept (Vannote *et al.,* 1980). More so, as described by the functional unit concept, fish are known to make transitions between microhabitats that facilitate their life history, (Figure 11; Cowx *et al.,* 2004). Thus, it is unlikely that an individual fish spends its entire life in one area, and migrations or movements between and within freshwater and marine habitats are a common adaption to facilitate ontogenesis in fish (Figure 12). Much effort has looked to improve fish passage for diadromous fish that must make migrations between freshwater and marine habitats. Although, given that potadromous fish spend their entire life in freshwater, they must then make movements between key habitats for spawning, feeding and refuge (predator and flow) (Wootton, 2002).

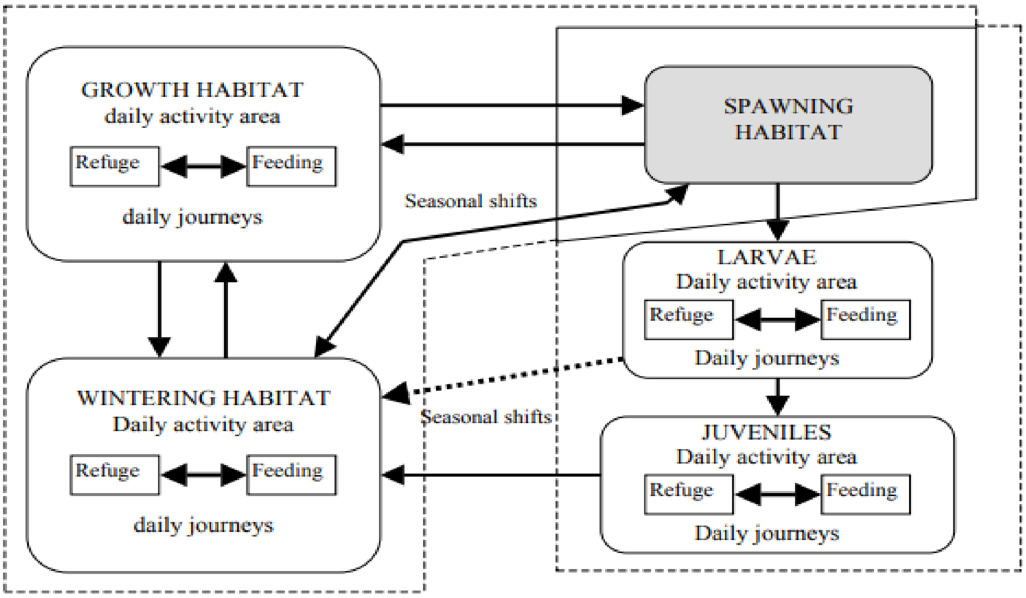


Figure 11 The functional unit concept for fish habitat requirements (Cowx & Welcomme, 1998; Cowx *et al.,* 2004).

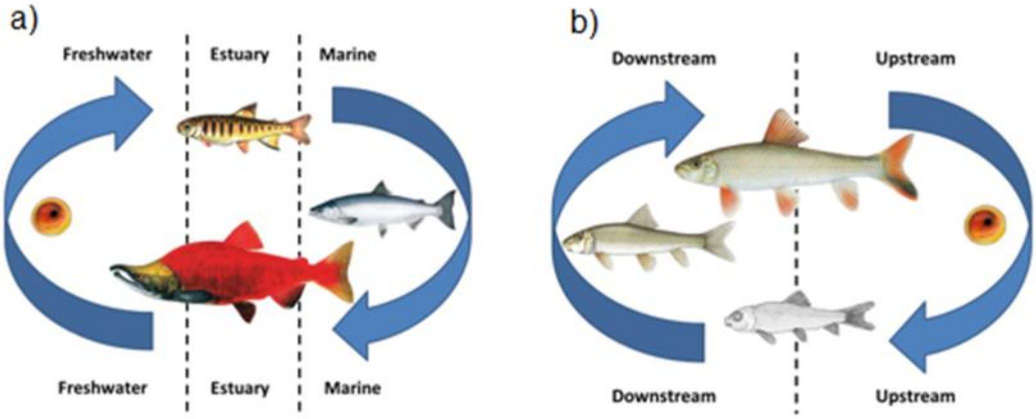


Figure 12 A schematic diagram of an (a) anadromous and (b) potadromous life cycle. (Cooney, 2013)

This is true of English coarse fish populations, which are often described as having home ranges where there is frequent use of a specific area that facilitates their behaviours (Hill & Grossman, 1987; Kramer & Chapman, 1999; Wootton, 2002 Knight *et al.,* 2009). Residency within these home ranges allows fish to identify suitable sites for feeding and shelter, and fish tend to thrive at sites with rich habitat heterogeneity where the main channel interacts with the river banks and stream complexity is usually high (Knight *et al.,* 2009).

Given how dramatically aquatic flora influences heterogeneity of riverine habitats, it is not surprising that spatiotemporal patterns in fish assemblage are linked to riparian cover (Marsh-Matthews & Matthews, 2000). The importance of riparian zones is widely recognised where they provide refuge from light, flow and predation and harbour food items for many species (Welcomme, 1979; Cowx & Welcomme, 1998; Pusey & Arthington, 2003). Riparian zones also provide spawning medium for plant-spawners including roach, bream, carp (*Cyprinus carpio*) and tench (*Tinca tinca*) who use bankside submerged macrophytes and weeds to attach their eggs (Everard, 2015). Gravel spawning species such as dace (*Leuciscus leuciscus*), chub (*Squalius cephalus*) and barbel (*Barbus barbus*) must all make migrations to habitats that have well-flushed clean gravels to facilitate the success of emerging larvae (Cowx *et al.,* 2004). Consequently, home range is often closely tied to the availability of spawning sites. For example, roach abundance is considerably higher in lowland rivers with dense macrophyte cover when compared to that of upstream reaches with poor riparian cover (Pitts *et al.,* 1995).

Table 1 Summary of common coarse fish species found in England and their habitat preferences (Modified from Cowx *et al.,* 2004; Bolland, 2008).

Family *Species*	Common name	Flow preference	Water velocity (cm s^{-1})	Habitat preference	Behaviour	Predators	Feeding	Migration
Cyprinidae								
Barbus barbus	Barbel	Rheophilic	35 – 49	Fast flow, gravels, macrophytes, 15-22°C	Shoals, close to river bed	Pike, chub	Insectivorous, piscivorous	Home range
Alburnus alburnus	Bleak	Eurytopic	5 – 20	Enriched nutrients, slow flow	Shoals, surface water	Pike, perch, chub	Insectivorous	Home range + spawning
Abramis brama	Bream	Eurytopic	5 - 20	Enriched nutrients, slack waters (adaptive)	Shoals, close to river bed	Pike	Insectivorous	Home range + spawning
Leuciscus cephalus	Chub	Rheophilic	20 - 50	Fast flow, gravels, macrophytes	Shoals	Pike, perch, chub	Insectivorous, piscivorous	Home range
Leuciscus leuciscus	Dace	Rheophilic	20 - 50	Fast flow, gravels	Shoals	Pike, perch, chub	Insectivorous	Home range
Rutilus rutilus	Roach	Eurytopic	>20	Slow flows, macrophytes (highly adaptable)	Shoals	Pike, perch, zander	Omnivorous	Home range
Scardinius erythrophthalmus	Rudd	Limnophillic	<5 or still	Shallow water, reeds, silt	Shoals	Pike, perch, zander	Omnivorous	Home range
Abramis bjoerkna	Silver bream	Eurytopic	5 - 20	Slack deep water macorphytes, silt	Shoals	Pike, perch	Omnivorous	Home range
Esocidae								
Esoc Lucius	Pike	Eurytopic	<5	Deep open water (adults)	Solitary	Pike	Piscivorous	Large home range
Percidae								
Perca fluviatilis	Perch	Eurytopic	Still	Dense macrophytes	Shoals	Pike, perch (adults)	Insectivorous, piscivorous	Large home range
Anguillidae								
Anguilla Anguilla	European eel	Eurytopic	>10	Slow flows, deep water, sand & macrophytes	Solitary	Pike	Insectivorous, piscivorous	Catadromous

Such habitat preferences are often categorised (Table 1), but many coarse fish in England have become opportunistic and tolerant of a greater range of conditions due to the persistence of anthropogenic modifications on rivers (Cowx *et al.,* 2004). Thus, it is likely that sub-optimal habitats may still be host to large numbers of coarse fish. Perhaps fish are able to facilitate regular trade-offs between feeding, reproduction and refuge by exploiting structural features of man-made structures where rivers are devoid of bankside refuge (Roff & Fairburn, 2007). Effectively, this would render man made river structures as attractive habitat for fish. At WPS, this attractiveness to fish would be undesired as eventual pump operation poses a high risk of entrainment (section 2.2.2).

4.3 Behavioural stimuli of riverine coarse fish movements

Behaviour of fishes is the outcome of internal (self) and external (environmental) cues that interact to produce a behavioural response. Fish behaviour is usually on an individual level where different responses may be produced to similar stimuli, or where individuals respond differently dependant on environmental (often structural) changes that directly affect a fishes ability to act (Figure 13).

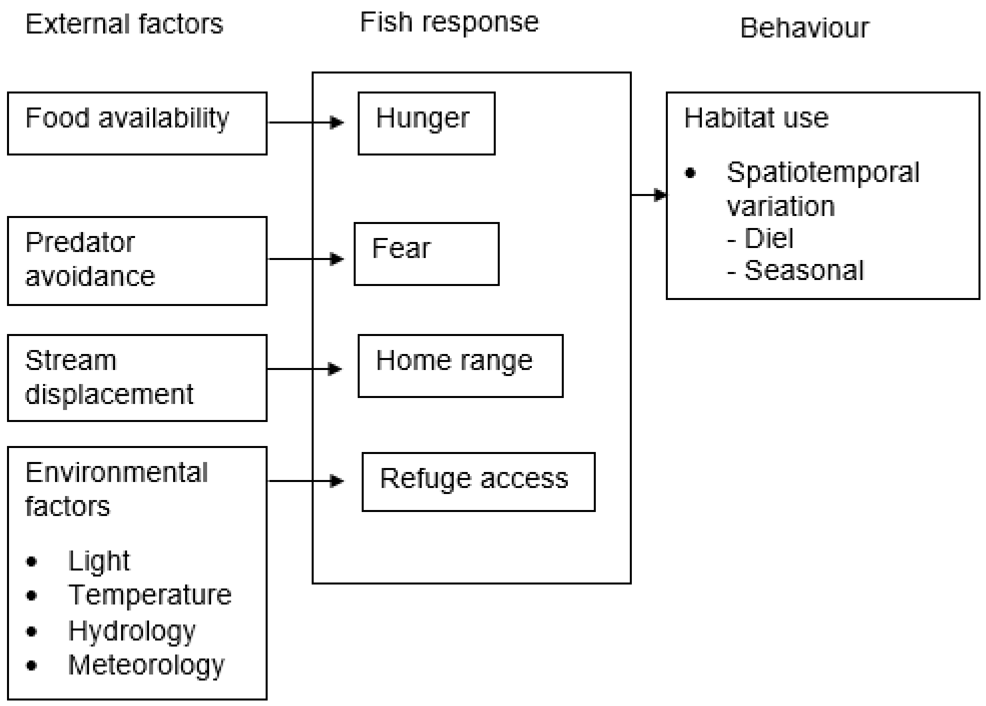


Figure 13 Box and flow schematic representation of the nature and influence of external factors which may influence habitat use in fishes (adapted from Lucas *et al.,* 2000).

4.3.1 River flow

The natural flow regime is essential for ecosystem integrity (Poff *et al.,* 1997; Figure 14), and seasonal connectivity of fluvial systems is an essential function for healthy river ecosystems during high flow and flooding events (Junk *et al.,* 1989; Sommer *et al.,* 2004; Tripp *et al.,* 2016). This has been demonstrated in The Flood Pulse Concept (FPC; Junk *et al.,* 1989) and Riverine Productivity Model (RPM; Thorp & Delong 1994) where the lateral connection between main river channel and available floodplain habitat is suggested as a major driver of fish behaviour in temperate river systems. Where rivers are unmodified, flooding is characterised by lateral expansion onto floodplain areas (Welcomme, 1979). Fluvial action during flooding creates essential fish habitats through the formation of backwaters, river channels and standing water bodies (Junk *et al.,* 1989; Amoros 2002). Backwaters in particular may provide important spawning and nursery habitats and are essential components of freshwater habitats where they are available year-round or seasonally (Reimer, 1991; Schiemer, 1999; Hohausova, 2000; Hohausova *et al.,* 2003). Similarly, these off-channel areas created during floods can offer increased survival, feeding and reproduction opportunities (Lyon *et al.,* 2010).

Fish have evolved several life history strategies associated with survival and exploitation of flood events, and in modified rivers, fish are inherently reliant on a hydrological regime that closely resembles the natural flow regime (Poff, 1997; Acreman *et al.,* 2010; Figure 15). For example, in rivers where seasonal

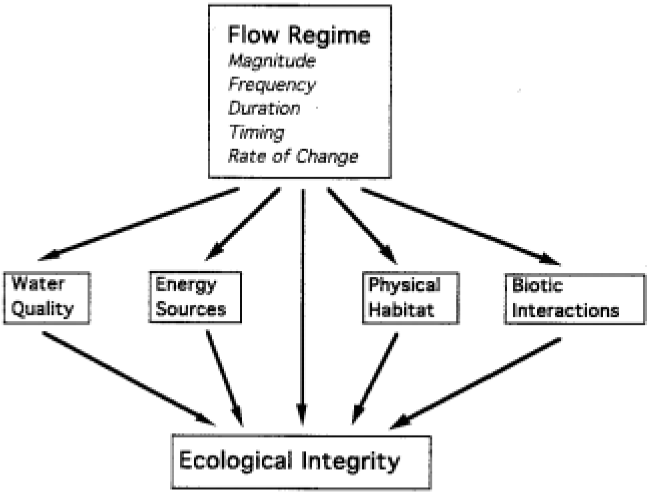


Figure 14 A schematic representation of the critical components of a flow regime and its direct and indirect effects on ecological integrity of water systems (Poff *et al.,* 1997).

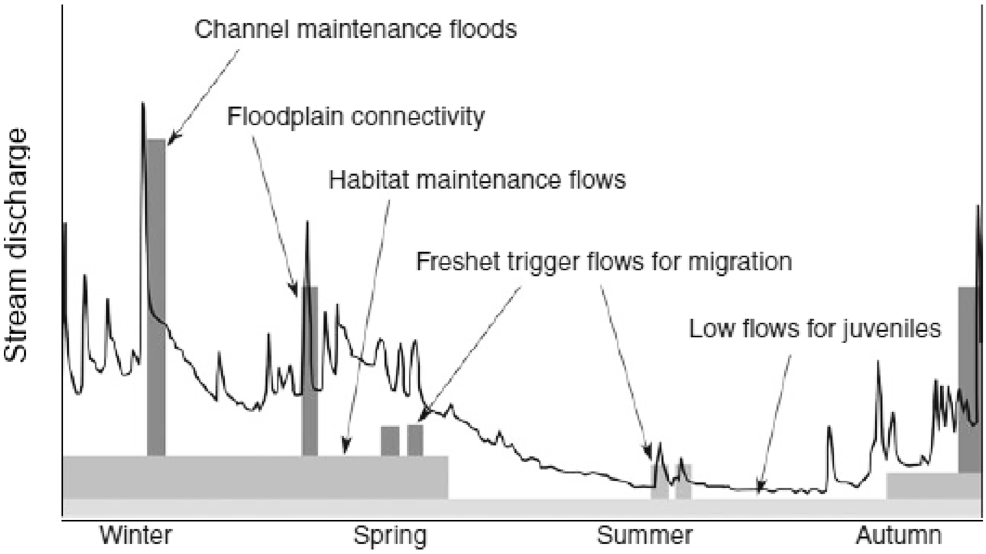


Figure 15 A natural flow regime (solid black line) with the building block approach laid over (light grey boxes). See Acreman *et al.* (2010) for the natural flow regime and building block approach to environmental flows.

flooding is predictable, many fish use high flows as migration and spawning cues which allows them to access upstream habitat that is unavailable during low flows (Matheney & Rabeni, 1995; David & Closs, 2002). Therefore, the availability and predictability of seasonal flows influences habitat use in fish, and in rivers, hydrological connectivity is essential for maintaining biodiversity (Snyder *et al.,* 2003; Thoms, 2003).

Unfortunately, many rivers and channels have now been modified for human use, and floodplain habitats have been replaced with urban developments. Manmade structures can completely separate the main river channel from the surrounding habitat and often prevent the formation of new floodplain habitat (Tockner & Bretschko, 1996). Because these habitats are potentially lacking in natural refuge and have an unnatural flow regime, fish have become increasingly at danger of mortality associated with flooding (Bolland *et al.,* 2006). For example, untimely high flows can wash eggs and larvae away (Jensen & Johnsen, 1999), and in constrained river systems, variable flows can cause mortality in adult fish (Weng *et al.,* 2001).

4.3.1.1 Swimming performance of fish

Swimming performance is a critical factor in determining how successful fish are in maintaining position during high flows and has a profound effect on how fish are dispersed in river systems (Wolter & Arlinghaus, 2003). Swimming speed and endurance directly relate to how successful a fish is in food capture, avoiding predation and at WPS, plays a key role in the ability to avoid entrainment (Domenici & Blake, 1997; Walker *et al.,* 2005; Piper *et al.,* 2013). Several variables influence swimming performance in fish such as fish size, skin composition (mucus; Sagnes *et al.,* 2000), water temperature (Bergman, 1988), dissolved oxygen content (Domenici *et al.,* 2000) and behaviour (i.e., shoaling; Svendsen *et al.,* 2003). Most fish species operate on a ‘reserve’ basis whereby they use very little of their swimming capabilities on a daily basis and instead reserve energy for specific requirements i.e., escaping predators or maintaining their position in the water column during high flow events (Clough & Turnpenny, 2000). Therefore, fish are expected to have different preferences for river flow depending on habitat pressures within their home range (Table 1; Knight *et al.,* 2009).

The function of swimming performance at WPS is critical as fish must be able to outswim high flows to mediate the risk of impingement and entrainment (section 2.2). Frequently, these structures are absent in stimuli that might allow fish to avoid intake areas (Clough & Turnpenny, 2000). Given, even where suitable stimuli are available, fish must be able to outswim the intake velocity to avoid entrainment. In many scenarios it becomes a question of endurance where fish must outcompete prolonged flow change. Similarly, a fishes ability to quickly employ evasive swimming (referred to as ‘burst speeds’ Clough *et al.,* 2004a) is essential on approach to pump intakes as powerful burst speeds may be sufficient to escape intake velocity.

These traits of swimming performance (endurance, burst) are both dependent on fish size and water temperature. For example, small (<10 cm) chub significantly outperform large chub (>15 cm) at low temperatures (<11 °C), but at high temperatures (>15 °C) the difference in burst speed is reduced (Clough *et al.,* 2004a). In dace, burst speed is similar in small and large fish at low temperatures (<11 °C), but at high temperatures (>15 °C), smaller fish outperform larger ones. A similar effect is demonstrated in roach and in perch, where smaller fish are able to outperform larger ones (Clough & Turnpenny, 2000; Clough *et al.,* 2004b). Large predatory fish such as pike typically have very powerful and fast burst speeds (160-245 m^{s-1}; Videler, 1996) to facilitate their feeding as ambush predators. However, endurance is limited when compared to other fish. Contrary to burst speed, endurance is thought to increase proportionally with fish length and therefore adult fish are expected to have increased endurance compared to juvenile fish (Clough *et al.,* 2004b). For example, adult bream and barbel are able to sustain their station position for longer in higher water temperatures than juveniles of the same species (Clough & Turnpenny, 2000).

4.3.1.2 Low flow refuge for fish

During periods of elevated flows the presence and function of refuge habitats is essential for the survival of fish who are unable to compete with flows due to their swimming performance and associated flow preferences (Table 1; Townsend, 1989; Lancaster & Hildrew, 1993; Lake, 2003). Fish are attracted to habitat choices with low flows because they are energetically favourable and avoid displacement in the main channel. Similarly, where metabolic capacity in fish is reduced (i.e., low temperature), flow refuge habitat is essential as the swimming performance in fish is reduced (Ruetz & Jennings, 2000).

The quantity and quality of low-flow refuge habitat is important for the survival of juvenile and adult fish during flooding and high flow events (Lancaster & Hildrew, 1993; Poff *et al.,* 1997). During elevated flows, fish populations are more stable where habitats are structurally complex and have low-flow refuge habitats available (Pearsons *et al.,* 1992). Flooding naturally increases the structural complexity of river systems whereby woody debris and vegetation enter the main river channel, creating pockets of low-flow refuge (Heggenes, 1988; McMahon & Hartman, 1989; Tullos *et al.,* 2015). Similarly, fish seek refuge around instream interstitial spaces, behind rocks and boulders and near river banks where riparian vegetation is dense (Lusk *et al.,* 2003; Lojkasek *et al.,* 2005; Gillette *et al.,* 2006).

Off channel areas (i.e., backwaters) provide key refuge from high flows in the main river channel and extend hydrological connectivity (Copp, 1999; Bell *et al.,* 2001). Although, in modified river systems, one of the most profound effects of regulation is the removal and loss of natural backwaters and side channels (Copp, 1999). In such rivers, the only potential off-channel refuges are commercial marinas, docks and purpose built channels for irrigation (Copp, 1999). In this scenario, fish may make use of manmade structures to facilitate their regular refuge from high flows. For off channel WPS this is undesired as their operation is likely to coincide with flooding and high-flow conditions.

4.3.2 Predation and fish behaviour

The effects of predation on prey communities has been widely considered in ecology (Wilbur, 1988). Fishes must make behavioural decisions that maximise feeding but minimise predation. Predation risk is species specific and in multi-species catchments, the community structure is likely influenced by behavioural patterns of predator and prey. Moreover, in constrained and modified river systems, predation becomes an increasing problem as survivorship in prey species is limited by access to refuge habitat. These factors play a key role in how and when fish move and therefore are expected to influence fish movements surrounding WPS.

Prey species must make informed choices that limit the number of interactions with predators and successful mediation of predator threat is usually achieved by access to refuge habitat (Christensen & Persson, 1993). But, these habitat choices can lead to fragmentation of riverine communities if predator threat remains high (Gilliam & Fraser, 2001). This is often particularly evident in larger rivers, whereby the presence of predators in the main channel can cause low densities of prey species in the river and high densities in its tributaries and backwaters (Fraser *et al.,* 1995; 1999). Similarly, fish may increase longitudinal migrations where predator presence is high in search of refuge habitat where rivers off poor habitat (Gilliam & Fraser, 2001). This behaviourally induced spatial fragmentation is widely demonstrated (i.e., Beecher *et al.,* 1988; Townsend & Crowl, 1991) and presents a scenario where WPS situated on or close to main river channels may serve as refuge for prey species.

Shoaling is a common behaviour employed by fish to decrease predation threat, and in many rivers, large shoals of similarly sized fish are often seen making coordinated movements between refuge habitats (i.e., Persson & Eklov, 1995; Lundvall *et al.,* 1999). In general, smaller fish species are more vulnerable to predation than larger ones and so the risk of predation changes for species and during growth (Wootton, 2002). For example, roach are predated by perch and pike as young (Copp, 1999), but when roach begin to make active habitat choice during early growth their sensitivity to predation is greatly reduced

(Brabrand & Faafeng, 1993). Because predation is likely to restrict habitat use in many fish, and many rivers are now lacking in natural refuge habitat it is anticipated that fish will be driven towards manmade river structures. Here, the concern is that fish may see WPS as attractive refuge habitat from predators.

4.3.3 Feeding and fish behaviour

The successful acquisition of food items is essential to maintain growth and energy in riverine fishes and it is widely recognised that the spatial distribution of fish is influenced by the abundance of predators and food availability (Metcalfe *et al.,* 1999). For prey species, the likelihood of being predated influences their choice of where to feed and subsequently influences habitat or food patch choice. Therefore, foragers are expected to be sensitive to the ratio of mortality (predator or otherwise) to food intake rate for potential food patches (Brown, 1992; Metcalfe *et al.,* 1999). Consequently, fish that have access to refuge habitats should favour foraging patches that minimise predation and maximise feeding (Gilliam & Fraser, 1987). The proportion of time spent in this patch depends on this fitness function and fish will spend less time in foraging patches that are plentiful in food items but have a high risk of predation when compared to patches that have fewer food items but also have fewer predators (Lindstrom, 1990).

This is true of the optimal foraging strategy where natural selection will favour individuals that are able to maximise foraging with minimum energy expenditure (Stein, 1977). Accordingly, the feeding strategy of a fish should be one that allows an individual to consume the highest amount of food whilst also expending the least amount of energy and avoiding predation. The habitat used by fishes has a key influence on prey availability and subsequently their diet (Grenouillet *et al.,* 2001). For example, main channel riverine zooplankton communities are dominated by rotifers, but larger bodied zooplankton are rarely present (Viroux, 1997). Conversely, in areas where there is low-flow refuge, zooplankton production is much higher and accordingly provides a better foraging site than in open water (Spaink *et al.,* 1998). Floodplain waterbodies and rivers with unmodified banks support greater populations of macrophytes than in rivers with modified banks (Grenouillet *et al.,* 2000; Cremona *et al.,* 2008). Subsequently, river habitats rich in macrophytes support a greater number of invertebrates and fish larvae, which provides enhanced foraging sites for fish migrating from main river channels (Freeman *et al.,* 1988).

Ambush predators maximise their feeding success by positioning themselves at the interface between two habitats, usually where one patch is more productive and the other is safer (Winemiller *et al.,* 1998). This is true of piscivorous fishes such as pike, who often feed at the beds of submerged macrophytes or low-flow habitats, areas that usually serve as refuge for prey (Kobler *et al.,* 2008). This combination of prey requiring refuge habitat, and predators seeking similar habitat for ambush contributes to a complicated system where both predator and prey must mediate their movements between river habitats that maximise feeding and safety respectively. Thus, prey species exhibit risk-sensitive foraging, where a fish must consider the potential costs and benefits of leaving a safe area to forage in a more dangerous area that offers higher quality resources (Turner & Mittelbach, 1990).

4.4 Spatiotemporal variation in movements of coarse fish

Day to night alternation of illumination has a large influence on fish behaviour and physiology, and is a controlling factor on habitat use in many fish (Lucas *et al.,* 2001). Diel migrations or movements are a common adaption to manage conflicting traits, and many fish exhibit a clear diurnal pattern where maximum activity is seen at dawn and dusk periods (Hohausova *et al.,* 2003; Horky *et al.,* 2008; Armstrong *et al.,* 2013). This regularity in both spatial and temporal presence has been demonstrated in many cyprinid fish species (Clough & Ladle, 1997; Lucas & Baras, 2008; Table 2).

Physical disturbance in aquatic ecosystems is often a major factor in structuring fish communities (Resh *et al.,* 1988; Poff & Allan, 1995; Lake, 2003; Magoulick & Kobza, 2003). Unsurprisingly, fish communities in lowland rivers are then strongly influenced by seasonal flows and droughts (Resh *et al.,* 1988; Poff *et al.,* 1997). Such seasonal changes to flow must change how fish use habitats and many aquatic organisms seek refuge from physical disturbance and/or have adaptions that mediate refuge (Rosenberger & Chapman, 2000). The extent and duration of flooding during wet seasons influences whether and how long fish can access important spawning and nursery habitats (Heiler *et al.,* 1995). For example, seasonal droughts may separate fish from the main river channel if side-channels become isolated (Bunn & Arthington, 2002). Mortality of fish trapped in isolated water bodies can then be high due to reductions in food and poor refuge from predators (Woodland & Ward, 1990). In constrained rivers where flow refuge is infrequently available, high flow events can flush fish downstream and into unfavourable habitats (Berland *et al.,* 2004). In such systems, fish may develop adaptions that facilitate their refuge during high flows. In Alexandre *et al.* (2016), the home range of barbel increased during high-flows, probably to aid access to a wider range of refuge habitat. Likewise, fish communities downstream of structures that adjust seasonal flows shift between suitable habitats to account for periodic reductions in habitat quality (Bunt *et al.,* 1999). There are also suggestions that home-range size increases with increasing water level in spring, although this is likely a function of lateral habitat expansion (Gardner *et al.,* 2015). Thus, seasonal flows events are important for determining fish community composition and at WPS it may be expected that the distribution of fishes is changed during pump operation.

Table 2 The effect of changes in light during day and night cycles on the activity of several key freshwater species found in UK rivers (adapted form Lucas & Baras, 2008).

Species	**Effect**
European eel *Anguilla anguilla*	Yellow eels predominantly nocturnal and swim faster during the day. Silver eels most active at night.
Northern pike *Esox lucius*	Migration of spawning adults into tributaries is greatest at night. Juvenile movement on bright days.
European grayling *Thymallus thymallus*	Peak movements of grayling out of nursery stream occur at start and end of night.
Dace *Leuciscus leuciscus*	Adults show little activity during day and night in summer. Rapid movement at dawn and dusk between day and night habitats. Juveniles move in and out of bays in response to predation risk at different light intensities.
Chub *Leuciscus cephalus*	Juveniles move into and out of bays in response to predation risk at different light intensities. Positive correlation between photoperiod and migration intensity.
Barbel *Barbus barbus*	Diel movements between refuge and foraging areas. Seasonal variety in peaks of activity in early morning and late evening in summer. Use overwintering habitats in winter.

Seasonal patterns in environmental conditions throughout rivers typically create a series of habitat patches that are used by fish to facilitate their life functions throughout seasonal change i.e., feeding, resting, refuge, spawning (Le Pichon *et al.,* 2016). Additionally, physical transport of nutrients, organic detritus and food between habitats, as well as fish movement between habitats, can greatly influence productivity and predator-prey interactions and food webs and fish are therefore vulnerable to seasonal changes (Polis *et al.,* 1996; Winemiller *et al.,* 1998). Because the use of long-term residency (until death in most coarse fish) in rivers is beneficial for optimal foraging (Huber & Kirchofer, 1997), fish congregate in habitats that exhibit seasonally high food abundance (Le Pichon *et al.,* 2016).

Spawning periods are often associated with lateral and longitudinal migrations (i.e., Welcome, 1985; Grift *et al.,* 2001) and therefore have an influence on daily activity. Perhaps the most extensive migrations of riverine fishes occur in late spring and early summer, where most coarse fish species spawn (Nunn *et al.,* 2009). During this period, peak metabolism in fishes occurs resulting in greater activity and a higher demand for habitat resources (Gardner *et al.,* 2015). For example, barbel migrate from main river channels to shallow streams with gravel beds for spawning in late spring when temperatures are 12-23°C (Lucas & Batley, 1996). This is true of other coarse fish, including perch, chub and roach who spawn in late spring (Hohausova *et al.,* 2003). However, such spawning migrations are energetically costly and thus the cessation of spawning is often followed by periods of inactivity where both home-range is reduced and diel patterns are flattened (Hohausova *et al.,* 2003).

Temperature has been described as an ecological resource, not dissimilar to that of food and habitat (Magnuson *et al.,* 1979), and is a controlling factor for growth in fish, such that the majority of coarse fish use spawning times that ensure the initial growth period of 0+ fish is during summer (Wootton, 2002). In many cases, year-class strength (YCS) is determined by growth in the first year of life (Mills & Mann, 1985; Cowx, 2001), with temperature correlations indicating that large adult populations often result from higher than average temperatures (Nunn *et al.,* 2003). Moreover, because fish typically show lethal, tolerance and performance factors associated with temperature (Fry, 1971), individuals often compete for habitats in their thermal preference that maximise their performance (Suski & Ridgway, 2009). Hence, temperature is often used to describe global patterns in species diversity (i.e., McAllister *et al.,* 1986; Allen *et al.,* 2002). Diet choices are closely matched with water temperature. For example, rudd switch from a piscivorous diet in early spring, to a predominately herbivorous one in summer (Guinan *et al.,* 2015), and roach begin to feed on detritus in late summer if zooplankton productivity is low (Nunn *et al.,* 2003). These changes are likely linked to increasing water temperatures that facilitate digestion of plant matter (Guinan *et al.,* 2015).

5. PHSYICAL AND BEHAVIOURAL FISH DETERRENTS

5.1 Introduction

In England and Wales, there are approximately 48,000 licenced water abstractions that use water intakes for the purpose of industrial water supply, irrigation, hydropower generation and flood defence (Clough *et al.,* 2014). These structures, such as WPS, impede the passage of European eels and carry a high risk of mortality for fishes living in the rivers they are situated on (section 2.2). Similarly, the replacement of natural riverine environments with artificial structures such as constrained side channels, canals, docks, marinas and waterways used for navigation has resulted in large changes to the physical structure of river systems and therefore, in many river systems, fish must use unnatural structures to facilitate their regular behaviours (section 4.3). Because of these undesired changes to fish behaviour, the use of mechanical or physical exclusion barriers (Turnpenny & O'Keeffe, 2005), fish guidance systems (Notach & Suski, 2012), and behavioural deterrents (Patrick *et al.,* 1988a & 1988b; Basov, 2007; Zielinkski & Sorensen, 2015) is a common practice to deter movements of fish and direct target species away from WPS.

The approach to successfully mediate mortality at WPS depends on the processes that lead to entrainment, and the behaviour of fishes living in the fore bay and/or making functional use of the pumping station structure. In all instances, a cost-effective solution must be identified. For eels attempting downstream passage of WPS, passage through pumps could be prevented by supplying an alternative bypass route and using technologies that minimise the likelihood of entrainment. For fish that use WPS to facilitate their regular fitness associated trade-off's (i.e., refuge use), movement into the fore bay of the pumping station could be prevented or minimised by physical or operational changes. Similarly, where fish show residency at WPS, fish could be removed prior to start-up and/or devices could be installed that render the facility unattractive to fish.

To modify an existing WPS so that it will not harm fish that are entrained is not as simple as replacing existing pumps with those that are 'fish-friendly' (Jackson, 2014; section 2.4.1). Instead, pump operators must target a pumping system that is fish-friendly as a whole, i.e. one that successfully incorporates a design or operation that *prevents* entrainment of fish. Whilst many water intakes throughout England are now in compliance with Eel Regulations (2009), WPS are perhaps the most prolific structure that fail to meet regulations (Solomon & Wright, 2012). From a management perspective, it is currently not cost-effective to replace all existing WPS with ones that are designed to mitigate entrainment of fish and eel. Therefore, for existing WPS to meet regulations, alternative solutions must be identified.

5.2 Positive exclusion screening techniques

The importance of screening water intakes in the UK was recognised more than 90 years ago, with the Salmon and Freshwater Fisheries Act (1923, revised 1975) (SAFFA) identifying the need for screening at intake and outfall structures (Turnpenny & Keeffe, 2005). Subsequently, the Water Resources Act (1991) (WRA) stipulates a requirement to screen water abstraction intakes and both the Habitat Regulations (1994) and the Water Framework Directive (WFD) (2003) provide legislation to target the recovery of all inland and coastal waters to ‘good’ status. At WPS, the use of screening technologies is widely applied, and in an effort to recover the critically endangered European eel, the practice of screening is now a statutory requirement (Council Regulation (EC) No. 1100/2007), and Eel regulations (2009) stipulate a requirement for the screening of water intakes which abstract more than 20 m^3s^{-1} a day unless exempted by the EA. The following does not aim to give a fully comprehensive review of screening technologies and instead presents a summarised overview. There has been some effort to highlight key features of available screening methods to divulge where screening may be appropriate.

5.2.1 Traditional mesh screens

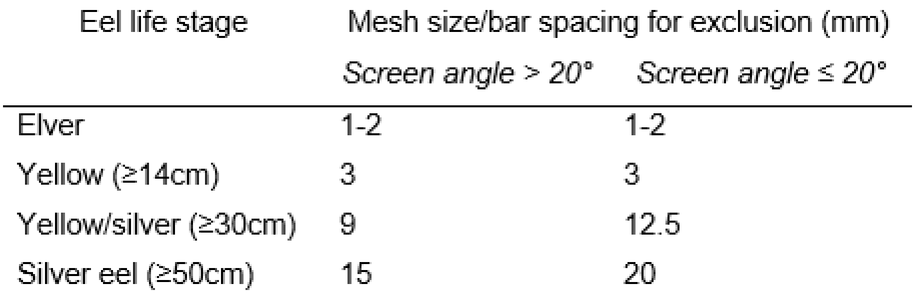
Mesh screens placed across pump entrances are often used to prevent the entrainment of fish at WPS (Turnpenny, 1981; Turnpenny & Keeffe, 2005; Sheridan *et al.,* 2014). A standard screen arrangement uses flat panels of mesh which are fixed to a frame. A suitable bywash must be provided where the screen is placed across a river channel and water velocity drawn at the screen should be low enough to prevent impingement of fish. Additionally, the mesh size should be small enough to ensure the exclusion of minimum target fish size and the screen should be set to an angle that flushes fish towards the bywash.

According to Turnpenny & Keeffe (2005), these screens can be targeted for all fish species and life stages which is advantageous in first order streams that show high biodiversity.

Appropriate mesh sizes are dictated by the size of the fish targeted (Table 3). This has seen the advent of technologies that target key life stages, such as those designed for protection of salmon smolts (smolt screens). Because most coarse fish have a lengthy growth period throughout their ontogeny, mesh sizes must be small enough to prevent entrainment at all life stages. This change in morphology throughout a fishes life cycle can be problematic for intake operators, and the use of screen technology at WPS is typically more or less effective depending on the target fish and life stage (Turnpenny & O'Keeffe, 2005; Table 4). This problem is widely demonstrated with regards to the European eel, a species that has a spawning period that is facilitated by downstream migration. As a result, the EA has now developed screening guidelines for the intakes of pumps targeted at increasing escapement of mature European eels (Sheridan *et al.,* 2014).

Screen suitability is increased by using mesh sizes that are less than the body width of an eel (Table 3). However, unlike coarse fish species that often display clear avoidance behaviour when they meet screens, eels have a tendency to show unpredictable responses (Boubee & Williams, 2006; Dixon, 2006). Eels have been observed approaching screen intakes at the bottom of the river bed and do not necessarily react to the presence of screens before making physical contact with them (Sheridan *et al.,* 2014).

Table 3 Mesh size selection and bar space width for eels at primary life stages (in accordance to Sheridan *et al.,* 2014).



Eel life stage	Mesh size/bar spacing for exclusion (mm)	
	Screen angle > 20°	*Screen angle ≤ 20°*
Elver	1-2	1-2
Yellow (≥14cm)	3	3
Yellow/silver (≥30cm)	9	12.5
Silver eel (≥50cm)	15	20

Table 4 Suitability of screening techniques for different fish species given as a rating (0-5), with zero not suitable at all, two low efficiency, three suitable for some life stages, four suitable for most life stages, and five suitable for all life stages. Costings are given as an approximation (£k) for WPS that draw up to $10m^3s^{-1}$, and are for equipment only and exclude installation. – Indicates no data (Adapted from Turnpenny & O'Keeffe, 2005).

