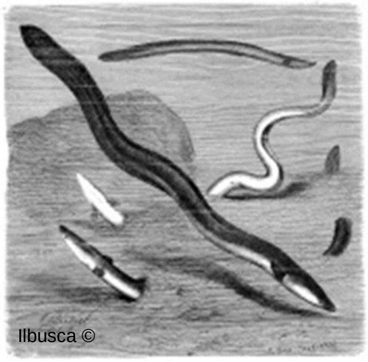
“No human being, however great, or powerful, was ever so free as a fish.”
John Ruskin 1819-1900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THE UNIVERSITY OF HULL

Mitigating the impacts of river flow regulation and barriers to fish spawning migrations

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by

Nicola Joanne Baker

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CONTENTS

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Haro, A.H., Wildman, T., Watten, B., Baker, N.J. & Bolland, J.D. *Passage of Downstream Migrant American Eels Through an Airlift Deep Bypass System,* IFM International Eel Symposium, London, UK, 2017

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DECLARATION OF AUTHORSHIP

I, Nicola Joanne Baker

declare that the work undertaken in this thesis entitled:

“Mitigating the impacts of river flow regulation and barriers to fish spawning migrations”

and the work presented here in is my own except when work has formed part of jointly authored publications has been included. The contribution from myself and the other authors to this work has been explicitly indicated below. I confirm that appropriate credit has been given within the thesis where reference has been made to the work of others.

Work that has been submitted:

(Chapter 6) Baker, N.J., Haro, A., Watten, B., Noreika, J. & Haro., A. (2018). Comparison of attraction, entrance and passage of downstream migrant American eels through airlift and siphon deep entrance bypass systems. *Ecological Engineering.*

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ABSTRACT

MITIGATING THE IMPACTS OF RIVER FLOW REGULATION AND BARRIERS TO FISH SPAWNING MIGRATIONS

Globally, migratory fish are threatened by anthropogenic modification to rivers. These create barriers that prevent fish accessing spawning grounds required for completion of life cycles. In order to make informed decsions, for mitigating the associated negative impacts, an understanding migratory behaviour when reaching barriers during the spawning migration is required. That said, there is a lack of information about the response of migratory fish to operational regimes in regulated rivers and the areas occupied, delays caused and routes taken around infrastructures. This study investigated the behaviour of three migratory fish species under operational regimes of three different infrastructures during each species' respective spawning season. The efficiency of a bypass channel that utilised the relationship between migratory behaviour and flow was also investigated for a further species.

The literature was reviewed to identify the different types of migratory life histories of fish, the impact of different riverine modification on the respective spawning migrations and how this can be mitigated. Fish have evolved in direct response to the natural flow regime and connectivity of riverine habitats, but barriers to migration exist from source to sea. This regulates or disrupts the flow regime and connectivity that fish depend upon, which has had considerable detriment to many migratory fish species globally. The main conclusion of the review was that knowledge gaps exist for the target species, and understanding the behaviour of the study species during the spawning migration is essential to improve access to spawning grounds in regulated rivers and ultimately conserve populations.

The effects of timing, magnitude and duration of eleven artificial flow (freshet) releases from two impounding reservoirs on river-resident brown trout (*Salmo trutta* L.), a species known to undertake spawning migrations, was investigated using radio telemetry in a regulated upland river in northern England. Most did not perform movements characteristic of spawning migrations; all were located within 10 m of the location occupied before freshets, and fish in a control reach behaved comparably. The largest unidirectional movements mostly occurred during elevated river level due to rainfall and reservoir overtopping events; other varied length movements occurred during natural peaks or low flow, indicating artificial freshets were not directly responsible, and may not be suitable to stimulate migration in river-resident fish in regulated rivers.

An acoustic telemetry study was conducted to determine the impact of a high-head hydropower station, associated diversion weir and spillway on downstream migrating shortfin eel (*Anguilla australis*) in the regulated Wairua catchment, Northland, New Zealand. Despite the diversion weir providing an alternative route, 88% (n = 21) of tagged eels that were detected here entered the power station forebay; of these, 52% were impinged onto intake screens, always when turbines were operating at greater than 3.04 MW/day. The rest (48%) passed the spillway and continued their migration, sometimes after long delays and having spent time immediately upstream of the intake where fitness could have been reduced due to high flows. Based on findings, the most effective mitigation here and at similar power schemes is considered to be operational or physical changes at the diversion weir to minimise entry of downstream migrating eels into the power canal during the migration period. Also discussed as potential solutions are turbine shutdowns, ensuring the spillway is available and provision of a bypass channel in the forebay.

At a pumping station in the Anglian region, UK, where the upstream river level is maintained primarily by a co-located gravity sluice door, route choice and behaviour of downstream migrating European eel (*Anguilla anguilla*) (n = 7) immediately upstream of both routes was investigated using acoustic telemetry. During the study, three eels passed through pumps despite only operating for 8% of the time the gravity sluice was open, and only two passed through the gravity sluice after arriving when it was closed; the remaining two retreated upstream. No eels were detected within 15 m of the gravity sluice when it was open and eel behaviour was indicative of reluctance to pass through pumps. Findings are discussed in terms of water resource management to implement operational changes, to make the gravity sluice an attractive downstream passage route for migrating eels and thus reduce passage through hazardous pumps.

The efficacy of two bypasses in attracting and passing downstream migrating American eels (*Anguilla rostrata*), designed to utilise the relationship between eel migratory behaviour and flow through two methods of flow creation, i.e. an airlift and a siphon, was tested in a simulated forebay environment, as a potential remediation measure at infrastructures requiring eel passage. Under entrance velocity of 1.2 m/s in eight test runs, both bypasses performed comparably and eels tested in each readily located, entered and passed. Test findings are discussed in relation to real-world application at sites with different characteristics, and the suitability of each design in successfully providing a safe route for downstream migrating eels.