	Type of screen		Species suitability (0 – 5)		
		Cost (£k) WPS up to $10m^3s^{-1}$	Salmonids	Eel & Lamprey	Cyprinids & other freshwater fish
Physical screening	Mesh screens	50+	5	5	5
	Angled bar racks	250+	5	2	3
	Rotatory disc screen	-	4	-	3
	Smolt safe screen	-	5	-	-
	Modular inclined screen	-	4	4	4
	Conada screen	-	5	5	5
	Labyrinth screen	-	5	4	3
Behavioural screening	Louvre barrier	50+	2	0	-
	Bubble curtain	15+	2	0	2
	Electric screen (intake)	18+	-	-	-
	Electric screen (outfall)	18+	4	4	4
	Acoustic device (Infrasound)	40+	4	2	4
	Acoustic device (BAFF)	400+	4	0	4
	Acoustic device (Ultrasound)	-	0	0	0
	Light (continuous)	20+	2	2	2
	Light (strobe)	40+	2	3	3
	Eel bypass	-	0	3	0
	Velocity cap	-	2	0	0
	Attraction flow	-	2	-	-

Where downstream passage is blocked by pumping intakes, eels can forcefully move through screens to attempt passage (Adams & Schwevers, 1997). This not only physically damages the eel, but also significantly increases the likelihood of entrainment.

For pump operators, targeting mesh sizes that prevent entrainment is an issue for intakes where smaller bar widths would impact water flow in a way that compromises operation. At WPS used for flood defence, small mesh sizes are commonly unsuitable as they do not meet the requirement for high water velocity. Similarly, retrofitting requires low water velocities, channel excavation and the construction of a suitable bywash, Consequently, retrofitted screens are generally not appropriate for large tidal and inland WPS, and are instead limited to streams with low water velocities (Turnpenny & Keeffe, 2005).

5.2.2 Angled bar racks (passive screening)

Angled bar racks are commonly used by WPS operators to function as trash/weed racks for debris exclusion. However, they may also be adapted for use as fish protection. Angled bar racks in principle function by construction of an array of vertical slats that are placed diagonally across flow field (i.e., pump intake) to create water turbulence in an effort to deter fish movements (Turnpenny & O’Keeffe, 2005). Angled bar racks work well for targeting large, strong fish with high swimming capabilities such as that in salmon (*Salmo salar)*, and provide reasonable protection for adult coarse fish, but have limited performance for eels (Table 4). Critical hydraulic conditions are required on site, as strong attraction flows are required to stimulate fish movements towards bypass channels (Simmons, 2000; Figure 16).

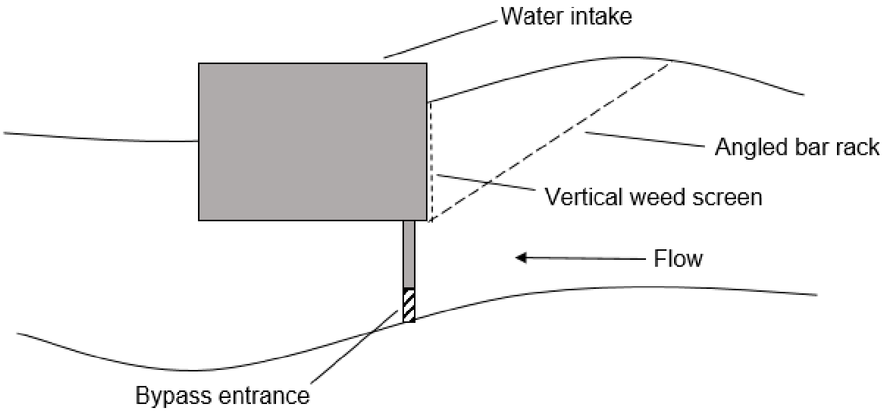


Figure 16 An example of an angled bar rack installation at a riverside water intake. Fish approach the angled bar rack were flow directs them towards the bypass entrance.

Subject to the correct spacing and sufficiently low approach velocity with high attraction flows, installed examples have functioned well for yellow and silver eels, but are ineffective for juvenile life stages (Sheridan *et al.,* 2014). Retrofitting applications present similar issues to those of mesh screening and costs here are particularly high due to the volume of raw materials required for the construction at large water intakes (Table 4). Although the spacing between angled bar racks can be targeted towards smaller fish, reduced bar widths are problematic for pumping efficiency, and pumping efficiency can be reduced as much as 50% where bar widths <3 mm are used (Clough *et al.,* 2014). A species specific understanding of angled bar racks is lacking, and a limited use throughout England means species specific fish behaviour is poorly understood.

5.2.3 Spillway screens

The principle of spillway screens is that a grid, mesh, or bar rack replaces part of the downstream face on a weir, where water passes through to be diverted towards pumps for irrigation or abstraction purposes (Turnpenny & O'Keeffe, 2005). These screens are largely inappropriate at WPS as they are designed to exploit the 'Coanda effect' of water rushing over a crest or outfall. This is also true of smolt-safe screens, which again are incorporated into a weir, but instead use fine mesh sizes targeted at early life stages of salmon.

5.2.4 Other screening technologies

5.2.4.1 Water Intake Protection (WIP)

In accordance with the Eel Regulations (2009), Beaudrey proposed the following guidelines in identifying screening solutions (see Fillon *et al.,* 2014).

- *Minimizing the impingement time (e.g. 30 seconds) and therefore substantially reducing the biota mortality*
- *Minimizing entrainment of smaller organisms*
- *Aquatic life must not be exposed to air*
- *Aquatic life must not be subjected to skin injury*
- *Aquatic life must not be subjected to injurious water pressure decreases nor to negative relative pressure*
- *Aquatic life must not fall from a height greater than 500 mm (an extra recommendation in some countries)*
- *There must be sufficient water to provide adequate return capability*

The Water Intake Protection (WIP) screen combines regular screening technology with a fish-recovery system. The system can be retrofitted to existing WPS using a pre-installed trash rack and utilises a rotating screen with a series of radial, deep storage compartments that are designed to trap fish that enter the screen. Once trapped in the compartments, fish are retained from water velocities drawn by the pumps and are therefore deemed safe. During operation, the screen works in cooperation with a Hidrostal fish-friendly pump (section 2.41), and moves fish away from pump intakes by depositing them adjacent to operating pumps using a backwash flow created by the rotating screen.

Currently, testing has been applied in the field to bluegill (*Lepomis macrochirus*), channel catfish (*Ictalurus punctatus*) and fathead minnows (*Pimephales promelas*), along with resident fish of the Missouri river. Fillon *et al*. (2014) demonstrated a 95% reduction in impingement losses when compared to control trials and was successful in preventing entrainment of all fish during the trial period. However, because testing was limited to a single report at a power cooling intake, it remains unclear as to its application at WPS. It is unlikely that a solution involving the use of pumping will be suitable for larger fish species, as eels are vulnerable to grinding and abrasion even in fish-friendly pumps.

5.2.4.2 Travelling screen barriers

Travelling water screens (TWS) are widely applied to intake points of power plants and are used to mediate entrainment of debris (Black & Perry, 2014). Typically, TWS utilise large mesh-panels that are attached to rotating drums and operated either sporadically (for cleaning) or continuously (for intakes in heavily weeded areas or for fish protection). As the screen rotates out of water, high-pressure water jets are used to remove debris and direct any trapped fish into the source water body (Black & Perry, 2014). For means of fish protection, successful remediation of entrainment is usually achieved by modifying TWSs with a finer mesh sizes (≤10 mm) and addition of ‘fish buckets’ that are designed to collect fish and move them to the top of the screen where they are deposited (Fletcher, 1990). The use of fish-buckets has previously been debated as entrapment here may be a source of injury and mortality in fish (Fletcher, 1990). However, modern designs typically incorporate improved designs (i.e., rounded edges) that offer better fish protection (Ronafalvy *et al.,* 2000).

Moving screens are thought to be beneficial at water intakes because screen movement may function to influence avoidance behaviours in fish. Accordingly, Black & Perry (2014) observed fish employing evasive swimming behaviours when coming into contact with moving screens. The authors concluded that TWS that are modified to function as fish deterrents are successful in reducing impingement mortality. Although, this laboratory based study may not translate to real-world scenarios, i.e, Svendsen *et al.,* 2010, where a TWS was unsuccessful in influencing the relative success of fish migrating past a water intake. Here, the authors concluded that their success was largely dependent on the volume of water abstracted by the facility, with higher water velocities resulting in increased survival of fish. Consequently, the success of such devices is probably dependant on both abiotic and biotic factors.

TWS also suffer similarly to mesh size issues associated with fixed mesh screens. Whilst mesh sizes may be adjusted seasonally and smaller mesh sizes (<2 mm) can be installed during key spawning periods to prevent entrainment of larvae, debris is likely to have a significant effect on survival of fish, and mortality of early life stages recorded as high as 100% where debris readily accumulate (Fletcher, 1994). More so, retrofit installations are also high cost due to the installation of mechanical parts and are generally limited to smaller intakes (i.e., bypass systems in streams).

5.2.4.3 Rotary disk screens

Rotary disk screens were originally designed to be used in sewage treatment works but have been modified for fish protection at intakes (Turnpenny & Keeffe, 2005). They use a series of discs stacked on top of each other, with interleaving columns rotating opposite directions. Rotary disk screens are relatively compact and thus can be easily retrofitted in replacement of traditional trash racks. In rivers with strong sweeping flows, rotating screens are suitable for deterring larger fish (i.e., roach, bream, perch) (Turnpenny & Keeffe, 2005). However, they are not suitable for large intake areas due to high costs and poor management of debris.

5.3 Behavioural deterrents

Behavioural deterrents function by targeting the sensitivity of the corresponding sensory system in fish i.e., vision, hearing and smell. The success of behavioural deterrent systems on fish movements relies on an aversive stimulus being produced in the fish (Noatch & Suski, 2012). This is then exploited by deterrent technology to block or direct fish away from targeted areas (i.e. water intakes) (Zielinski *et al.,* 2014). Hence, these practices differ from mechanical or physical barriers by not obstructing water flow (Noatch & Suski, 2012) and offer potential remediation for structures with water intakes that require high water velocities. Reponses to stimuli vary by species, life stage, size and physiological condition. Consequently, it is important to identify the most suitable remediation measure with regards to target species and life stage.

5.3.1 Velocity barriers and Louver screening

Natural instream flow can be manipulated to create a velocity barrier that exceeds the swimming capabilities of a fish (Notach & Suski, 2012). This is usually accomplished by constricting water flow using either a culvert or flume-like design. Potential sites usually require a channel small enough that would see an increase in flow rate if a culvert type design was incorporated. Suitable species are usually those that have swimming thresholds that can be exceeded by high flowing water. Velocity barriers have been used to increase bypass efficiency of weak swimmers like lamprey (Heinrich *et al.,* 2003). However, these systems are generally ineffective for species with strong swimming capabilities, or high burst speeds as is many coarse fish throughout the England (section 4.3.1.1)

5.3.1.1 Louver screening

Following the principle of angled bar racks, louver screens have been used extensively throughout the development of water intake protection and are often considered an effective option for reducing entrainment of salmonids and larger coarse fish that are predisposed to flow attractions (i.e., Solomon, 1992; Turnpenny & O’Keeffe, 2005). Whilst considered a behavioural deterrent, they rely on construction of a physical screen that manipulates water velocities, and in turn creates a velocity barrier. The louver screen functions based on the reaction of fish to currents generated by water flowing over louver slats. The structure is positioned in front of the water intakes, and fish that approach the structure are attracted towards shearing flows (velocity gradient across different parts of the fishes body) and as a result avoid entering the screen.

Louver screening is relatively cost-effective when compared to the installation of angled bar racks, although, application of louver screens is limited by channel depth, and in deep water (i.e. ≥4 m), louver construction does not usually extend to the full depth of the channel. This makes louver screening mostly unsuitable for benthic or bottom dwelling fish such as the eel and larger cyprinids i.e., pike (Table 4; Kynard & Buerkett, 1997; Turnpenny & O'Keeffe, 2005). Similarly, they can be ineffective for fish that swim through apposing flows. However, some applications can be altered, and the angle of the screen to the axis of flow is often manipulated to reduce fish penetration. Louver screens are usually most effective between 10° and 15°, with 30° being the maximum offset. For applications where fish can swim through apposing flows, fish penetration can be reduced by the addition of fine screening close to the bywash entrance (Solomon, 1992).

5.3.2 Electric barriers

Electrical fields can frighten, attract, stun, or kill fish and this has been exploited by fisheries biologists for years using electric fishing (Vandergoot *et al.,* 2011). Electrical energy applied to water is transferred to fish which can lead to taxis (forced swimming), and immobilisation (Reynolds, 1996). In worse case scenarios, electrical currents can cause trauma or death, but when used at prescribed intensities, electrical fields can be used as effective fish deterrents by promoting a behavioural avoidance response (i.e., Katopodis *et al.,* 1994; Figure 17). Electrical fish deterrent systems utilise the passing of electrical current between a series of anodes and cathodes placed in the water column. As electricity passes from one side to the other, it effectively creates a physical barrier that should deter fish. Graduated Field Fish Barriers (GFFB) function by using an array of electrical fields that increase in intensity as fish swim upstream into the deterrent (Figure 17; Burger *et al.,* 2012). Fish that are sensitive to electrical currents are expected to find water where the electric intensity is lower, subsequently swimming into the bypass channel.

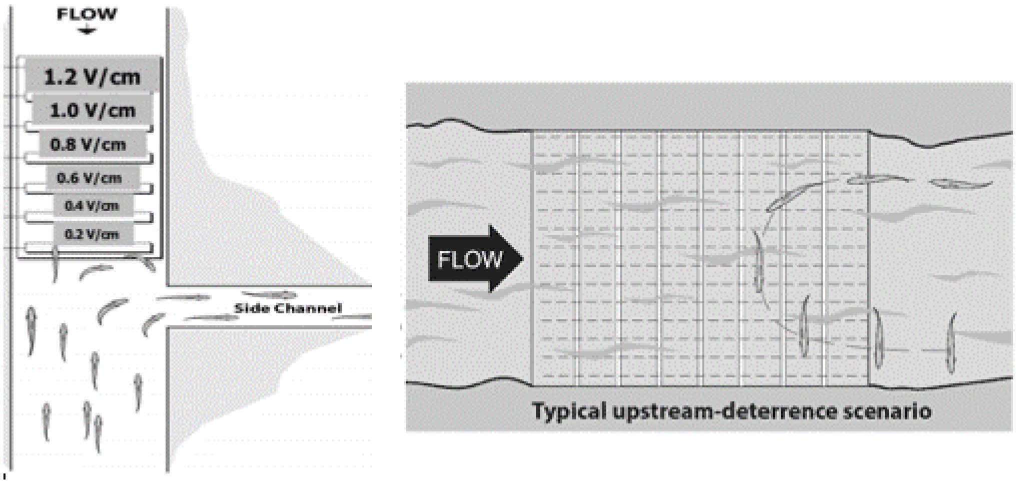


Figure 17 An example of an electric fish deterrent with an increasing electric array designed to target fish towards a bypass channel (Figure adapted form Burger *et al.,* 2012).

Electrical barriers have been widely applied to prevent the spawning and movements of invasive species between water bodies (Noatch & Suski, 2012; Johnson *et al.,* 2014, Parker *et al.,* 2015; Kim & Mandrak, 2017). The electric Aquatic Nuisance Species Dispersal Barrier in the Chicago Sanitary and Shipping Canal was successful in controlling downstream movements of the river goby (*Awaous banana*), and has also been adapted to prevent upstream movements of carp with great success (Sparks *et al.,* 2010). Similarly, electric barriers have been used at water intakes to prevent fish entrainment (Burrows, 1957; Davis *et al.,* 2016), and the use of improved ultra-low frequency electric deterrents are successful in reducing entrainment at water intakes (Stoot *et al.,* 2018). However, fish size can be a limiting factor, as smaller fish generally require a greater amount of electrical power to cause taxis than larger fish (Henry *et al.,* 2003).

The effects of electricity on fish is largely dependent on target species (Dolan & Miranda, 2003), deterrent design (Notach & Suski, 2012), direction of current and water conductivity (Hll & Willis, 1994). Because the effects of electricity dissipate in water, fish that are further from the source are less likely to suffer taxis, and thus display avoidance behaviours when contacting electrical fields. Although limited in understanding, Egg *et al.* (2019) demonstrated the effectiveness of electrical barriers at a dyke-based WPS, where they reported a ‘turning rate’ (fish repelled by electrical field) of 72%. But, their wider application under different structural conditions is currently unexplored, and retrofitted applications are expected to be limited by access to bypass channels. Their installation is also costly when compared to other deterrents (Table 4). Unfortunately, there are currently large knowledge gaps on the effectiveness of electric barriers as retrofitted applications. The effectiveness of these barriers is quite varied, and testing is generally lacking for many coarse fish species expected in UK rivers.

5.3.3 Light based deterrents

Light levels influence fish behaviour by modulating orientation, access to foraging, intra and interspecific communications, predator avoidance and circadian movements associated with diel patterns (see section 4.7.1; Li & Maaswinkel, 2007). Thus, it is expected that the introduction of artificial lights may be useful as a deterrent for fish movements if it can be used to induce a behavioural avoidance. Light can be used to illuminate existing physical or behavioural screens so that fish can orientate themselves in a way that maximises the deterrent, or it can be used directly to attract or deter fish. The use of lighting is appropriate for structures where construction of physical barriers to fish would otherwise impair water flow (Turnpenny & O’Keeffe, 2005).

The use of lights as fish deterrents extends at least 60 years for applications in aquaculture and as a method to reduce entrainment at water intakes (Johnson *et al.,* 2005; Hamel *et al.,* 2008). High impingement and entrainment at night can be mitigated by the installation of lights that improve fish orientation by illuminating structural features such as fish screens, weed screens and bar racks. This has been used to great effect, with reduction in entrainment of cyprinids as high as 90% (Pavlov, 1989).

Illumination can also function as a deterrent by exploiting species specific criteria based on spectral sensitivity of retinal photo pigments. For example, in the eel, a species with strong phototaxis and rheotaxis, light can be used to discourage from following water flow that would result in entrainment (Hadderingh & Smythe, 1997; Figure 18). Because there are usually pronounced diel fluctuations in swimming activity where swimming performance is positively associated with illumination, it is typical of fish to cease or reduce swimming activities when illumination is below the threshold required for visual orientation (Hocutt, 1980). Indeed, fish may or may not be able to orientate

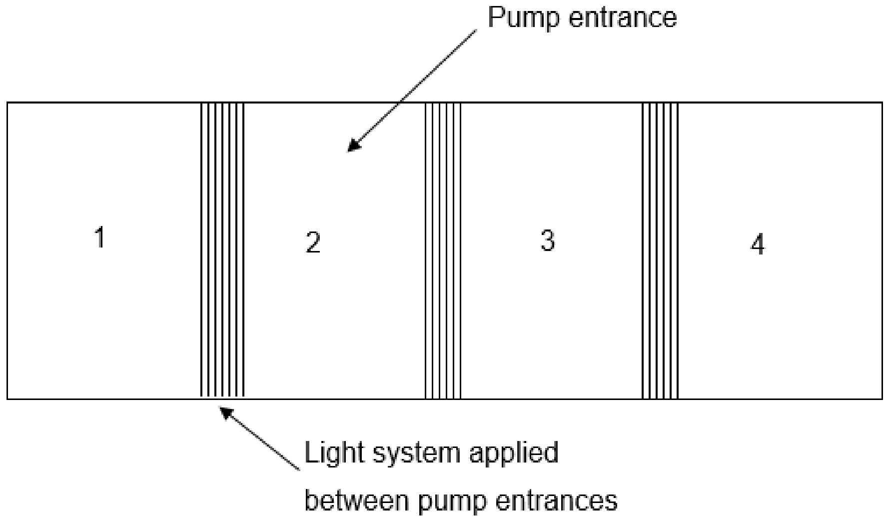


Figure 18 An example of a pumping station with four individual pumps and an installed fish deterrent using strobe lighting.

themselves to flow in dark or highly turbid water and thus it may be advantageous to use lighting as an attraction to guide fish away from intakes at night.

Fixed lighting is limited in its applications, and many argue that strobe lighting is more effective against a wider range of fish (Notach & Suski, 2012). When submerged and installed at the entrance of turbine intakes, strobe lighting can be used to deter fish from turbines and minimise entrainment (Brown, 2002). Again, these lighting deterrents are effective against juvenile and adult eels, showing reductions up to 90% in both field and laboratory testing (Patrick *et al.,* 2001). Flash rates of pulsing strobe lights can be adjusted for best effect, where for example, 300 flashes per minute (FPM) is highly effective in reducing entrainment of perch and trout, whereas other fish require higher or lower FPM (Johnson *et al.,* 2001). Although, there are suggestions that strobe lighting alone is not effective enough where complete deterrence is the goal, because individual species react differently to light (i.e., Hamel *et al.,* 2008). For example, in Hadderingh (1982), strobe lighting reduced entrainment of perch by up to 100%, but increased entrainment of three-spined sticklebacks (*Gasterosteus aculeatus*). Whilst lighting can be retrofitted to existing structures with relative ease when compared to that of physical screening, lighting must be submerged to minimise light pollution, which often results in high installation and maintenance costs and is undesired by pump operators.

Their application is also only realistically suitable in clear water, which presents issues for WPS that draw heavy loads of silt. However, this is improving as technology develops, and new hardware has improved ease of fitting, increased life span and can be operated remotely. Most early work focused on mercury vapour lights (i.e., Patrick *et al.,* 1985), and white strobe lights (Richards *et al.,* 2007), which are a comprise as they do not exploit the full availability of the light spectrum (Sullivan *et al.,* 2016). Modern LED lighting now allows an installed device to be programmed to best target fish species based on spatiotemporal presence and individual species response to different light frequencies (red, green, blue, white). Early laboratory studies suggest coloured light accompanied by light pulses provokes an improved avoidance behaviour when compared to traditional lighting (Sullivan *et al.,* 2016). Maintenance must be considered, and in heavily weeded rivers lighting may not be suitable if equipment is persistently covered by vegetation.

5.3.4 Acoustic deterrents

Sound can be used as a fish deterrent where visual stimulation is not suitable, such as where turbidity is high and/or river channels are deep. When used underwater, Acoustic Fish Deterrents (AFD) exploit phonotaxis by generating pressure waves that are unpleasant to fish (Schilt, 2007). AFD began to gain popularity almost 30 years ago, where Klinect *et al.* (1992) discovered that noise generated by an underwater turbine was deterring fish. As with other behavioural deterrents, the effectiveness of AFD varies considerably with target species (Maes *et al.,* 2004).

Hearing ability in fish can be broadly generalised as “generalists” that detect frequencies below 1KHz, and “specialists” who detect a wider range of frequencies (Notach & Suski, 2012). The highly specialised ear present in cyprinids may predispose them to a greater auditory range and thus susceptibility to AFD (Hocutt, 1980). Operators can therefore adjust AFD to best reflect target species and AFD have been widely applied to meet similar goals to that of visual deterrents, with some success at reducing impingement/entrainment at water intakes (Ross *et al.,* 1993; Maes *et al.,* 2004). This is especially true of experiments that have targeted cyprinid fish where entrainment was reduced by as much as 80% (Sonny *et al.,* 2006). Knudsen *et al.* (1994) demonstrated the successful use of an AFD to prevent

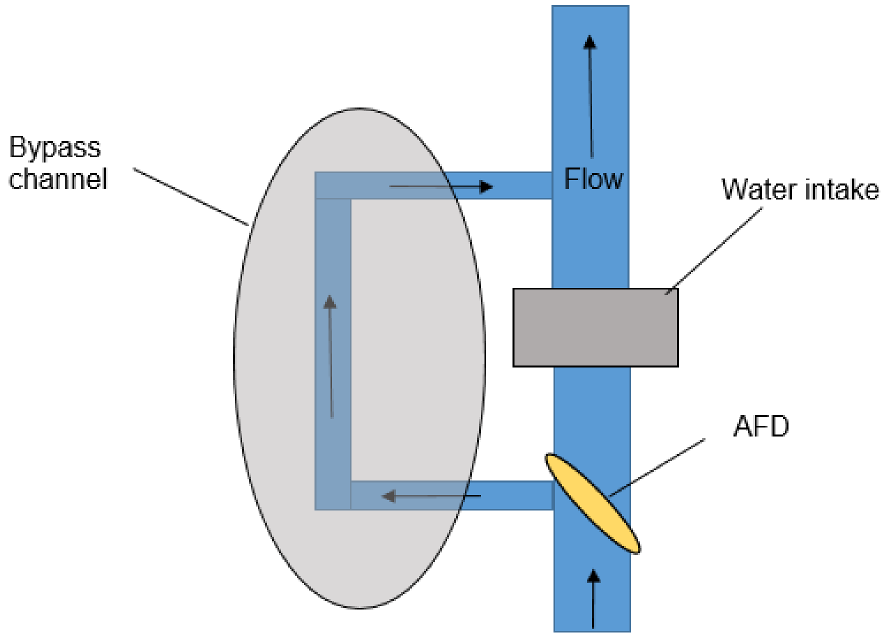


Figure 19 An example of an Acoustic Fish Deterrent (AFD) installed on a river where a water intake spans the width of the channel.

salmon from entering river side channels, which may lend itself to applications at off-channel WPS. Similarly, in Murchy *et al*. (2017), a WFD application installed at each side of a lock barrier was successful in controlling entry of carp, with 80-90% of all fish being repelled by the AFD.

AFD work best when used in cooperation with other deterrents, which must be incorporated in any cost-benefit analysis (Welton *et al.,* 2002). Particularly, the use of lighting to accompany sound is often cited (Patrick *et al.,* 1985). For certain applications, bypass channels must also be constructed where intake areas span the width of a river channel (i.e., Figure 19). there is also a requirement for consideration of site specific conditions including bathymetry and hydrology, which are deciding factors in determining usable frequency ranges for the suitability of AFD for retrofit applications, (Popper & Carlson, 1998). Low-frequency sound waves as a deterrent show poor performance in shallow waters (Turnpenny & O'Keeffe, 2005). Pure tones should not be used because fish tend to habituate to them, showing poor reaction and overall deterrent efficiency (Vetter *et al.,* 2015). Thus, it is often appropriate to use a range of sounds, or pulses of audio as opposed to consistent transmission. While this broad-brush approach can provoke avoidance behaviours in a wider range of fish, it inherently loses some precision, and is less likely to be effective against fish with specialist hearing.

5.3.5 Bubble curtains

Bubble curtains are amongst the simplest deterrents and have been used with varying success to attract or deter fish from water intakes. Using a similar principle to that of a louver screen (i.e., creating an artificial screen by exploiting hydrology), compressed air is pumped through a perforated tube laid across the riverbed which creates a wall of bubbles. The tube is positioned at an angle to the flow and directs fish towards a bywash (Turnpenny & O’Keeffe, 2005). Their installation is simple, cheap and low maintenance, and adjustments to the size and spacing of bubbles, air discharge water pressure and illumination can be made to best reflect species specific considerations (Solomon, 1992). Bubble curtains often attract interest from fisheries managers because of their low installation costs (Table 4), but as a standalone fish deterrent have shown limited potential (i.e., Dawson *et al.,* 2006). For example, laboratory based investigations show pike and carp being deflected by bubble screens, but they had no effect on trout (Turnpenny & O’Keeffe, 2005). Patrick et al. (1985) indicated up to 70% of baitfish avoided air bubbles, with similar results from Stewart (1981) suggesting pollack (*Pouachius pollachius*) would not cross a bubble barrier under experimental conditions. Their effectiveness for targeting English river residents is limited (Table 4).

It has long been understood that bubble screens are inherently reliant on interactions with other stimuli (electric, sound, light) (Notach & Suski, 2012). The relationship between the effectiveness of these devices is complicated and site specific. Bubble curtains have been used in conjunction with acoustic deterrents with great success for controlling downstream movements of fish (Welton *et al.,* 2002; Perry *et al.,* 2014). Many cite their effectiveness as highest during the day and lowest at night, suggesting that light reflected on bubble curtains is an important factor (Patrick *et al.,* 1985; Ruebush *et al.,* 2012; Stewart *et al.,* 2014). Using this understanding, a combination of deterrents using bubble curtains and strobe lights has shown some success in deterring estuarine fish from tidal entrances (McIninch & Hocutt, 1987). However, other studies have reported that some fish are attracted to such deterrents (i.e., Sager *et al.,* 1987). Particularly, in Stafford-Glase & Homa (1997), age 0 rainbow smelt (*Osmerus mordax*) were repelled by such barriers, but juveniles and adults were not, and a similar technique showed poor effectiveness in reducing the fish loss at a dam slipway (Stewart *et al.,* 2014).

5.3.6 Chemical barriers

Chemical alteration of aquatic habitats has been used to deter fish movements. In principle, these chemical deterrents function by influencing key factors that contribute towards overall water quality. For example, the manipulation of dissolved oxygen (DO) has the potential to create a chemical barrier where oxygen saturation is unfavourable for fish. This functions on the principle that areas of hypoxic water negatively influence fish distributions (Hasler *et al.,* 2009). Similarly, with respiration being a limiting factor for fish, increased carbon dioxide concentration is expected to deter fish movements. Currently, there are few examples of chemical manipulation being used to deter fish movements. In areas where natural episodes of hypoxia are common it may be possible to construct a permanent hypoxic zone that would hypothetically block fish passage (Scheier *et al.,* 2008). Persistent mixing of waters upstream of WPS through pump operation may render chemical barriers less effective.

6. MATERIALS AND METHODS

6.1 Study catchment

The Yorkshire Ouse (hereafter referred to as the River Ouse) is a river in North Yorkshire, England. When combined with the River Ure tributary, the River Ouse is approximately 200 km long, extending from its source near Hawes (SE806971). The river is formed at the confluence between the River Ure and the Ouse Gill Beck, where it flows through the city of York before joining the River Trent and then forms the Humber Estuary at its mouth (SE862235).

The River Ouse has a series of tributaries (namely, the Aire, Don, Wharfe, Ure and Foss) that form a catchment area of approximately 3315 km^2. Of these, the Swale, Ure and Nidd drain much of the upland reach of North Yorkshire, where water flows south easterly from the Yorkshire Dales. Due to heavy rainfall in the region, much of the lower Ouse catchment is susceptible to flooding. Flooding in York has been recorded for many centuries and the frequency and magnitude of flooding has continued to increase during the last century (Environment Agency, 2016a). In response to continued flooding events, the York Flood Alleviation scheme was devised consisting of the Castle Mills Lock, Castle Mills Sluice and the Foss barrier.Working in conjunction with the adjacent Castle Mills bypass sluice, Castle Mills Lock now functions exclusively to maintain the upstream stretch of the River Foss at 7.6 mAOD. The remaining downstream stretch of the river forms Foss basin, which is maintained by Foss barrier and its adjacent pumping station.

The River Ouse contains relativley unpolluted habitats in its lowland reaches, but following a legacy of pollution in the Humber estuary, the river has poor salmonid populations, probably because its tidal reaches are heavily polluted (Environment Agency, 2020). In the upper reaches there are some remaining healthy populations of brown trout, but much of the river, and especially the lowland reaches, are predominantly coarse fish (particularly cyprinids) (Lucas *et al.,* 1998; Lucas *et al.,* 2008).

6.1.1 The study site

The study site was located at Foss WPS situated in Foss basin (Figure 20). When constructed, the site had a total pumping capacity of 32 m^{3}s^{-1}, but following a catastrophic flooding event in 2015, the site was redeveloped. As of

2016, Foss WPS has eight xylem pumps, each with a capacity of 6.5 m^3s^{-1} and provides a total pumping capacity of 52 m^3s^{-1} for response to extreme flooding. The screened intake measures roughly 27m across with fish protection limited to a slow start-up procedure. Unlike many other pumping sites throughout England, Foss WPS is unique in that pumps are generally operated at a much lower frequency, whereas other WPS often pump on a daily basis. Foss WPS remains non-operational during regular flows and is only used in response to flood events.

The Foss barrier is a turnover lift gate and straddles the River Foss where the confluences of the River Ouse and the River Foss meet in York city centre. The floodgate is designed to prevent floodwater backing up in the Foss where it meets the surge water of the River Ouse and is unable to drain away. When the River Ouse reaches 7.6m mAOD the flood gate is lowered. Whilst the floodgate is down, downstream fish passage from the Foss to the River Ouse is prevented, as water is unable to flow into the River Ouse naturally. Therefore,

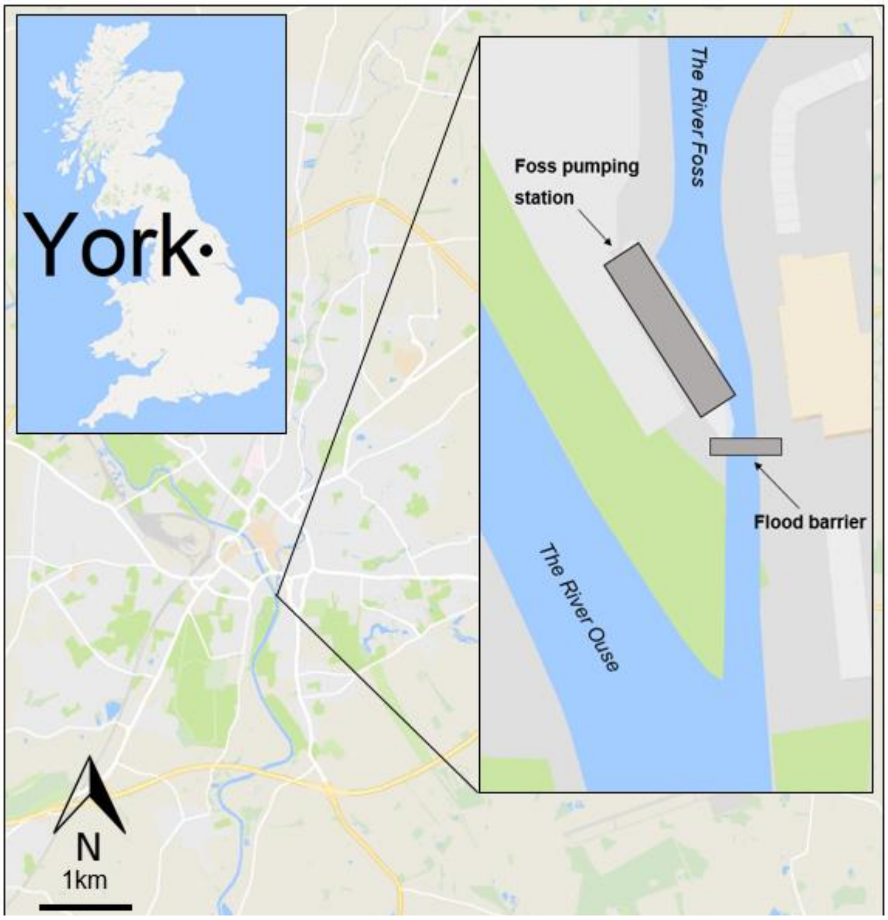


Figure 20 The position of York (top left) with the rivers Ouse and Foss meeting in the city centre (map insert). Foss pumping station is situated at the confluence of the Ouse and Foss immediately adjacent to Foss flood defense gate (SE605512).

free passage of fishes in the Foss is blocked and individuals within Foss basin are vulnerable to entrainment from pumping operations. When the WPS is in operation, water is pumped from Foss basin and passed through the facility and into the pump housing, before being discharged downstream of the floodgate into the River Ouse via a discharge culvert. The pumps are managed by computer software that maintains the water level of Foss basin at approximately 7.6mAOD. Pumps remain operational until flood level water in the River Ouse subsidies and equalises with Foss basin.

Foss WPS is currently recognised as high priority under the Eel Regulations due its potential impacts on upstream and downstream passage of eels. Following cost-benefit analysis by the EA, it has been deemed that screening the intake for European eels is unsuitable due to the physical space and pumping capacity required and the relative risk of debris accumulating under operation. Therefore, alternative remediation measures need to be considered.

6.2 Fish monitoring

6.2.1 Monitoring technique

The ability to observe fish in their natural environment can be difficult to achieve. Traditionally fisheries surveys have relied on biologists interacting directly with fish through trapping and handling methods. Whilst this is practical and sometimes essential to collect biological data, it is potentially damaging to fish as it can alter their natural behaviour. Physical handling of the fish is inherently difficult, and in many cases, relies on favourable environmental conditions for capture. Consequently, it is desirable to use methods that do not involve removing individuals from their environment, and instead allow passive biological observations.

The use of underwater sonar imaging was deemed an appropriate tool for examination of fish movements in Foss basin following expert opinion from members of Hull International Fisheries Institute (HIFI) and the EA. Fish monitoring was performed using a Dual Frequency Identification Sonar (DIDSON 300m, Sound Metrics, USA). The high-resolution multi-beam sonar is capable of imaging objects in turbid and dark waters and is therefore extremely useful for capturing fish movements at both day and night. The user is able to image underwater scenes in near video-like quality and review footage with variable playback speeds, automated fish counting and measurement tools. The technique is unobtrusive; allowing fishes to be monitored without the need for capture. Therefore, fish movements within Foss basin can be passively monitored using DIDSON.

6.2.2 Installation and operation

In late October 2017, the DIDSON was installed at Foss pumping station using scaffold via a bankside railing and submerged within the channel to a depth of 3 m (Figure 21). The unit was located immediately adjacent to the pumping station, 35 m from the flood defence barrier and 145 m from the nearest upstream barrier (Castle Mills Lock). The DIDSON was operated at high frequency (1.8 MHz; 96 beams ordinated 0.3º apart) and had an observable field of view (FOV) of 10m (5 m to 15 m window length).

All software inputs were completed using manufacturer supplied SoundMetrics software. The frame rate was set to six frames per second (fps), the maximum frame rate available for the setup, and receiver gain and focus were left at default. Equipment was contained in a weatherproof box and had remote access via TeamViewer software using a wireless internet connection.

Figure 21 DIDSON installation at Foss

Continuous observations were captured to an external hard drive which was exchanged with bi-weekly site visits. The files were time and date stamped and recorded at ten minute intervals. Images were recorded throughout October, November, December 2017 and January, February and March 2018 (*N* = 153 nights).

6.2.2.1 Regular flows

From its position fixed on the leading bank of Foss WPS, the DIDSON was orientated to face across Foss basin (Position 1; Figure 22a). As the standard

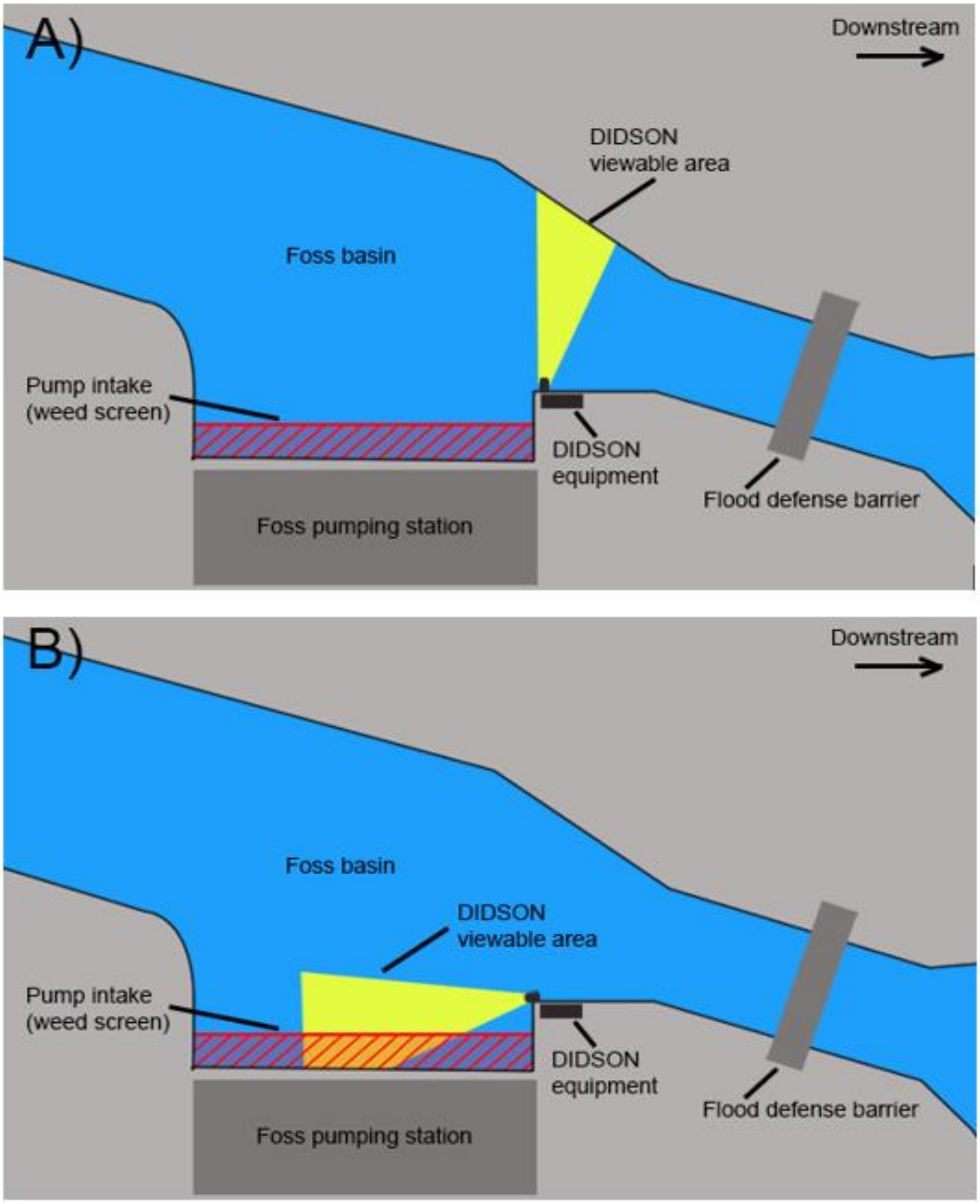


Figure 22 A schematic diagram of Foss pumping station with the DIDSON orientated to face position 1 (a) and position 2 (b).

operating position, the DIDSON was able to image fish moving in the channel between Foss basin and the River Ouse. Position one was confirmed visually by aligning the DIDSON beam with the steel bank wall. In this scenario, the flood defence barrier is open, and the pumps are not operational.

6.2.2.2 During pump operation

When pumps were to be operated the DIDSON was repositioned by rotating the scaffold bar and reorienting the DIDSON to image across the weed screen (Position 2; Figure 22b). Prior to pumping taking place, EA staff contacted the author who provided remote assistance with re-positioning the DIDSON. Due to the size of the intake at Foss, the number of pumps that could be imaged at one time was reduced. In all pumping scenarios, the DIDSON was orientated to image pumps three, four and five. Therefore, images captured during pumping are representative of around 40% of the pump intake.

Position two was confirmed by visual observation of the weed screen in the image (Figure 23). When the DIDSON is orientated to this position, the flood defence barrier is down and pumps are operational.

6.3 DIDSON analysis

6.3.1 Coarse fish

6.3.1.1 Regular flows

The recorded images were viewed using SoundMetrics DIDSON software. To reduce processing time, an early sampling trial using footage captured during October 2017 was used to determine an appropriate sub-sampling frequency. A total of two days was sampled by visual counting of fish at 1 frame every 15 minutes. Due to the initially large volumes of fish observed in the entire frame, it was determined that subsequent samples would be taken from the centre of the DIDSON array in a 2 m^2 window. Therefore, estimated fish abundance is given as individuals·2 m^{-2}. Following this, histograms of fish abundance were constructed at 15, 30 and 60 minute intervals. This revealed that all intervals were appropriate for identification of diel activity of fishes in Foss basin. Although, analysis time increased by 100% for every interval of sampling, and due to the size of the data set it was determined that hourly intervals would be appropriate. Additionally, background subtraction was used during this sample period and was later determined to be detrimental in most cases as it eliminated fish that were stationary on the bed of Foss basin.

The following analysis in November and December 2017, and January, February and March 2018 was based on visual counting of individual fish abundance during a 1 frame·h^{-1} subsample. The sample was taken at five minutes past the hour (±5 s), which allowed the observer to move the image and determine which objects were fish. This was repeated for a 14-day period per month which were determined by availability of consecutive data (i.e, few interruptions). Playback speeds were adjusted between 4x and 16x speed for easier discrimination of non-fish targets.

Fish size was measured using the measurement tool in SoundMetrics software, and then grouped into six size classes; 0-10 cm, 11-20 cm, 21-30 cm, 31-40

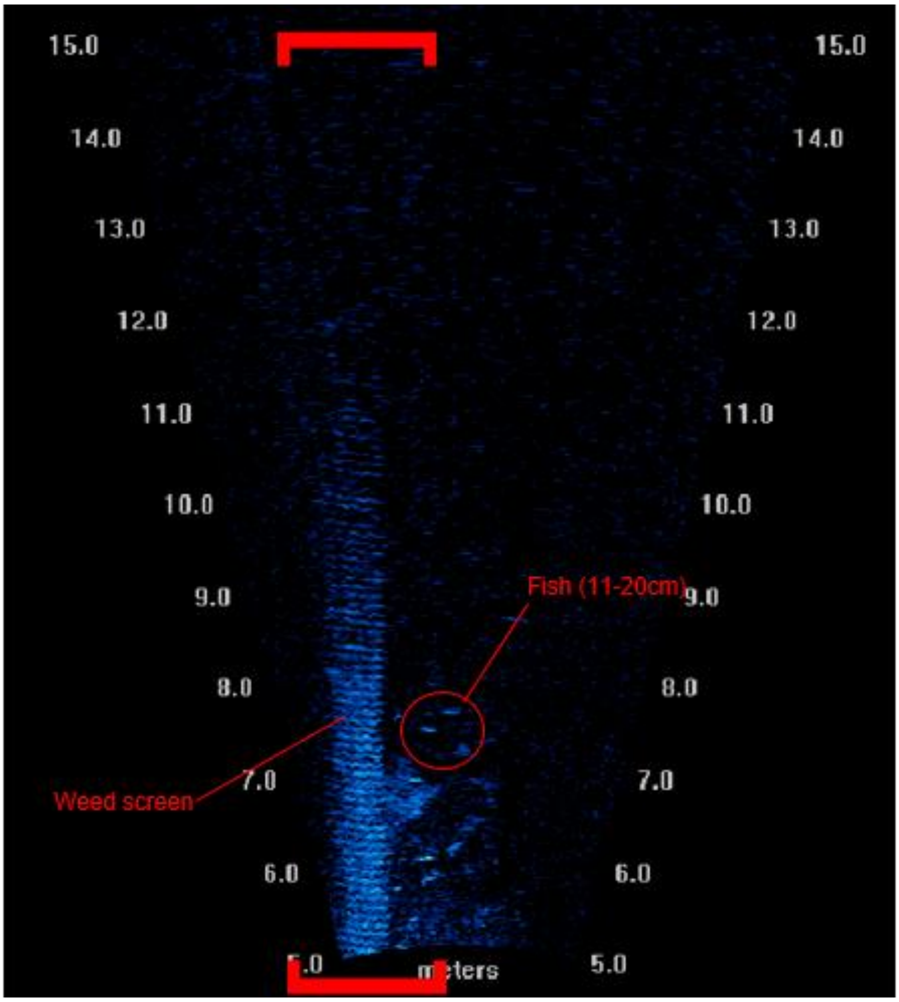


Figure 23 An example image of the DIDSON orientated to face the weed screen during pump operation. Screen capture taken directly from DIDSON software. The red brackets indicate the position of the weed screen, and a group of fish is highlighted by the red circle.

cm, 41-50 cm and >50 cm. This allowed processing time to be reduced by not measuring each individual. Following initially low counting of larger individuals (>50 cm), these fish were measured individually in all cases. The final dataset was constructed in Microsoft Excel and sorted by date, time, size class, and total count (per hour).

6.3.1.2 During pumping

It was decided that a true representation of pumping requires a more fine-scale approach than that used to determine diel patterns in fish presence. Thus, the subsampling method appropriate for regular flows was adjusted accordingly. Here, analysis were based on visual counting of individual fish movements during a one minute·15minute^{-1} subsample. Additionally, the whole beam was sampled instead of a 2m^2 window. Playback speeds were also adjusted to 10x speed. Fish were counted as ‘in’ if they entered the weed screen, and ‘out’ if they exited it. Fish that appeared to approach the weed screen, or swim along the width of the weed screen were counted as ‘approached’.

6.3.2 European eels

In addition to studying coarse fish behaviour at Foss, efforts were dedicated to identifying if any European eels attempted downstream passage of Foss pumping station. Due to the labour required for such a temporally extensive data set, a literature review was conducted to identify an appropriate sub-sample period. This suggested that onset of migration in mature silver eels is stimulated by reduction in moonlight, and many authors conclude that downstream movements of eels occur during the third quarter and new moon lunar phases (i.e., Deedler 1970; Deedler, 1984; Tesch, 2003; Acout *et al.,* 2008). Similarly, it appears to be widely acknowledged that European eels display negative phototactic behaviours associated with a nocturnal life style (Dou & Tsukamoto 2003; Rodriguez *et al.,* 2009). Following this a ten day sample period was reviewed minute by minute (24h) at 10x speed between the 9th and 18th November 2017 (Table 5). The playback speed was considered suitable following attempts at 2.5x, 5x and 10x revealed the same moving objects could be discerned at all speeds. During this sample period a total of zero eels were imaged in both day and night periods. As a result, December and January were analysed using a sub-sample process containing DIDSON footage recorded between the last quarter and third moon phases and at a night-time period between 21:00h and 04:00h (Table 5).

6.4 Environmental parameters

6.4.1 In-stream

Gauged Daily Flow (GDF) was recorded at the EA Skelton gauging station on the River Ouse, located 6.7 km upstream of Foss pumping station. GDF is a measure of the mean river flow in cubic metres per second (m^3s^{-1}) based on a 24h day from records every 15 minutes. This is usually in line with calendar days.

River levels are recorded nationally and are used to determine the relative flood risk posed to flood-prone catchments. River level (mAOD) was provided by the EA using water levels recorded in hourly intervals at two points within the catchment; Foss basin (L2472/SE6057951091) and in The River Ouse downstream of Foss barrier (L2404/SE6057951091). In all cases where pumping operation was taking place, river level data from Foss basin was used to determine the differences upstream and downstream of Foss barrier. Otherwise, recordings from the River Ouse were used, as they were indicative of river level during non-pumping hours.

An average (means) daily river level was taken for comparison with GDF. Similarly, because GDF and river level (Ouse) were recorded daily, for regression analysis it was necessary to sum daily total fish counts. This is described as ‘the sum of estimated fish abundance’ in the following results.

Table 5 Sunrise and sunset times (to the nearest five minutes), total hours per light period (day, night) and lunar phase dates in association with expected movements of migrant eels (i.e., Lowe, 1952; Tesch 2003; Durif *et al.,* 2005; Time and date, 2018).

	Sunlight		*Total*		*Lunar phase*	
Month	Sunrise	Sunset	Day light (hours)	Darkness (hours)	Third quarter	New moon
October	07:00	18:30	11 ½	12 ½	12/10/17	19/10/17
November	07:00	16:00	9	15	10/11/17	18/11/17
December	08:00	15:45	7 ¾	15 ¾	10/12/17	18/12/17
January	08:20	16:00	7 ⅓	16 ⅔	08/01/17	17/01/18
February	07:45	17:00	9 ¼	14 ¾	07/02/18	15/02/18
March	06:30	16:00	9 ½	14 ½	09/03/18	17/03/18

From February 2018, temperature (°C) was recorded every 15 minutes using a temperature logger (Tinytag Aquatic 2 tg-4100) attached to the pole supporting the DIDSON. Temperature was then summarised as a daily average.

6.4.2 Light period

The setting and rising of the sun was used to determine differences in fish abundance during day and night light periods (Table 5). For example, in November, day time was classified as the hours between 07:00 and 16:00, thus, allowing fish abundance across light periods to be compared.

6.4.3 Historical site data

Historical site data was limited to anecdotal reports and no consistent record of pumping was available. However, it was possible to determine the number and duration of pumping events in the previous 20 years using river level data from the River Ouse and Foss basin. This was used to determine the potential frequency of interactions with coarse fish and downstream migrations of mature European eels.

6.5 Statistical methods

6.5.1 Software

All statistical analysis was performed using R 3.4.2 (R Core Team, 2017) and the extended GUI provided with RStudio. GGplot2 was used to draw boxplots and regressions (Wickham, 2009). Microsoft Excel (2016) was used to tabulate data and draw histograms and environmental scatterplots.

6.5.2 Statistical analysis

In all cases initial analysis was attempted using parametric testing and the residuals were then checked for normality by observation of histogram and Shapiro-Wilk testing. Kruskal-Wallis rank sum test was used to determine the difference in fish abundance between months, and between light periods (regular flows, pumping), and the difference in environmental parameters between months (GDF, river level, temperature). The test reports a χ^2 test statistic and a p value to reveal if the test was insignificant $p>0.05$, significant $p<0.05$ and of high significance $p<0.01$. Post-hoc testing was applied using Dunn's test (Dinno, 2017) to determine which levels of the independent variable differ from each other across the categorically variable (i.e., how fish abundance varies across light period and month). The test uses the same level of significance as kruskal-wallis.

Linear regression was used to determine the correlation between environmental factors (River level (Ouse), GDF and temperature) and the sum of estimated fish abundance. This method quantifies the relationship between two variables by producing an equation for the best line of fit ($y=a+\beta x$), which uses the independent variable (x) as a predictor of the dependant variable (y). The regression estimates the values of the slope gradient (β) and the intercept (a) of the line of best fit. The line of best fit is the line which minimises the sum of the squared residuals (differences between observed dependant value and the prediction from the regression equation). Regression assumes that there is a linear relationship between the independent and dependant variable, the residuals are normally distributed and show homoscedasticity, and that observations are independent and have minimal leverage on the data. This is confirmed by visual assessment of the diagnostic plots. The model can then be fitted to the observed data by plotting the computed regression line over the data points.

7. RESULTS

7.1 Historical pumping at Foss (1996-2017)

Anthropogenic modifications to the rivers Foss and Ouse have taken place for several centuries, and modifications to the natural flow regime in The River Foss has existed since at least the late 1700s following the construction of Castle Mills lock and sluice system. Both downstream and upstream flows in the River Foss are now actively managed as part of the York Flood Alleviation Scheme, which includes the structures at Castle Mills, Foss WPS and its adjacent flood defence barrier. However, whilst Foss WPS has been operating for at least 30 years, a consistent record of operational history is data-poor and is limited to anecdotal reports.

However, using historical river level data from the rivers Ouse and Foss it was possible to provide an estimation of the frequency and duration of pumping throughout the past 21 years. Observed peaks in the scatterplot appear to reveal flood events in the Ouse catchment, which show seasonal trends in the interannual relationship between flooding and pump operation (Figure 24).

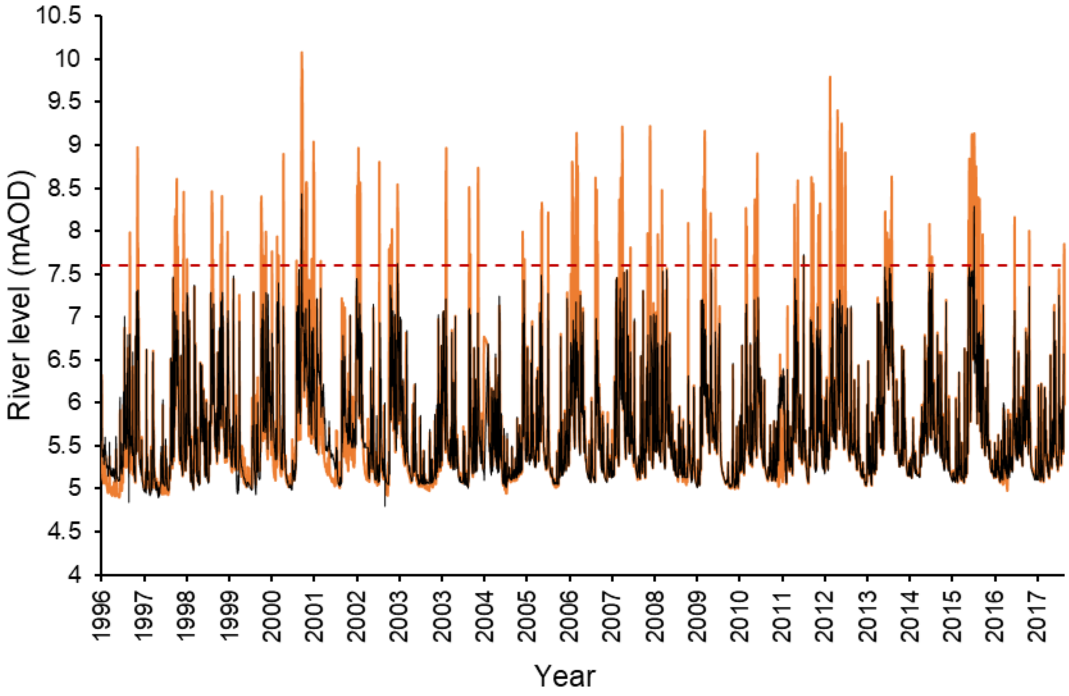


Figure 24 Annual river level (mAOD) series for the River Ouse (orange) and Foss basin (black). Floodgate closed and pumping presumed to be operational at 7.6±0.2 mAOD (red dashed line). Data provided by the Environment Agency. Values were recorded once per day at 9am

Because the River Foss is a regulated system where the river level is maintained at 7.6 mAOD upstream of Castle Mills Lock, river levels in Foss basin are the same as the River Ouse until the Ouse reaches 7.6mAOD and pumping takes place to prevent floodwater entering the River Foss. Using this presumption of the Foss flood gate barrier closing when the River Ouse reaches 7.6±0.2 mAOD, there has been at least 121 pumping events between 1996 and 2017 (Table 6; Figure 25a). This is validated by visual representation of the differences between levels of the rivers Ouse and Foss (Figure 24).

Throughout the 21 year period tabulated, cumulative pumping events have not exceed ten per year, and on average there were five to six pumping events per year (Figure 25a). Foss WPS was only pumping for five percent of the year and on average was only operational for 20 days a year (Figure 25b). River levels more than 8 mAOD were recorded in in all years except 1996, 2005 and 2017 (Figure 24). The catchment is susceptible to extensive flooding, and the highest river level was recorded at 10 mAOD in 2000, during which Foss WPS operated for 17 consecutive days. A similar event was recorded in 2012, which was later followed by a large flood in December 2015. Referenced as the boxing day floods, in 2015 a record flood overwhelmed Foss WPS where pumping took place for 20 consecutive days.

Interannual trends largely show stochasticity and thus a clear pattern is hard to determine (Figure 25a; Table 6). Although, as expected, peak flows can be

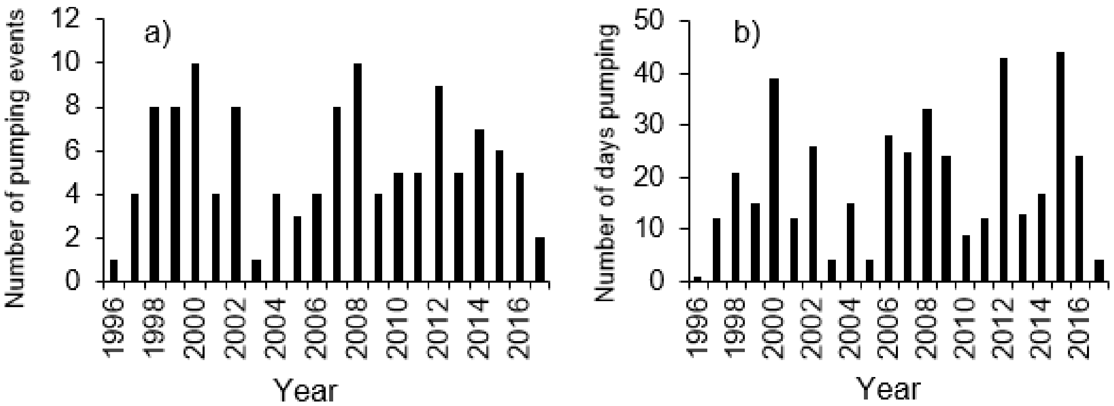


Figure 25 (a) Total number of pumping events by year, (b) total number of days pumping by year. Represenititve of May 1996 - December 2017.

Table 6 The total number of pumping events between the years 1996 and 2017 as determined by pump operation occurring when The River Ouse river level reaches 7.6 mAOD. the number of pumping events is coloured on a red to green colour scale, with solid red indicating no pumping, and solid green indicating higher frequency of pumping events.

	Number of pumping events																						
	Year																						
Month	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	Total
Jan		0	3	2	1	2	0	1	0	0	0	3	2	1	2	2	1	1	3	4	2	0	30
Feb		2	0	0	0	1	2	0	1	0	0	0	1	0	1	1	1	1	3	0	1	0	15
Mar		0	2	1	1	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	1	1	9
Apr		0	1	1	2	1	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	8
May	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	2
Jun	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	4
Jul	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	3
Aug	0	0	0	0	0	0	1	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	4
Sep	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2
Oct	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	5
Nov	0	0	1	0	2	0	2	0	0	2	1	0	1	1	2	0	0	0	0	1	1	1	15
Dec	1	2	0	4	2	0	1	0	0	0	1	2	2	1	0	2	1	3	1	1	0	0	24
Total	1	4	8	8	10	4	8	1	4	3	4	8	10	4	5	5	9	5	7	6	5	2	121

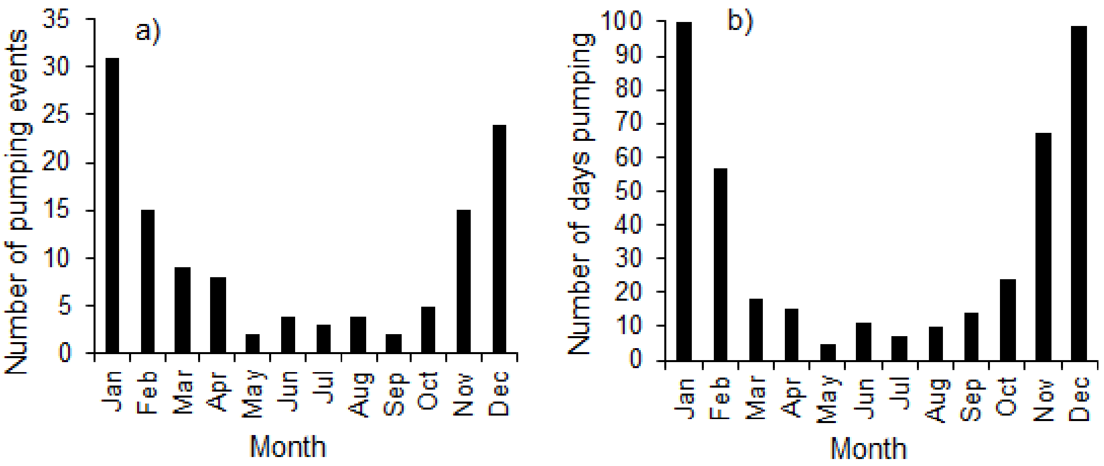


Figure 26 (a) Total number of pumping events by month, (b) Total number of days pumping by month. Representative of May 1996 - December 2017.

predicted on a seasonal basis, and all major flood events were recorded in late autumn or winter (October – March), except for high summer flows recorded in June and July. There also appears to be a general trend in increasing frequency and duration of pumping from August to January (Figure 26). Thus, the frequency of pumping is low in the summer and high in late autumn and throughout winter (Figure 26a). The frequency of pumping is highest in January and December, where there have been more than 30 pumping events in January and more than 20 in December (Figure 26a). Similarly, January and December both reach a total of 100 days pumping and thus both the frequency and duration of pumping is high in these months. The relationship between number of pumping events and days pumping appears to be linear (Figure 26). This is true of all months except September, October and November, where pumping events appear to be longer in duration, probably in response to early winter flows (Figure 26b).

The risk posed by Foss WPS does not follow a linear relationship throughout time, and there are large interannual fluctuations in pumping effort that influence the relative likelihood of eels facing possible entrainment or delays to their migration. For example, flows, and thus pumping, have been low in 2003, 2005 and 2017, presenting a smaller risk to migrant eels than years 2000, 2012 and 2015 where flows and pump operation were high (Figure 24; Table 6). What is not clear when relying on river levels for operational history is how different pumping scenarios influence the relative risk to eels and coarse fish. For example, it is currently unknown as to the number of pumps that have been operated per event, the flows they generate in Foss basin, and whether eels are able to successfully avoid pump intakes by residing in Foss basin during pump operation. The variation in these factors is expected to significantly influence the relative risk to eels attempting passage of Foss WPS.

7.2 2017/2018 European eels

It was not possible to sample October 2017 due to a late deployment of the DIDSON. However, a sample period in November, December and January was analysed in accordance with the lunar cycle in an effort to image any eels which may have suffered delays to their migration.

A total of two eels were recorded in Foss basin in December 2017 during a 10-day sample period (December 1st – 10th). Eel_120901 was recorded at 22:22:40 on the 9th December 2017 (Figure 27a), and Eel_120902 was recorded shortly after at 22:36:18 the same evening (Figure 27b). Eel_120901 entered the array from the left (upstream), was measured at 73 cm and was in the array for a total of 22 seconds. Eel_120902 entered the array from the left, was measured at 64 cm and was in the array for a total of 62 seconds. Both eels appeared to exit the

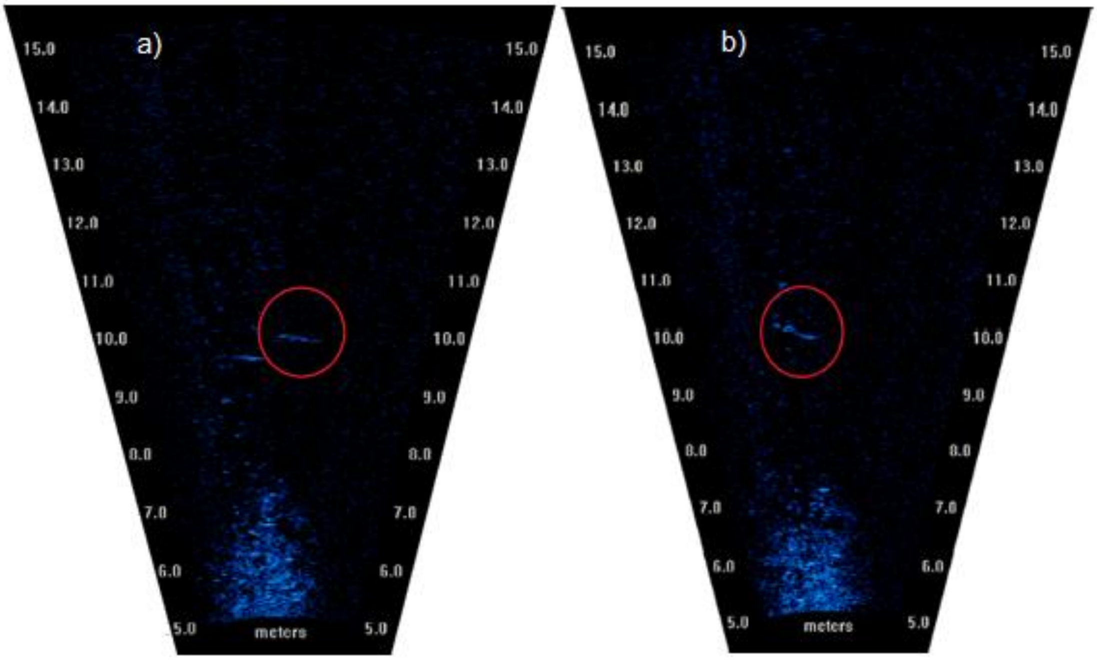


Figure 27 (a) Eel ID = Eel_120901, size=73cm, entry=left, total time in array=22seconds. (b) Eel ID = Eel_120902, size=64cm, entry=left, total time in array = 62 seconds. Eels indicated by red circle.

Figure 28 An eel retrieved from the weed screen during November 2017 (left), compared with boot (right).

beam to the right and it is therefore assumed that they made successful downstream passage of Foss WPS as there are no further barriers. No eels were identified during a 10-day sample period in January.

7.2.1 During pumping

In an isolated pump test during November 2017, one individual eel was retrieved from the weed screen during routine weed clearance. The eel appeared to display characteristics indicative of a yellow eel and was likely residing in Foss basin during its growth phase (Figure 28). There was no indication of the presence of eels during pumping events.

7.3 Coarse fish movements during regular flows

7.3.1 Data examined

Although the DIDSON was deployed for a total of 153 days, hardware failure resulted in the DIDSON not recording for a total of 12 days. Because the sub-sample was based on 14 days per month (to minimise operator hours required for post processing), the loss of footage was not reflected in November and December. There was a loss of two days in January and the sampling period was adjusted to 12 days in March due to unit failure at the end of the data set.

7.3.1.1 Pumping events

During the study period there was a total of four pumping events. Pumping took place on the 24th November 2017 for four consecutive days, on the 4th January 2018 for three consecutive days, on the 24th January for two consecutive days, and on the 13th March 2018 for six days. The sampling periods for December

2017, January 2018 and February 2018 all took place after pumping events and therefore the following fish abundance results are expected to be influenced by pump operation. The dataset in March 2018 does not follow a pumping event.

7.3.2 Key findings

Throughout the five month deployment, there was a total of 6,217 individual fish identified based on sampling a 2 m^{2} window during a 1 frame·h^{-1} subsample (medians= 3, ITQ=4, min=0, max=19). In order by month, a total of 2146 individual fish were recorded in November 2017, 1405 in December 2017, 1069 in January 2018, 882 in February 2018, and 715 in March 2018. A highly significant kruskal-wallis suggested that total counts of fish abundance was different between months ($\chi^{2}_{4,\ 1617}$ = 132.81, p= <0.001; Table 7). This was followed by a post-hoc Dunn's test (1964), which showed that all months were significantly different from each other except for December 2017 and February 2018 (Z=-0.23, p=0.4).

7.3.3 Diel patterns in fish abundance

7.3.3.1 Light period

A Wilcoxon rank sum test revealed that estimated fish abundance was significantly different between day (median 4 individuals·2m-^{2}, ITQ=7) and night (median 2 individuals·2m^{-2}, ITQ=3) light periods (W=421950, p=<0.001) (Figure 29). This was followed by a kruskal-wallis test that revealed estimated fish abundances assorted by light period were significantly different between months ($\chi^{2}_{9,\ 1612}$ = 335.24, p=<0.001) (Table 8). A post-hoc Dunn's test revealed that day and night estimated fish abundances were significantly different in all months except March where day and night were not significantly different (Z=-0.7, p=0.27) (Figure 30).

When comparing light periods between months, estimated fish abundance at night was not significantly different except in November which was different to all other months; December (z=-3.41 p=<0.001), January (z=-34.37, p=<0.001), February (Z=-2.62, p=0.006), March (Z=-3.05, p=0.001). However, when comparing day, all months were significantly different except for December and February (z=1.4, p=0.1).

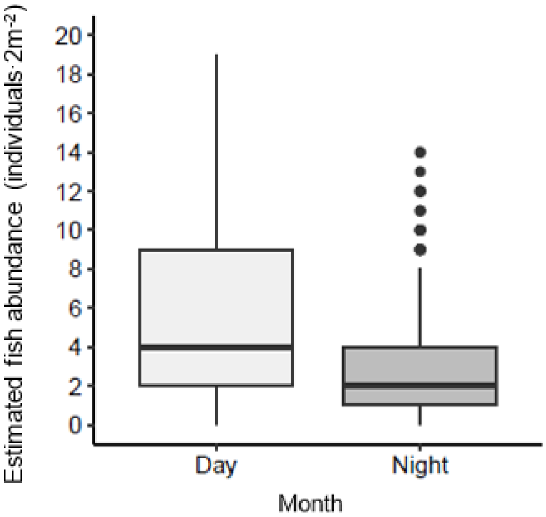


Figure 30 Estimated fish abundance given as light period; day (white) and night (grey). Vertical lines represent quartile 1 to the smallest non-outlier, and quartile 3 to the largest non-outlier (as given by solid points).

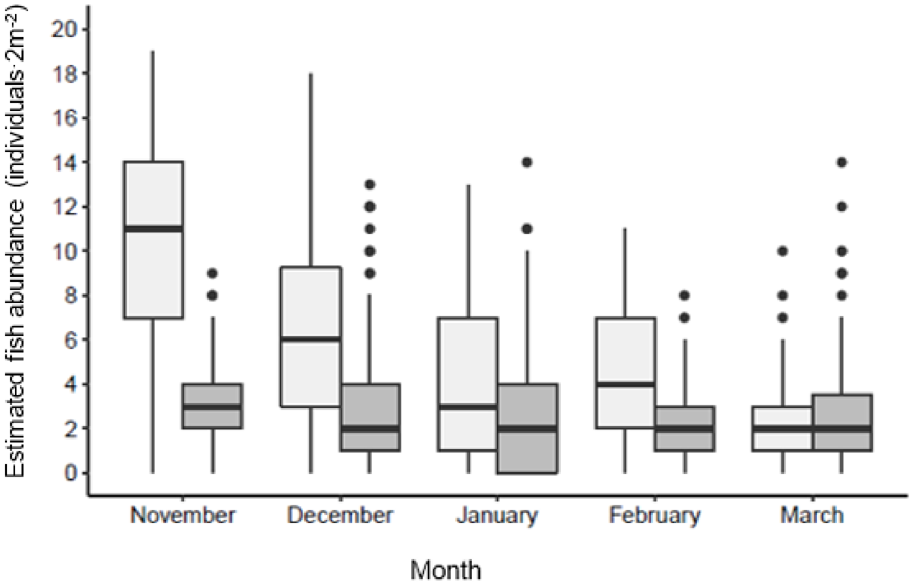


Figure 29 Estimated fish abundance given as light period; day (light grey) and night (dark grey). Data is separated by month, vertical lines represent quartile 1 to the smallest non-outlier, and quartile 3 to the largest non-outlier (as given by solid points).

7.3.3.2 November 2017

Construction of a bar histogram revealed that fish movements during November 2017 followed a clear and predictable pattern throughout the 14-day sample period, whereby estimated fish abundance increased and decreased at well-defined times of the day (Figure 31). These peaks and troughs in the histogram appear to represent diel activity of fishes at Foss. Here, it is apparent that light period influences the number of fish present at any one-time. At dawn there was a large and notable increase in fish presence at the point of sampling. During this period, fish numbers were typically recorded between 15 and 19

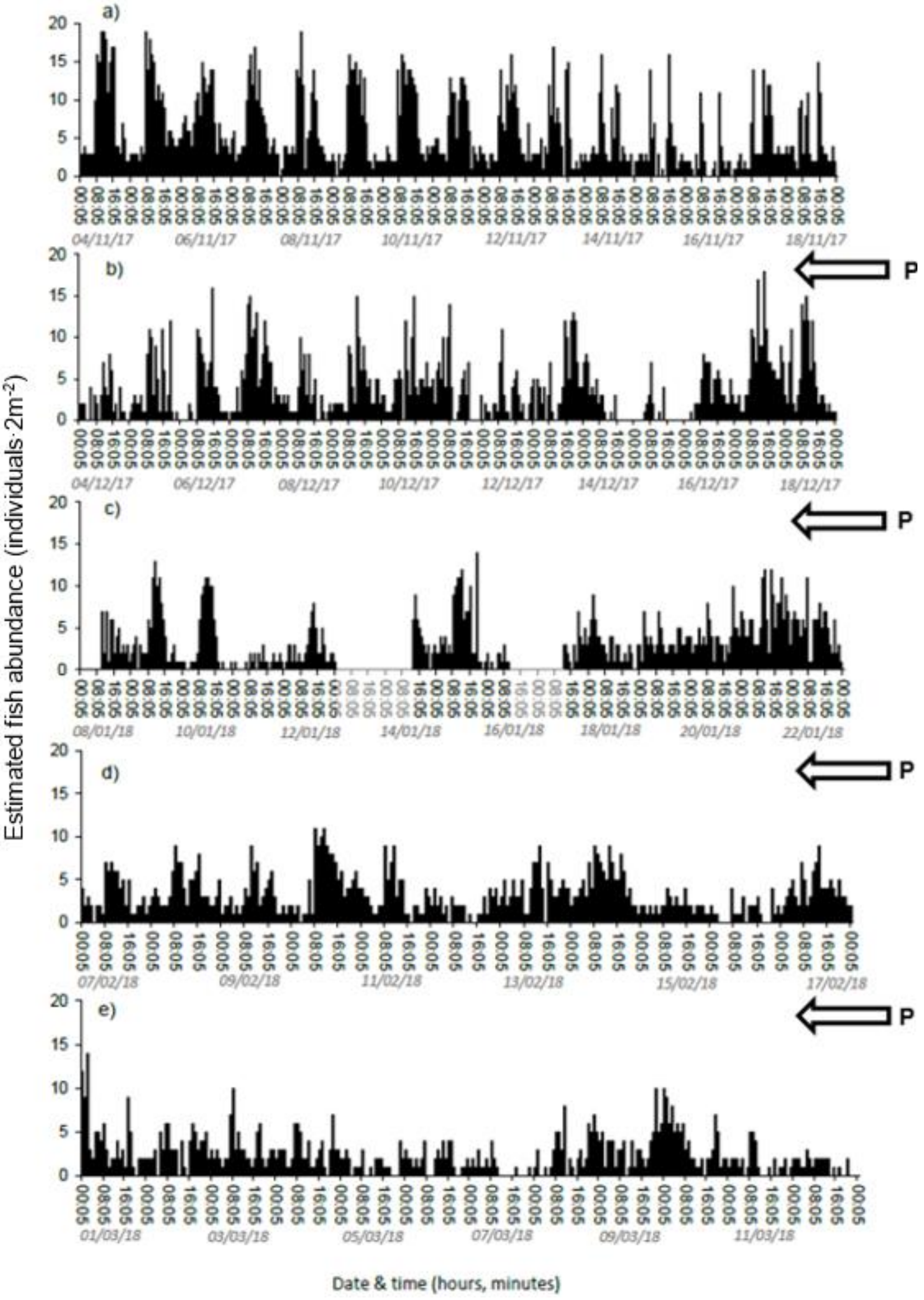


Figure 31 Estimated fish abundance at Foss WPS, York. a) November, b) December, c) January, d) February, e) March. Missing data is indicated by light grey axis. Pumping events are indicated by bold arrow and P (taking place between months).

individuals·2m^{-2}, and fish abundance peaked at 19 individuals·2m^{-2}at 07:00. Consequent days showed typical peaks of fish numbers within three hours of dawn. Estimated fish abundance was highest during daylight hours (Table 8). In some cases fish count remained as high as that noted at dawn (i.e., 10/11/17 Figure 32). This was usually followed by a net decrease in fish numbers after dusk, where fish was typically recorded between seven and 17 individuals·2m^{-2}, and fish abundance peaked at 17 individuals·2m^{-2} 16:00 followed by four individuals·2m^{-2} at 17:05. Throughout the evening (i.e., 16:00 – 20:00), estimated fish abundances remained lower than during the day, but were still consistently recorded as high as those noted at dawn. These trends begin to breakdown towards the end of the sample period where observed peaks and troughs were not as well defined with daytime fish presence being reduced, whilst evening fish presence began to increase. Pumping did not take place in the sample period in November 2017.