1 INTRODUCTION

Rivers are diverse – fish utilise this by migrating between habitats

Riverine ecosystems are some of the most diverse on Earth (McCluney *et al*., 2014). Fish have evolved over millions of years to synchronize their behaviour, including migration for reproduction, feeding and predator avoidance, with specific parts of the natural flow regime in free-flowing rivers, such as floods in spring/winter or low flows in summer (Lehner *et al*., 2011). Migration is defined as relocation on a much greater scale than daily movements, between separate habitats where conditions are alternately favourable or unfavourable, and involves a substantial part of a population that move seasonally with predictability or synchronicity in time (Northcote, 1984; Baras & Lucas, 2001; Dingle & Drake, 2007; Shaw & Couzin, 2012; Brönmark *et al*., 2013). Migration is a major factor in the life history of many freshwater species (Rankin, 1985) and spawning migrations are usually the longest movements (Rustadbakken *et al*., 2004; Zimmer *et al*., 2010). It is undoubtedly one of the most extraordinary aspects of ecology that has generated a lot of interest in the scientific community and amongst the public (Crook *et al*., 2014); two fascinating examples being the return of salmonids to natal streams and the transoceanic migrations of anguillid eels to spawning grounds. Riverine ecosystems and fish migration also depend upon longitudinal connectivity, or connections between upstream and downstream sections of a river network (Junk, Bayley & Sparks, 1989; Poff *et al*., 1997; Cote *et al*., 2009; Anderson *et al*., 2015; Brink *et al*., 2018) to access the required habitats. Thus, free-flowing rivers are essential to sustain migratory fish, the habitat they depend on and ultimately for completion of life cycles.

Pressure on rivers results in removal of the flow regime and blockage of migration routes

From source to sea, riverine ecosystems have been modified and exploited by humans for the resources they provide for thousands of years. Installation of weirs and dams to divert flow allow power to be generated and machinery to be driven, as well as water to be stored for drinking and sanitation, which has been integral to the growth of the population and society (Vorosmarty *et al.,* 2010). As a result of these modifications, the flow regime that fish depend upon is often completely removed or regulated, and associated infrastructure becomes a barrier that prevents fish migration (Gerlier & Roche, 1998; Rustadbakken *et al.,* 2004) or a partial barrier that interrupts migration and can cause delays for some or all individuals. A barrier may be considered as anything that impedes movement of organisms between habitats, and for fish can be physical, such as the aforementioned infrastructure; hydraulic, such as high velocities created by such infrastructure; chemical, thermal or a matter of distance itself (Silva *et al*., 2018). Such disruptions to longitudinal connectivity have, in part, led to the worldwide 40% decline within migratory fish populations (Bacalbasa-Dobrovici, 1985; Cowx & Welcomme, 1998; Dudgeon, 2006; Brink *et al*., 2018). Increasing recognition of this has resulted in legislation calling for restoration of longitudinal connectivity at man-made obstacles in many countries (Lucas & Baras, 2001; Brink *et al*., 2018) in order to alleviate the pressures on natural resources.

It is essential to understand migratory fish movements and behaviour in response to regulated flow regimes and around associated barriers so species-specific remediation measures can be designed and implemented. This is increasingly recognized as valuable in understanding the impacts of barriers to migration, however, it is one of the least studied areas of fish biology (Silva *et al*., 2018) and there is still a dearth of information on fish movements during the spawning migration in regulated catchments and the behaviour upon reaching barriers. For example, there is still a paucity of information about:

- The response of potamodromous species to reservoir freshet (flow) releases of differing timing, magnitude and duration, intended to promote spawning migrations downstream of potable supply reservoirs
- The route choice and fine-scale behaviour of downstream migrating catadromous eels in rivers where flow is regulated by hydropower and pumping stations, respectively, where there are multiple routes available and upon reaching barriers associated with infrastructure, i.e. areas occupied directly upstream before passage
- The influence of operational regime on the timing of adult eel approach and behaviour at said infrastructure, including the delay caused, ability to complete onward migration after passage through various routes and fate
- The efficiency of bypass channels for attracting and passing adult downstream migrating eels, including flows required, how different flow generation methods affect eel behaviour and eel behaviour before entry, during passage and the effects post-passage

State of the art, most appropriate telemetry techniques (determined by locally specific conditions) were employed in order to fill these gaps for the study species. Such research is consequently essential for management and conservation of these migratory species that are especially vulnerable to anthropogenic influences due to the complex requirements in order for life cycles to be fulfilled.

The overall aim of the study was to investigate the impact of river flow regulation by reservoirs, a hydropower station and a pumping station on migratory fish access to spawning grounds, and, where necessary, help identify remediation measures to conserve fish. To this end, the study was divided into key topics that are addressed in Chapters 2 to 7. Specific aims and objectives are provided at the start of each chapter.

Chapter 2 reviews different types of fish spawning migration, highlighting the importance of habitat connectivity and the natural flow regime for fish life cycles, with reference to key concepts and principles. It reviews current literature documenting the anthropogenic alterations to rivers which create barriers to migration, the impact this has on fish species worldwide and the consequent requirement for mitigation measures to be incorporated into management decisions, in order to meet legislative requirements. This will be discussed as well as examples of mitigation measures.

Chapter 3 investigates the effectiveness of reservoir freshet (flow) releases of different timing, magnitude and duration on facilitating the upstream spawning migration of river-resident brown trout (in an upland river in West Yorkshire, UK, with emphasis on how the fish movements in this study compare to movement patterns characteristic of a spawning migration. The necessity of freshet releases for brown trout to perform spawning migrations is discussed. A freshet is defined as a rise in water level, in this case it is being released from a reservoir so is an artificial flow release.

Chapter 4 investigates the impact of the operation of a high-head hydropower station on downstream migrating shortfin eels, including timing of arrival, behaviour and route choice at an associated diversion weir, power station intake and spillway in Northland, New Zealand, with recommendations on how operational changes hold promise to reduce impingement onto the power station intake screens and allow adult eels to safely exit the catchment, such as management of the diversion weir and managing forebay level to increase spill in order to make alternative routes more attractive. The potential for a bypass channel to be implemented and setting a maximum generation level during migration season is also discussed.

Chapter 5 investigates the behaviour of downstream migrating European eels in the forebay of a pumping station with a co-located gravity sluice in Lincolnshire, UK, with emphasis on how pump operation affects route choice and availability, areas occupied immediately upstream and how operational changes to make the gravity sluice more attractive to eels hold promise to improve safe passage.

Chapter 6 compares the attraction, entrance and passage of downstream migrant American eels through two bypass channels; airlift and siphon deep entrance bypass systems trialled in a simulated forebay, with emphasis on the efficacy of such measures in providing passage solutions to downstream migratory eels at various infrastructure globally.

Chapter 7 summarises the information gained from chapters 3 to 6 in the context of the literature review in chapter 2, summarises global management implications and suggests recommendations for further study. The information in this thesis aims to provide guidance for water resource managers worldwide. This is in relation to the global requirement to alleviate impacts to rivers and migratory fish as demands on water resources and fish stocks increase, which is giving rise to legislation that requires water resource managers to do so. Thus, the recommendations aim to inform cost-effective remediation; specifically, the outputs will inform operational changes and design of alternative bypass routes to improve fish passage at infrastructure. Based on findings, this will minimise the costs of remediation and maximise the environmental benefits, which is in the best interests of both managers and fish inhabiting affected catchments. Further, the information aims to provide evidence to help understand the issue of barriers to fish migration, ideally to aid in the development of future less impactful riverine modifications that are designed with fish passage in mind.

2 LITERATURE REVIEW ON THE EFFECT OF FLOW REGULATION FROM SOURCE TO SEA

2.1 Introduction

Free-flowing, connected rivers provide a range of habitats, flows, temperatures and food webs to inhabiting biota (Brink *et al*., 2018). Migratory fish are sustained in rivers when the needs of all life stages are met, including that spawning grounds in either freshwater or the ocean can be accessed. The evolution of movement between freshwater and the ocean is discussed to have arisen as a result of "migration maximising fitness or the lifetime product of reproductive success x survivorship; therefore occurring when the gain in fitness from using a second habitat minus the migration costs of moving between habitats exceeds the fitness from staying in only one habitat… the relative availability of food in freshwater and seawater zones being the most important biological variable" (Gross, 1987). The natural flow regime is what has made such movements possible; hence fish life history strategies have evolved primarily in direct response to it (Bunn & Arthington, 2002) and consequently depend on it to provide cues and opportunities for free migration between different habitats required for different life stages. Although fish are adaptable and can evolve in response to man-made flow regimes, flow modification is broadly recognised as disrupting fish and fish habitats (e.g. Murchie *et al*., 2008). This is partly due to fish requiring longitudinal connectivity, which is often disrupted in rivers where flow is controlled by humans. Longitudinal connectivity refers to connections between upstream and downstream sections of a river network (Cote *et al*., 2009) and is essential for normal riverine ecosystem functioning and for fish to perform migrations to habitats required in order to complete their life cycle. In some systems, lakes are also present, which are important to ecosystem functioning, but for the purpose of the Thesis, rivers will be used to refer to the entire freshwater system and the prescence of lakes is implicit. Migratory fish are threatened globally, partly due to disruptions to longitudinal connectivity (Stanford & Ward, 2001; Anderson *et al*., 2015; Brink *et al*., 2018) (Figure 2.1) as infrastructure is constructed in rivers to meet the needs of humans which can act as a partial or full barrier to fish migration. In recent years, there has been increasing recognition of the importance of longitudinal connectivity, but the effects of disruption on inhabiting biota remain poorly understood. Understanding migratory fish behaviour is at the forefront of ecological research to allow mitigation measures to be identified and recommended to improve the situation.

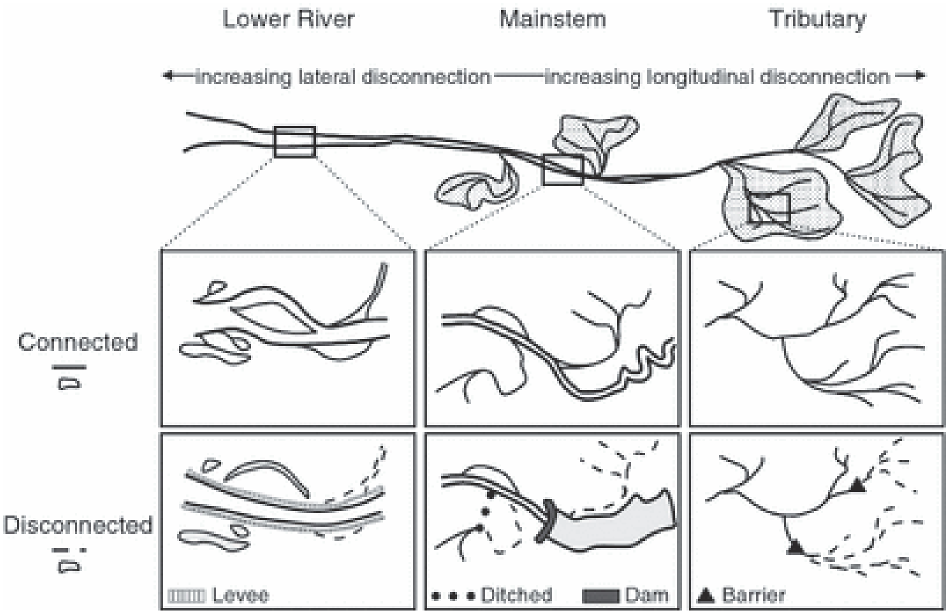


Figure 2.1. Schematic diagram showing river sections and areas from source to sea that are connected or disconnected by anthropogenic influences. Longitudinal disconnections are often seen among habitats in tributaries, whereas in lower reaches, lateral disconnections are also common (adapted from Fullerton *et al*., 2010).

The aim of this literature review is to understand the different types of fish spawning migrations, the mechanisms driving them and how they are intrinsically linked with diverse natural river ecosystems. The review also aims to determine the effects of anthropogenic alterations to rivers on migratory fish and how these can be alleviated. More specifically, objectives are to 1) determine the different types of fish spawning migrations that occur in part or completely in rivers, 2) discuss current status and reasons for decline of these fishes, 3) establish causes for river modification with particular emphasis on dams and impoundments, hydropower and pumping stations and their effect on migratory fish, and 4) explore how these impacts can be mitigated, with particular reference to replicating the natural flow regime and providing efficient fish passage solutions, with emphasis on understanding the behaviour of the species in question and utilising this to provide cost-effective passage solutions or prevent entry into undesired areas.