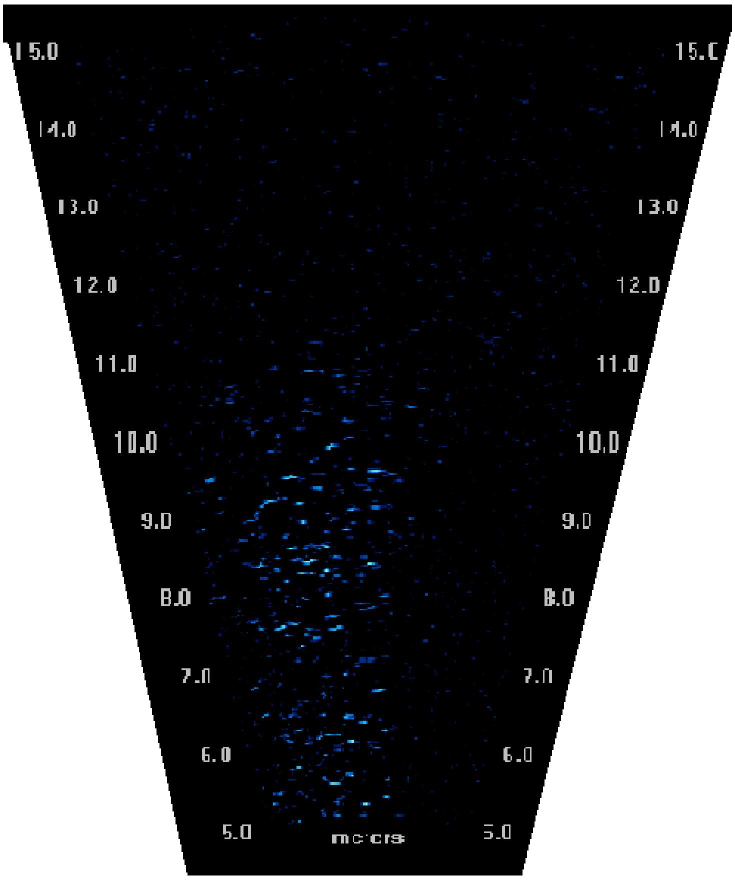


Figure 32 An example image indicative of fish presence at dawn in Foss basin, York. Image recorded 10/11/2017 08:05:00. Screen capture taken directly from DIDSON software background subtraction enabled. Estimated fish abundance *n*=16 individuals·2m-^{2}.

7.3.3.3 December 2017

The trends observed in the November 2017 sample continued to breakdown during December 2017. Unlike those seen in November 2017, increases in fish abundance did not consistently occur at dawn and dusk periods and the predictability of diel movements became harder to discern. Here, fish abundance did not exceed 14 individuals·$2m^{-2}$ at dawn and 12 individuals·$2m^{-2}$ at dusk. Additionally, the overall count of fish abundance during December was considerably lower than that of November 2017. Although estimated fish abundance remained higher during the day, the trend was not as visible as that of November (Figure 31b, Table 7). However, there was still some evidence of diel patterns similar to those in November 2017, although the peaks were less pronounced. On one occasion fish abundance was low during the day (<5 individuals·$2m^{-2}$), before peaking at dusk and increasing during the evening and night (13 individuals·$2m^{-2}$ 20:05 13/12/17).

7.3.3.4 January 2018

As found in December 2017, diel patterns in fish abundance continued to breakdown during January 2018 and fish abundance was largely different to that seen in the previous two months (Figure 31c). Patterns whereby fish abundance increased during the evening in December 2017 became more relevant here as observed peaks in activity surrounding dawn and dusk periods were not present (Table 5). Fish abundance appeared to increase later in the day, with peak numbers at an estimated 13 individuals·$2m^{-2}$ 11:05 09/01/18 (Figure 31c; Table 8). The sum of estimated fish abundance continued to decline when compared to November and December 2017, although this may be influenced by two periods of missing data in January (13/01/18 & 16/01/18). This was also the first month where little or no fish presence was observed throughout a 24h period (15/01/18). Towards the end of the sample period, patterns in fish abundance became unpredictable and followed no observable pattern despite pumping not taking place within the sample period.

7.3.3.5 February 2018

Whilst the histogram of fish presence appears to flatten during February 2018, there was some return to the diel patterns observed in November 2017, where fish presence was predictable by dawn and dusk periods (i.e., 10/02/18).

Particularly, fish abundances peaked at dawn with an estimated 11 individuals·2m^{-2} 08:00 10/02/18 (Figure 31d; Table 8). Subsequent days showed similar abundances within three hours of dawn. At dusk, fish abundance was observed to peak at 8 individuals·2m^{-2} 16:00 08/02/18. The sum of estimated fish abundance continued to decline when compared to the previous three months. Similar to findings in January 2018, there was also several occasions where fish abundance appeared to increase throughout the evening and peak during the night.

7.3.3.6 March 2018

Throughout the 12-day sample period in March 2018, diel fish presence became unpredictable for the most part and instead fish counts were consistent throughout a 24h period, with little observable peaks that coincided with marked diel periods (i.e., dawn, dusk) (Figure 31e). In complete contrast to previous months, fish abundance was highest at night where 14 individuals·2m^{-2} was recorded at 02:00 01/03/18 (Table 8). The highest recorded fish abundance at dawn was seven individuals·2m^{-2} 7:00 03/03/18. Similarly, dusk only produced a high of nine individuals·2m^{-2} 17:00 01/03/18. The sum of estimated fish abundance continued to decline when compared to the previous four months. Although, this could be a result of the sample period being immediately before high flows in the River Ouse

Table 7 Gauged Daily Flow recorded at Skelton, Ouse. River level recorded on the Ouse. Temperature recorded at the point of sample (DIDSON), and the sum of estimated fish abundance. All Values were recorded between November 2017 and March 2018.

	GDF (m^3s^{-1})				River level (Ouse) (mAOD)				Temperature (℃)				Sum of estimated fish abundance (individuals·$2m^{-2}$·1 frame·h^{-1})			
Month	*median*	*ITQ*	*min*	*max*	*median*	*ITQ*	*min*	*max*	*median*	*ITQ*	*min*	*max*	*median*	*ITQ*	*min*	*max*
November	21.40	33.60	14.90	206	5.30	0.50	5.20	7.80	-	-	-	-	4	8	0	19
December	39.80	32.40	19.80	117	5.60	0.30	5.20	6.00	-	-	-	-	3	5	0	18
January	89.80	65.60	37.70	228	6.20	0.80	5.50	8.00	-	-	-	-	2	4	0	14
February	53.90	35.10	27.80	106	5.70	0.40	5.30	6.50	3.40	0.80	2.10	5.20	3	3	0	11
March	77.70	89.00	25.50	201	6.00	1.00	5.30	7.80	5.20	2.80	0.50	7.60	2	2	0	14

Table 8 Estimated fish abundance (individuals·$2m^{-2}$·1 frame·h^{-1}) across day and night light periods, as derived from visual counts of DIDSON footage captured between November 2017 and March 2018.

	Day					Night				
Month	*median*	*ITQ*	*min*	*max*	*total*	*median*	*ITQ*	*min*	*max*	*total*
November	11	7	0	19	1495	3	2	0	9	651
December	6	6.3	0	18	742	2	3	0	13	661
January	3	6	0	13	504	2	4	0	14	565
February	4	5	0	11	498	2	2	0	8	384
March	2	2	0	10	742	2	2.5	0	14	661

7.3.4 Environmental parameters

Visual plotting of GDF and river level (Ouse) confirmed these parameters were suitable for determining when pump operation was likely to occur (Figure 34). Both plots appear to be largely similar and the four pumping events recorded during the study are clearly visible by observed peaks and troughs in the scatter plots (Figure 33; Figure 34). Using GDF parameters from the Skelton gauging station suggested that flows respond quickly to rainfall in the catchment and high flows (exceeding $150m^3{\cdot}s^{-1}$) typically peaked within three days and returned to regular flows after one to two days (Figure 33). Thus, some certainty can be applied to timing and duration of pumping events at Foss when combined with information on river level (Figure 34). GDF and the River Ouse level was recorded for a total of 151 days.

Median GDF was recorded as $54.2m^3{\cdot}s^{-1}$ (ITQ=56) across the duration of five months, with the highest value being recorded in January ($228m^3{\cdot}s^{-1,}$ ITQ=65.5) and the lowest recorded in February 2018 ($53.85\ m^3{\cdot}s^{-1}$, ITQ=35.08) (Table 7). A kruskal-wallis test confirmed that GDF was significantly different between months ($\chi^2_{1,\ 149} = 54$, p= <0.001), with a post-hoc Dunn's test (1964), showing that all months were significantly different from each other except for November

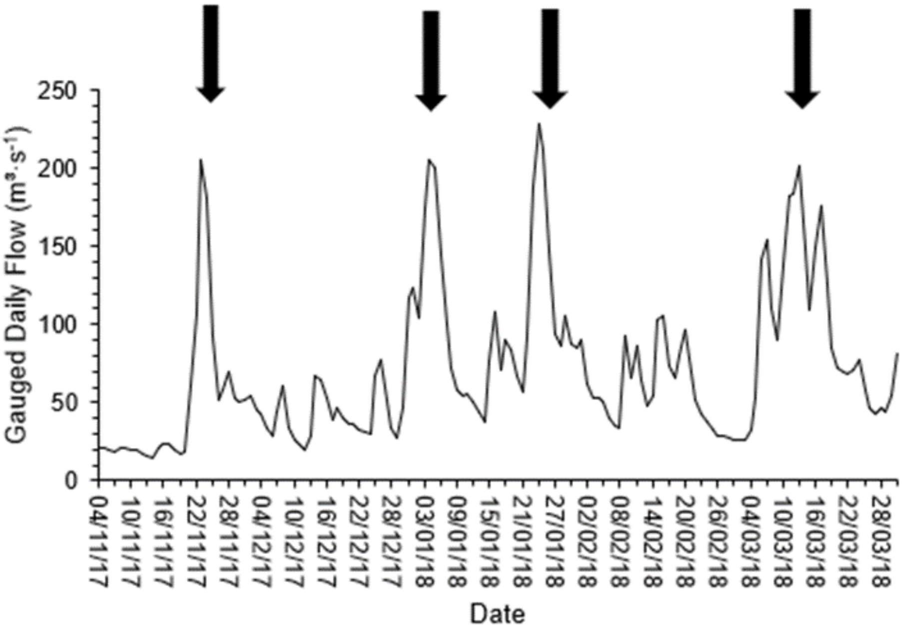


Figure 33 Gauged Daily Flow (GDF) recorded at Skelton, Ouse. GDF based on a water-day (9:00am - 9:00pm). Arrows indicative of pumping events at Foss pumping station, York. Data provided by the EA and logged on a daily basis.

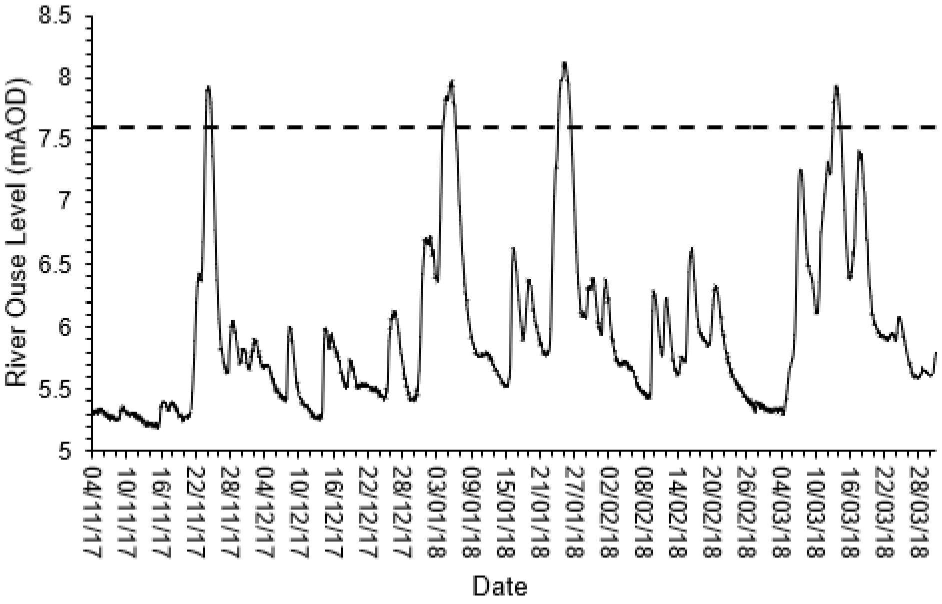


Figure 34 Rive level recorded in The River Ouse (L2404/SE6057951091). The dashed line measuring 7.6mAOD is indicative of pumping at Foss pumping station. Data provided by the EA and logged on an hourly basis.

and December 2017 (Z=-1.2, p=0.12), and January and March 2018 (Z=1.17, p=0.11).

The trends for river level (Ouse) were largely similar to that of GDF, although the ITQ ranges were smaller which may be due to an increased accuracy (as to pumping) when measuring river level as opposed to GDF. The median river level (Ouse) was recorded as 5.7 mAOD (ITQ=0.4) across the duration of five months, with the highest value being recorded in January 2018 (8 mAOD, ITQ=0.8) and the lowest in December 2017 (6mAOD, ITQ=0.3) (Table 7). As for GDF, a kruskal-wallis test confirmed that river level was significantly different between months ($\chi^2_{1,\,149}$ = 51.8, p= <0.001), with a post-hoc Dunn's test, showing that all months were significantly different from each other except for November and December 2017 (Z=-1.4, p=0.08), January and March 2018 (Z=1.5, p=0.07), and February and March 2018 (Z=-1.4, p=0.08).

Temperature was recorded for a total of 37 days. Median temperature was recorded as 4.7℃ (ITQ=2.6), with the highest value being recorded in March (5.5℃, ITQ=2.8) and the lowest in February 2018 (3.4℃, ITQ= 0.8) (Figure 35). A kruskal-wallis test indicated there was no significant difference between February and March 2018 ($\chi^2_{1,\,36}$ = 3.7, p=0.05).

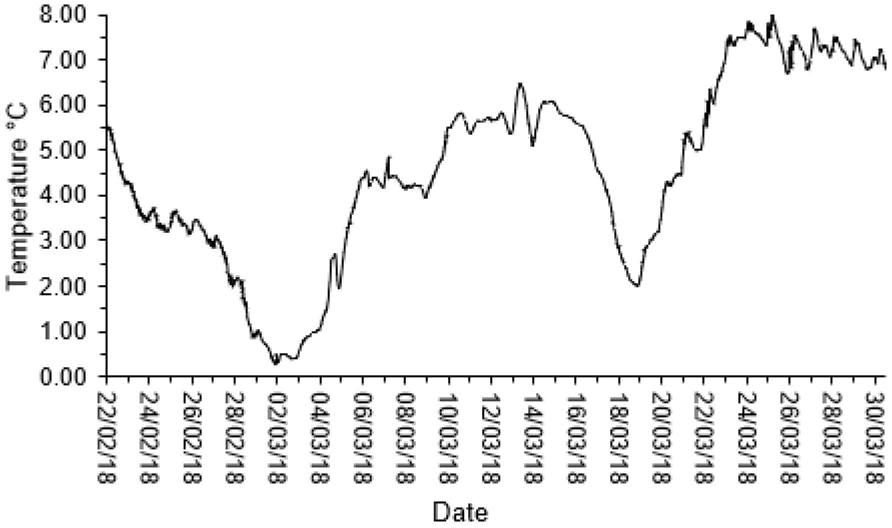


Figure 35 River temperature in Foss basin. Data recorded at the immediate point of sampling (DIDSON) on an hourly basis.

7.3.4.1 Regression analysis of fish abundance and environmental data

A reverse stepwise linear regression was calculated to investigate the relationship between the sum of estimated fish abundance (individuals·2m-^{2}) and the predictors GDF, and average river level. Average temperature was not included as the sample sizes were unequal due to temperature recording not starting until February 2018. However, a regression for temperature is presented exclusive of the stepwise model. The reverse stepwise process revealed that a model containing only average river level was the minimal model required to best explain the variation in the sum of estimated fish abundance. This was confirmed by a significant regression equation ($F_{1,66}$ = 31, p <0.001) and an R^2 of 0.32 suggested 32% of the variation in the sum of estimated fish abundance was explained by average river level. The predicted sum of estimated fish abundance was equal to 416.15 -57.12 (average river level) individuals·2m-^{2} when average river level was measured in mAOD. A scatterplot showed that there was a negative relationship between average river level and the sum of estimated fish abundance (Figure 36a), which was confirmed by a Pearson’s correlation coefficient of 0.57. According to this model, the sum of estimated fish abundance was reduced by 57 for every increase in average river level (Ouse).

Visual inspection of the diagnostic plots suggested that the residuals were normally distributed, which was confirmed by Shapiro-wilk test (W = 0.99, p = 0.97). Similarly, the relationship between the independent and dependant variables appears to be linear, showing little pattern in the standardised residuals with no observations having large leverage, and thus the assumptions of the test were met. A significant regression equation was also found for a model containing only GDF ($F_{1, 64} = 25$, $p < 0.001$). An R^2 of 0.26 suggested 26% of the variation in the sum of estimated fish abundance was explained by a model containing only GDF. The predicted sum of estimated fish abundance was equal to 127.3515 -0.6354 (GDF) individuals·2m-^{2} when GDF was measured in cumecs.

A scatterplot showed that there was a negative relationship between GDF and sum of estimated fish abundance (Figure 36b), which was confirmed by a Pearson's correlation coefficient of -0.5. The sum of estimated fish abundance was reduced by 0.6 for every increase in GDF. All assumptions of the model were met, and normal distribution of the residuals was confirmed by Shapiro-wilk (W = 0.99, p = 0.93).

The interactions between GDF and average river level was removed from the model and did not significantly explain the variation seen in the sum of

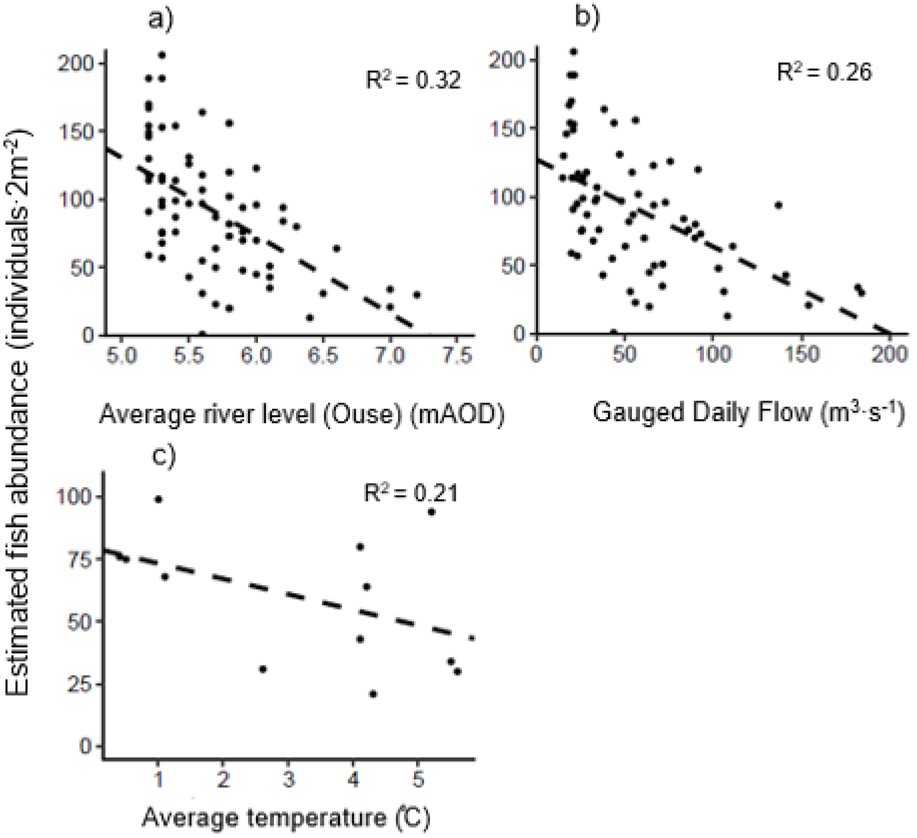


Figure 36 Linear regressions for the sum of estimated fish abundance a) Average river level (Ouse) p=<0.001, b) Gauged daily flow p=<0.001, c) Average temperature p=0.13.

estimated fish abundance. Temperature data for February 2018 was not included as it was outside the DIDSON sample period. A linear regression was unable to find a significant regression equation for a model containing average temperature in March 2018 ($F_{1,10}$= 2.71, p = 0.13). An R^2 of 0.21 suggested 21% of the variation in the sum of estimated fish abundance in March could be explained by average temperature. Similarly, a scatterplot showed no real correlation between average temperature and sum of estimated fish abundance (Figure 36c), which was confirmed by an insignificant Pearson's correlation coefficient (p= 0.13).

As there were no other independent variables to add to the model, 42% of the variation in the sum of estimated fish abundance was unexplained in the current study. From visual analysis of the plots it appears that the relationship between the predictor factors and sum of estimated fish abundance was influenced by monthly sample period. To ascertain this, a more complex model including the interaction of average river level and month, and GDF and month was constructed to plot an individual slope per month.

A plot for average river level confirmed that the negative relationship between total fish abundance and average river level was true for all months except January 2018, although this trend may also be a function of an unknown predictor as fish abundance appeared to decline over time (month) (Figure 37a). Similarly, a plot for GDF supports a negative correlation, but again highlights a general decline in fish abundance that may be influenced by a factor other than GDF (Figure 37b).

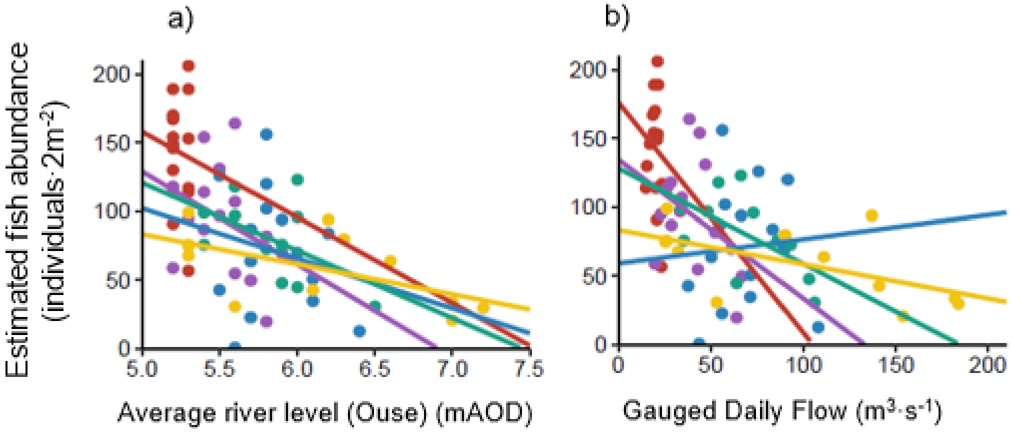


Figure 37 Linear regression for the sum of estimated fish abundance as coloured by month, November (red), December (purple), January (blue), February (green) and March (yellow). A) Average river level (Ouse), b) Gauged daily flow.

7.3.5 Size distribution of imaged fish

In all cases it was possible to classify fish by size from DIDSON sampling. Fish size class analysis was limited due to the variation in coarse fish identified during the sampling period (Tables 9 – 13). Fish >50cm were measured individually, and a note made on their size. There was no formal species identification protocol because species identification was not practical or consistent due to limitations of the DIDSON image. That said, it is likley that smaller fish (11-20 cm) were species such as roach, dace and perch, with medium fish (31-40 cm) probabaly bream. Larger fish (>50 cm) are expected to be pike, zander or large barbel. Although, this is largely speculative without a consistent species ID protocol and thus does not influence further analysis.

Fish abundance appears to be concentrated around the size class’s 0-10 cm, 11-20 cm and 21-30 cm (Figure 38). But, fish in the size range 11-20 cm accounts for the majority of fish abundance (Figure 38). This was true of all months, although it was particularly clear in November, where fish abundance was higher than all other months, regardless of size class (Figure 38). When analysing months in chronological order, the length-frequency histograms begin to flatten, although this was perhaps a function of a general decline in fish abundance and the trends in size distribution remained similar. However, it was clear that there were some temporal fluctuations in size composition (Figure 39). 70% of the fish identified at Foss were categorised as 11-20 cm (Figure 39). In December there was an increase in fish categorised as 21-30 cm from 190 in November to 215. Although 0-10 cm fish are present at the start of the sample period (46 recorded 07/12/17) they decreased quickly (0 recorded 9/12/17) and were replaced by 21-30 cm fish (40 recorded 10/12/17) (Figure 39b). Size composition in January was similar to November, although size composition in February and March differed considerably (Figure 39). In particular, in February the proportion of fish 21-30 cm increased (Figure 39d), and in March, the concentration of 0-10 cm fish increased (Figure 39e).

Assessment of cumulative sum revealed a sharp increase in 11-20 cm fish in all months (Figure 40). Trends in successive size classes were also largely similar across months (Figure 40). As found with general trends in fish abundance (i.e., Figure 38), there appeared to be some variation in fish size between night and day periods. Particularly, in November the smallest size class (0-10 cm) only

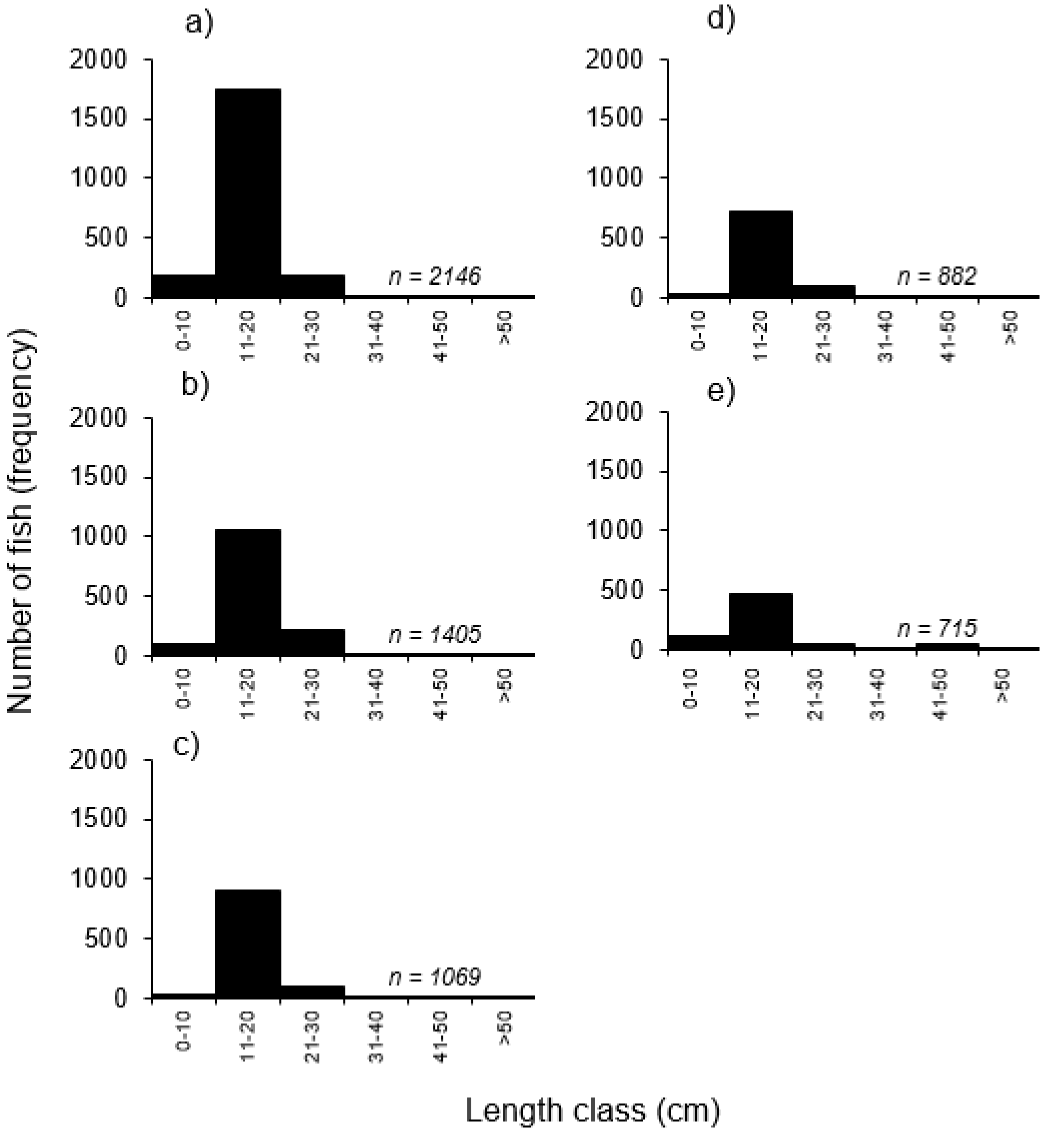


Figure 38 length frequency distribution of fish at Foss pumping station, York. A) November, b) December, c) January, d) February, e) March.

appeared to be present during the day (Table 9), whereas all other size classes show no real predictability by light period. In December, smaller fish (0-10 cm) become more present during early evening (Table 10), and in January and February these trends were less apparent (Tables 11, 12). In March there was a general increase in larger fish (31-40, 41-50 cm) (Figure 39), although this did not appear to be associated with light period (Table 13).

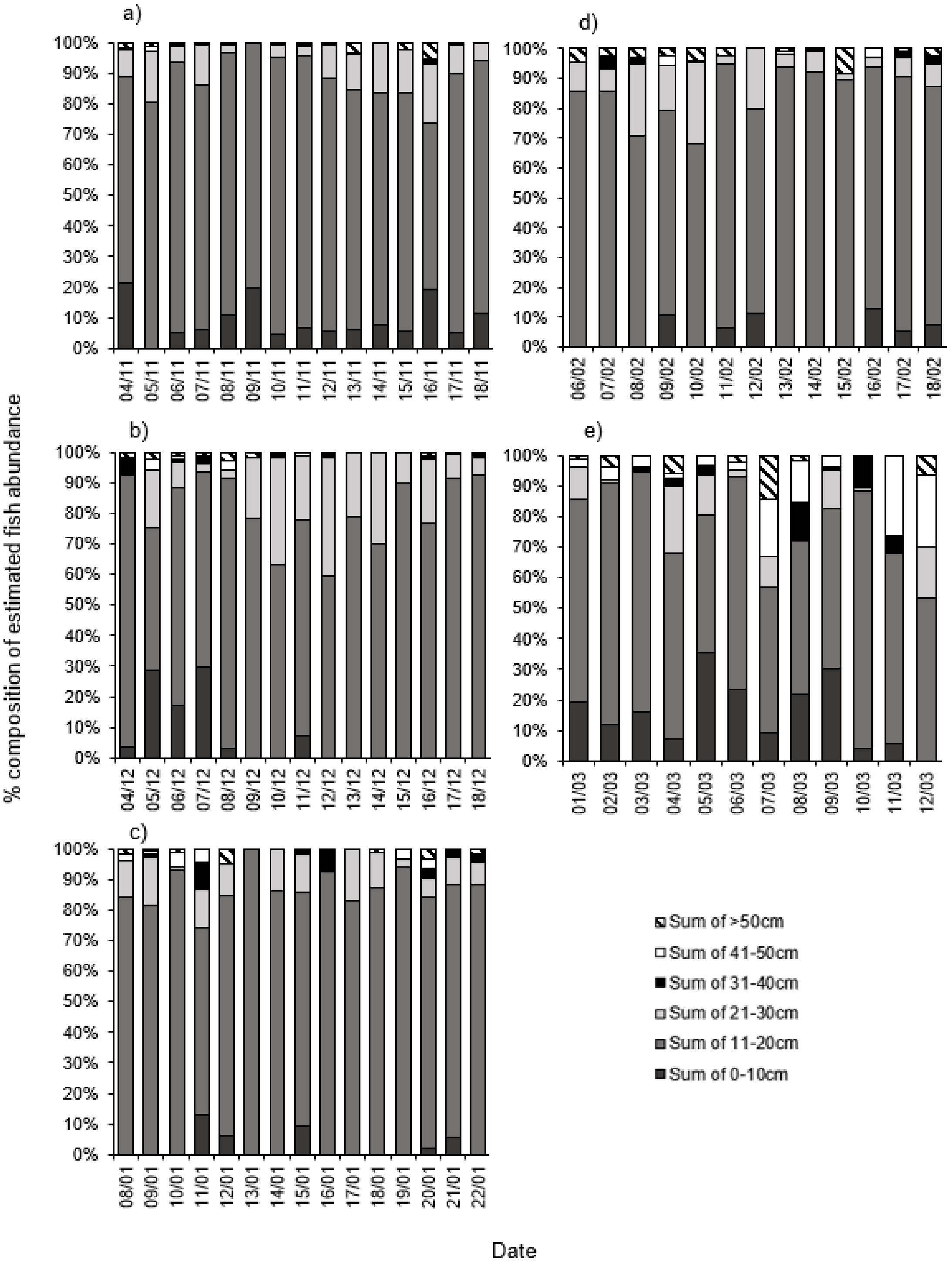


Figure 39 Size composition of fish identified at Foss pumping station, York. A). November, b) December, c) January, d) February, e) March.

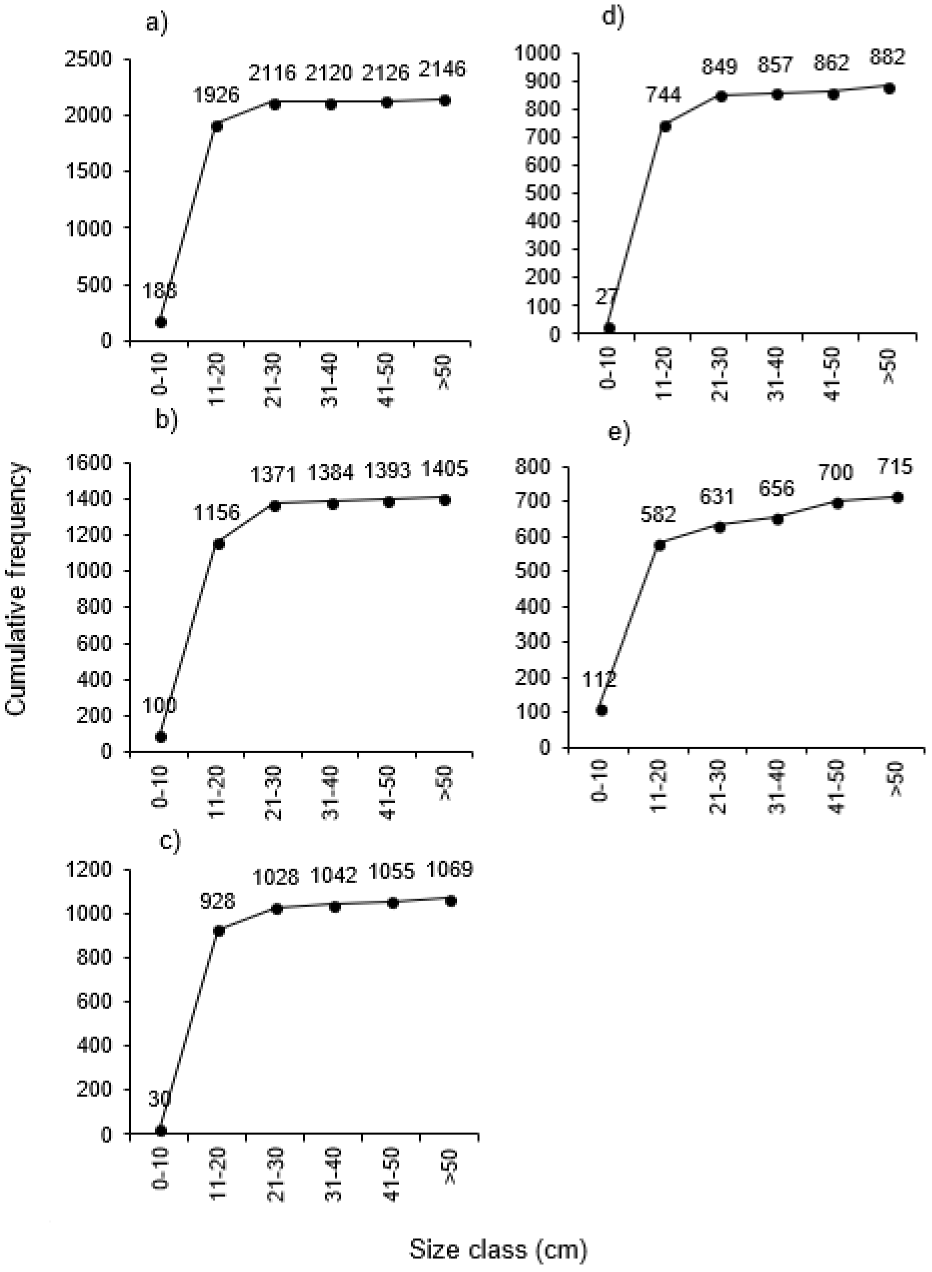


Figure 40 Cumulative frequency plots for size class distribution of fishes at Foss pumping station, York. Solid points represent actual values (given above points). A) November, b) December, c) January, d) February, e) March.

Table 9 Average (mean) abundance (individuals·2m^{-2} ± SD) of fish counted at Foss WPS for all size classes during a 14-day period in November 2017. Samples taken from a 1 frame·hour^{-1} sub sample.

Time	*Size class (cm)*						
	0-10	11-20	21-30	31-40	41-50	>50	Total
00:05:00	0.00±0.00	2.14±2.41	0.52±1.12	0.10±0.40	0.00±0.00	0.14±0.44	2.90±2.16
01:05:00	0.00±0.00	2.62±2.66	0.41±1.23	0.00±0.00	0.00±0.00	0.10±0.30	3.14±2.48
02:05:00	0.00±0.00	1.97±2.11	0.76±1.66	0.00±0.00	0.03±0.18	0.07±0.25	2.83±2.00
03:05:00	0.00±0.00	1.72±1.72	0.83±1.55	0.00±0.00	0.00±0.00	0.17±0.46	2.72±1.64
04:05:00	0.00±0.00	1.76±1.90	0.69±1.73	0.10±0.55	0.00±0.00	0.10±0.30	2.66±1.93
05:05:00	0.00±0.00	1.83±1.77	0.76±1.40	0.03±0.18	0.07±0.25	0.00±0.00	2.69±1.98
06:05:00	0.00±0.00	2.62±2.27	0.17±0.60	0.07±0.25	0.03±0.18	0.03±0.18	2.93±2.15
07:05:00	2.93±4.72	5.83±5.45	0.52±1.61	0.17±0.65	0.03±0.18	0.00±0.00	9.48±6.10
08:05:00	1.79±4.38	7.14±5.66	0.59±1.65	0.00±0.00	0.10±0.40	0.00±0.00	9.62±6.39
09:05:00	2.45±4.50	6.24±5.59	0.72±1.77	0.14±0.58	0.00±0.00	0.03±0.18	9.59±6.78
10:05:00	1.33±4.02	6.27±5.69	0.47±1.04	0.07±0.25	0.00±0.00	0.03±0.18	8.17±6.36
11:05:00	1.30±3.59	5.43±5.62	0.37±1.15	0.03±0.18	0.03±0.18	0.03±0.18	7.20±6.23
12:05:00	0.53±2.08	5.43±5.24	0.43±1.16	0.13±0.57	0.00±0.00	0.10±0.54	6.63±5.40
13:05:00	2.00±4.89	5.83±4.88	0.50±1.38	0.10±0.54	0.00±0.00	0.00±0.00	8.43±6.16
14:05:00	0.07±0.36	6.30±5.11	0.07±0.25	0.20±0.76	0.00±0.00	0.13±0.57	6.77±4.99
15:05:00	0.80±2.12	6.93±5.33	0.43±1.16	0.13±0.57	0.07±0.36	0.10±0.40	8.47±5.41
16:05:00	0.60±2.41	6.90±4.79	0.40±1.35	0.20±1.09	0.03±0.18	0.03±0.18	8.17±4.75
17:05:00	0.00±0.00	3.20±2.35	0.43±1.13	0.00±0.00	0.00±0.00	0.13±0.57	3.77±2.16
18:05:00	0.00±0.00	2.27±2.08	0.80±1.37	0.07±0.36	0.00±0.00	0.13±0.34	3.27±2.09
19:05:00	0.30±1.64	2.17±2.22	0.50±1.16	0.07±0.36	0.03±0.18	0.03±0.18	3.10±2.29
20:05:00	0.23±1.27	1.83±2.16	1.20±1.86	0.03±0.18	0.07±0.36	0.00±0.00	3.37±2.37
21:05:00	0.00±0.00	2.03±2.52	0.63±1.29	0.30±1.05	0.00±0.00	0.13±0.43	3.10±2.59
22:05:00	0.00±0.00	1.30±1.93	1.60±2.69	0.00±0.00	0.03±0.18	0.20±0.48	3.13±2.50
23:05:00	0.00±0.00	1.47±1.83	0.67±1.06	0.03±0.18	0.03±0.18	0.17±0.46	2.37±1.67

Table 10 Average (mean) abundance (individuals·2m^{-2} ± SD) of fish counted at Foss WPS for all size classes during a 14-day period in December 2017. Samples taken from a 1 frame·hour^{-1} sub sample.

Time				*Size class (cm)*			
	0-10	11-20	21-30	31-40	41-50	>50	Total
00:05:00	0.00±0.00	1.69±2.02	0.38±1.25	0.00±0.00	0.00±0.00	0.00±0.00	2.06±2.08
01:05:00	0.00±0.00	1.25±1.18	0.56±1.99	0.00±0.00	0.00±0.00	0.00±0.00	1.81±1.97
02:05:00	0.19±0.75	1.56±2.06	0.81±1.83	0.00±0.00	0.00±0.00	0.00±0.00	2.56±2.42
03:05:00	0.13±0.50	1.56±2.15	0.81±1.47	0.00±0.00	0.00±0.00	0.00±0.00	2.50±2.96
04:05:00	0.13±0.51	1.27±1.57	0.07±0.25	0.00±0.00	0.00±0.00	0.07±0.25	1.53±1.45
05:05:00	0.00±0.00	2.67±2.55	0.20±0.41	0.00±0.00	0.07±0.25	0.07±0.25	3.00±2.39
06:05:00	0.20±0.77	2.00±1.55	0.07±0.25	0.00±0.00	0.00±0.00	0.00±0.00	2.27±1.83
07:05:00	0.00±0.00	2.80±2.54	0.40±0.73	0.00±0.00	0.00±0.00	0.13±0.35	3.33±2.81
08:05:00	0.00±0.00	6.73±4.81	1.27±2.18	0.07±0.25	0.00±0.00	0.07±0.25	8.13±3.96
09:05:00	0.13±0.51	5.80±4.98	1.33±2.43	0.07±0.25	0.00±0.00	0.00±0.00	7.33±4.53
10:05:00	0.00±0.00	4.47±4.24	0.13±0.51	0.20±0.56	0.00±0.00	0.13±0.35	4.93±4.57
11:05:00	0.00±0.00	5.20±5.42	0.40±0.82	0.13±0.51	0.00±0.00	0.07±0.25	5.80±5.46
12:05:00	0.20±0.77	4.53±4.43	0.33±0.72	0.20±0.56	0.13±0.35	0.00±0.00	5.40±4.53
13:05:00	0.00±0.00	4.07±3.39	0.27±0.59	0.07±0.25	0.07±0.25	0.07±0.25	4.53±3.71
14:05:00	0.00±0.00	4.07±3.76	1.47±2.85	0.00±0.00	0.07±0.25	0.13±0.35	5.73±4.28
15:05:00	1.07±3.61	3.87±3.24	2.67±4.90	0.00±0.00	0.00±0.00	0.00±0.00	7.60±4.64
16:05:00	1.13±3.27	3.33±2.89	0.27±0.59	0.00±0.00	0.07±0.25	0.00±0.00	4.80±3.40
17:05:00	1.07±2.84	1.73±2.25	0.60±1.29	0.07±0.25	0.07±0.25	0.00±0.00	3.53±2.74
18:05:00	0.60±1.84	1.73±2.65	0.80±1.69	0.00±0.00	0.07±0.25	0.00±0.00	3.20±3.40
19:05:00	1.33±3.24	2.20±3.09	0.33±0.89	0.00±0.00	0.07±0.25	0.07±0.25	4.00±4.05
20:05:00	0.00±0.00	2.07±3.12	0.07±0.25	0.00±0.00	0.00±0.00	0.00±0.00	2.13±3.09
21:05:00	0.20±0.77	1.53±2.09	0.53±0.99	0.00±0.00	0.00±0.00	0.00±0.00	2.27±2.63
22:05:00	0.27±0.79	2.00±2.36	0.13±0.51	0.00±0.00	0.00±0.00	0.00±0.00	2.40±2.58
23:05:00	0.00±0.00	1.87±1.92	0.27±1.03	0.07±0.25	0.00±0.00	0.00±0.00	2.20±2.07

Table 11 Average (mean) abundance (individuals·2m^{-2} ± SD) of fish counted at Foss WPS for all size classes during a 14-day period in January 2018. Samples taken from a 1 frame·hour^{-1} sub sample.

Time	*Size class (cm)*						
	0-10	11-20	21-30	31-40	31-50	>50	Total
00:05:00	0.00±0.00	1.56±1.96	0.38±0.61	0.00±0.00	0.00±0.00	0.06±0.25	2.00±2.25
01:05:00	0.00±0.00	1.80±2.36	0.20±0.56	0.00±0.00	0.00±0.00	0.00±0.00	2.00±2.42
02:05:00	0.00±0.00	2.40±2.64	0.33±0.72	0.00±0.00	0.00±0.00	0.00±0.00	2.73±2.93
03:05:00	0.00±0.00	1.60±2.26	0.33±0.81	0.00±0.00	0.00±0.00	0.00±0.00	1.93±2.31
04:05:00	0.13±0.51	1.60±1.95	0.20±0.77	0.00±0.00	0.07±0.25	0.07±0.25	2.07±2.15
05:05:00	0.20±0.77	2.00±1.85	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	2.20±2.11
06:05:00	0.00±0.00	1.73±1.57	0.07±0.25	0.00±0.00	0.00±0.00	0.07±0.25	1.87±1.59
07:05:00	0.13±0.51	1.80±2.78	0.07±0.25	0.00±0.00	0.00±0.00	0.07±0.25	2.07±2.73
08:05:00	0.00±0.00	2.47±2.99	0.40±1.54	0.00±0.00	0.00±0.00	0.07±0.25	2.93±2.98
09:05:00	0.00±0.00	2.47±3.50	0.47±1.30	0.13±0.35	0.07±0.25	0.00±0.00	3.13±3.52
10:05:00	0.00±0.00	4.13±3.85	0.40±0.82	0.33±0.61	0.07±0.25	0.00±0.00	4.93±4.21
11:05:00	0.20±0.77	3.80±4.66	0.27±0.70	0.00±0.00	0.13±0.35	0.00±0.00	4.40±4.92
12:05:00	0.00±0.00	4.13±3.96	0.20±0.56	0.27±0.59	0.00±0.00	0.00±0.00	4.6±4.03
13:05:00	0.00±0.00	3.87±3.75	0.07±0.25	0.07±0.25	0.13±0.35	0.13±0.35	4.27±3.55
14:05:00	0.00±0.00	4.67±3.65	0.53±0.74	0.07±0.25	0.00±0.00	0.00±0.00	5.27±3.65
15:05:00	0.07±0.25	3.33±2.81	0.47±1.06	0.07±0.25	0.00±0.00	0.13±0.51	4.07±2.93
16:05:00	0.20±0.77	2.27±2.34	0.47±1.30	0.00±0.00	0.07±0.25	0.00±0.00	3.00±2.87
17:05:00	0.20±0.77	2.07±1.70	0.07±0.25	0.00±0.00	0.00±0.00	0.13±0.35	2.47±2.16
18:05:00	0.00±0.00	2.20±2.51	0.13±0.51	0.00±0.00	0.07±0.25	0.07±0.25	2.47±2.35
19:05:00	0.73±2.34	2.40±2.41	0.67±1.23	0.00±0.00	0.07±0.25	0.00±0.00	3.87±3.97
20:05:00	0.00±0.00	2.67±2.66	0.20±0.56	0.00±0.00	0.00±0.00	0.00±0.00	2.87±2.77
21:05:00	0.00±0.00	1.60±2.55	0.20±0.56	0.00±0.00	0.07±0.25	0.00±0.00	1.87±2.44
22:05:00	0.13±0.51	1.73±2.12	0.40±1.29	0.00±0.00	0.00±0.00	0.00±0.00	2.27±2.21
23:05:00	0.00±0.00	1.47±1.12	0.13±0.35	0.00±0.00	0.13±0.51	0.13±0.51	1.87±1.35

Table 12 Average (mean) abundance (individuals·2m^{-2} ± SD) of fish counted at Foss WPS for all size classes during a 10-day period in February 2018. Samples taken from a 1 frame·hour^{-1} sub sample.

Time				*Size class (cm)*			
	0-10	11-20	21-20	31-40	41-50	>50	Total
00:05:00	0.00±0.00	1.75±1.05	0.42±0.79	0.08±0.28	0.00±0.00	0.08±0.28	2.33±0.98
01:05:00	0.00±0.00	2.17±1.40	0.33±0.88	0.00±0.00	0.00±0.00	0.00±0.00	2.50±1.31
02:05:00	0.00±0.00	1.92±0.99	0.33±0.77	0.00±0.00	0.00±0.00	0.00±0.00	2.25±0.75
03:05:00	0.00±0.00	2.00±1.53	0.25±0.62	0.08±0.28	0.00±0.00	0.08±0.28	2.42±1.37
04:05:00	0.00±0.00	1.83±1.85	0.17±0.38	0.08±0.28	0.00±0.00	0.00±0.00	2.08±1.92
05:05:00	0.00±0.00	1.58±1.08	0.17±0.57	0.08±0.28	0.00±0.00	0.08±0.28	1.92±0.90
06:05:00	0.08±0.28	1.58±1.88	0.67±1.49	0.08±0.28	0.00±0.00	0.08±0.28	2.50±2.06
07:05:00	0.25±0.86	2.83±2.32	0.25±0.45	0.00±0.00	0.00±0.00	0.08±0.28	3.42±1.92
08:05:00	0.00±0.00	5.17±3.21	0.58±0.99	0.00±0.00	0.00±0.00	0.00±0.00	5.75±3.67
09:05:00	0.00±0.00	4.50±3.00	0.08±0.28	0.00±0.00	0.00±0.00	0.08±0.28	4.67±2.90
10:05:00	0.64±2.11	4.09±3.33	0.55±0.82	0.09±0.30	0.00±0.00	0.09±0.30	5.45±2.97
11:05:00	0.42±1.44	4.83±2.79	0.25±0.62	0.00±0.00	0.08±0.28	0.00±0.00	5.58±2.67
12:05:00	0.00±0.00	4.00±2.66	0.17±0.38	0.08±0.28	0.08±0.28	0.08±0.28	4.42±2.90
13:05:00	0.00±0.00	4.08±3.44	0.50±0.79	0.08±0.28	0.00±0.00	0.08±0.28	4.75±3.25
14:05:00	0.00±0.00	3.50±2.23	0.50±1.16	0.08±0.28	0.00±0.00	0.08±0.28	4.17±2.20
15:05:00	0.00±0.00	2.92±2.10	0.50±1.16	0.00±0.00	0.00±0.00	0.00±0.00	3.42±2.39
16:05:00	0.00±0.00	3.25±2.34	0.75±1.42	0.00±0.00	0.00±0.00	0.17±0.38	4.17±2.16
17:05:00	0.00±0.00	2.50±2.39	0.83±1.74	0.00±0.00	0.00±0.00	0.08±0.28	3.42±2.53
18:05:00	0.00±0.00	2.25±1.71	0.33±0.88	0.00±0.00	0.00±0.00	0.08±0.28	2.67±1.55
19:05:00	0.00±0.00	1.75±1.21	0.33±0.65	0.00±0.00	0.08±0.28	0.08±0.28	2.25±1.13
20:05:00	0.42±0.99	1.75±1.28	0.08±0.28	0.00±0.00	0.08±0.28	0.25±0.62	2.58±1.56
21:05:00	0.75±1.42	1.58±1.88	0.17±0.57	0.00±0.00	0.08±0.28	0.25±0.45	2.83±1.26
22:05:00	0.00±0.00	2.42±1.56	0.17±0.38	0.00±0.00	0.00±0.00	0.08±0.28	2.67±1.61
23:05:00	0.00±0.00	1.42±1.31	1.00±1.75	0.00±0.00	0.00±0.00	0.08±0.28	2.50±1.24

Table 13 Average (mean) abundance (individuals·2m^{-2} ± SD) of fish counted at Foss WPS for all size classes during a 12-day period in March 2018. Samples taken from a 1 frame·hour^{-1} sub sample.

Time				*Size class (cm)*			
	0-11	11-20	21-30	31-40	41-50	>50	Total
00:05:00	0.67±1.55	2.58±3.20	0.17±0.38	0.00±0.00	0.08±0.28	0.08±0.28	3.58±3.60
01:05:00	0.42±1.44	2.42±3.02	0.33±0.77	0.08±0.28	0.17±0.57	0.17±0.57	3.58±2.67
02:05:00	0.67±1.77	1.92±2.42	0.33±0.65	0.00±0.00	0.33±0.65	0.00±0.00	3.25±3.69
03:05:00	0.50±1.16	1.58±2.27	0.08±0.28	0.00±0.00	0.50±1.00	0.00±0.00	2.67±2.01
04:05:00	0.25±0.86	1.00±0.95	0.17±0.38	0.17±0.57	0.00±0.00	0.00±0.00	1.58±1.50
05:05:00	0.33±0.88	2.08±1.97	0.00±0.00	0.08±0.28	0.00±0.00	0.08±0.28	2.58±1.97
06:05:00	0.00±0.00	1.67±1.87	0.42±0.79	0.08±0.28	0.00±0.00	0.00±0.00	2.17±1.52
07:05:00	0.50±1.24	2.33±2.38	0.58±1.72	0.00±0.00	0.08±0.28	0.08±0.28	3.58±2.27
08:05:00	0.25±0.86	3.33±2.93	0.08±0.28	0.42±1.44	0.25±0.86	0.08±0.28	4.42±2.53
09:05:00	0.42±0.99	1.67±1.66	0.08±0.28	0.17±0.57	0.42±0.99	0.25±0.62	3.00±1.75
10:05:00	0.58±1.50	1.00±1.27	0.00±0.00	0.17±0.57	0.17±0.38	0.00±0.00	1.92±1.62
11:05:00	0.67±1.77	0.75±1.05	0.33±0.65	0.17±0.57	0.17±0.57	0.17±0.57	2.25±2.00
12:05:00	0.25±0.86	1.00±1.41	0.08±0.28	0.00±0.00	0.17±0.57	0.08±0.28	1.58±1.62
13:05:00	0.58±1.08	0.75±0.86	0.17±0.57	0.17±0.38	0.08±0.28	0.00±0.00	1.75±1.28
14:05:00	0.17±0.57	1.25±1.35	0.00±0.00	0.00±0.00	0.08±0.28	0.00±0.00	1.50±1.24
15:05:00	0.00±0.00	0.42±0.79	0.58±0.90	0.17±0.38	0.08±0.28	0.00±0.00	1.25±1.13
16:05:00	0.42±1.16	0.83±1.33	0.17±0.57	0.00±0.00	0.25±0.62	0.08±0.28	1.75±1.42
17:05:00	0.67±0.98	2.08±2.15	0.33±0.88	0.00±0.00	0.17±0.38	0.00±0.00	3.25±2.49
18:05:00	0.75±1.60	1.08±1.50	0.00±0.00	0.00±0.00	0.08±0.28	0.17±0.38	2.08±2.15
19:05:00	0.25±0.62	1.17±2.28	0.00±0.00	0.08±0.28	0.17±0.57	0.00±0.00	1.67±2.14
20:05:00	0.08±0.28	1.75±1.81	0.00±0.00	0.08±0.28	0.33±0.88	0.00±0.00	2.25±2.26
21:05:00	0.64±1.56	2.36±2.50	0.09±0.30	0.00±0.00	0.00±0.00	0.00±0.00	3.09±3.14
22:05:00	0.18±0.60	2.64±1.85	0.00±0.00	0.09±0.30	0.09±0.30	0.00±0.00	3.00±2.09
23:05:00	0.18±0.60	2.09±1.75	0.09±0.30	0.18±0.40	0.00±0.00	0.00±0.00	2.55±1.69

7.4 Coarse fish activity during pump operation

7.4.1 Pumping events recorded

A pumping event during January 2018 was imaged. River flow in the Ouse began to rise on 3rd January 2018, where GDF was recorded at $174m^3 \cdot s^{-1}$ and corresponding river levels reached 7.4mAOD. The floodgate at Foss WPS was closed during the early hours (00:15) of the 4th January, where GDF had risen to 205 $m^3 \cdot s^{-1}$ and river levels (Ouse) began to rise above 7.6mAOD. The pumps operated throughout a three day period between the 4th and 6th January (N=57 hours). On the 6th of January, GDF at Skelton had fallen to 145 $m^3 \cdot s^{-1}$ and pumping ended at 9:00am when river level (Ouse) had fallen to 7.5mAOD. The floodgate was then opened, and the Foss was free to flow into the Ouse. Unfortunately, there was a period of non-operation where the DIDSON failed and subsequently there was a seven hour gap in the recorded data period (Figure 41).

7.4.2 January 2018

In a sample representative of the pumping event during January 2018, there was a total of 921 fish recorded in a 57 hour period. Of this, 278 were counted as ‘in’ (entered the weed screen), 226 counted as ‘out’ (exited the weed screen) and a further 417 were counted as ‘approached’ (swam towards the weed screen and/or displayed behaviours that seemed to avoid contact with the weed screen) (Figure 41). The maximum number of fish was 9 $individuals \cdot 1min \cdot 15min^{-1}$ (one minute per 15 minute sample) (in), 4 $individuals \cdot 1min \cdot 15min^{-1}$ (out) and 20 $individuals \cdot 1min \cdot 15min^{-1}$ (approached), with an overall total of 29 $individuals \cdot 1min \cdot 15min^{-1}$. The minimum number of fish recorded was 0 $individuals \cdot 1min \cdot 15min^{-1}$ (in, out, approach). A Wilcox rank sum tests suggested there was no significant difference between the number of fish that were counted as in (medians=1 $individuals \cdot 1min \cdot 15min^{-1}$, ITQ=2) and out (medians= 0 $individuals \cdot 1min \cdot 15min^{-1}$, ITQ=2) (W=20908, p=0.15). Similarly, there was no significant difference between the number of fish in and those that approached (Wilcox; W=20640, p=0.23), or out and approached (Wilcox; W=19480, p=0.94). However, a Wilcox rank sum test revealed that the total number of fish recorded between day (medians=1 $individuals \cdot 1min \cdot 15min^{-1}$,

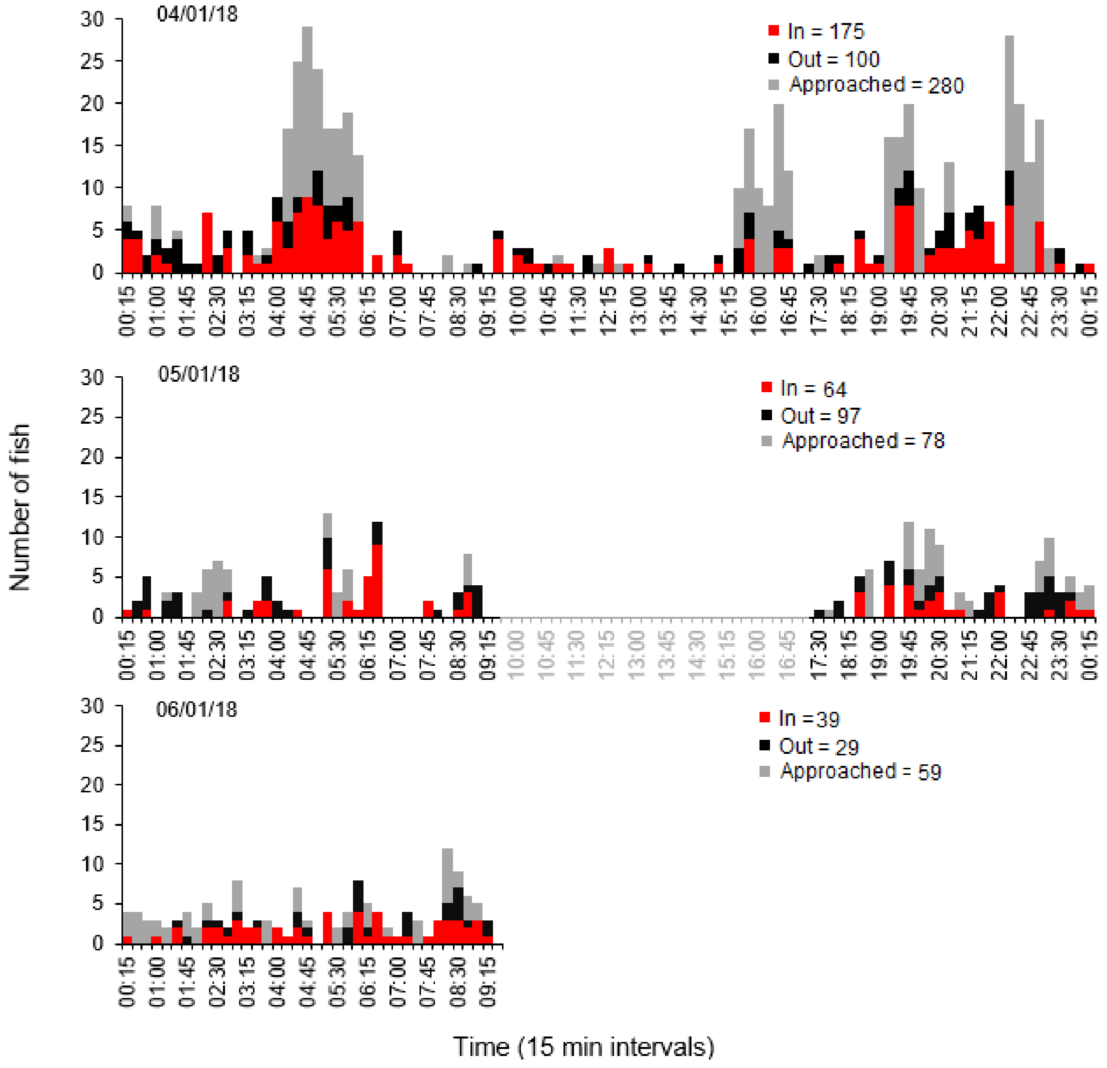


Figure 41 Pumping event in January 2018. Number of fish counted as in, out and approaching the weed screen during the three day pumping scenario (N=57 hours). The grey axis indicates missing data.

ITQ=3) and night periods (medians=4 individuals·1min·15min^{-1}, ITQ=7) was significantly different (W=2050, p=0.0019) (Figure 42).

The recorded fish numbers steadily declined throughout the duration of the event, with a total reduction of 505 fish from the start to the end of the end of the event. Fish numbers were recorded as 555 (mean= 5.5 individuals·1min·15min^{-1}), 239, (mean= 3 individuals·1min·15min^{-1}), and 127 (mean= 3.5 individuals·1min·15min^{-1}), on days one, two and three respectively. However, on day two there was a loss of eight hours of DIDSON footage and day three was of limited duration, which likely contributed to an under recording of fish. However, it is possible that a drop in fish numbers was due to entrainment. It is also important to note that the DIDSON installation could only image half of the weed screen, and pumping operation typically cycles through

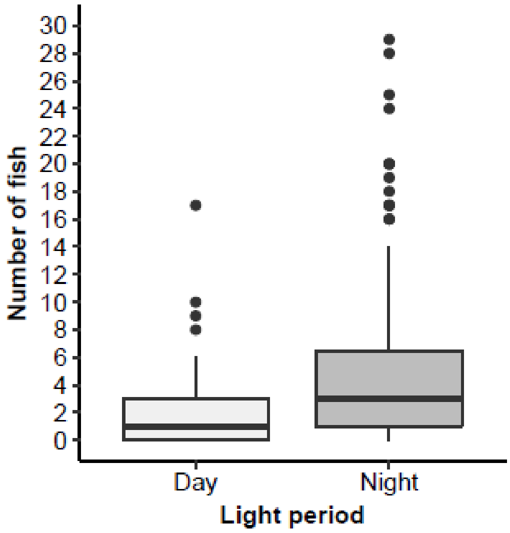


Figure 42 Number of fish recorded during January 2018 pumping event given as light period; day(white) and night (grey). Vertical lines represent quartile 1 to the smallest non-outlier, and quartile 3 to the largest non-outlier (as given by solid points).

pumps one to eight. This presents a possibility that fish activity was concentrated around pump intakes that are not being imaged. Therefore, numbers of fish described represent absolute minimums as opposed to definite numbers.

8. DISCUSSION

8.1 Introduction

In this study, a lengthy deployment of an underwater sonar allowed for a unique opportunity to capture diel and seasonal patterns in fish presence and develop the understanding of fish behaviour at WPS. Foss WPS was determined to be a suitable study site based on its off-channel structural position, adjacent flood defence barrier, and seasonal operation where pumps are operational for as little as 5% of the year. Additionally, fish protection at the WPS is currently limited to a slow start-up procedure, and Foss WPS was identified as a high priority structure in accordance to the Eel Regulations (2009). The Rivers Ouse and Foss are vulnerable to extreme flooding, and the structural position of Foss WPS at the confluences of these rivers provided a unique opportunity to record fish movements during regular flows, and during periods of flood when the WPS becomes operational.

The installation of a DIDSON at Foss WPS provided an opportunity to collect data without the need for traditional invasive fisheries monitoring techniques. Acoustic data collected by the DIDSON was processed by eye in accordance to a sub-sampling technique derived from a trial period. Thousands of fish were imaged throughout the five month sample period, and subsequently the WPS has been identified to present a risk of entrainment to fish. Visual counting of fish revealed diel and seasonal trends, where predictable changes in fish abundance were associated with dawn and dusk periods during November and December 2017. The same trends were not present in a sample period during January, February and March 2018. Recorded fish abundance was significantly different between all months, and there was a linear decline in fish abundance throughout the five month study period. Light period was a significant predictor of fish abundance, and there was significantly more fish counted during day time periods than at night time. Size class analysis indicated that the majority of fish imaged were smaller cyprinids, such as roach and dace, with the exception of larger fish recorded that were probably pike or bream. This was similar to typical coarse fish species expected in lowland reaches of UK rivers (i.e., Cowx *et al.,* 2004). A reverse stepwise linear regression process revealed that river level (Foss barrier, Ouse: L2404/SE6057951091) was the main predictor of fish abundance throughout the study where a rise in river level was associated with a decline in fish presence. But, it was determined that this was probably influenced by a general decline in fish abundance throughout the study. One pumping event was successfully monitored which showed a potentially high rate of fish entrainment associated with declining fish abundance over a three day pumping period.

8.2 Site history and entrainment risk

The River Ouse and Foss basin are isolated from the River Foss by a permanent impediment at Castle Mills lock and sluice which significantly reduces the longitudinal connectivity for fish between the rivers Foss and Ouse. The river level in the River Foss upstream of Castle Mills lock is now exclusively regulated by automatic spill over releases at the sluice and water pumping activities between Foss basin and the River Ouse when Foss Barrier is lowered. Because of this, it is likely that fish populations residing in the River Foss above Castle Mills have become completely isolated from those in the River Ouse. Thus, any fish community residing in the upstream reach of the River Foss is probably unaffected by pumping operations at Foss WPS if they do not pass over the sluice during flood periods. But, when considering the site as a whole, Foss WPS and the adjacent flood defence barrier, inclusive of upstream lock gate and sluice, show high potential for negative impacts on immediate fish populations. For example, impoundments at the mouth of the Foss present high likelihood of preventing free passage of migrant fish between the Foss and the Ouse, and water pumping activities can remove fish from the river via entrainment.

Following a historical assessment of Foss WPS, it was determined that the WPS has likely presented a high risk of entrainment to fish that reside in the River Ouse, and migrate into the Foss basin, since its construction in 1988. Estimates on the number of pumping events since 1996 support the conclusion that pumping operation at Foss WPS poses a significant threat of entrainment to fish. The site typically operates on a seasonal cycle, and fish are exposed to a dangerous risk of entrainment all year round, as sporadic high summer flows can result in several small pumping events, and predictable maximization of pumping during winter ascertains a predisposed risk to fishes entering Foss basin. As yet, there is no evidence base to suggest the volume of such pumping events, and thus it must be assumed that all pumping events have comparable rates of fish entrainment.

A seasonally high operational cycle during winter at Foss WPS shows potential to coincide with expected downstream movements of migrant European eels that attempt escapement of the River Foss (Vollestad *et al.,* 1986; Jansen *et al.,* 2007). This is particularly true for the potential of late eel migrants, that may be attempting passage of the structure in November and December where pumping is beginning to peak. Thus, there is a reasonably high likelihood of eels meeting pumping operations between August and October. Whilst pumping is high in January, February and March, it is unlikely to present any real risk to migrant eels unless they have faced serious delays by upstream structures such as Castle Mills Lock (i.e., Eyler *et al.,* 2016).

8.3 The status of European eel at Foss WPS

In light of the critically endangered status of the European eel, it has now been recognised that the facilitation and effective protection of seaward migrating eels from WPS is a critical component of their conservation (Feunteun, 2002; Han *et al.,* 2008; Piper *et al.,* 2015). At Foss WPS, the problem of eel management is complicated as the structure exists between two large lock impediments and thus there is some uncertainty as to catchment wide eel numbers. Additionally, complications with installation of monitoring equipment at Foss WPS meant that a peak window for eel migration was missed (October 2017). Given these issues, a total of two eels were successfully imaged during December 2017.

Underwater sonar images revealed that both eels were able to locate the entrance/exit channel of Foss basin and thus it is assumed that they achieved successful seaward migration of Foss WPS. Both eels were identified at night-time and their passage occurred at the onset of the third quarter moon phase. The river level was low (5.4mAOD) and it does not appear that eels moved during high flows (Ouse at Skelton recorded as $34m^3 \cdot s^{-1}$). Whilst this downstream movement in association with the lunar cycle is in support of several authors who cite the period between the third and first quarter moon phases as a key migration stimuli (i.e., Cullen & McCarthy, 2003; Miyai *et al.,* 2014), it is of direct contrast to a large body of literature that suggest high flows as the most prevalent stimuli (Boubee *et al.,* 2001; Cullen & McCarthy, 2003; Bolland *et al.,* 2018). Although, there are examples where river flow is not associated with downstream eel movements (Boubee & Williams, 2006), it is perhaps applicable to suggest that heavy regulation of flow in the River Foss may dilute flow stimulus usually associated with downstream movements of European eels. Similarly, regulation of such system is reliant on automatic sluicing and as the present study uses GDF measured on the main channel, it is unclear if flow in the River Foss was significant enough to function as downstream stimuli and therefore requires further investigation.

Seaward migration in eels can be delayed where WPS impedes or prevents free passage of fish (Marmulla, 2001; Verhelst *et al.,* 2018; Bolland *et al.,* 2018). There is currently a lack of understanding regarding delayed eel movements, although it is thought that such delays can result in an increased risk of predation, and because migration in eels is preceded by a cessation to regular feeding, delays at riverine structures can lead to starvation and/or otherwise eels may move in unfavourable physiological and hydrological conditions. Similarly, when eels arrive at WPS they may be deterred by such structures and return upstream (Bolland *et al.,* 2018). In this scenario the silvering process can reverse (Durif *et al.,* 2005; Eyler *et al.,* 2016). Moreover, European eel may have already experienced upstream delays by Castle Mills lock and sluice, and there is a possibility that eels recorded at Foss WPS may have already stopped silvering and began reverting to a growth phase (Durif *et al.,* 2005). However, eels that have previously ceased slivering in upstream reaches may fulfil the process at a later date and thus the effect of delays by WPS is unclear and requires further investigation (Eyler *et al.,* 2016).

A number of studies at water intakes typically record a higher number of eels than in this study, which holds bearing for the relative risk to eels at Foss WPS in light of their critically endangered status (i.e., Piper *et al.,* 2012; Piper *et al.,* 2013; Brown *et al.,* 2014; Buysee *et al.,* 2014; van Esch & Spierts, 2014; Piper *et al.,* 2015; Eyler *et al.,* 2016). Indeed, the structural position of Foss WPS, including its off-channel location and intermittent operation, may reduce its negative implications associated with seaward eel migration, and whilst the WPS is inherently a dangerous risk to eels in the catchment, it is unlikely that this structure alone is reducing escapement of eels (Feunteun, 2002).

Foss WPS was constructed between two major river impediments, namely Naburn lock gate and weir 8.86km downstream of the site, and Castle Mills Lock and sluice 145m upstream of the pumping station (Figure 43). Naburn lock is the first major riverine structure that eels must pass following their entry from the Humber estuary, and forms a barrier between the tidal and non-tidal stretches of the River Ouse. Castle Mills Lock and sluice regulates the upstream river level of the River Foss, and differences in upstream and downstream river levels here present a largely impassable structure to elvers. The lock gate previously had an elver pass but has been removed due to poor performance. Eel entry into the River Foss may be prevented all together if immigrants attempt migration into the River Foss when Foss WPS is operating with the adjacent flood defence barrier down. But, despite both structures existing without elver passes, a well-timed immigration process may lend itself to success if eels move during flood periods, or when lock gates are opened for navigation. Similarly, elvers should be able to pass between gaps in lock structures. Where there are large volumes of immigrant eels there is a reasonable probability that enough will pass to maintain population status upstream of Foss WPS but this requires further investigation via population assesment.

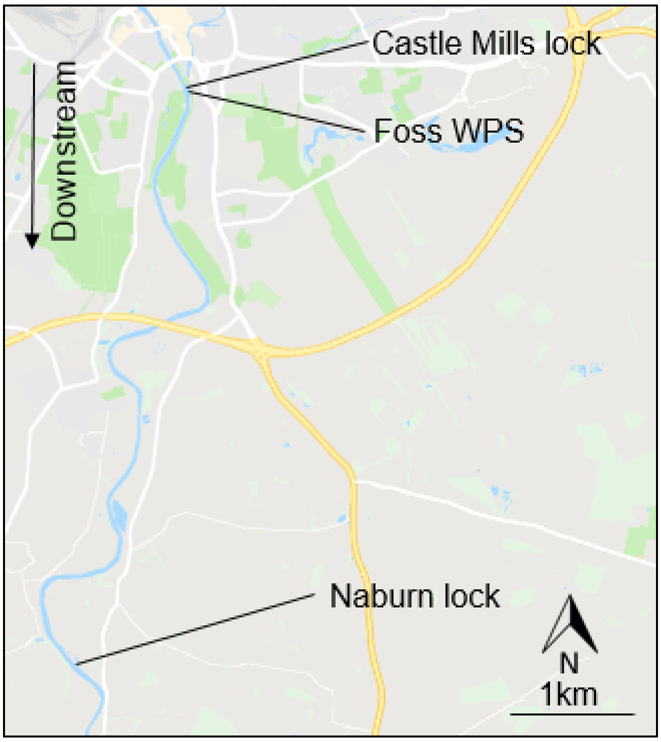


Figure 43 The position of Naburn lock, Foss WPS and Castle Mills lock on the River Ouse.

8.4 Factors influencing fish distribution around Foss WPS

Coarse fish are a major component of fish communities in UK rivers (Lucas & Baras*,* 2008). Despite being one of the UK's richest aquatic resources, there is currently a paucity in the understanding of anthropogenic influence on coarse fish following a surge in research throughout mid to late 20th century. At present, the problem of fish movements around riverine structures is one that has come to much attention following the implementation of the Water Framework Directive (WFD) and a multitude of supportive legislation that target habitat connectivity, biodiversity and water quality.

However, it has to be said that few papers exist that directly look to explore the interactions of coarse fish with WPS in England, and there is currently a lack in understanding of coarse fish behaviour at WPS. However, anecdotal reports provide a general suggestion that WPS offer refuge habitat to fish in habitat devoid rivers. This study attempts to improve this understanding by addressing a question as to which factors may present fish an opportunity to utilise WPS structures and ultimately how this influences entrainment risk.

8.4.1 Diel and seasonal patterns in fish abundance

In this study there were marked changes in the diel presence of fish imaged by the sonar at Foss WPS. During a sample period beginning in November 2017, there was a diel pattern in fish abundance where fish count was highest during the day with peak activity occurring at dawn and dusk periods. This is in direct support of literature that suggests dawn and dusk to be a key predictor of fish activity, usually associated with feeding and predation responses marked by periods of illumination (i.e., Hohausova *et al.,* 2003; Horky *et al.,* 2008; Armstrong *et al.,* 2013). But, in this study, this trend showed a tendency to break down where the predictability of fish presence at dawn and dusk periods become less clear, and fish abundance typically peaked within three hours of dawn and dusk throughout December 2017 to March 2018. Also, there appeared to be some switch to nocturnal activity, particularly in the 2018 winter period.