2.2 Drivers for spawning migrations

Due to previous recognition that our understanding of the movements of organisms has in the past been hindered by inaccurate terminology (Dingle & Drake, 2007), it is important to first determine the difference between movement and migration. Movement is defined as the act of changing position or location, mostly occurring within a relatively well defined area, or home range (Dingle, 1996). Home range is an area that provides resources necessary for survival, i.e. food, shelter and mates; movements occur between areas within the home range, to obtain resources and requirements necessary for breeding, maintenance or both (e.g. Dingle & Drake, 2007). This area develops in response to local resources, in order to obtain food or avoid predators; hence to survive (Morais & Deverat, 2016).

Migration is more specialized, often but not limited to larger temporal and spatial scales (Morais & Deverat, 2016). As discussed by Dingle (1996), migration results in relocation to a new habitat; this is not driven by resources in the first habitat such as food, and during migration fish will not respond to sensory cues from these resources, i.e. their motivation is not driven by these resources as it usually would be when moving around in the home range. The most recent definition of migration which encorporates that of the recognised Northcote (1978) definition with four overlapping concepts, is that migration is (1) a type of locomotory activity that is notably persistent, undistracted and straightened out, i.e. without straying from the directional path in another direction; (2) a relocation of the animal that is on a much greater scale, involving movement of a much longer duration than those in its normal daily activities, (3) a seasonal to–and–fro movement of populations between regions where conditions are alternately favourable or unfavourable; and (4) movements that lead to redistribution or mixing (of individuals, that leaves the location and spatial extent of the population un-changed) or dispersal (when animals in a population move apart) Dingle & Drake, 2007).

2.3 Why do fish migrate?

Migrations are impressive, regardless of distance and require longitudinal connectivity

Migration is described as resulting from key resources and optimal habitats for growth, survival and reproduction being separated in space and time (Northcote, 1984; Lucas & Baras, 2001). Research demonstrates that migrating between habitats allows fish to optimize growth by accessing more productive areas, improve survival through increased growth, increased overwinter survival, access to refugia from severe conditions and predator avoidance, as well as potential for increased reproductive fitness through improved adult condition and access to optimal spawning habitat (Morais & Deverat, 2016) (Figure 2.2). Its' evolution therefore ultimately maximises lifetime reproductive success (Gross, 1987). Indeed, all freshwater fish species worldwide, are said to migrate to some extent between feeding and breeding areas in order to complete their life cycles (Lucas & Baras, 2001; Brink *et al*., 2018) (Figure 2.2).

Spawning migrations, the focus of this review, are some of the most significant in the life history, varying greatly temporally and spatially and extending up to thousands of kilometres. Despite distance not being a primary criterion, migrations that cover extreme distances are often seen as being iconic (Lucas & Baras, 2001; Brink *et al.*, 2018) due to the vast distances and obstacles overcome in order to reach spawning grounds. Some examples are the return of salmonids to the streams in which they were born, or the transoceanic migrations of anguillid eels. Though less reported, there are migratory species in developing countries that are described as being "every bit as charismatic as Northern Hemisphere salmon and eel" such as largemouth yellowfish (*Labeobarbus kimberleyensis*, Gilchrist & Thompson, 1913) in South Africa, spotted sorubim (*Pseudoplatystoma corruscans*, Spix & Agassiz, 1829), the curimba (*Prochilodus lineatus,* Valenciennes, 1837), or the salmon-like dourado (*Salminus brasiliensis*, Cuvier, 1816) species in South America (Carolsfeld, 2003; Brink *et al.*, 2018) which has resulted in significant conservation interest to date.

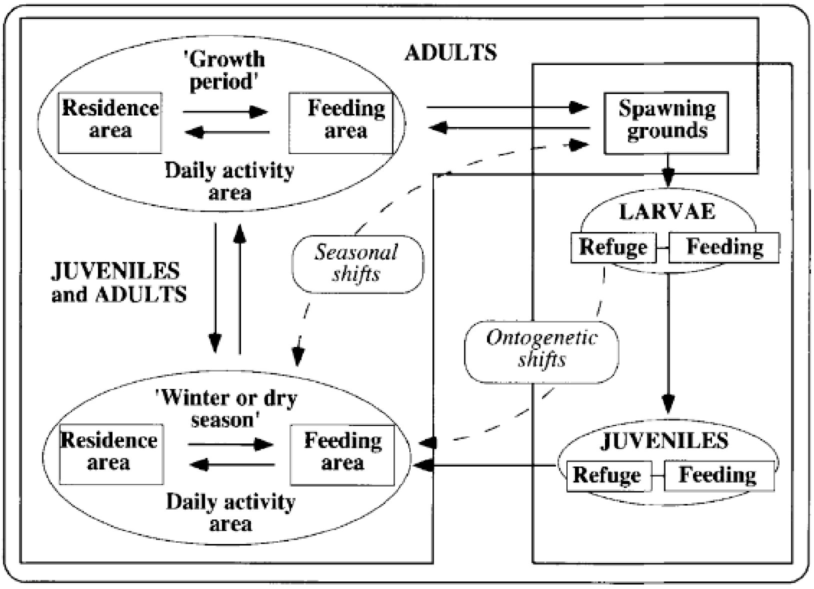


Figure 2.2. Schematic illustration of the habitats required by fish for different life stages (circled) and the movements between those habitats (arrows), demonstrating the functional life concept in fish. Taken from Lucas and Barras, (2001).