Because fish make coordinated movements between habitats that best reflect resource availability (Dingle & Drake, 2007), the structural presence of WPS may be more or less attractive habitat depending on seasonal predictors (i.e., Nunn *et al.,* 2009). This is usually associated with physical habitat features and refuge opportunities that are exploited on a diel basis .Thus, changes in presence of fish may then be associated with movements between distinct day and night habitats (Clough & Ladle, 1997).

Whether these recorded diel movements are the result of a circadian rhythm associated with the setting and rising of the sun or are behavioural responses to physical and biological stimuli is unclear (Reebs, 2002). When an endogenous circadian rhythm is involved, fish are usually synchronised to a 24h cycle that exerts some influence by zeitgebers (external factors that regulate circadian rhythms). Yet, where an endogenous cycle is not present, diel activity patterns in coarse fish show variation on an individual level where they directly reflect external factors (Reebs, 2002). Coarse fish show a need for seasonal dispersal to gain access to important refuge habitats associated with illumination, predation, feeding, flow and temperature (Lucas *et al.,* 2001). Thus, there is an expectation of fish to display activity patterns that reflect trade-offs between negative habitat conditions (i.e., Roff & Fairbairn, 2007).

Accordingly, fish exploit habitat heterogeneity by conducting movements between habitats that offer different environmental resources (Armstrong *et al.,* 2013). Observed diel changes in the activity of coarse fish are then often linked to movements between refuge habitats. This is demonstrated in Copp & Jurajda (1999), where the number of fish caught in refuge habitat (shallow river banks) was higher at night than during the day. Similarly, which time of day fish choose to move between rivers and tributaries or off-channel areas that offer refuge opportunities shows considerable variation between winter and summer (Nunn *et al.,* 2009). In spring and winter fish may emigrate from tributaries to the main channel during daylight and immigrate from main channel to tributaries at night and in contrast, the opposite movement occurs during summer (Nunn *et al.,* 2009). This suggests that physiological traits associated with activity period may display plasticity (Reebs, 2002). If so, then the unpredictability of fish activity at Foss WPS may be associated with fish provisionally choosing differing refuge resources driven by seasonal changes (Fraser *et al.,* 1995).

8.4.2 Illumination and day night alteration

The emphasis on a day night cycle is widely accepted as one of the main factors contributing towards the characteristic patterns observed in fish behaviour (i.e., Helfman *et al.,* 1986). Behaviour in fish can be mediated by differences in illumination periods which extends to inner (physiology) and outer (environmental) factors. Illumination facilitates fish behaviour directly where chemical processes induce changes in physiology associated with light and dark periods (Lopez-Olmeda *et al.,* 2006). Particularly so, the onset of night is associated with reductions to swimming ability (Lopez-Olmeda *et al.,* 2006), feeding and thermal tolerance in diurnal fish. Coarse fish must then make use of the setting and rising of the sun to make informed habitat choices (Copp *et al.,* 2005). Differences in fish counts during day and night may also be explained by variation in group activities, particularly those associated with rest and refuge at night (Holfman *et al.,* 1986).

Such high fish counts during the day in the present study suggests that the fish community in the River Ouse is predominately composed of diurnal species. A reduction in night-time activity is usually associated with a circadian regulation of melatonin, which has a controlling factor over activity and diel patterns in fish by regulating sleep-like behaviours (Lopez-Olmeda *et al.,* 2006). This process does, however, have negative connotations for prey species, as nocturnal predators like pike hunt well during darkness (Andersen *et al.,* 2008). This is also supported in this study by an increased tendency for larger fish to be recorded at night. Many fish seek refuge habitats in darkness for rest and predator avoidance which may at least partially explain high activity during dusk periods. Although, refuge that is safe during the night may not be safe during the day and diel patterns surrounding WPS may be influenced by dispersal from day and night habitats.

A simple explanation for the reasons why this pattern of day-night activity was diminished in the December to March period at Foss WPS is not immediately apparent. Although, this a period of seasonal transition where daylight hours are steadily reduced throughout the winter period and thus is expected to be a period for readjustment for fish. Most fish are quick to adjust their activity patterns to differing light-dark cycles and fish may begin to make habitat decisions that are not influenced by an endogenous cycle (Reebs, 2002). The overbearing stimuli of light may “mask” the circadian rhythm of fishes, and if a circadian rhythm is present, it is probably one that allows for fluctuations in the zeitgeber, or is easily readjusted to external factors (Mrosovsky, 1999).

Changes to recorded diel activity in the present study may also be associated with a transition to a fish community where behaviour of nocturnal fish is easier to discern. For example, fish that are generally active during the day may become more sedentary at the onset of winter and thus activity of nocturnal fish may become more pronounced (Okun *et al.,* 2005). Indeed, the composition of fish communities can shift throughout seasons (Schlosser, 1982; Schiemer, 1999; Orsi *et al.,* 2018). Previous studies on the River Ouse tend to reveal large numbers of roach, perch and other smaller cyprinids that show differences in activity period (diurnal, nocturnal) (Lucas *et al.,* 1998; 2008), and thus it is likely that differences in diel patterns at Foss WPS may be associated with changes to community structure, but this requires further investigation with a more robust species identification.

8.4.3 Foraging and predation of fish

Many fish experience diel fluctuations in predation risk and food availability. Because habitat safety is not uniform through day and night periods, fish must make decisions about when is the optimal time to feed or seek refuge during a 24 hour period (Railsback *et al.,* 2005). Changes to coordinated diel patterns may then be associated with periods of elevated predation, such is true for riverine fish species that delay migrations where predation is high (i.e., Aarestrup *et al.,* 2005). Indeed, prey species must adapt to ongoing changes in illumination period as exposure will likely incur an additional hazard of predation if it is to coincide with periods of high activity and abundance in predatory fishes (Helfman *et al.,* 1986). For example, juvenile perch have been observed moving from open water habitats at night into macrophyte refuge in the morning (Jacobson & Berg, 1998). This is also true of nocturnal fish like roach that forage at night and stay hidden during the day. Given, stochastic fluctuations associated with predation threat is expected to change on a spatiotemporal scale. Perhaps then, fish may make decisions that do not reflect predictable factors (i.e., sunlight) if predation risk is costly.

Fish are expected to move between day and night habitats on a diel basis to facilitate feeding (Clough & Ladle, 1997), and WPS are likely to have limited food resources due to pumping activities. In the example of Foss WPS, fish probably have access to good food resources during summer when pump activity is lowest. Accordingly, as fish deplete limited food resources, they move between patches that offer higher food abundance (Schilling, 2005). Any fish situated around Foss WPS probably makes foraging migrations between Foss basin and the River Ouse. Because of these trends associated with food abundance, cyprinid foragers may congregate at food patches according to seasonal predictors (Freeman & Grossman, 1993). High foraging opportunities in the Ouse has negative connotations associated with an increased susceptibility to predation and thus fish must make informed habitat choices that facilitate both feeding and predator refuge. If fish are able to avoid predators when not feeding by adjusting patterns in their daily migrations, then the optimal feeding period should be the time of the day when the trade-off between predation and feeding is minimised rather than when feeding is maximised (Clark & Levy, 1988). Seasonal differences in fish activity surrounding WPS may then be linked to differences in food availability and predation threat but requires further investigation into food availability around WPS.

8.4.4 River flow and its relationship with refuge

In this study, the structural position of Foss WPS, including its off-channel position and placement within a basin like environment, was considered to be a key factor in influencing fish abundance. Although situated at the confluence of the rivers Ouse and Foss, Foss basin effectively functions as artificial backwater habitat extending as an off-channel area from the River Ouse because Castle Mills Lock severs hydrological connectivity between the River Foss and the River Ouse.

This variation in channel morphology is expected to account for recurring patterns of fish movements (i.e., Visintainer *et al.,* 2006), and diel movements of fish to and from off-channel river backwaters and floodplains are a common adaption associated with exploitation of habitat heterogeneity (Hohausova, 2000; Hohausova *et al.,* 2003; Nunn *et al.,* 2009). Fish presence in off-channel areas is mediated by river size (Bischoff & Scholten, 1996; Copp, 2004), and in off-channel areas of large rivers, fish densities tend to peak during the day

(Copp *et al.,* 2005). More so, in Hohausova *et al.* (2003), roach, bleak and chub moved from a backwater to river at dawn, whereas perch moved throughout the day and rudd were bi-modal (moved at mid-day, midnight) which may suggest species-specific movement patterns between rivers and their off-channel areas. Perhaps, variability in diel patterns in this study may then be the result of species-specific movements between the River Ouse and Foss basin.

Access to low-flow refuge during flood events is critical for the survival of fish (Poff *et al.,* 1997), especially so in modified rivers where channelisation and modifications of bankside habitats has removed low-flow refuge. Because the River Ouse is heavily constrained by flood banks, and has poor longitudinal and latitudinal connectivity, any fish present in the River Ouse may see Foss basin as a suitable habitat where this offers relief from high flows in the main river channel (Bell *et al.,* 2001). Thus, the presence of Foss WPS on a flood prone river system is expected to influence fish movements where hydrological connectivity between the pumping structure and main river channel is good. Indeed, the use of marinas, private docking areas and other man-made off-channel areas as flow refuge may be an important factor in determining fish survival in habitat devoid rivers (Copp, 1997). However, if fish enter Foss basin during flood events it is highly likely that they may become trapped when the flood defence barrier is lowered. In this scenario coarse fish become vulnerable to prolonged flow changes when the WPS is operating and must seek flow refuge within Foss basin or otherwise face prolonged flow changes during pump operation. Once fish become trapped in Foss basin, the issue of flow refuge is expected to far exceed those of foraging and predatory responses, and the provision of flow refuge becomes essential for fish survival. For WPS operators this is undesired as their operation is likely to coincide with periods of flood and high-flow condition.

In this study, a negative association between river flow and river level and fish abundance was unexpected, as it is generally accepted that fish activity should increase during high flows as fish make foraging movements where food resources increase (Munn & Brusven, 1991), are usually displaced from refuge habitats (Andre *et al.,* 2016), and are expected to leave the main river channel and enter off-channel areas, with the opposite occurring when river levels return back to normal (Hocutt, 1980). The timing and duration of high flow events can also serve as a cue for spawning migrations in fish (Welcomme, 1985). However, it is important to note that the relationship between flow and fish movements at Foss WPS probably differs from that typically observed. For example, where flooding is usually associated with high fish abundance, the same is probably not true at Foss WPS due to pumping coinciding with the operation of the flood defence barrier. Changes to water level also shift the availability of important refuge habitats (Cowx *et al.,* 2004), and rising river levels in the River Ouse may increase the number of available refuge habitats outside of Foss basin which may reduce fish abundance if fish disperse into the River Ouse (Bunn & Arthington, 2002).

8.4.5 Winter and overwintering of fish

A winter period was associated with both a decline in fish abundance and a change from a predictable diel pattern in fish activity to one where pronounced peaks in the histogram were reduced (Figure 31). This may be explained by a change to fish behaviour that best reflects winter resources such as temperature (Suski & Ridgway, 2009) and food availability (Shuter *et al.,* 2012). The fact that winter is often associated with periods of high fish mortality is well-documented (Hurst, 2007), and the onset of winter is associated with decreases in metabolism, swimming performance (Wardle, 1980; Binder *et al.,* 2015), feeding and predation response (Le Morvan *et al.,* 1997; Suski & Ridgway, 2009), and also exacerbates problems associated with external stressors such as parasites and toxic substances (Butler & Fairchild, 2005).

There is a question as to whether a reduction in diel activity patterns at Foss WPS may be associated with an overwintering period for fish that enter Foss basin. Indeed, fish may prepare for winter through energy allocation, physiological adaptions (i.e., Johnston *et al.,* 1990; Guderly, 2004) and identification of suitable overwintering habitats (Shuter *et al.,* 2012; Binder *et al.,* 2015). Fish may use storage strategies that rely on energy stored during summer feeding to facilitate their winter survival (Shuter *et al.,* 2012), and then the location of habitats that allow a fish to reduce energy expenditure is generally more important than the costs associated with predation and access to food (Suski & Ridgway, 2009). Such winter movements usually involve fish seeking out larger, deeper habitats with slow moving waters as they provide shelter from winter flows (Allouche *et al.,* 1999). Consequently, backwaters are often important areas for shelter during winter as they offer reduced flow and thermal advantages when compared to cooler main channel areas (Bodensteiner & Lewis, 1994; Allouche *et al.,* 1999).

Accordingly, fish may be expected to make coordinated movements into artificial backwater habitats like Foss WPS if they offer refuge from winter flows and predators (Brodersen *et al.,* 2008). The successful identification of overwintering habitat largely depends on the proximity of suitable winter refuge in relation to a fishes home-range, and as a result, seasonal migrations are often more prevalent in fish communities close to larger rivers than at periphery of suitable habitats (Butler & Fairchild, 2005). Indeed, Foss basin is situated immediately adjacent to the River Ouse, and it may be seen as an attractive overwintering habitat for fish that are seeking 'safe' refuge from the River Ouse. Conversely, if fish are to use Foss basin as an overwintering habitat, than this may be expected to increase their relative entrainment risk due to a combination of a maximization in pumping events, and a reduced swimming performance associated with low temperatures (Ruetz & Jennings, 2000).

8.4.6 Home range and residency

Although there are few studies using telemetry to track and study the movements of riverine coarse fish, there has been some indication that coarse fish utilise home ranges to facilitate their movements between habitat patches in rivers (Clough & Ladle, 1997; Lucas *et al.,* 2008). In unregulated rivers, the turnover and frequency of microhabitats that offer refuge, feeding and spawning opportunities is high. Accordingly, the home range of fish in these systems is usually small because fish have access to most key habitat features they require, but in regulated rivers, fish may employ extended home ranges that facilitate access to a wider range of resources because key habitat features are further apart (Lucas *et al.,* 2008).

The scenario is complicated at WPS that offer structural features that are 'attractive' to fish, as a concentration of habitat resources may be associated with a reduction in home range. More so, the spatiotemporal scales that fish use to make habitat choices is expected to change in accordance with seasonal predictors (Andre *et al.,* 2016), which may present an increased likelihood for fish to utilise Foss WPS if it provides local refuge opportunities that are unavailable in the River Ouse. Then, a limited home range that is associated with Foss WPS may present an increased susceptibility to environmental fluctuations for fish (Heupel *et al.,* 2006).

Currently, most effort directed towards reducing entrainment at facilities that use turbines or water pumping has focused primarily on fish that have extensive home ranges, or are downstream migratory fishes (Martins *et al.,* 2014). However, fish may associate themselves with river structures if they offer refuge opportunities during their learning period. Foss basin is a large, open environment that could support several thousand fish, and because Foss WPS is expected to offer refuge (flow, predation) opportunities when not operational, fish may display residency surrounding these structures. If structural features at WPS satisfy individual fish refuge needs, then it becomes a question of whether fish are expected to have any desire to leave.

Dedicated information about the spatial patterns of fish in the River Ouse and at Foss WPS is in its infancy and thus it remains unclear whether fish observed on underwater sonar images are residents of the structure or not. At Foss WPS the problem is further complicated by a seasonally high operational cycle that may coincide with critical life stages, or an entrainment risk that has a species-specific bias. Indeed, entrainment risk is expected to vary between species, life stage, time, and operational cycle (Grimaldo *et al.,* 2009). Temporal variation in entrainment risk may then be linked to changes in physical (pump operation, temperature, light) and biological (predatory and prey distribution) factors that would affect forebay use (Martins *et al.,* 2013). Patterns in diel activity may become unpredictable if fish are persistently searching for improved habitat options (Andre *et al.,* 2016), and residency around pumping structures may then influence diel behaviour where fish are directly affected by pumping operations but this requires further investigation.

8.5 Pump operation at Foss WPS

Analysis based on the singular pumping event revealed entrainment of fish at Foss WPS was consistent with findings at other WPS where fish outside of pumps become entrained upon operation (i.e., Solomon & Wright, 2012). A pumping event spanning three days was consistent with those discerned from a historical assessment of Foss WPS, suggesting that the present pumping event was representative of pumping operations at the site. Because fish imaged at Foss WPS were unable to leave the forebay of the structure during pumping, it was assumed that declining fish counts throughout the three day pumping event were a result of fish being removed from the forebay via pump entrainment or had found upstream refuge, but this requires validation. Similarly, this may help explain declining fish numbers throughout the duration of the study, where pumping scenarios between monthly fish count sample periods may have removed fish from the population. It may then be expected that the remaining fish display different behaviours that possibly reflect changes to patterns in diel activities reflected in the present results.

A high number of fish counts during pump operation associated with night-time was expected because a reduced metabolic capacity in diurnal fish associated with darkness means most fish are poor swimmers at night (Wardle, 1980; Binder *et al.,* 2015). Fish surrounding WPS at night are then more vulnerable to entrainment than during the day. A number of attempts have been made to determine the critical water velocity thresholds that lead to entrainment at pump intakes (i.e., Salmon Advisory Committee 1997). Such broad-brush criteria however do not account for the variation observed in swimming performance at different life stages (Clough & Turnpenny, 2000; Clough *et al.,* 2004a, b; section 4.3.1.1). They also fail to take into account daily and seasonal variation and/or incorporate ideas surrounding fish physiology and swimming performance and are thus currently unreliable for determining entrainment risk during pump operation.

Most coarse fish are vulnerable to entrainment at WPS because their swimming capabilities are usually poor when compared to that of Salmonids (Cowx *et al.,* 2004). In particular, endurance performance is important as fish surrounding the forebay of Foss WPS are vulnerable to prolonged flow changes where they are unable to leave Foss basin until pumping has ceased. Similarly, the structure is lacking in alternative habitat stimuli (i.e. viability of low-flow refuge) that would allow fish to position themselves away from pump intakes and it is therefore unlikely that any fish present in the forebay is able to locate alternative refuge habitat. One of the main concerns at pumping stations during pumping is at start-up where fish are unprepared for changes in water flow. At Foss WPS, a slow start-up procedure is used that is designed to allow fish in the immediate vicinity of the pumps chance to swim away and outswim contending flows. However, because the flood defence barrier is lowered, fish are essentially trapped in Foss basin until water pumping has sufficiently relived the River Foss of flood water.

Once fish have entered Foss basin and the flood defence barrier is lowered, the ability of fish to locate suitable flow refuge becomes a greater priority than that of feeding and predation response. Indeed, any fish surrounding the forebay of Foss WPS are then much more vulnerable to prolonged changes in flow than they are that of predation or other factors.

8.6 Remediation targets

The installation and incorporation of devices or regimes that best target fish-friendly pumping practises at Foss WPS has been considered. Primarily, there are three potential options; engineered solutions, natural solutions and operational changes. Engineered solutions are usually achieved by modifications and additions to structural features of WPS which are expected to, in a best case scenario, prevent the entrainment of fish into pumping structures. But, the successful mitigation of mortality at WPS is much more than installing a ‘fish-friendly’ pump (Jackson, 2014). Indeed, the installation of ‘fish-friendly’ pumps is often not possible at WPS used for flood defence as such situations require high volumes of water to be pumped. Thus, identification and installation of alternative devices is essential at many WPS. In any case, pump operators must also seek behavioural study of fish using such structures as it is likely that operation of pumps and remediation devices can be made a multitude more effective by careful consideration of operating times (section 4.7.1).

Pumping stations that extract more than 20 m^3s^{-1} of water a day are required to install screens (size dependant on local eel stocks) in accordance to the Eel Regulations (2009). However, this is not suitable at Foss WPS due to site characteristics, including an intake area that would impair pumping significantly if screened, and a seasonal pumping cycle that creates extreme hydrological conditions surrounding Foss WPS. Moreover, whilst the Eel Regulations (2009) stipulate a necessity to screen water intakes, it does so with consideration to cost i.e., ‘Best available technology not entailing excessive cost’ and a cost-benefit analysis at Foss WPS revealed a disproportionate cost if screening measures were installed (Kendall, 2016). Indeed, there is little to be gained by the installation of expensive screening measures that would ultimately impair pumping operation. With the limited data available there has yet been a quantification of eel behaviour at Foss WPS and thus installing screens based off pre-emptive findings is not expected to improve eel escapement at the site.

Behavioural deterrents that use nonphysical stimuli to moderate fish movements are a good alternative as they are often less expensive, can be manipulated for navigation and it is easier to implement taxon-specific considerations (Popper & Carlson, 1998; Noatch & Suski, 2012). Modifications to the fore bay of pumping structures to include physical screening techniques, bypass channels and installation of devices that function as behavioural deterrents has become common practice (i.e., section five). However, these modifications can fail to incorporate a site-specific understanding of fish behaviour and WPS often penned as ‘fish-friendly’ can remain to have high fish mortality (Solomon & Wright, 2012). A combination of site characteristics including the structural position and operational regime of Foss WPS do not lend themselves well to retrofitted behavioural applications. Louver screening is not suitable due to the sites operation with a flood defence barrier, and it is unclear if the physical installation of electrical, sounding and lighting devices would be suitable due to the sites operation on as an off-channel basin. Given, there is a consideration that the installation of such devices at the entrance to Foss basin may function to deter fish from entering. Although, their operation is likely to incur a disproportionate cost due to the sites limited operation schedule and thus requires further investigation.

8.6.1 Operational changes

One potential solution to reduce fish entrainment at Foss WPS is to make adjustments to the operational regime that best reflect fish-friendly pumping practices. A combination of temporal and spatial trends in fish behaviour are useful in determining an appropriate operational cycle. Indeed, if behaviour of fish changes their susceptibility to entrainment in accordance to specific diel periods, then pumping operations can be timed to avoid peak activity periods. Even low levels of adult mortality through entrainment can have a significant impact on the populations and the environment Agency considers 100 coarse fish kills to be a major incident (Environment Agency, 2016b). Given, it is important to incorporate an understanding of the factors associated with entrainment into management plans associated with pump operation (Martins *et al.,* 2013). Consequently, a site-specific understanding of daily and seasonal trends in fish behaviour is essential if managers are to make biologically informed decisions about pump operations.

One solution at Foss WPS would be to adjust the timing of the closure of the defence flood barrier. Although not certain, it is likely that fish are entering Foss basin from the River Ouse during high flow periods. If so, the barrier could be lowered in advance of high flows which should reduce the number of fish vulnerable to entrainment at the site. Additionally, pumping hours could be adjusted to best reflect diel trends in fish activity at the site. For instance, fish counts are generally highest during the day and then focusing a pumping operation during the night may reduce entrainment. To facilitate such changes a daily decision-making process should be incorporated that allows for flexibility, especially during small-scale pumping scenarios (Sambrook & Cowx, 2008). The effectiveness of changes to operational regime is expected to show seasonal variation. For example, a period of operation that best avoids peak fish numbers during dawn and dusk periods should prove very effective during November, but has little bearing in other months in the current understanding. Similarly, as a whole, fish are present at Foss WPS during the day and night, and therefore adjusting operation to avoid either of these periods is still going to incur entrainment.

Adjusting the operational cycle at Foss WPS is challenging, as a seasonally high operational cycle coincides with a downstream migration period in eels. A best-case scenario would be to cease pumping between September and December, but this is simply not possible as the site must become operational in response to seasonal flood periods. Additionally, given that the timing of seaward migration in eels differs to that of coarse fish movements at Foss WPS, the ability to mitigate fish entrainment at the site is complicated (Rytwinksi *et al.,* 2017). It is essential that any operational change made to WPS do not disrupt regular pumping activities, and at Foss WPS it is imperative that operational changes do not increase the risk of flooding to properties and land surrounding the rivers Ouse and Foss (Bolland *et al.,* 2018). This study has highlighted that the fish community at Foss WPS is unpredictable, and because behaviour of fishes surrounding WPS shows temporal variation, a consistent operational change may not be suitable. Additionally, changes to the operational regime that best target fish-friendly practises are further complicated by stochastic environmental features, and it is expected that flexibility in operational regime is inherently reliant on prevailing hydrological characteristics of the site.

8.6.2 Flow refuge

Engineered solutions such as physical screening are expected to have reduced functionality at Foss WPS due to its position in a basin-like environment and both difficult installation in a navigation channel and maintenance of deterrent systems. Additionally, such practices often fail to incorporate multi-species considerations, which has negative implications for a potentially diverse fish community at Foss WPS. The vast majority of fish present at Foss WPS are considered to be non-migratory, show a tendency to be at the structure during day and night, and although in reduced numbers, are present throughout winter. Preventing fish entry to Foss basin is a best-case scenario and it is unlikely that an engineered solution, such as installing lighting at the entrance to Foss basin in the River Ouse would be successful in ceasing fish entry at Foss WPS without further investigation. Regression analysis revealed an unpredictable trend in fish counts associated with water level and flow, and therefore the installation and implementation of remediation measures that best target a ‘natural’ solution are expected to have increased performance when compared to engineered practices.

Fish entry to Foss basin is a major concern as elevated flows in the Rivers Ouse and Foss may occur during times of reduced metabolic capacity in fish. Because fish that enter Foss basin preceding pump operation subsequently become ‘trapped’, the provision and access to areas of low-flow refuge are essential if fish are too avoid entrainment during pumping. Although yet determined, if fish are residents of the basin surrounding Foss WPS, then the population is expected to decline throughout the winter season where fish are lost to pumping activities if they are unable to outswim prolonged changes to flow. Therefore, it is advised that the addition of structures and/or habitats that increase the provision of low-flow refuge is installed in Foss basin. The implementation of structures such as flow deflectors are common practice in UK river restoration/rehabilitation projects (Biron *et al.,* 2004; Harvey, 2007; Smith *et al.,* 2014), and the addition of in-stream structures that manipulate flow to offer habitats with low-flow refuge are expected to attract fish as they offers benefits associated with energy use. This allows fish to employ a greater degree of predator vigilance or otherwise perform tasks that would be hindered by high-flows (Lancaster, 1993; Magoulick & Kobza, 2003; Liao, 2007).

There is now a demand for an increased effort focusing on ecohydraulic research at Foss WPS. Flow characteristics are expected to vary spatially and temporally and any solution targeting flow-refuge must then be developed in association with an understanding of site-specific flows, especially so where pump operation can be predicted seasonally. Firstly, the construction of a bathymetric profile of Foss basin is expected to reveal possible areas of low-flow refuge if they are associated with morphological features of the river bed/channel (Wedding *et al.,* 2008). In addition, computational fluid dynamics (CFD) can be used to determine the distribution of flow across intake areas (Turnpenny *et al.,* 1998), which provides a more realistic description of site-specific flows compared to older models (Keylock *et al.,* 2012).

Using CFD it would be possible to create a flow model for Foss basin that would identify areas of low-flow refuge (Lane *et al.,* 1998; Chang *et al.,* 2013). This can then be adjusted to reflect a multitude of different pumping scenarios i.e. one to eight pumps at varying capacities, which is anticipated to reveal opportunities for the provision of low-flow refuge areas. Thus, a combination of bathymetric profiling and CFD can be used to inform the construction of an appropriate low-flow refuge habitat in Foss basin. The more habitat provided in these key areas should provide protection from prolonged flow changes when Foss WPS is operational. Although, this does potentially concentrate fish populations, and then any installation must be done with consideration for predators which requires further study into the provision of low-flow habitats that prevent predator access.

8.6.3 Habitat offsetting

Because of the spatial presence of Foss WPS at the confluences between a main river channel and a tributary, one alternative approach to reducing fish entrainment at the site may be to prevent fish entering the site from the River

Ouse. The idea of creating habitat to compensate for habitat lost through river modification has seen some success through the implementation of like-for-like habitats such as the addition of in-channel habitat, riparian revegetation, and low-flow areas (Scruton *et al.,* 2005; Quigley & Harper, 2006). Biodiversity offsetting uses a similar approach, but with a goal of protecting areas where there is a predicted loss of biodiversity (Gibbons *et al.,* 2016). Offsetting habitat can be used to compensate for adverse impacts on rivers and aquatic life that remain following habitat modifications.

The success of such habitat compensations is inherently reliant on an understanding of how fish utilise habitats. More so, the volume of fish utilising new habitats is likely to increase rapidly where fish use social cues to advertise the availability of new habitats to conspecifics (Elvidge *et al.,* 2017). Thus, successful river rehabilitation projects must incorporate an understanding of how fish utilise habitats. Importantly, if fish imaged at Foss WPS are residents to the structure, then the formation of new habitat features in the River Ouse should function to deter fish movements from Foss WPS if they are provided with habitat features that offer increased refuge opportunities. Thus, the addition of habitat features that offer refuge opportunities in the River Ouse may be used to offset the attractiveness of Foss basin. At present there is no evidence base to suggest whether fish imaged at Foss WPS are living in Foss basin or are residents of the River Ouse and therefore further research needs to target an improved understanding of how and when fish are accessing Foss WPS

8.7 Conclusions and recommendations for future biological assessments of fish populations at WPS

This study has demonstrated the use of biological assessments at WPS to be a useful tool to identify suitable operational regimes to mitigate fish entrainment at WPS. By analysing the diel and seasonal patterns in fish activity at WPS, it is expected that **pump operators may be able to improve the timing of pump operations to best reflect fish-friendly pumping practices**. Following a five-month data collection period, large variation in diel and seasonal trends of fish activity have been identified at Foss WPS. The main advantage of such a large data set is avoiding pitfalls associated with snap-shot data collection. During November 2017, fish followed modulated activity patterns, where activity was highest at dawn and dusk, and during the day. Based on these results **it is**

recommended that pump operation is timed to best avoid day time pumping. At this WPS, the flood defence barrier can also be lowered in advance of pump operation to reduce the number of fish entering the structure. This period of operation would avoid peak periods of fish activity that occur during the day and instead focus pumping at night where fish activity is reduced. However, subsequent sampling showed that although there is a consistent decrease in fish activity during the night, these patterns can break down and the fish community may be unpredictable where modulated patterns operate stochastically. **It is therefore recommended that further investigation is undertaken, including a second and third year data sampling.** It is expected that this will reveal if these trends associated with fish activity operate on a population level or are the result of external factors (site operation, environmental).

The problem of fish activity at WPS is complicated as these structures may offer habitats that are attractive to fish and thus trends in diel activity around WPS may be associated with an increased efficiency in the use of key habitats i.e, refugia (flow, predation, temperature) (Kramer & Chapman, 1999). The majority of coarse fish have limited home ranges and it may be costly for fish to search for higher quality habitats if WPS facilitate regular trade-offs. Because the use of WPS by fish is inevitable, **it is recommended that the availability and quantity of key habitat features, such as backwaters and refuge habitats is assessed on the rivers WPS are located on in association with a biological fish community assessment.** This is expected to reveal whether fish have alternative habitat options if they are deterred from WPS.

The importance of eel escapement at WPS is stipulated in the Eels Regulations (2009), therefore many pump operators are now investigating remediation measures that best target free passage of European eels due to their status as a critically endangered fish. Screening all WPS is largely inappropriate from an economical and biological view without biological assessments to ascertain this necessity. In this study, an assessment of historical pumping revealed an operational regime that likely coincides with the migration movements of European eels. But, operational adjustments here are difficult due to a seasonally high operational regime. The identification of two eels at Foss WPS is enough to suggest that the WPS should incorporate eel protection.

Additionally, a delayed deployment of monitoring equipment may have missed a key migratory window and poor image sampling shows potential for eels to be under recorded. Therefore, it is probably safe to suggest that there is a greater number of European eels attempting passage of Foss WPS than those identified in the present study**, but this requires further investigation to determine suitable remediation options.**

This study has also identified thousands of coarse fish residing in the structures surrounding Foss WPS. Differences in fish behaviour, body size and activity period suggest that this is a large unpredictable multi-species community and therefore pump operators must also incorporate interactions with coarse fish in their management plans. Because the effectiveness of physical and behavioural barriers tends to show species-specific bias (Clark & Harvey, 2002), **remediation measures that target individual species are unlikely to be effective at reducing overall fish entrainment at WPS**. A switch to multi-species plans is expected to reduce negative impacts associated with prioritising species that share habitat with non-target species (Jewell, 2000), and **it is therefore recommended that any remedial measures incorporated into pumping operations are done so with multi-species considerations**.

Additionally, there is currently a lack of a sophisticated environmental analysis at Foss WPS, and with limited data, regression analysis of GDF and river level did not explain all of the variation in fish abundance, suggesting other environmental factors to be important. **It is recommended that biological assessments of fish behaviour around WPS are conducted simultaneously with environmental (i.e. GDF, river level, temperature) surveys over a daily sample period.** Because there is currently no model to validate entrainment during pump operation, it is unclear whether a reduction in fish activity was associated with pumping that had taken place between monthly sample periods. Based on these results, **further investigation is required to determine if pump operation reduces the number of fish imaged and more data of pumping operations is required.**

Although the use of behavioural stimuli as a fish deterrent is widely understood (i.e., Noatch & Suski, 2012), this study identified thousands of potadromous fish that only perform in river migrations, show activity during the day and night and throughout winter, and a poor regression analysis was in support of an unpredictable fish community. **It is recommended to let this community to continue to function naturally as it is currently unclear if engineered solutions would operate efficiently.** It is considered here that the provision of low-flow refuge is an important factor in determining fish survival at WPS and **it is therefore recommended that a combination of bathymetric profiling and CFD are performed around WPS to identify the availability and provision of low-flow refuge for fish.** These surveys would provide essential information for biologists and pump operators, and combined with an extended sample period would form the basis of a PhD research project that aims to identify natural habitat remediation solutions to entrainment at WPS.

There is a definite need to improve study methods used to asses WPS for European eel passage in order to ascertain their numbers and migratory status. **It is recommended that Environmental DNA (EDNA) is collected upstream and downstream of WPS to determine species presence.** Additionally, there is currently a lack of validation model for the body characteristics of imaged eels, and **in order to protect European eels it is necessary to support underwater sonar images with tracked fishing movements (using electronic tags).** Additionally, the use of a DIDSON underwater sonar provided a broad-scale interpretation into the diel and seasonal patterns in fish activity around a WPS. Images captured by the sonar contained detailed information on fish behaviour that would be otherwise unobtainable by traditional sampling techniques. The successful identification of modulated patterns in fish activity confirmed the techniques ability for biological fish assessments. **It is recommended that future biological assessments at WPS incorporate the use of non-invasive technologies such as underwater sonar.** However, the DIDSON is vulnerable to poor image quality **and this could be improved on by using an adaptive resolution imaging sonar (ARIS) which provides a higher-resolution image**

These results suggest that detecting the ecological impacts of manmade structures requires large-scale behavioural studies. Whilst such biological investigations are expensive, they offer a wealth of knowledge that should prove key to identifying the most appropriate remediation measures. It is perhaps ignorant to assume an approach taken in one location is applicable to a given structure, as both hydrological and biological function varies considerably between different aquatic environments (marine, estuarine and freshwater). It is therefore expected that the success of remediation is dependent on several factors in a best case scenario, namely; a behavioural assessment of fish surrounding the WPS, the identification of cost-beneficial remediation measures that best target species present (multi-species), and, operational changes that reflect best practice operation in relation to spatiotemporal patterns in fish presence. **For existing structures it is recommended that changes are made to the way pumping is operated, and for new structures this should be implemented through early consultation with regulatory bodies and fisheries scientists.**

9. REFERENCES

Acreman, M.C. & Ferguson, A.J.D. (2010) Environmental flows and the European water framework directive. *Freshwater Biology*, *55*(1), 32-48.

Acou, A., Lefebvre, F., Contournet, P., Poizat, G., Panfili, J. & Crivelli, A. J. (2003) Silvering of female eels (Anguilla anguilla) in two sub-populations of the Rhone Delta. *Bulletin Francais De La Peche Et De La Pisciculture*(368), 55-68.

Acou, A., Boury, P., Laffaille, P., Crivelli, A.J., Feunteun, E. (2005) Towards a standardized characterization of the potentially migrating silver European eel (Anguilla anguilla, L.). *Archiv für Hydrobiologie*, *164*(2), 237-255.

Acou, A., Laffaille, P., Legault, A., Feunteun, E. (2008). Migration pattern of silver eel (Anguilla anguilla, L.) in an obstructed river system. *Ecology of Freshwater Fish*, 17(3),.432-442.

Adams, N. S., & Schwevers, D.U. (1997). Behavioral surveys of eels (*Anguilla rostrata*) migrating downstream under laboratory conditions. Institute of Applied Ecology, Neustader Weg 25, 36320 Kirtorf-Wahlen, Germany.

Alerstam, T., Hedenstrom, A. & Akesson, S. (2003) Long-distance migration: evolution and determinants. *Oikos*, 103(2), 247-260.

Alexandre, C. M., Almeida, P. R., Neves, T., Mateus, C. S., Costa, J. L. & Quintella, B. R. (2016) Effects of flow regulation on the movement patterns and habitat use of a potamodromous cyprinid species. *Ecohydrology*, 9(2), 326-340.

Allen, A. P., Brown, J. H. & Gillooly, J. F. (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, 297(5586), 1545-1548.

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.

Amoros, C. & Bornette, G. (2002) Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology*, 47(4), 761-776.

Andersen, M., Jacobsen, L., Gronkjaer, P. & Skov, C. (2008) Turbidity increases behavioural diversity in northern pike, Esox lucius L., during early summer. *Fisheries Management and Ecology*, 15(5-6), 377-383.

Angling Trust (2011) Angling Trust Position Paper: Run of River Hydropower

Aoyama, J. (2009) Life History and Evolution of Migration in Catadromous Eels (GenusAnguilla). *Aqua-BioScience Monographs*, 2(1).

Arai, T. (2014) Do we protect freshwater eels or do we drive them to extinction? *Springerplus*, 3.

Archer, S., Hope, A. & Partridge, J. C. (1995) The molecular basis for the green-blue sensitivity shift in the rod visual pigments of the European eel. *Proceedings of the Royal Society B-Biological Sciences*, 262(1365), 289-295.

Armstrong, J. B., Schindler, D. E., Ruff, C. P., Brooks, G. T., Bentley, K. E. & Torgersen, C. E. (2013) Diel horizontal migration in streams: Juvenile fish exploit spatial heterogeneity in thermal and trophic resources. *Ecology*, 94(9), 2066-2075.

Astrom, M. & Dekker, W. (2007) When will the eel recover? A full life-cycle model. *Ices Journal of Marine Science*, 64(7), 1491-1498.

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

Basov, B. M. (2007) On electric fields of power lines and on their perception by freshwater fish. *Journal of Ichthyology,* 47, 656–661.

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.

Becker, J. M., Abernethy, C. S., Dauble D. D. (2003). Identifying the effects on fish of Changes in Water pressure during turbine passage. *Hydro Review*, 22 (5).

Beecher, H. A., Dott, E. R. & Fernau, R. F. (1988) Fish Species Richness And Stream Order In Washington State Streams. *Environmental Biology of Fishes*, 22(3), 193-209.

Bell, E., Duffy, W. G. & Roelofs, T. D. (2001) Fidelity and survival of juvenile coho salmon in response to a flood. *Transactions of the American Fisheries Society*, 130(3), 450-458.

Belpaire, C. G. J., Goemans, G., Geeraerts, C., Quataert, P., Parmentier, K., Hagel, P. & De Boer, J. (2009) Decreasing eel stocks: survival of the fattest? *Ecology of Freshwater Fish*, 18(2), 197-214.

Bergman, E. (1988). Foraging abilities and niche breadths of two percids, Perca fluviatilis and Gymnocephalus cernua, under different environmental conditions. *Journal of Animal Ecology,* 57 (2), 443-453.

Berland, G., Nickelsen, T., Heggenes, J., Okland, F., Thorstad, E. B. & Halleraker, J. (2004) Movements of wild Atlantic salmon parr in relation to peaking flows below a hydropower station. *River Research and Applications*, 20(8), 957-966.

Besson, M. L., Trancart, T., Acou, A., Charrier, F., Mazel, V., Legault, A. & Feunteun, E. (2016) Disrupted downstream migration behaviour of European silver eels (Anguilla anguilla, L.) in an obstructed river. *Environmental Biology of Fishes*, 99(10), 779-791.

Bilotta, G. S., Sibley, P., Hateley, J. & Don, A. (2011) The decline of the European eel Anguilla anguilla: quantifying and managing escapement to support conservation. *Journal of Fish Biology*, 78(1), 23-38.

Binder, T. R., O'Connor, C. M., McConnachie, S. H., Wilson, S. M., Nannini, M. A., Wahl, D. H. & Cooke, S. J. (2015) Is winter worse for stressed fish? The consequences of exogenous cortisol manipulation on over-winter survival and condition of juvenile largemouth bass. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology*, 187, 97-102.

Binner, M., Kloas, W. & Hardewig, I. (2008) Energy allocation in juvenile roach and burbot under different temperature and feeding regimes. *Fish Physiology and Biochemistry*, 34(2), 103-116.

Bischoff, A. & Scholten, M. (1996) Diurnal distribution patterns of 0+ barbel Barbus barbus in two different types of habitats in the River Sieg, Germany. *Folia Zoologica*, 45, 13-20.

Black, J. L. & Perry, E. S. (2014) Laboratory Evaluation of the Survival of Fish Impinged on Modified Traveling Water Screens. *North American Journal of Fisheries Management*, 34(2), 359-372.

Boetius J. (1976) Elvers, Anguilla anguilla and Anguilla rostrata from two Danish localities. Size, body weight, developmental stage and number of vertebrae releated to time of ascent. *Meddelelser Da. Fisk. Havunders*, 7, 199-220.

Boetius, J. (1967) Experimental indication of lunar activity in European silver eels, Anguilla anguilla (L.). *Meddelelser fra Danmarks Fiskeri-og Havundersogelser*, 6, 1–6.

Bolland, J. Cowx, I. G., Martyn, C. L. (2006) Factors affecting the dispersal of coarse fish. R & D Report, Environment Agency.

Bolland, J., Murphy, L., Stanford, R., Angelopoulos, N., Baker, N., Wright, R., Reeds, J. & Cowx, I. (2018) Direct and indirect impacts of pumping station operation on downstream migration of critically endangered European eel. *Fisheries Management and Ecology*, 26(1), 76-85.

Brabrand, A. & Faafeng, B. (1993) Habitat Shift In Roach (Rutilus-Rutilus) Induced By Pikeperch (Stizostedion-Lucioperca) Introduction - Predation Risk Versus Pelagic Behavior. *Oecologia*, 95(1), 38-46.

Bracken, F. S. A. & Lucas, M. C. (2013) Potential Impacts Of Small-Scale Hydroelectric Power Generation On Downstream Moving Lampreys. *River Research and Applications*, 29(9), 1073-1081.

Brackley, Robert (2016) Interactions between migrating salmonids and low-head hydropower schemes. PhD thesis.

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.

Bromage, N., Porter, M. & Randall, C. (2001) The environmental regulation of maturation in farmed finfish with special reference to the role of photoperiod and melatonin. *Aquaculture*, 197(1-4), 63-98.

Brown, J. S. (1992) Patch Use Under Predation Risk .1. Models And Predictions. *Annales Zoologici Fennici*, 29(4), 301-309.

Brown, R. S., Carlson, T. J., Welch, A. E., Stephenson, J. R., Abernethy, C. S., Ebberts, B. D., Langeslay, M. J., Ahmann, M. L., Feil, D. H., Skalski, J. R. & Townsend, R. L. (2009) Assessment of Barotrauma from Rapid Decompression of Depth-Acclimated Juvenile Chinook Salmon Bearing Radiotelemetry Transmitters. *Transactions of the American Fisheries Society*, 138(6), 1285-1301.

Brown, R. S., Colotelo, A. H., Pflugrath, B. D., Boys, C. A., Baumgartner, L. J., Deng, Z. D., Silva, L. G. M., Brauner, C. J., Mallen-Cooper, M., Phonekhampeng, O., Thorncraft, G. & Singhanouvong, D. (2014) Understanding Barotrauma in Fish Passing Hydro Structures: A Global Strategy for Sustainable Development of Water Resources. *Fisheries*, 39(3), 108-122.

Brusle, J. (1991) The Eel (Anguilla Sp) And Organic-Chemical Pollutants. *Science of the Total Environment*, 102, 1-19.

Bruijs, M. & Durif, C. (2009) Silver Eel Migration and Behaviour. In: Thillart, G., Dufour, S., Rankin, J. C. Spawning Migration of the European Eel. Reproduction index, a useful tool for conservation management.

Bryhn, A. C., Bergenius, M. A. J., Dimberg, P. H. & Adill, A. (2013) Biomass and number of fish impinged at a nuclear power plant by the Baltic Sea. *Environmental Monitoring and Assessment*, 185(12), 10073-10084.

Bunn, S. E. & Arthington, A. H. (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, 30(4), 492-507.

Bunt, C. M., Cooke, S. J., Katopodis, C. & McKinley, R. S. (1999) Movement and summer habitat of brown trout (Salmo trutta) below a pulsed discharge hydroelectric generating station. *Regulated Rivers-Research & Management*, 15(5), 395-403.

Burger, C. V., Zeligs, J. Z., Bock, G., Cooney, P. (2012) Non-Lethal Electric Guidance Barriers for Fish and Marine Mammal Deterrence: A Review for Hydropower and Other Applications

Burrows, R.E. (1957) Diversion of adult salmon by an electric field. U. S. Fish and Wildlife Service Special Scientific Report: Fisheries 246. US Fish and Wildlife Service, Washington, DC.

Butler, L. H. & Fairchild, G. W. (2005) Response of fish assemblages to winter in two adjacent warmwater streams. *American Midland Naturalist*, 154(1), 152-165.

Buysse, D., Mouton, A. M., Baeyens, R. & Coeck, J. (2015) Evaluation of downstream migration mitigation actions for eel at an Archimedes screw pump pumping station. *Fisheries Management and Ecology*, 22(4), 286-294.

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.

Cada, G. F. (2001) The development of advanced hydroelectric turbines to improve fish passage survival. *Fisheries*, 26(9), 14-23.

Cada, G. F., Garrison, L. A., Fisher, R. K. (2007) Determining the effect of shear stress on fish mortality during turbine passage. *Journal of Hydraulic Engineering*, 26(7), 52.

Cairns, D. K. & Hooley, P. J. D. (2003) Lunar cycles of American eepls in tidal waters of the southern Gulf of St. Lawrence, Canada, *American Fisheries Society Symposium*, 33, 265 – 274.

Calles, O., Olsson, I. C., Comoglio, C., Kemp, P. S., Blunden, L., Schmitz, M. & Greenberg, L. A. (2010) Size-dependent mortality of migratory silver eels at a hydropower plant, and implications for escapement to the sea. *Freshwater Biology*, 55(10), 2167-2180.

Calles, O., Karlsson, S., Hebrand, M. & Comoglio, C. (2012) Evaluating technical improvements for downstream migrating diadromous fish at a hydroelectric plant. *Ecological Engineering*, 48, 30-37.

Chang, W. Y., Constantinescu, G., Lien, H. C., Tsai, W. F., Lai, J. S. & Loh, C. H. (2013) Flow Structure around Bridge Piers of Varying Geometrical Complexity. *Journal of Hydraulic Engineering*, 139(8), 812-826.

Christensen, B. & Persson, L. (1993) Species-specific antipredatory behaviours: effects on prey choice in different habitats. *Behavioral Ecology and Sociobiology*, *32*(1), 1-9.

Ciccotti, E. (2005) Interactions between capture fisheries and aquaculture: the case of the eel (Anguilla anguilla L., 1758).

Clark, J. A. & Harvey, E. (2002) Assessing multi-species recovery plans under the endangered species act. *Ecological Applications*, 12(3), 655-662.

Clough, S. C., Turnpenny, A. W. H. (2000) Swimming Speeds in Fish: Phase 1. R & D Report, Environment Agency.

Clough, S.C., Lee-Elliott, I.E., Turnpenny, A.W.H., Holden, S.D.J., Hinks, C. (2004a) Swimming Speeds in Fish: Phase 2 Literature Review. R & D Report, Environment Agency.

Clough, S.C., Lee-Elliott, I.E., Turnpenny, A.W.H., Holden, S.D.J., Hinks, C. (2004b) Swimming Speeds in Fish: Phase 2. R & D Report, Environment Agency

Colotelo, A. H., Pflugrath, B. D., Brown, R. S., Brauner, C. J., Mueller, R. P., Carlson, T. J., Deng, Z. D., Ahmann, M. L. & Trumbo, B. A. (2012) The effect of rapid and sustained decompression on barotrauma in juvenile brook lamprey and Pacific lamprey: Implications for passage at hydroelectric facilities. *Fisheries Research*, 129, 17-20.

Copp, G. H. & Jurajda, P. (1999) Size-structured diel use of river banks by fish. *Aquatic Sciences*, 61(1), 75-91.

Copp, G. H., Spathari, S. & Turmel, M. (2005) Consistency of Diel behaviour and interactions of stream fishes and invertebrates during summer. *River Research and Applications*, 21(1), 75-90.

Copp, G.H. (2004) Behaviour of young and small fishes in the River Lee (Hertfordshire) over a twenty-four-hour cycle in midsummer. *The London Naturalist*, 83, 87–95.

Copp, G.H., Spathari, S., Turmel, M. (2005) Consistency of diel behaviour and interactions of stream fishes and invertebrates during summer. *River Research and Applications,* 21, 75–90.

Cooney, P. (2013) Anadromous, Catadromous, Amphidromous, Oceanodromous, or Potamodromous ; The Fisheries Blog. Available online: https://thefisheriesblog.com/2013/05/20/anadromous-catadromous-amphidromous-oceanodromous-or-potamodromous/ [Accessed 16/10/2019].

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.

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

Cowx I.G. (2000) Factors influencing coarse fish populations in lowland rivers. R&D Report, Environment Agency.

Cowx I.G. (2001) Factors influencing coarse fish populations in rivers. R&D Report, Environment Agency.

Cowx, I. G., Noble, R. A., Dunn., A. D. Harvey, J. P., Welcomme, R. L. Halls, A. S. (2004) Flow snf Level Criteria for Coarse Fish and Conservation Species. R & D Report, Environment Agency.

Cowx, I. G. & Aya, M. P. (2011) Paradigm shifts in fish conservation: moving to the ecosystem services concept. *Journal of Fish Biology*, 79(6), 1663-1680.

Cullen, P. & McCarthy, T. K. (2003) Hydrometric and meteorological factors affecting the seaward migration of silver eels (Anguilla anguilla, L.) in the lower River Shannon. *Environmental Biology of Fishes*, 67(4), 349-357.

Curry, R. A., Currie, S. L., Arndt, S. K. & Bielak, A. T. (2005) Winter survival of age-0 smallmouth bass, Micropterus dolomieu, in north eastern lakes. *Environmental Biology of Fishes*, 72(2), 111-122.

Cremona, F., Planas, D., Lucotte, M. (2008). Biomass and composition of macroinvertebrate communities associated with different types of macrophyte architectures and habitats in a large fluvial lake. *Fundamental and Applied Limnology / Archiv für Hydrobiologie*, 171(2),.119-130.

Cresci, A., Paris, C., Durif, C., Shema, S., Bjelland, R., Skiftesvik, A. & Browman, H. (2017) Glass eels (Anguilla anguilla) have a magnetic compass linked to the tidal cycle. *Science Advances*, 3(6).

Daverat, F. & Tomas, J. (2006) Tactics and demographic attributes in the European eel Anguilla anguilla in the Gironde watershed, SW France. *Marine Ecology Progress Series*, 307, 247-257.

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. J., Jackson, P. R., Engel, F. L., LeRoy, J. Z., Neeley, R. N., Finney, S. T. & Murphy, E. A. (2016) Entrainment, retention, and transport of freely swimming fish in junction gaps between commercial barges operating on the Illinois Waterway. *Journal of Great Lakes Research*, 42(4), 837-848.

Dawson, H. A., Reinhardt, U. G. & Savin, J. F. (2006) Use of electric or bubble barriers to limit the movement of Eurasian ruffe (Gymnocephalus cernuus). *Journal of Great Lakes Research*, 32(1), 40-49.

DEFRA (2010) Eel Management plans for the United Kingdom Overview for England and Wales.

Deelder CL (1954) Factors affecting the migration of the silver eel in Dutch inland waters. *Journal du Conseil Permanent International Pour l'Exploration de la Mer*, 20, 177–185

Deelder, C. (1970) Synopsis of biological data of the eel *Anguilla anguilla* (Linnaeus, 1758). *FAO Fish. Synop.*, 80: 68.

Deelder, C.L. (1984) Synopsis of biological data on the eel Anguilla anguilla (Linnaeus, 1758). Rome: FAO Fisheries Synopsis 80, FAO, 73.

Dekker W, Casselman JM, Cairns DK, Tsukamoto K, Jellyman D, Lickers H (2003) Québec Declaration of Concern: worldwide decline of eel resources necessitates immediate action. *Fisheries*, 28, 28–30.

Dekker, W. (2002) Monitoring of glass eel recruitment Volume 1: Thematic overview. Netherleands institute for fisheries research. 1 – 284.

Dekker, W. (2003a) On the distribution of the European eel (Anguilla anguilla) and its fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*, 60(7), 787-799.

Dekker, W. (2003b) Did lack of spawners cause the collapse of the European eel, Anguilla anguilla?. *Fisheries Management and Ecology*, 10(6), 365-376.

Deng, Z. Q., Carlson, T. J., Duncan, J. P., Richmond, M. C. & Dauble, D. D. (2010) Use of an autonomous sensor to evaluate the biological performance of the advanced turbine at Wanapum Dam. *Journal of Renewable and Sustainable Energy*, 2(5).

Deng, Z. Q., Carlson, T. J., Dauble, D. D. & Ploskey, G. R. (2011) Fish Passage Assessment of an Advanced Hydropower Turbine and Conventional Turbine Using Blade-Strike Modeling. *Energies*, 4(1), 57-67.

Deng, Z. Q., Guensch, G. R., McKinstry, C. A., Mueller, R. P., Dauble, D. D. & Richmond, M. C. (2005) Evaluation of fish-injury mechanisms during exposure to turbulent shear flow. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(7), 1513-1522.

Dinno, A. (2017) Dunn's Test of Miltiple Comparisions Using Rank Sums.

Dolan, C. R. & Miranda, L. E. (2003) Immobilization thresholds of electrofishing relative to fish size. *Transactions of the American Fisheries Society*, 132(5), 969-976.

Domenici, P., Steffensen, J. F. & Batty, R. S. (2000) The effect of progressive hypoxia on swimming activity and schooling in Atlantic herring. *Journal of Fish Biology*, 57(6), 1526-1538.

Dou, S. Z. & Tsukamoto, K. (2003) Observations on the nocturnal activity and feeding behavior of Anguilla japonica glass eels under laboratory conditions. *Environmental Biology of Fishes*, 67(4), 389-395.

Dufour, S., Burzawa-Gerard, E., Le Belle, N., Shaihi, M., Vidal, B. (2003) Reproductive endocrinology of the European eel. In: Aida, K., Tsukamoto, K., Yamauchi, K. (Eds.), *Eel Biology*. Springer-Verlag, Tokyo, 373–383.

Durif, C., Dufour, S. & Elie, P. (2005) The silvering process of Anguilla anguilla: a new classification from the yellow resident to the silver migrating stage. *Journal of Fish Biology*, 66(4), 1025-1043.

Durif, C., Guibert, A., Elie, P. (2009) Morphological discrimination of the silvering stages of the European eel, *American Fisheries Society Symposium*, 58, 103-111

Durif, C., Browman, H., Phillips, J., Skiftesvik, A., Vøllestad, L. Stockhausen, H. (2013) Magnetic Compass Orientation in the European Eel. *PLoS ONE*, 8(3), 59212.

Ehrler, C. P., Steinbeck, J. R., Laman, E. A., Hedgepeth, J. B., Skalski, J. R. & Mayer, D. L. (2003) *A process for evaluating adverse environmental impacts by cooling-water system entrainment at a California power plant*.

Elie P., Lecompte-Finiger R., Cantrelle I., Charlon N. (1982) Definition of the limits of the pigmented stages of the cielle Anguilla anguilla L., *Vie Milieu,* 32, 145-157.

Elvidge, C. K., Cooke, E. L. L., Cunjak, R. A. & Cooke, S. J. (2017) Social cues may advertise habitat quality to refuge-seeking conspecifics. *Canadian Journal of Zoology*, 95(1), 1-5.

Everard, M., (2015). *River habitats for coarse fish: how fish use rivers and how we can help them*. Old Pond Publishing.

Environment Agency (2010) Mapping Hydropower Opportunities and Sensitivities in England and Wales.

Environment Agency (2012) Good practice guidelines to the environment agency hydropower handbook: The environmental assessment of proposed low head hydropower developments.

Environment Agency (2013) Screening at intakes and outfalls: measures to protect eel, The Eel Manual.

Environment Agency (2016a) How we’re reducing the risk of flooding for York.

Environment Agency (2016b) Incidents and their classification: the Common Incident Classification Scheme (CICS)

Environment Agency (2020) *Environment Agency - Catchment Explorer.* Available online: https://environment.data.gov.uk/catchment-planning/OperationalCatchment/3280/Summary [Accessed 17/06/2020]

Esteve, C. & Alcaide, E. (2009) Influence of diseases on the wild eel stock: The case of Albufera Lake. *Aquaculture*, 289(1-2), 143-149.

Ferguson, J. W., Ploskey, G. R., Leonardsson, K., Zabel, R. W. & Lundqvist, H. (2008) Combining turbine blade-strike and life cycle models to assess mitigation strategies for fish passing dams. *Canadian Journal of Fisheries and Aquatic Sciences*, 65(8), 1568-1585.

Feunteun, E. (2002) Management and restoration of European eel population (Anguilla anguilla): An impossible bargain. *Ecological Engineering*, 18(5), 575-591.

Fillon, M. Jackson, P. Lindsay, J. (2014) WIP screens: a new technology for fish protection at water intakes. In: International Fish Screening Tecniques.

Fletcher, R. I. (1990) Hydraulic and Mechanical Considerations, an Addendum to a Review of Reported Fine Mesh Screen Applications for High Volume Water-Intake Systems and Recommendations for Further Investigations.

Fletcher, R. I. (1994) Comments of Fine-Mesh Investigations as Reported in the Draft Environmental Impact Station.

Fraser, N. H. C., Metcalfe, N. B. & Thorpe, J. E. (1993) Temperature-Dependent Switch Between Diurnal And Nocturnal Foraging In Salmon. *Proceedings of the Royal Society B-Biological Sciences*, 252(1334), 135-139.

Fraser, D. F., Gilliam, J. F. & Yiphoi, T. (1995) Predation As An Agent Of Population Fragmentation Ln A Tropical Watershed. *Ecology*, 76(5), 1461-1472.

Fraser, N. H. C., Heggenes, J., Metcalfe, N. B. & Thorpe, J. E. (1995) Low Summer Temperatures Cause Juvenile Atlantic Salmon To Become Nocturnal. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 73(3), 446-451.

Fraser, D. F., Gilliam, J. F., MacGowan, M. P., Arcaro, C. M. & Guillozet, P. H. (1999) Habitat quality in a hostile river corridor. *Ecology*, 80(2), 597-607.

Freeman, M. C. & Grossman, G. D. (1993) Effects Of Habitat Availability On Dispersion Of A Stream Cyprinid. *Environmental Biology of Fishes*, 37(2), 121-130.

Fry, F. E. J. (1971) The effect of environmental factors on the physiology of fish. 1–98 in: W. S. Hoar and D. J. Randall, (eds) *Fish Physiology*, Volume VI. Academic Press Inc., New York, USA.

Fu, T., Deng, Z. D., Duncan, J. P., Zhou, D. Q., Carlson, T. J., Johnson, G. E. & Hou, H. F. (2016) Assessing hydraulic conditions through Francis turbines using an autonomous sensor device. *Renewable Energy*, 99, 1244-1252.

Fukuda, N., Miller, M. J., Aoyama, J., Shinoda, A. & Tsukamoto, K. (2013) Evaluation of the pigmentation stages and body proportions from the glass eel to yellow eel in Anguilla japonica. *Fisheries Science*, 79(3), 425-438.

Gardner, C. J., Deeming, D. C. & Eady, P. E. (2015) Seasonal Water Level Manipulation For Flood Risk Management Influences Home-Range Size Of Common Bream Abramis Brama L. In A Lowland River. *River Research and Applications*, 31(2), 165-172.

Geeraerts, C. & Belpaire, C. (2010) The effects of contaminants in European eel: a review. *Ecotoxicology*, 19(2), 239-266.

Gibbons, J. W. & Andrews, K. M. (2004) PIT tagging: Simple technology at its best. *Bioscience*, 54(5), 447-454.

Gibbons, P., Evans, M. C., Maron, M., Gordon, A., Le Roux, D., von Hase, A., Lindenmayer, D. B. & Possingham, H. P. (2016) A Loss-Gain Calculator for Biodiversity Offsets and the Circumstances in Which No Net Loss Is Feasible. *Conservation Letters*, 9(4), 252-259.

Gillette, D. P., Tiemann, J. S., Edds, D. R. & Wildhaber, M. L. (2006) Habitat use by a Midwestern USA riverine fish assemblage: effects of season, water temperature and river discharge. *Journal of Fish Biology*, 68(5), 1494-1512.

Gilliam, J. F. & Fraser, D. F. (1987) Habitat Selection Under Predation Hazard - Test Of A Model With Foraging Minnows. *Ecology*, 68(6), 1856-1862.

Gilliam, J. F. & Fraser, D. F. (2001) Movement in corridors: Enhancement by predation threat, disturbance, and habitat structure. *Ecology*, 82(1), 258-273.

Gilligan, D. & Schiller, C. (2004) Downstream transport of the eggs, larvae and juvenile fish in the Murray river: Impacts of river regulation on downstream dispersal. *Proceedings of the MDBC Workshop on Downstream Fish Migration*, 41-50.

Greenwood, M. F. D. (2008) Fish mortality by impingement on the cooling-water intake screens of Britain's largest direct-cooled power station. *Marine Pollution Bulletin*, 56(4), 723-739.

Grenouillet, G. & Pont, D. (2001) Juvenile fishes in macrophyte beds: influence of food resources, habitat structure and body size. *Journal of Fish Biology*, 59(4), 939-959.

Grenouillet, G., Pont, D. & Olivier, J. M. (2000) Habitat occupancy patterns of juvenile fishes in a large lowland river: interactions with macrophytes. *Archiv Fur Hydrobiologie*, 149(2), 307-326.

Grift, R. E., Buijse, A. D., Breteler, J., Van Densen, W. L. T., Machiels, M. A. M. & Backx, J. (2001) Migration of bream between the main channel and floodplain lakes along the lower River Rhine during the connection phase. *Journal of Fish Biology*, 59(4), 1033-1055.

Guderley, H. (2004) Metabolic responses to low temperature in fish muscle. *Biological Reviews*, 79(2), 409-427.

Guinan, M. E., Kapuscinski, K. L. & Teece, M. A. (2015) Seasonal diet shifts and trophic position of an invasive cyprinid, the rudd Scardinius erythrophthalmus (Linnaeus, 1758), in the upper Niagara River. *Aquatic Invasions*, 10(2), 217-225.

Hadderingh, R. H. (1982) Experimental Reduction Of Fish Impingement By Artificial Illumination At Bergum-Power-Station. *Internationale Revue Der Gesamten Hydrobiologie*, 67(6), 887-900.

Hadderingh, R.H. & Smythe, A.G. (1997). Deflecting eels from power stations with light. Electric Power Research Institute, Palo Alto, USA

Haro., A. (2003) Downstream Migration of Silver-Phase Anguillid Eels, In: Eel Biology.

Halls, A.S. & M. Kshatriya (2009) Modelling the cumulative barrier and passage effects of mainstream hydropower dams on migratory fish populations in the Lower Mekong Basin MRC, Mekong River Commission, Vientiane. 104.

Hamel, M. J., Brown, M. L. & Chipps, S. R. (2008) Behavioral responses of rainbow smelt to in situ strobe lights. *North American Journal of Fisheries Management*, 28(2), 394-401.

Han, Y. S., Liao, I. C., Huang, Y. S., He, J. T., Chang, C. W. & Tzeng, W. N. (2003) Synchronous changes of morphology and gonadal development of silvering Japanese eel Anguilla japonica. *Aquaculture*, 219(1-4), 783-796.

Hansen L.P., Jonsson N., Jonsson B. (1995) Factors affecting upstream and downstream migration in anadromous European salmonids and catadromous eel. International Council for the Exploration of the Sea, Aalborg, Denmark, 29 September.

Hansen, E. A. & Closs, G. P. (2005) Diel activity and home range size in relation to food supply in a drift-feeding stream fish. *Behavioral Ecology*, 16(3), 640-648.

Haraldstad, O., Vollestad, L. A. & Jonsson, B. (1985) Descent Of European Silver Eels, Anguilla-Anguilla L In A Norwegian Watercourse. *Journal of Fish Biology*, 26(1), 37-41.

Hasler, C., Suski, C., Hanson, K., Cooke, S., Tufts, B. (2009). The Influence of Dissolved Oxygen on Winter Habitat Selection by Largemouth Bass: An Integration of Field Biotelemetry Studies and Laboratory Experiments. *Physiological and Biochemical Zoology*, 82(2), 143-152.

Hecker, G. E. & Cook, T. C. (2005) Development and evaluation of a new helical fish-friendly hydroturbine. *Journal of Hydraulic Engineering-Asce*, 131(10), 835-844.

Heggenes, J. (1988) Effects Of Short-Term Flow Fluctuations On Displacement Of, And Habitat Use By, Brown Trout In A Small Stream. *Transactions of the American Fisheries Society*, 117(4), 336-344.

Heiler, G., Hein, T., Schiemer, F. & Bornette, G. (1995) Hydrological connectivity and flood pulses as the central aspects for the integrity of a river-floodplain system. *Regulated Rivers-Research & Management*, 11(3-4), 351-361.

Heinrich, J., Mullett, K., Hansen, M., Adams, J., Klar, G., Johnson, D., Christie, G. Young, R. (2003). Sea Lamprey Abundance and Management in Lake Superior, 1957 to 1999. *Journal of Great Lakes Research*, 29, 566-583.

Helfman, G. S., Facey, D. E. Hales, S., Bozeman, E. L. (1987) Reproductive ecology of the American eel, American Fisheries Society Symposium Series, 1, 42-56.

Henderson, P. A., Turnpenny, A. W. H. & Bamber, R. N. (1984) Long-Term Stability Of A Sand Smelt (Atherina-Presbyter Cuvier) Population Subject To Power-Station Cropping. *Journal of Applied Ecology*, 21(1), 1-10.

Henry, T.B., Grizzle, J.M., Johnston, C.E., Osborne, J.A. (2004) Susceptibility of ten fish species to electroshock-induced mortality. *Transactions of the American Fisheries Society*, *133*(3), 649-654.

Hill, J. & Grossman, G.D. (1987). Home range estimates for three North American stream fishes. Copeia 1987, 376–380.

Hill, T.D. & Willis, D.W. (1994) Influence of water conductivity on pulsed AC and pulsed DC elecrofishing catch rates for largemouth bass. *North American Journal of Fisheries Management*. 14(1), 202‑207.

Hocutt, C.H. (1980) Behavioral barriers and guidance systems, In: C.H. Hocutt, J.R. Stauffer Jr., J.E. Edinger, L.W. Hall Jr., R.P. Morgan II (Eds.), Power Plants: Effects on Fish and Shellfish Behavior, Academic Press, New York (1980), pp. 183-205

Hohausova, E. (2000) Exchange rate and small-scale movements of fish between a river and its backwater. *Archiv Fur Hydrobiologie*, 147(4), 485-504.

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.

Holmlund, C. M. & Hammer, M. (1999) Ecosystem services generated by fish populations. *Ecological Economics*, 29(2), 253-268.

Horky, P., Slavik, O. & Bartos, L. (2008) A telemetry study on the diurnal distribution and activity of adult pikeperch, Sander lucioperca (L.), in a riverine environment. *Hydrobiologia*, 614(1), 151-157.

Hu, W. Y., Jones, P. D., DeCoen, W., King, L., Fraker, P., Newsted, J. & Giesy, J. P. (2003) Alterations in cell membrane properties caused by perfluorinated compounds. *Comparative Biochemistry and Physiology C-Toxicology & Pharmacology*, 135(1), 77-88.

Huber, M. & Kirchhofer, A. (1997) Habitat use of radiotagged adult nase (Chondrostoma nasus) in a regulated river. *Folia Zoologica*, 46, 67-77.

Huertas, M., Canario, A. V. M. & Hubbard, P. C. (2008) Chemical communication in the Genus Anguilla: a minireview. *Behaviour*, 145, 1389-1407.

Huet M. (1959) Profiles and biology of Western European streams as related to fish management, *Transactions of the American Fisheries Society,* 88, 155 163.

Humphries, P., Serafini, L. G. & King, A. J. (2002) River regulation and fish larvae: variation through space and time. *Freshwater Biology*, 47(7), 1307-1331.

Hurst, T. P. (2007) Causes and consequences of winter mortality in fishes. *Journal of Fish Biology*, 71(2), 315-345.

Huss, M., Bystrom, P., Strand, A., Eriksson, L. O. & Persson, L. (2008) Influence of growth history on the accumulation of energy reserves and winter mortality in young fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 65(10), 2149-2156.

International Council for the Exploration of the Sea (ICES) (2006) Report of the 18th session of the Joint EIFAC/ICES Working Group on Eels (WGEEL), Rome (Italy), 23–27 January 2006. ICES CM 2006/ACFM:16; EIFAC Occasional Paper No. 38. ICES Advisory Committee on Fisheries Management, Rome, Italy, 122.

International Council for the Exploration of the Sea (ICES) (2016). European eel (Anguilla anguilla) throughout its natural range. ICES Advice on fishing opportunities, catch, and effort. Northeast Atlantic. ICES Advice Book 9, 1-6.

Jansen, H.M., Winter, H.V., Bruijs, M.C., Polman, H.J. (2007) Just go with the flow? Route selection and mortality during downstream migration of silver eels in relation to river discharge. *ICES Journal of marine Science*, *64*(7), 1437-1443.

Jackson, D. (2014) Implications of the Eel Regulations on the design of a pumping plant. WIT Transactions on State of the Art in Science and Engineering, 71.

Jacobsen, L. & Berg, S. (1998) Diel variation in habitat use by planktivores in field enclosure experiments: the effect of submerged macrophytes and predation. *Journal of Fish Biology*, 53(6), 1207-1219.

Jacoby, D. & Gollock, M. (2014) *Anguilla anguilla*. *The IUCN Red List of Threatened Species* 2014

Jensen, A. J. & Johnsen, B. O. (1999) The functional relationship between peak spring floods and survival and growth of juvenile Atlantic Salmon (Salmo salar) and Brown Trout (Salmo trutta). *Functional Ecology*, 13(6), 778-785.

Jessop, B. M., Shiao, J. C., Iizuka, Y. & Tzeng, W. N. (2004) Variation in the annual growth, by sex and migration history, of silver American eels Anguilla rostrata. *Marine Ecology Progress Series*, 272, 231-244.

Jewell, S.D. (2000) Multi-species recovery plans. *Endangered Species*, *25*(3), 31.

Johnson, P. N., Goetz, F. A. & Ploskey, G. R. (2001) Evaluation of strobe lights for vertically displacing juvenile salmon near a filling culvert intake at the Hiram M. Chittenden Locks, Seattle, Washington, in Coutant, C. C. (ed), *Behavioral Technologies for Fish Guidance*. American Fisheries Society Symposium, 13-

25.

Johnson, R.L., McKinstry, C.A., Cook, C.B., Tano, D.K., Faber, D. M., Francis, S., Simmons, M.A., Simmons, C.S., Brown, R.S., Thorsten, S.L., LeClaire, R. (2005) Strobe light deterrent efficacy test and fish behavior determination at Grand Coulee Dam third powerplant forebay. Pacific Northwest National Laboratory.

Johnson, N. S., Thompson, H. T., Holbrook, C. & Tix, J. A. (2014) Blocking and guiding adult sea lamprey with pulsed direct current from vertical electrodes. *Fisheries Research*, 150, 38-48.

Johnston, I. A., Fleming, J. D. & Crockford, T. (1990) Thermal-Acclimation And Muscle Contractile Properties In Cyprinid Fish. *American Journal of Physiology*, 259(2), R231-R236.

Jones, V. (2009) On the sex and distribution of the freshwater eel (Anguilla anguilla). *Journal of Zoology*, 150(3), 371-385.

Jonsson, B. & Jonsson, N. (1993) Partial Migration - Niche Shift Versus Sexual-Maturation In Fishes. *Reviews in Fish Biology and Fisheries*, 3(4), 348-365.

Jonsson, N. (1991) Influence of water flow, water temperature and light on fish migration in rivers. *Nordic journal of freshwater research*, 66(1991), 20-35.

Junk WJ, Bayley PB, Sparks, R. E. (1989) The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic* Sciences, 106, 110–127.

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

Katopodis, C., E. M. Koon, L. Hanson. (1994) Sea Lamprey Barriers: New Concepts and Research Needs. Ann Arbor, MI.

Kemp, P. S., Gessel, M. H. & Williams, J. G. (2005) Fine-scale behavioral responses of Pacific salmonid smolts as they encounter divergence and acceleration of flow. *Transactions of the American Fisheries Society*, 134(2), 390-398.

Kendall, J. (2016) Foss Barrier Recovery Project: Eel Regulations Compliance Document

Kennish, M. J. (1992) *Ecology of Estuaries: Anthropogenic Effects*. Boca Raton, FL: CRC Press.

Kettle, A. J., Bakker, D. C. E. & Haines, K. (2008) Impact of the North Atlantic Oscillation on the trans-Atlantic migrations of the European eel (Anguilla anguilla). *Journal of Geophysical Research-Biogeosciences*, 113(G3).

Kettle, A. J., Vollestad, L. A. & Wibig, J. (2011) Where once the eel and the elephant were together: decline of the European eel because of changing hydrology in southwest Europe and northwest Africa? *Fish and Fisheries*, 12(4), 380-411.

Keylock, C. J., Constantinescu, G. & Hardy, R. J. (2012) The application of computational fluid dynamics to natural river channels: Eddy resolving versus mean flow approaches. *Geomorphology*, 179, 1-20

Kimura, S. & Tsukamoto, K. (2006) The salinity front in the North Equatorial Current: A landmark for the spawning migration of the Japanese eel (Anguilla japonica) related to the stock recruitment. *Deep-Sea Research Part Ii-Topical Studies in Oceanography*, 53(3-4), 315-325.

Kim, J. & Mandrak, N.E., (2017) Effects of vertical electric barrier on the behaviour of common carp. *Management*, *8*(4), 497-505.

Kirk, R. S. (2003) The impact of Anguillicola crassus on European eels. *Fisheries Management and Ecology*, 10(6), 385-394.

Klinect, D. A., Loeffelman, P. H., Vanhassel, J. H. & Amer Power, C. (1992) *A New Signal Development Process And Sound-System For Diverting Fish From Water Intakes*, *54*.

Knight, C. M., Kenward, R. E., Gozlan, R. E., Hodder, K. H., Walls, S. S. & Lucas, M. C. (2009) Home-range estimation within complex restricted environments: importance of method selection in detecting seasonal change. *Wildlife Research*, 36(3), 213-224.

Knudsen, F. R., Enger, P. S. & Sand, O. (1994) Avoidance Responses To Low-

Frequency Sound In Downstream Migrating Atlantic Salmon Smolt, Salmo-Salar. *Journal of Fish Biology*, 45(2), 227-233.

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.

Kock, T. J., Evans, S. D., Liedtke, T. L., Rondorf, D. W. & Kohn, M. (2009) Evaluation of Strobe Lights to Reduce Turbine Entrainment of Juvenile Steelhead (Oncorhynchus mykiss) at Cowlitz Falls Dam, Washington. *Northwest Science*, 83(4), 308-314.

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

Kultz, D. (2012) The Combinatorial Nature of Osmosensing in Fishes. *Physiology*, 27(4), 259-275.

Kramer, D.L. & Chapman, M.R., (1999) Implications of fish home range size and relocation for marine reserve function. *Environmental biology of Fishes*, *55*(1-2), 65-79.

Kynard, B. & Buerkett, C. (1997). Passage and Behavior of Adult American Shad in an Experimental Louver Bypass System. *North American Journal of Fisheries Management*, 17(3), 734-742.

Lake, P. S. (2003) Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology*, 48(7), 1161-1172.

Lancaster, J. & Hildrew, A. G. (1993) Characterizing In-Stream Flow Refugia. *Canadian Journal of Fisheries and Aquatic Sciences*, 50(8), 1663-1675.

Lane, S. N., Bradbrook, K. F., Richards, K. S., Biron, P. A. & Roy, A. G. (1999) The application of computational fluid dynamics to natural river channels: three-dimensional versus two-dimensional approaches. *Geomorphology*, 29(1-2), 1-20.

Langford, T. E. (1983). *Electricity Generation and the Ecology of Natural Waters*. Liverpool: Liverpool University Press.

Larsson, P., Hamrin, S. & Okla, L. (1990) Fat-Content As A Factor Inducing Migratory Behavior In The Eel (Anguilla-Anguilla L) To The Sargasso Sea. *Naturwissenschaften*, 77(10), 488-490.

Lapointe, N.W., Cooke, S.J., Imhof, J.G., Boisclair, D., Casselman, J.M., Curry, R.A., Langer, O.E., McLaughlin, R.L., Minns, C.K., Post, J.R. and Power, M. (2013) Principles for ensuring healthy and productive freshwater ecosystems that support sustainable fisheries. *Environmental Reviews*, *22*(2), 110-134.

Le Morvan, C., Troutaud, D. & Deschaux, P. (1998) Differential effects of temperature on specific and nonspecific immune defences in fish. *Journal of Experimental Biology*, 201(2), 165-168.