Many species display plasticity in their life history and associated migration strategy, which is defined as "the ability of a single genotype to produce multiple phenotypes in response to variation in the environment" (Pfennig *et al.*, 2010). This can contribute to the occurrence of both resident and migrant individuals occurring within the same population; a phenomenon known as partial migration (Jonsson & Jonsson, 1993;

Secor, 1999; Chapman *et al*., 2012; Gillanders *et al*., 2015). Individuals will undergo a trade-off between maximising fitness (growth, reproduction) with the resources available throughout the year (Morais & Deverat, 2016). Migration as a life history may be selected for if the energetic demand of migrating to explore distant resources outweighs the cost of staying resident, which could be unfavourable due to predation risk and intraspecific competition from residents (Morais & Deverat, 2016). In this case, the risk of seeking out new habitats, where these factors may be more favourable may outweigh the cost of staying resident. Thus, evolution and genetics are partly responsible but are thought to be intertwined with environmental factors (Pulido, 2007) and the scale of spawning migrations seen in those that migrate depends on a range of factors. In terms of genetics, the evolution of a life history strategy such as migration evolves as it maximises fitness of individuals and populations (Gross, 1987), where individual fitness is reproductive success throughout the ontogeny (Morais & Deverat, 2016) and at a population level also includes interactions between individuals where strategies develop depending on other individuals in the population (Gross, 1987). This evolution results in an increase of resilience and stability at a population level. Thus, aforementioned plasticity in the life history has allowed fish to adapt and survive in present day rivers using strategies that evolved long before heavy modification to rivers. Despite this, the innate drivers for fish migration are maintained throughout generations, namely utilising flow to aid in migration to areas required for spawning.

2.4 Different types of spawning migrations

Fish migrations that occur exclusively within freshwater are defined as ‘potamodromous’; this is the broad term for fish that may be more commonly classified as ‘non-anadromous’, ‘river-resident’ or ‘inland’ (Morais & Deverat, 2016). When fish migrate between fresh and salt water, these migrations are classified as being ‘diadromous’ and are broken down further based on the direction of the spawning migration. ‘Anadromous’ species migrate from the sea to spawn in freshwater and ‘catadromous’ species migrate from freshwater into the sea to spawn (Dingle, 1980; McDowall, 1987). Diadromous species spend most of the ontogeny in the area used for growth and migrate to the alternate environment to breed (Myers, 1949). Diadromous species provide both direct and indirect benefits to the ecosystem as they inhabit multiple habitats and act as consumers, ecosystem engineers, modulators of biogeochemical processes and transport vectors (Flecker *et al.,* 2010). In order to survive in such different habitats, large demands are placed on the physiology of anadromous fish. Fish can also adopt an ‘amphidromous’ – where migration between the sea and freshwater is not directly associated with reproduction but occurs regularly at another definite stage of the life cycle (Myers, 1949) – or an ‘oceanodromous’ life history, when migration between necessary habitats and the entire life history is carried out within the ocean (Morais & Deverat, 2016). The latter two are beyond the scope of this thesis as the focus is on spawning migrations in freshwater.

Homing back to natal sites to spawn or ‘philopatry’, though not a requirement for fish to be classified as migratory (Waldman *et al*., 2008), is exhibited in anadromous (Dittman & Quinn, 1996), catadromous (Hunter *et al*., 2003) and potamodromous species (Rakowitz *et al*., 2009). In evolutionary terms, this behaviour is advantageous as it ensures eggs are deposited in suitable habitat and also balances the number of spawners within the reproductive capacity of the area (Northcote, 1997). This will also be affected by density dependence regulating the number of spawners in the area, depending on competition for resources such as space or suitable spawning locations (e.g. Rose *et al*., 2001). Ultimately this relies on density dependent mortality to regulate the distribution of populations (e.g. Hixon & Jones, 2005). This behaviour indicates evolution of mechanisms in response to relatively predictable environmental conditions or rhythmic patterns of changes (Lucas & Baras, 2001). Whilst the conditions that resulted in selection of homing traits prevail, this will remain the most adaptive strategy.

It has been discussed that spawning migrations are normally the longest movements carried out within each year, even in landlocked fish (Rustadbakken *et al*., 2004; Zimmer *et al*., 2010). However, Dingle & Drake, (2007) and Morais and Deverat, (2016) discuss that “classic” examples of migration in migratory fish and across all taxa might be extreme cases and the exception rather than the rule (Dingle & Drake, 2007). This information is important when aiming to understand the migratory behaviour of a population in order to conserve it and highlights the need for further research in this area, to prove or disprove such suggestions. There is consequently increasing recognition that a broad range of behaviours are exhibited within populations, i.e. displaying alternate life history strategies (or life history plasticity) (see Morais & Deverat, 2016).

The strong imprinting of migration in fishes is evidenced in examples such as landlocked diadromous fish (described as the first cases of alternative life histories) that have been discussed to potentially mimic migratory behaviour in the new restricted habitat and even started to migrate again after the removal of barriers (McDowall, 1988). In brown trout, barrier removal resulted in an increase in spawning success by adults, fry survival, recruitment and smolt migration success as well as more adults migrating to the sea and adults spawning in areas further upstream (Birnie-Gauvin *et al*., 2018). Variation in migratory tendency occurs between species, between populations within a species (Gillanders *et al*., 2015) and between individuals within a population, but the latter has received less attention (Chapman *et al*., 2011) and is important when aiming to understand the migratory behaviour of a species in order to conserve them. There are a number of factors determining whether a species migrates and the distance of migrations.

Food availability is an important factor determining both where migratory fishes occur (Gross, 1987) and the direction of movement; Gross *et al*., (1988) previously attributed diadromous fish distribution to global patterns in aquatic productivity. When feeding and reproductive areas are separated temporally (i.e. in migratory species, in part due to reproductive seasons being constrained by environmental factors), being able to feed at one time of year and breed at another is favourable (Bonnet, Bradshaw, & Shine, 1998). This is particularly suited to a capital breeding strategy, which relies on energy acquired previously in the feeding area (and hence ‘capitalised’) to be drawn upon during reproduction (McBride *et al*., 2013). This is linked to semelparity; where the animal only spawns once in a lifetime (Bonnet, Bradshaw & Shine, 1998) as opposed to iteroparous animals known to carry out several reproductions (Morais & Deverat, 2016).

Energy stored in somatic and visceral tissues is used during reproductive development, for example Sockeye salmon *Oncorhynchus nerka* (W) use around 80% of their total energy stores during upstream migration and spawning (Brett, 1986). This influences whether an animal can survive after spawning (Jonsson, Jonsson & Hansen, 1997) and explains why semelparous animals only spawn once then are ‘spent’ and die. Repeated spawning is seen in some populations, for example in Atlantic salmon (*Salmo salar* (Linnaeus, 1758)) (e.g. Jonsson *et al*., 1991), which is possible if less energy has been allocated for a single reproductive event. Glebe & Legett, (1981b) previously linked semelparity to fish investing more than 60% of their total energy in migration and spawning, based on observations of several populations of American shad *Alosa sapidissima* (Wilson, 1811) and some observations of salmonids (*Oncorhynchus* and *Salmo*). Further, the largest individuals in Nauyuk Lake, Northwest Territories, Canada were thought to have never been able to spawn again due to the amount of energy allocated for reproduction (Jonsson, Hansen and Jonsson, 1991). For eels, the total amount of energy allocated to gonad growth and migration has been calculated to be 75% in female eels which is said to be extremely high in relation to other teleosts (cf. Wootton, 1979).

Based on a capital spawning life history strategy, feeding during the migration in unknown environments is unnecessary. It can be costly as it poses other constraints such as energy required for finding and catching prey and digestion that could be used for directed swimming so could potentially cause delays (Lucas & Baras, 2001).The alternative strategy is income breeding, where energy is acquired locally, throughout a prolonged spawning season and is directly allocated to reproduction; many species exhibit mixed capital- and- income breeding patterns and the scale of this is affected by ontogeny or in relation to environmental conditions (McBride *et al*., 2015). Ultimately, flexible processes of energy acquisition allow energy to be invested cautiously in order to maximise lifetime reproductive value (McBride *et al*., 2013) and the advantages of capital versus income breeding depend on the abundance, predictability and temporal stability of food availability (Chastel *et al*., 1995).

Starting a migration with maximum fuel reserves has been described as an optimum strategy as long as sufficient energy is stored beforehand (Lucas & Baras, 2001). However, conditions during the migration may result in more energy expenditure, making reserves insufficient; in which case feeding would be required. In Atlantic salmon, the maturation is a step-wise process (Thorpe, 1994). This is said to be for obvious reasons - that when the prospects of successful reproduction and survival are jeopardized, the maturation process can stop (Svedäng & Wickström, 1997). The maturation process in eels is also discussed to be a step wise process based on fat content analysis that would make it impossible for eels to reach the Sargasso Sea if this was the only reserve available (Svedäng & Wickström, 1997).

Migrating to habitats where conditions are different requires morphological and physical changes in order for animals to survive in the new habitat, which also places energetic demands on the animal. Further, some of the required changes would make feeding difficult, for example, the increase in jaw size of adult male salmon to aid in competing for females at the spawning grounds, amongst other functions (Quinn and Foote, 1994; see Witten & Hall, 2003) and the silvering process in mature adult eels (Brujis & Durif, 2009) to allow for survival in the ocean. These are perhaps some of the most iconic and impressive morphological differences exhibited in migratory fishes.

Some fish do not display diadromy despite having access to the ocean (Loughlin *et al*., 2017), rendering them partially migratory. In such populations, there is said to be a selective balance between migratory and resident individuals (Alerstam *et al*., 2003), with factors such as age-, sex- and dominance affecting expression of the ‘migratory urge’ (Lack, 1968), Also, it would only be beneficial for a certain proportion of the population to migrate, due to aforementioned density dependence. As well as changes in food availability, harshness of seasonal shifts and difficulty of migration may determine whether residency or migration is favoured (Alerstam *et al*., 2003). Southern rivers that have high and predictable temperature regimes, for example, select for early age at maturity and an increase in expenditure on reproduction when compared to rivers at higher latitudes, such as in American shad where age at sexual maturity and frequency of repeat spawners increased with latitude (Leggett and Carscadden,1978; Glebe & Leggett, 1981a,b). This is further supported by Solomon & Templeton (1976), where a population of brown trout perform localised movements where spawning, nursery and feeding habitats were within close proximity to the home range, negating the need to move further.

There are three different types of migratory strategy; obligate migrants, that migrate regardless of environmental and individual conditions; facultative migrants, that potentially migrate depending on environmental and individual conditions; or obligate residents, that stay resident irrespective of environmental conditions (Dingle & Drake, 2007; Brodersen *et al*., 2014). An example of obligate migration is seen in salmon (*Oncorhynchu*s and *Salmo* spp; Dingle, 1996) whereas facultative migration is seen roach (*Rutilus rutilus* (L.) that migrate from the lake to connected streams, displaying partial migration, before returning to the lake the following spring (e.g. Brodersen *et al*., 2008). Brodersen *et al*., (2014) found that there is a positive relationship between somatic body condition and the probability of migration, but only in individuals that adopt a migratory strategy at some point in the ontogeny; and discuss that in obligate residents, this does not influence individual participation in migration.

Miller & Bond (2015) suggest that resident individuals may potentially adopt a migratory life history later in life, but until they discovered that older individuals individuals in a population of Dolly varden trout ((*Salvelinus malma* (Walbaum, 1792)) “retired from anadromy”, it was not known that migratory individuals became resident. The authors suggested that size benefits of marine foraging declined in older fish, in this case the authors hypothesize that this is viable in this particular population due to foraging opportunities being subsidized by the predictable annual supply of energy-rich eggs and carcasses of spawning Pacific salmon (*Oncorhynchus* spp) (Miller & Bond, 2015) .