Le Pichon, C., Tales, E., Gorges, G., Baudry, J. & Boet, P. (2016) Using a continuous riverscape survey to examine the effects of the spatial structure of functional habitats on fish distribution. *Journal of Freshwater Ecology*, 31(1), 1-19.

Lee, T. (1982) Ageing and growth of eel population, Anguilla anguilla, in the lagoons of Arcachon Bay (France), *The Oceanographic Society of Japan*, 17, 83-94.

Li, L. & Maaswinkel, H. (2007) Visual sensitivity and signal processing in teleosts. In Hara, T.J., and Zielinski, B.S. Elsevier (eds). *Sensory systems neuroscience*. Amsterdam. 180‑227.

Liao, J. C. (2007) A review of fish swimming mechanics and behaviour in altered flows. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 362(1487), 1973-1993.

Liermann, C. R., Nilsson, C., Robertson, J. & Ng, R. Y. (2012) Implications of Dam Obstruction for Global Freshwater Fish Diversity. *Bioscience*, 62(6), 539-548.

Lindstrom, A. (1990) The role of predation risk in stopover habitat selection in migrating bramblings, Fringilla montifringilla. *Behavioral Ecology*, 1(2), 102-106.

Lojkasek, B., Lusk, S., Halacka, K., Luskova, W. & Drozd, P. (2005) The impact of the extreme floods in July 1997 on the ichthyocenosis of the Oder Catchment area

(Czech Republic). *Hydrobiologia*, 548, 11-22.

Lopez-Olmeda, J. F., Bayarri, M. J., de Lama, M. A. R., Madrid, J. A. & Sanchez-Vazquez, F. J. (2006) Effects of melatonin administration on oxidative stress and daily locomotor activity patterns in goldfish. *Journal of Physiology and Biochemistry*, 62(1), 17-25.

Lowe, R.H. (1952) The influence of light and other factors on the seaward migration of the silver eel (Anguilla anguilla L.). *Journal of Animal Ecology,* 21, 275–309

Lucas, M. C. & Batley, E. (1996) Seasonal movements and behaviour of adult barbel Barbus barbus, a riverine cyprinid fish: Implications for river management. *Journal of Applied Ecology*, 33(6), 1345-1358.

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

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*, 223-232.

Lucas, M. & Baras, E., (2008) *Migration of freshwater fishes*. John Wiley & Sons.

Lundvall, D., Svanbäck, R., Persson, L. Byström, P. (1999) Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. *Canadian Journal of Fisheries and Aquatic Sciences*, *56*(7), 1285-1292.

Lundquist, C. J., Diehl, J. M., Harvey, E. & Botsford, L. W. (2002) Factors affecting implementation of recovery plans. *Ecological Applications*, 12(3), 713-718.

Lusk, S., Halacka, K. & Luskova, V. (2003) Rehabilitating the floodplain of the lower River Dyje for fish. *River Research and Applications*, 19(3), 281-288.

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.

Maes, J., Turnpenny, A. W. H., Lambert, D. R., Nedwell, J. R., Parmentier, A. & Ollevier, F. (2004) Field evaluation of a sound system to reduce estuarine fish intake rates at a power plant cooling water inlet. *Journal of Fish Biology*, 64(4), 938-946.

Magnuson, J. J. (1986) Exploitation Of Marine Communities - May,Rm. *Science*, 232(4756), 1447-1447.

Magnuson, J. J., Crowder, L. B. & Medvick, P. A. (1979) Temperature As An Ecological Resource. *American Zoologist*, 19(1), 331-343.

Magoulick, D. D. & Kobza, R. M. (2003) The role of refugia for fishes during drought: a review and synthesis. *Freshwater Biology*, 48(7), 1186-1198.

Marmulla, G. (2001) Dams, fish and fisheries: opportunities challenges and conflict resolution. FAO.

Marsh-Matthews, E. & Matthews, W. J. (2000) Geographic, terrestrial and aquatic factors: which most influence the structure of stream fish assemblages in the midwestern United States? *Ecology of Freshwater Fish*, 9(1-2), 9-21.

Martins, E. G., Gutowsky, L. F. G., Harrison, P. M., Patterson, D. A., Power, M., Zhu, D. Z., Leake, A. & Cooke, S. J. (2013) Forebay use and entrainment rates of resident adult fish in a large hydropower reservoir. *Aquatic Biology*, 19(3), 253-263.

Martins, E., Gutowsky, L., Harrison, P., Flemming, J., Jonsen, I., Zhu, D., Leake, A., Patterson, D., Power, M. & Cooke, S. (2014) Behavioral attributes of turbine entrainment risk for adult resident fish revealed by acoustic telemetry and state-space modeling. *Animal Biotelemetry*, 2(1), 13.

Matheney, M. P. & Rabeni, C. F. (1995) Patterns Of Movement And Habitat Use By Northern Hog Suckers In An Ozark Stream. *Transactions of the American Fisheries Society*, 124(6), 886-897.

Mathur, D., Heisey, P. G., Skalski, J. R. & Kenney, D. R. (2000) Salmonid smolt survival relative to turbine efficiency and entrainment depth in hydroelectric power generation. *Journal of the American Water Resources Association*, 36(4), 737-747.

McAllister, D. E., Platania, F. W., Schueler, M. E., Baldwin, D. S. (1986) Ichthyofaunal patterns on a geographic grid. 17–51 in: C. H. Hocutt & E. O. Wiley, (eds) *The Zoogeography of North American Freshwater Fishes.* Wiley Interscience, New York.

McIninch, S. P. & Hocutt, C. H. (1987) Effects Of Turbidity On Estuarine Fish Response To Strobe Lights. *Journal of Applied Ichthyology-Zeitschrift Fur Angewandte Ichthyologie*, 3(3), 97-105.

McMahon, T. E. & Hartman, G. F. (1989) Influence Of Cover Complexity And Current Velocity On Winter Habitat Use By Juvenile Coho Salmon (Oncorhynchus-Kisutch). *Canadian Journal of Fisheries and Aquatic Sciences*, 46(9), 1551-1557.

Metcalfe, N.B., Fraser, N.H. and 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.

Miller, M. J. & Tsukamoto, K. (2004) An introduction to leptocephali: Biology and identification. *Ocean research Institute, Tokyo*

Miller, M.J., Kimura, S., Friedland, K.D., Knights, B., Kim, H., Jellyman, D.J., Tsukamoto, K. (2009) Review of ocean-atmospheric factors in the Atlantic and Pacific oceans influencing spawning and recruitment of anguillid eels. In Challenges for Diadromous Fishes in a Dynamic Global Environment. *American Fisheries Society Symposium*, 69, 231-249.

Miller, M. and Tsukamoto, K. (2017) The ecology of oceanic dispersal and survival of anguillid leptocephali*. Canadian Journal of Fisheries and Aquatic Sciences*, 74(6), 958-971..

Mills, C. A. & Mann, R. H. K. (1985) Environmentally-Induced Fluctuations In Year-Class Strength And Their Implications For Management. *Journal of Fish Biology*, 27, 209-226.

Miyai, T., Aoyama, J., Sasai, S., Inoue, J. G., Miller, M. J. & Tsukamoto, K. (2004) Ecological aspects of the downstream migration of introduced European eels in the Uono River, Japan. *Environmental Biology of Fishes*, 71(1), 105-114.

Moriarty, C. (2003) The yellow eel. In: Aida, K., Tsukamoto, K., Yamauchi K. *Eel Biology*. Springer: Tokyo.

Moriarty, C. and Dekker, W. (1997). Management of the European Eel. Marine Institute.

Moyle, P. B. & Israel, J. A. (2005) Untested assumptions: effectiveness of screening diversions for conservation of fish populations. *Fisheries*, 30(5), 20-+.

Mrosovsky, N. (1999) Masking, history, definitions, and measurements. *Chronobiology International.* 16, 415–429.

Murchy, K., Cupp, A., Amberg, J., Vetter, B., Fredricks, K., Gaikowski, M. and Mensinger, A. (2017). Potential implications of acoustic stimuli as a non-physical barrier to silver carp and bighead carp. *Fisheries Management and Ecology*, 24(3), pp.208-216.

Munn, M. D.& M. A. Brusven. (1991) Benthic invertebrate communities in nonregulated and regulated waters of the Clearwater River, Idaho, USA. *Regulated Rivers: Research and Management* 6, 1–11.

Neitzel, D. A., Dauble, D. D., Cada, G. F., Richmond, M. C., Guensch, G. R., Mueller, R. R., Abernethy, C. S. & Amidan, B. (2004) Survival estimates for juvenile fish subjected to a laboratory-generated shear environment. *Transactions of the American Fisheries Society*, 133(2), 447-454.

Newbold, S. C. & Iovanna, R. (2007) Population level impacts of cooling water withdrawals on harvested fish stocks. *Environmental Science & Technology*, 41(7), 2108-2114.

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.

Nishi, T., Kawamura, G. & Matsumoto, K. (2004) Magnetic sense in the Japanese eel, Anguilla japonica, as determined by conditioning and electrocardiography. *Journal of Experimental Biology*, 207(17), 2965-2970.

Northcote, T. G. (1998) *Migratory behaviour of fish and its significance to movement through riverine fish passage facilities*.

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

Nunn, A. D., Cowx, I. G., Frear, P. A. & Harvey, J. P. (2003) Is water temperature an adequate predictor of recruitment success in cyprinid fish populations in lowland rivers? *Freshwater Biology*, 48(4), 579-588.

Nunn, A., Copp, G., Vilizzi, L., Carter, M. (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.

Odeh, M. (1999). A Summary of Environmentally Friendly Turbine Design Concepts. United States department of Energy, Report DOE/ID 13741

Okamura, A. K., Yamada, Y., Tanaka, S., Horie, N., Utoh, T., Mikawa, N., Akazawa, A. & Oka, H. P. (2002) Atmospheric depression as the final trigger for the seaward migration of the Japanese eel Anguilla japonica. *Marine Ecology Progress Series*, 234, 281-288.

Okun, N., Mendonca, R. & Mehner, T. (2005) Diel shifts in community composition and feeding of juvenile fishes in the pelagic area of a large shallow lake. *Limnologica*, 35(1-2), 70-77.

Oliveira, K. & McCleave, J. D. (2002) Sexually different growth histories of the American eel in four rivers in Maine. *Transactions of the American Fisheries Society*, 131(2), 203-211.

Otake T (2003) Metamorphosis. In: Aida K, Tsukamoto K, Yamauchi K (eds) Eel biology. Springer, Tokyo, 61–74.

Pacariz, S., Westerberg, H. & Bjork, G. (2014) Climate change and passive transport of European eel larvae. *Ecology of Freshwater Fish*, 23(1), 86-94.

Pankhurst, N. W. & Lythgoe, J. N. (1983) Changes In Vision And Olfaction During Sexual-Maturation In The European Eel Anguilla-Anguilla (L). *Journal of Fish Biology*, 23(2), 229-240.

Pankhurst, N. W. (1982) Changes In Body Musculature With Sexual-Maturation In The European Eel, Anguilla-Anguilla (L). *Journal of Fish Biology*, 21(4), 417-428.

Papi, F. (2006) Navigation of marine, freshwater and coastal animals: concepts and current problems. *Marine and Freshwater Behaviour and Physiology*, 39(1), 3-12.

Parker, A. D., Glover, D. C., Finney, S. T., Rogers, P. B., Stewart, J. G. & Simmonds, R. L. (2015) Direct observations of fish incapacitation rates at a large electrical fish barrier in the Chicago Sanitary and Ship Canal. *Journal of Great Lakes Research*, 41(2), 396-404.

Parmeggiani, A., Govoni, N., Zannoni, A., Di Biase, A., Sirri, R., Forni, M., Mandelli, M. & Mordenti, O. (2015) Effect of photoperiod on endocrine profiles and vitellogenin expression in European eels Anguilla anguilla during artificially induced ovarian development. *Theriogenology*, 83(4), 478-484.

Patrick, P. H., Christie, A. E., Sager, D., Hocutt, C. & Stauffer, J. (1985) Responses Of Fish To A Strobe Light Air-Bubble Barrier. *Fisheries Research*, 3(2), 157-172.

Patrick, P.H., R. S. McKinley, W. C. Micheletti (1988a). Field testing of behavioral barriers for cooling water intake structures—Test Site 1—Pickering Nuclear Generating Station. In Proceedings: fish protection at steam and hydroelectric power plants. EPRI/AP-5663. Electric Power Research Institute. Palo Alto, 13–25.

Patrick, P. H., R. S. McKinley, A. E. Christie, J. G. Holsapple. (1988b). Fish protection: sonic deterrents. In Proceedings: fish protection at steam and hydro-electric power plants. EPRI/AP-5663. Electric Power Research Institute. Palo Alto, 1–2.

Patrick, P. H., Poulton, J. S. & Brown, R. (2001) Responses of American eels to strobe light and sound (preliminary data) and introduction to sound conditioning as a potential fish passage technology, in Coutant, C. C. (ed), *Behavioral Technologies for Fish Guidance*. American Fisheries Society Symposium, 1-11.

Patrick, P. H., Mason, E., Powell, J., Milne, S. & Poulton, J. S. (2014) Evaluating the Effectiveness of the Pickering Nuclear Generating Station Fish Diversion System Barrier Net. *North American Journal of Fisheries Management*, 34(2), 287-300.

Pavlov, D.S. (1989). Structures assisting the migrations of non-salmonid fish: USSR. FAO Fisheries Technical Paper No. 308. Rome, Fisheries and Agriculture Organization of the United Nations. .

Pearsons, T. N., Li, H. W. & Lamberti, G. A. (1992) Influence Of Habitat Complexity On Resistance To Flooding And Resilience Of Stream Fish Assemblages. *Transactions of the American Fisheries Society*, 121(4), 427-436.

Pennock, C. A., Bender, D., Hofmeier, J., Mounts, J. A., Waters, R., Weaver, V. D. & Gido, K. B. (2018) Can fishways mitigate fragmentation effects on Great Plains fish communities? *Canadian Journal of Fisheries and Aquatic Sciences*, 75(1), 121-130.

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.

Persson, L. & Eklov, P. (1995) Prey Refuges Affecting Interactions Between Piscivorous Perch And Juvenile Perch And Roach. *Ecology*, 76(1), 70-81.

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.

Piper, A., Manes, C., Siniscalchi, F., Marion, A., Wright, R., Kemp, P. (2015). Response of seaward-migrating European eel (Anguilla anguilla) to manipulated flow fields. *Proceedings of the Royal Society B: Biological Sciences*, 282(1811).

Piper, A. T., Svendsen, J. C., Wright, R. M. & Kemp, P. S. (2017) Movement patterns of seaward migrating European eel (Anguilla anguilla) at a complex of riverine barriers: implications for conservation. *Ecology of Freshwater Fish*, 26(1), 87-98.

Pitts, C. S., van Breukelen, S. W. F., Hayward, P. J., Cowx, I. G., Smith, K. L. (1995) Modelling Habitat Requirements of Coarse Fish in Lowland Rivers. R & D Report. National Rivers Authority.

Poff, N. L. & Allan, J. D. (1995) Functional-Organization Of Stream Fish Assemblages In Relation To Hydrological Variability. *Ecology*, 76(2), 606-627.

Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E., Stromberg, J.C. (1997) The natural flow regime. *BioScience*, 47(11), 769-784.

Polis, G. A., Holt, R. D., Menge, B. A., Winemiller, K. O. (1996). Temporal and spatial components of food webs. In Polis, G. A. & Winemiller, K. O. (eds) *Food Webs: Integration of Patterns and Dynamics*, 435–460. New York: Chapman & Hall.

Popper, A. N. & Carlson, T. J. (1998) Application of sound and other stimuli to control fish behavior. *Transactions of the American Fisheries Society*, 127(5), 673-707.

Post, D. M., Kitchell, J. F. & Hodgson, J. R. (1998) Interactions among adult demography, spawning date, growth rate, predation, overwinter mortality, and the recruitment of largemouth bass in a northern lake. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(12), 2588-2600.

Pracheil, B. M., DeRolph, C. R., Schramm, M. P. & Bevelhimer, M. S. (2016) A fish-eye view of riverine hydropower systems: the current understanding of the biological response to turbine passage. *Reviews in Fish Biology and Fisheries*, 26(2), 153-167.

Prignon, C., Micha, J.C., Gillet, A. (1998) Biological environmental characteristics of fish passage at the Tailfer Dam of the Meuse River, Belgium. In: Jungwirth, M., Schmutz, S. & Weiss, S. (eds) *Fish migration and fish bypasses*. Fishing New Books. Oxford: Blackwell Science, 69–84.

Pringle, C. (2003) What is hydrologic connectivity and why is it ecologically important? *Hydrological Processes*, 17(13), 2685-2689.

Pusey, B. & Arthington, A. (2003). Importance of the riparian zone to the conservation and management of freshwater fish: a review. *Marine and Freshwater Research*, 54(1), p.1.

Quigley, J. T. & Harper, D. J. (2006) Effectiveness of fish habitat compensation in Canada in achieving no net loss. *Environmental Management*, 37(3), 351-366.

Railsback, S. F., Harvey, B. C., Hayse, J. W. & LaGory, K. E. (2005) Tests of theory for diel variation in salmonid feeding activity and habitat use. *Ecology*, 86(4), 947-959.

Reckordt, M., Ubl, C., Wagner, C., Frankowski, J. & Dorow, M. (2014) Downstream migration dynamics of female and male silver eels (Anguilla anguilla L.) in the regulated German lowland Warnow River. *Ecology of Freshwater Fish*, 23(1), 7-20.

Reimer, G. (1991) The Ecological Importance Of Floodplains For Fish At The River March (Austria). *Archiv Fur Hydrobiologie*, 121(3), 355-363.

Resh, V. H., Brown, A. V., Covich, A. P., Gurtz, M. E., Li, H. W., Minshall, G. W., Reice, S. R., Sheldon, A. L., Wallace, J. B. & Wissmar, R. C. (1988) The Role Of Disturbance In Stream Ecology. *Journal of the North American Benthological Society*, 7(4), 433-455.

Reynolds, J. B. (1996) Electrofishing. In Murphy, B. R. & D. W. Willis (eds), *Fisheries Techniques*, 2nd ed. American Fisheries Society, Bethesda, 221–253.

Richards, N. S., Cawps, S. R. & Brown, M. L. (2007) Stress response and avoidance behavior of fishes as influenced by high-frequency strobe lights. *North American Journal of Fisheries Management*, 27(4), 1310-1315.

Richmond, M., Serkowski, J., Ebner, L., Sick, M., Brown, R. & Carlson, T. (2014) Quantifying barotrauma risk to juvenile fish during hydro-turbine passage. *Fisheries Research*, 154, 152-164.

Rodriguez, A., Castello-Orvay, F. & Gisbert, E. (2009) Somatic growth, survival, feed utilization and starvation in European elver Anguilla anguilla (Linnaeus) under two different photoperiods. *Aquaculture Research*, 40(5), 551-557.

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

Ronafalvy, J. P., Cheesman, R. R., Matejek, W. M. (2000) Circulating water traveling screen modifications to improve fish survival and debris handling at Salem Generating Station. *Environmental Science and Policy,* 3, 377– 382.

Rosenberger, A. E. & Chapman, L. J. (2000) Respiratory characters of three species of haplochromine cichlids: Implications for use of wetland refugia. *Journal of Fish Biology*, 57(2), 483-501.

Ross, Q.E., Dunning, D.J., Thorne, R., Menezes, J.K., Tiller, G.W., Watson, J.K. (1993) Response of alewives to high-frequency sound at a power plant intake on Lake Ontario, *North American Journal of Fisheries Management*, 13(2), 291‑303.

Rossi, R. (1979) An estimate of the production of the eel population in the Valli of Comacchio (Po Delta) during 1974–1976. *Bolletino di zoologia*, 46(3), 217-223.

Ruebush, B. C., Sass, G. G., Chick, J. H. & Stafford, J. D. (2012) In-situ tests of sound-bubble-strobe light barrier technologies to prevent range expansions of Asian carp. *Aquatic Invasions*, 7(1), 37-48.

Ruetz, C. R. & Jennings, C. A. (2000) Swimming performance of larval robust redhorse Moxostoma robustum and low-velocity habitat modeling in the Oconee River, Georgia. *Transactions of the American Fisheries Society*, 129(2), 398-407.

Rummer, J. L. & Bennett, W. A. (2005) Physiological effects of swim bladder overexpansion and catastrophic decompression on red snapper. *Transactions of the American Fisheries Society*, 134(6), 1457-1470.

Russell, I. C. & Potter, E. C. E. (2003) Implications of the precautionary approach for the management of the European eel, Anguilla anguilla. *Fisheries Management and Ecology*, 10(6), 395-401.

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).

Sagnes, P., Champagne, J. Y. & Morel, R. (2000) Shifts in drag and swimming potential during grayling ontogenesis: relations with habitat use. *Journal of Fish Biology*, 57(1), 52-68.

Salmon Advisory Committee (1997) Fish Passes And Screens For Salmon – Report of the Salmon Advisory Committee

Satpathy, K. K., Mohanty, A. K., Biswas, S., Sahu, G. & Selvanayagam, M. (2015) An unusual fish impingement event in the cooling water system of a nuclear power plant. *Indian Journal of Geo-Marine Sciences*, 44(9), 1323-1330.

Sbaihi, M., Fouchereau-Peron, M., Meunier, F., Elie, P., Mayer, I., Burzawa-Gerard, E., Vidal, B. & Dufour, S. (2001) Reproductive biology of the conger eel from the south coast of Brittany, France and comparison with the European eel. *Journal of Fish Biology*, 59(2), 302-318.

Schiemer, F. (1999) Conservation of biodiversity in floodplain rivers. *Archiv Fur Hydrobiologie*(3), 423-438.

Schilling, N. S. (2005) Survival of the fittest: fish in patchy environments show ideal free distribution. *Eukaryon*. 1, 11 16.

Schilt, C. R. (2007) Developing fish passage and protection at hydropower dams. *Applied Animal Behaviour Science*, 104(3-4), 295-325.

Schlosser, I.J. (1982) Fish community structure and function along two habitat gradients in a headwater stream. *Ecological monographs*, *52*(4), 395-414

Schmidt J. (1906) Contributions to the life-history of the eel (Anguilla vulgaris Flem.). Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 5, 137-264.

Schmidt, J. (1923) IV.—The breeding places of the eel. *Philosophical Transactions of the Royal Society. B*, *211*(382-390), 179-208.mille

Schmidtnielsen, K. (1972) Locomotion - Energy Cost Of Swimming, Flying, And Running. *Science*, 177(4045), 222

Scruton, D. A., Clarke, K. D., Roberge, M. M., Kelly, J. F. & Dawe, M. B. (2005) A case study of habitat compensation to ameliorate impacts of hydroelectric development: effectiveness of re-watering and habitat enhancement of an intermittent flood overflow channel. *Journal of Fish Biology*, 67, 244-260.

Sheridan, S., Turnpenny, A.W.H., Horsfield, R., Solomon, D., Bamford, D., Bayliss, B., Coates, S., Dolben, I., Frear, P., Hazard, E., Tavner, I., Trudgill, N., Wright, R., Aprahamian, 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.

Shuter, B. J., Finstad, A. G., Helland, I. P., Zweimuller, I. & Holker, F. (2012) The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. *Aquatic Sciences*, 74(4), 637-657.

Shuter, B. J., Ihssen, P. E., Wales, D. L. & Snucins, E. J. (1989) The Effects Of Temperature, Ph And Water Hardness On Winter Starvation Of Young-Of-The-Year Smallmouth Bass, Micropterus-Dolomieui Lacepede. *Journal of Fish Biology*, 35(6), 765-780.

Simmons, R. (2000). Effectiveness of a fish bypass with an angled bar rack at passing atlantic salmon and steelhead trout smolts at the Lower Saranac hydroelectric project. In: Odeh, M. Advances in fish passage technology

Simpson, W. G. & Ostrand, K. G. (2012) Effects of Entrainment and Bypass at Screened Irrigation Canals on Juvenile Steelhead. *Transactions of the*

American Fisheries Society, 141(3), 599-609.

Snyder, E. B., Arango, C. P., Eitemiller, D. J., Stanford, J. A. & Uebelacker, M. L. (2003) Floodplain hydrologic connectivity and fisheries restoration in the Yakima River, USA, in Wetzel, R. G. (ed), *International Association of Theoretical and Applied Limnology, Vol 28, Pt 4, Proceedings*. International Association of Theoretical and Applied Limnology Proceedings, 1653-1657.

Solomon D.J. (1992). *Diversion and entrapment of fish at water intakes and outfalls*. R & D Report, National Rivers Authority, Bristol.

Solomon, D.J. & Wright, R. (2012) Prioritising pumping stations for facilities for the passage of eels and other fish: Final report version 1.1. Environment Agency, Kelvedon, Essex

Sommer, T. R., Harrell, W. C., Solger, A. M., Tom, B. & Kimmerer, W. (2004) Effects of flow variation on channel and floodplain biota and habitats of the Sacramento River, California, USA. *Aquatic Conservation-Marine and Freshwater Ecosystems*, 14(3), 247-261.

Sonny, D., Knudsen, F. R., Enger, P. S., Kvernstuen, T. & Sand, O. (2006) Reactions of cyprinids to infrasound in a lake and at the cooling water inlet of a nuclear power plant. *Journal of Fish Biology*, 69(3), 735-748.

Spaink, P. A., Ietswaart, T. & Roijackers, R. (1998) Plankton dynamics in a dead arm of the River Waal: a comparison with the main channel. *Journal of Plankton Research*, 20(10), 1997-2007.

Sparks, R.E., Barkley, T.L., Creque, S.M., Dettmers, J.M., Stainbrook, K.M., (2010) Evaluation of an electric fish dispersal barrier in the Chicago Sanitary and Ship Canal. In *American Fisheries Society Symposium*, 74.

Spierts I.L.Y & Vis, H. (2012) Test on fish survivability of Bedford Pumps model SAF 90.05.12, Nieuwegein, the Netherlands.

Suski, C.D. & Ridgway, M.S. (2009) Winter biology of centrarchid fishes. *Centrarchid fishes: diversity, biology, and conservation*,264-292.

Sullivan, B., Wilson, A., Gutowsky, L., Patrick, P., Sills, M., Cooke, S. (2016). The Behavioral Responses of a Warmwater Teleost to Different Spectra of Light-Emitting Diodes. *North American Journal of Fisheries Management*, 36(5), 1000-1005.

Stafford-Glase, M. & J. Homa. (1997) An evaluation of fish entrainment and the effectiveness of the strobe light deterrent system at Milliken Station on Cayuga Lake, Thompkins County, and New York. Prepared for New York State Electric and Gas Corporation, Binghampton.

Stein, R.A., (1977) Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. *Ecology*, *58*(6), 1237-1253.

Stephenson, J. R., Gingerich, A. J., Brown, R. S., Pflugrath, B. D., Deng, Z. Q., Carlson, T. J., Langeslay, M. J., Ahmann, M. L., Johnson, R. L. & Seaburg, A. G. (2010) Assessing barotrauma in neutrally and negatively buoyant juvenile salmonids exposed to simulated hydro-turbine passage using a mobile aquatic barotrauma laboratory. *Fisheries Research*, 106(3), 271-278.

Stoot, L., Gibson, D., Cooke, S., Power, M. (2018). Assessing the potential for using low-frequency electric deterrent barriers to reduce lake sturgeon (Acipenser fulvescens) entrainment. *Hydrobiologia*, 813(1), 223-235.

Stewart, P.A. (1981) An investigation into the reactions of fish to electrified barriers and bubble curtains. *Fisheries Research*, *1*, 3-22.

Svendsen, J. C., Aarestrup, K., Deacon, M. G. & Christensen, R. H. B. (2010) Effects Of A Surface Oriented Travelling Screen And Water Abstraction Practices On Downstream Migrating Salmonidae Smolts In A Lowland Stream. *River Research and Applications*, 26(3), 353-361.

Svendsen, J. C., Skov, J., Bildsoe, M. & Steffensen, J. F. (2003) Intra-school positional preference and reduced tail beat frequency in trailing positions in schooling roach under experimental conditions. *Journal of Fish Biology*, 62(4), 834-846.

Tesch, F. W. (2003) *The Eel: Biology and Management of Anguillid Eels.* Blackwell Publishing. London

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*, 305-308.

Thoms, M. C. (2003) Floodplain-river ecosystems: lateral connections and the implications of human interference. *Geomorphology*, 56(3-4), 335-349.

Tockner, K. & Bretschko, G. (1996). Spatial distribution of particulate organic matter (POM) and benthic invertebrates in a river-floodplain transect (Danube, Austria): importance of hydrological connectivity. *Archiv für Hydrobiologie Supplement*, 115, 11-27.

Todd, P. (1981) Timing and periodicity of migrating New Zealand freshwater eels (Anguillaspp.). *New Zealand Journal of Marine and Freshwater Research*, 15(3), 225-235

Townsend, C. R. & Crowl, T. A. (1991) Fragmented Population-Structure In A Native New-Zealand Fish - An Effect Of Introduced Brown Trout. *Oikos*, 61(3), 347-354.

Townsend, C. R. (1989) The Patch Dynamics Concept Of Stream Community Ecology. *Journal of the North American Benthological Society*, 8(1), 36-50.

Travade, F., Larinier, M., Boyer-Bernard, S., Dartiguelongue, J. (1998) Performance of for fish pass installations recently built on two rivers in South-west France. In: Jungwirth, M., Schmutz, S., Weiss, S. (eds) *Fish migration and fish bypasses*. Fishing New Books. Oxford: Blackwell Science, 146–179.

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.

Tsukamoto K., Aoyama J. (1998) Evolution of freshwater eels of the genus Anguilla: a probable scenario.

Tsukamoto, K. & Arai, T. (2001) Facultative catadromy of the eel Anguilla japonica between freshwater and seawater habitats. *Marine Ecology Progress Series*, 220, 265-276.

Tsukamoto, K. (2009) Oceanic migration and spawning of anguillid eels. *Journal of fish biology*, *74*(9), 1833-1852.

Tullos, D. & C. Walter (2015) Fish use of turbulence around wood in winter: Physical experiments on hydraulic variability and habitat selection by juvenile coho salmon, Oncorhynchus kisutch. *Environmental Biology of Fishes*, 98, 1339–1353

Turner, A. M. & Mittelbach, G. G. (1990) Predator Avoidance And Community Structure - Interactions Among Piscivores, Planktivores, And Plankton. *Ecology*, 71(6), 2241-2254.

Turnpenny. A. W. H., & O' Keeffe, N. (2005) Screening for intake and outfalls. Environment Agency.

Tzeng, W. N., Wang, C. H., Wickstrom, H. & Reizenstein, M. (2000) Occurrence of the semi-catadromous European eel Anguilla anguilla in the Baltic Sea. *Marine Biology*, 137(1), 93-98.

Van Dijk, P. L. M., Hardewig, I. & Holker, F. (2005) Energy reserves during food deprivation and compensatory growth in juvenile roach: the importance of season and temperature. *Journal of Fish Biology*, 66(1), 167-181.

Van Den Thillart, G.E.E.J., Van Ginneken, V., Körner, F., Heijmans, R., Van der Linden, R., Gluvers, A. (2004) Endurance swimming of European eel. *Journal of Fish Biology*, *65*(2), 312-318.

van Esch, B. P. M. & Spierts, I. L. Y. (2014) Validation of a model to predict fish passage mortality in pumping stations. *Canadian Journal of Fisheries and Aquatic Sciences*, 71(12), 1910-1923.

van Ginneken, V. J. T. & Maes, G. E. (2005) The european eel (Anguilla anguilla, Linnaeus), its lifecycle, evolution and reproduction: a literature review. *Reviews in Fish Biology and Fisheries*, 15(4), 367-398.

Van Ginneken, V., Durif, C., Balm, S. P., Boot, R., Verstegen, M. W. A., Antonissen, E. & Van den Thillart, G. (2007) Silvering of European eel (Anguilla anguilla L.):

seasonal changes of morphological and metabolic parameters. *Animal Biology*, 57(1), 63-77.

Vandergoot, C. S., Murchie, K. J., Cooke, S. J., Dettmers, J. M., Bergstedt, R. A. & Fielder, D. G. (2011) Evaluation of Two Forms of Electroanesthesia and Carbon Dioxide for Short-Term Anesthesia in Walleye. *North American Journal of Fisheries Management*, 31(5), 914-922.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R., Cushing C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences,* 37, 130-137

Verhelst, P., Buysse, D., Reubens, J., Pauwels, I., Aelterman, B., Van Hoey, S., Goethals, P., Coeck, J., Moens, T. & Mouton, A. (2018) Downstream migration of European eel (Anguilla anguilla L.) in an anthropogenically regulated freshwater system: Implications for management. *Fisheries Research*, 199, 252-262.

Versonnen, B. J., Goemans, G., Belpaire, C. & Janssen, C. R. (2004) Vitellogenin content in European eel (Anguilla anguilla) in Flanders, Belgium. *Environmental Pollution*, 128(3), 363-371.

Vetter, B.J., Cupp, A.R., Fredricks, K.T., Gaikowski, M.P., Mensinger, A.F., (2015) Acoustical deterrence of silver carp (Hypophthalmichthys molitrix). *Biological invasions*, *17*(12), 3383-3392.

Videler, J. J. (1996). *Fish Swimming.* London, Chapman & Hall, 1-260.

Viroux, L. (1997) Zooplankton development in two large lowland rivers, the Moselle (France) and the Meuse (Belgium), in 1993. *Journal of Plankton Research*, 19(11), 1743-1762.

Vis, H. & J.H. Kemper. (2012) Test Fish Survivability Bedford Pumps SAF.90.05.12 Pump at 330 rpm (1.3m3/s). VisAdvies BV, Nieuwegein, the Netherland.

Visintainer, T. A., Bollens, S. M. & Simenstad, C. (2006) Community composition and diet of fishes as a function of tidal channel geomorphology. *Marine Ecology Progress Series*, 321, 227-243.

Voigt, R., Carton, A. G. & Montgomery, J. C. (2000) Responses of anterior lateral line afferent neurones to water flow. *Journal of Experimental Biology*, 203(16), 2495-2502.

Vollestad, L. (1986) Temperature-dependent activity of brackish water yellow eels, Anguilla anguilla L. *Aquaculture Research*, 17(3), 201-205.

Vollestad, L. (1992) Geographic Variation in Age and Length at Metamorphosis of Maturing European Eel: Environmental Effects and Phenotypic Plasticity. *The Journal of Animal Ecology*, 61(1), 41.

Vollestad, L. A. (1992) Geographic-Variation In Age And Length At Metamorphosis Of Maturing European Eel - Environmental-Effects And Phenotypic Plasticity. *Journal of Animal Ecology*, 61(1), 41-48.

Vollestad, L. A., Jonsson, B., Hvidsten, N. A. & Naesje, T. F. (1994) Experimental Test Of Environmental-Factors Influencing The Seaward Migration Of European Silver Eels. *Journal of Fish Biology*, 45(4), 641-651.

Vollestad, L. A., Jonsson, B., Hvidsten, N. A., Naesje, T. F., Haraldstad, O. & Ruudhansen, J. (1986) Environmental-Factors Regulating The Seaward Migration Of European Silver Eels (Anguilla-Anguilla). *Canadian Journal of Fisheries and Aquatic Sciences*, 43(10), 1909-1916.

Vowles, A.S., Don, A.M., Karageorgopoulos, P., Worthington, T.A., Kemp, P.S. (2015) Efficiency of a dual density studded fish pass designed to mitigate for impeded upstream passage of juvenile E uropean eels (A nguilla anguilla) at a model C rump weir. *Fisheries management and ecology*, *22*(4), 307-316.

Walker, J., Ghalambor, C., Griset, O., Mckenney, D. Reznick, D. (2005). Do faster starts increase the probability of evading predators?. *Functional Ecology*, 19(5), 808-815.

Ward, J.V. & Stanford, J.A. (1983). The serial discontinuity concept of lotic ecosystems. In Fontaine, T.D. & Bartell, S.M (eds) Dynamics of Lotic Ecosystems, 29-42. Ann Arbor Science Publishers.

Wardle, C. S. (1980) Effects of temperature on the maximum swimming speed of fishes. In: Ali., M. (eds) *Environmental Physiology of Fishes*. Plenum Press, New York, USA.

Wedding, L. M., Friedlander, A. M., McGranaghan, M., Yost, R. S. & Monaco, M. E. (2008) Using bathymetric lidar to define nearshore benthic habitat complexity: Implications for management of reef fish assemblages in Hawaii. *Remote Sensing of Environment*, 112(11), 4159-4165.

Welcomme, R. L. (2001). The status of large river habitats. In: Cowx, I.G., ed. *Rehabilitation of freshwater fisheries*. Oxford: Fishing News Books, Blackwell Science, 11-20.

Welcomme, R.L. (1979) *Fisheries Ecology of Floodplain Rivers.* London: Longman, 325.

Welcomme, R.L. (1985) River Fisheries. FAO Technical paper, 262.

Welton, J. S., Beaumont, W. R. C. & Clarke, R. T. (2002) The efficacy of air, sound and acoustic bubble screens in deflecting Atlantic salmon, Salmo salar L., smolts in the River Frome, UK. *Fisheries Management and Ecology*, 9(1), 11-18.

Weng, Z. Y., Mookerji, N. & Mazumder, A. (2001) Nutrient-dependent recovery of Atlantic salmon streams from a catastrophic flood. *Canadian Journal of Fisheries and Aquatic Sciences*, 58(8), 1672-1682.

Wickham, D. A. (1973) Attracting And Controlling Coastal Pelagic Fish With Nightlights. *Transactions of the American Fisheries Society*, 102(4), 816-825.

H. Wickham. (2016) ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York,

Wilbur, H. M. (1988) Interactions between growing predators and growing prey. In B. Ebenmann & L. Pensson. (eds) *Interactions in size-structured populations: from individual behavior to ecosystem dynamics.* Springer-Verlag, Berlin, Germany.

Winemiller, K. O. & Jepsen, D. B. (1998) Effects of seasonality and fish movement on tropical river food webs. *Journal of Fish Biology*, 53, 267-296.

Wippelhauser, G. & McCleave, J. (1988) Rhythmic activity of migrating juvenile American eels Anguilla rostrata. *Journal of the Marine Biological Association of the United Kingdom*, 68(01), 81.

Wolter, C. & Arlinghaus, R. (2003) Navigation impacts on freshwater fish assemblages: the ecological relevance of swimming performance. *Reviews in Fish Biology and Fisheries*, 13(1), 63-89.

Woodland, D. J. & P. J. Ward. (1990) Fish communities in sandy pools of Magela Creek, Alligator Rivers Region. Supervising Scientist for the Alligator Rivers Region, 81.

Wootton, R. (2002). *Fish Ecology*. Cham: Blackie Academic

Zhang, J., Chen, G. B., Chen, Z. Z., Qiu, Y. S. & Xiong, D. (2016) Application of hydroacoustics to investigate the distribution, diel movement, and abundance of fish on Zhubi Reef, Nansha Islands, South China Sea. *Chinese Journal of Oceanology and Limnology*, 34(5), 964-976.

Zielinski, D. P. & Sorensen, P. W. (2015) Field test of a bubble curtain deterrent system for common carp. *Fisheries Management and Ecology*, 22(2), 181-184.