Specific environmental conditions are required for fish to reproduce (Morais & Deverat, 2016). In a river with a natural flow regime, potamodromous, anadromous, and catadromous fish typically perform spawning migrations during high flow events as they provide cues for migration and allow access and movement to spawning sites located in different areas (Lucas & Barras, 2001). The flow regime is described as a 'master variable' (Poff *et al*., 1997) which controls or influences not only the timing of migration and reproduction of many organisms but also other aspects of the physical aquatic environment (Lytle & Poff, 2004). Timing of spawning migration has been related to environmental factors including lunar cycle, diel cycle and increased turbidity (Hellawell *et al*., 1974; Lucas & Baras, 2001) with seasonal changes said to be vital in governing the rate and onset of sexual maturation in salmonids (Brink *et al*., 2018) and reduced photoperiod during the autumn/winter spawning season being discussed to provide the cue for salmonids to become sexually mature and ready to migrate (Crisp, 2000). Trancart *et al*., (2013) discuss that for anguillid eels, rainfall is the most relevant factor for analysis of factors that influence migration as it is a proxy for other cues affecting migrations (river flow, temperature change, wind, atmospheric pressure, turbidity and effects on luminosity from associated cloud cover). Further, certain species have temperature thresholds that trigger spawning migrations, for example in brook lamprey (*Lampetra planeri* (Bloch)) (7.5^{o}c) (Malmqvist, 1980), Atlantic eels (*Anguilla)* (10 – 18^{o}c) (Haro, 1991) and striped bass (*Morone saxatilis* (Walbaum)) (17–18°C) (Carmichael *et al*., 1998). In recent research into salmonid migration, the importance of social cues for timing of salmon migration has been discussed, with findings that individual sockeye salmon alter their behaviour in response to annual fluctuations in population density (Berdahl *et al*., 2017).

2.4.1 Potamodromy

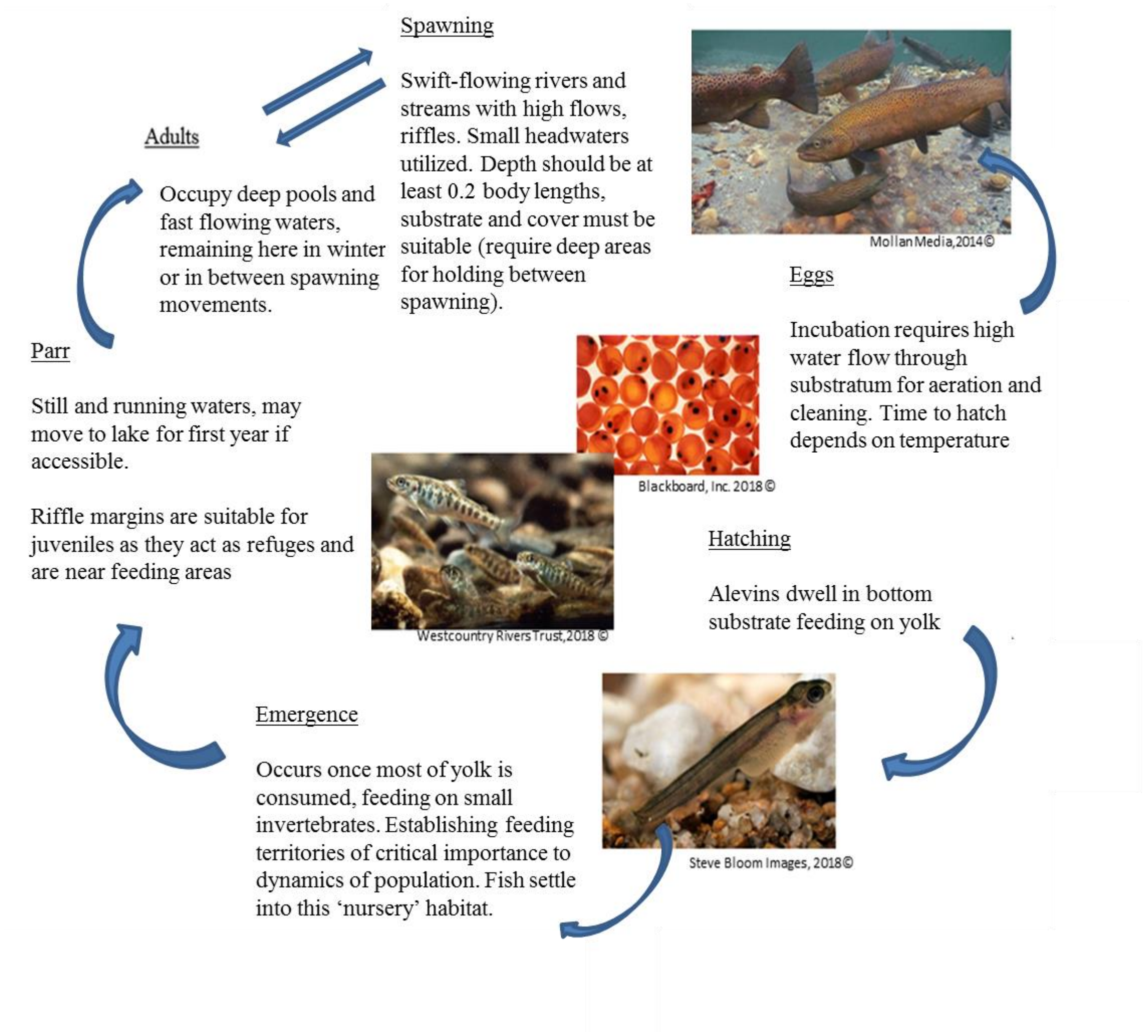
Information and distribution

Of the world's 33,592 fish species, 40% are reported to reside in freshwater (~13,440) and it is likely more than 13,000 of these are potamodromous (~96%) (Morais & Deverat, 2016). Potamodromous fishes are reported to inhabit mostly the Northern Hemisphere but are present in numerous parts of the world (Morais & Deverat, 2016). This could therefore be due to fewer and more recent studies in the Southern Hemisphere as a result of an increase in research interest in response to the decline in species in the Northern Hemisphere, motives for research or quality of past data (e.g. Funge-Smith, 2018). Potamodromous species support essential commercial and recreational fisheries worldwide (Morais & Deverat, 2016), some of the most well recognised and iconic species being large catfish in South America and Asia, and salmonids such as brown trout that are abundant in many river systems on a global scale (Jonsson & Jonsson, 2011), being non-native in many countries where they have been introduced.

Species example and information

Brown trout are a favoured model study species for a potamodromous life history as they are one of the most genetically diverse vertebrates known (Ferguson, 1989) and display plasticity in the migratory life history (Rieman & Dunham, 2000; Klemetsen *et al*., 2003). This makes them highly adaptable. They are also ecologically valuable in terms of assessing habitat quality and understanding anthropogenic impacts to rivers due to their sensitivity to many anthropogenic pressures such as habitat modification, flow regulation and chemical pollution (Pont *et al*., 2006). They occur in habitats ranging from very small streams to large rivers and even coastal ranges (Klemetsen *et al*., 2003), which makes them a good ecological indicator as their status can reveal the qualitative status of the environment in comparison to other environments where they reside, including the impact of differing flow regimes (Milner *et al*., 2012). This also applies to other trout species (Wenger *et al*., 2011).

In brown trout, individuals display seasonal movements between habitats, have different requirements for different life stages (Figure 2.3) and are capable of being highly motile, but like many species display large variation in migration distances. They have been extensively reported to migrate upstream to find appropriate spawning habitat (reviewed in Banks, 1969; Solomon & Templeton, 1976; Beard & Carline, 1991; Young 1994, 1999; Arnekleiv & Kraabol, 1996, Ovidio *et al*., 1998; Ovidio, 1999; Burrell *et al*., 2000; Arnekleiv & Ronning, 2004; Bettinger & Bettoli, 2004; Bendall *et al*., 2005; Popoff & Neumann, 2005; Saraniemi *et al*., 2008; Quinn *et al*., 2011), but can also be relatively sedentary (Bridcutt *et al*., 1993; Burrell *et al*., 2000; Brown *et al*., 2001; Knouft & Spolita, 2002; Popoff & Neumann, 2005). Brown trout have also been discussed to possibly migrate downstream for spawning (Gosset *et al*., 2006). The variation in migratory distance and direction has been related to spatial distribution of appropriate spawning habitat relative to adult feeding or refuge areas (Lucas & Baras, 2001).



Spawning

Swift-flowing rivers and streams with high flows, riffles. Small headwaters utilized. Depth should be at least 0.2 body lengths, substrate and cover must be suitable (require deep areas for holding between spawning).

MollanMedia,2014©

Eggs

Incubation requires high water flow through substratum for aeration and cleaning. Time to hatch depends on temperature

Blackboard, Inc. 2018©

Hatching

Alevins dwell in bottom substrate feeding on yolk

Steve Bloom Images, 2018©

Emergence

Occurs once most of yolk is consumed, feeding on small invertebrates. Establishing feeding territories of critical importance to dynamics of population. Fish settle into this ‘nursery’ habitat.

Westcountry Rivers Trust,2018 ©

Parr

Still and running waters, may move to lake for first year if accessible.

Riffle margins are suitable for juveniles as they act as refuges and are near feeding areas

Adults

Occupy deep pools and fast flowing waters, remaining here in winter or in between spawning movements.

Figure 2.3. The life cycle of brown trout. Adapted from information in); Heggenes, (1990); Armstrong *et al*., (2003); Jonsson & Jonsson, (2011); Quinn *et al*., (2011); The Wild Trout Trust, (2014).

Current status and reasons for decline

Potamodromous fish are described as being one of the most threatened faunal groups worldwide (Beatty *et al*., 2014) with more than 20% in the world being classified as extinct, threatened or endangered (Revenga *et al*., 2000). Habitat degradation, invasive species and overharvesting as well as dams that cause barriers to migration are amongst the most impactful pressures (Brink *et al*., 2018). When assessing the impact of dams for global freshwater fish diversity, Liermann *et al*., (2012) reported that of the 397 freshwater ecoregions evaluated, 50% were obstructed by large and medium sized dams and ~27% faced additional obstruction, highlighting the significance of this impact worldwide. Climate change is also recognised as being one of the most significant pressures on potamodromous fishes, as it adds to current and future anthropogenic stressors (Beatty *et al*., 2014, and references therein). Broad-scale studies of climate change focus mainly on temperature, but altered flows can also decrease the amount of suitable habitat. For example, four trout species in the interior Western United States (~1 million km^2) are predicted to decline by between 35 – 77% in response to increased temperature and frequency of winter floods as a result of warmer, rainier winters that are predicted during future climate change (Wenger *et al*., 2011).

2.4.2 Anadromy

Information and distribution

Anadromous fishes spend most of their lives in the sea and individuals in a population migrate into freshwater to breed at a specific time in the ontogeny (Myers, 1949; Morais & Deverat, 2016). It is currently estimated that there are 175 (Riede, 2004) anadromous species worldwide, with potentially more that are yet to be discovered, which currently only equates to ~0.5% of the world’s fish species (Morais & Deverat, 2016). Many populations are a valuable resource for many countries in terms of having high economic value for fisheries of small and large scale, high market value such as sturgeons and salmonids high recreational value in fishing lakes, which is important for tourism in certain coutries, are valued for the necessity for protein sources, and also have cultural value (Morais & Deverat, 2016), such as eels (e.g. Righton & Walker, 2013).

The reasons for the evolution of anadromy have been discussed by numerous authors over the past few decades (reviewed in Morais & Deverat, 2016). Most recently, it is discussed that this life history strategy is an adaptation in evolutionary history in a particular environment, potentially in response to predation, competition or geological history (Bloom and Lovejoy, 2014), independent of marine or freshwater origin. In salmonids there is a gradient of tactics from freshwater residency to anadromy (e.g. Jonsson & Jonsson, 1993). This ‘facultative diadromy’ indicates that neither of these life history strategies is better than the other, but one will be favoured under certain circumstances, as discussed in section 2.4 (McDowall, 1988) and emphasizes the effect of environmental conditions on which life history is selected.

Species example and information

Some of the most iconic anadromous migrations are those of salmonids in various regions of the Northern Hemisphere that migrate to the ocean for feeding and back to natal streams for breeding (Banks, 1969) such as Atlantic salmon (Figure 2.4). Migration into the sea for feeding where food resources are more abundant allows for larger growth (McDowall, 2001), for example Pacific salmon (*Oncorhynchus* spp) obtain more than 95% of their biomass in the marine environment (Naiman *et al*., 2002). Salmonids also require cold, well-oxygenated streams for spawning as lower temperatures result in increased concentration of dissolved oxygen (Wetzel, 2001) and consequently increasechance of egg survival. These are often found in headwaters but may vary depending on location, i.e. in mountainous areas; this may be very close to the head of the tide (Banks, 1969).

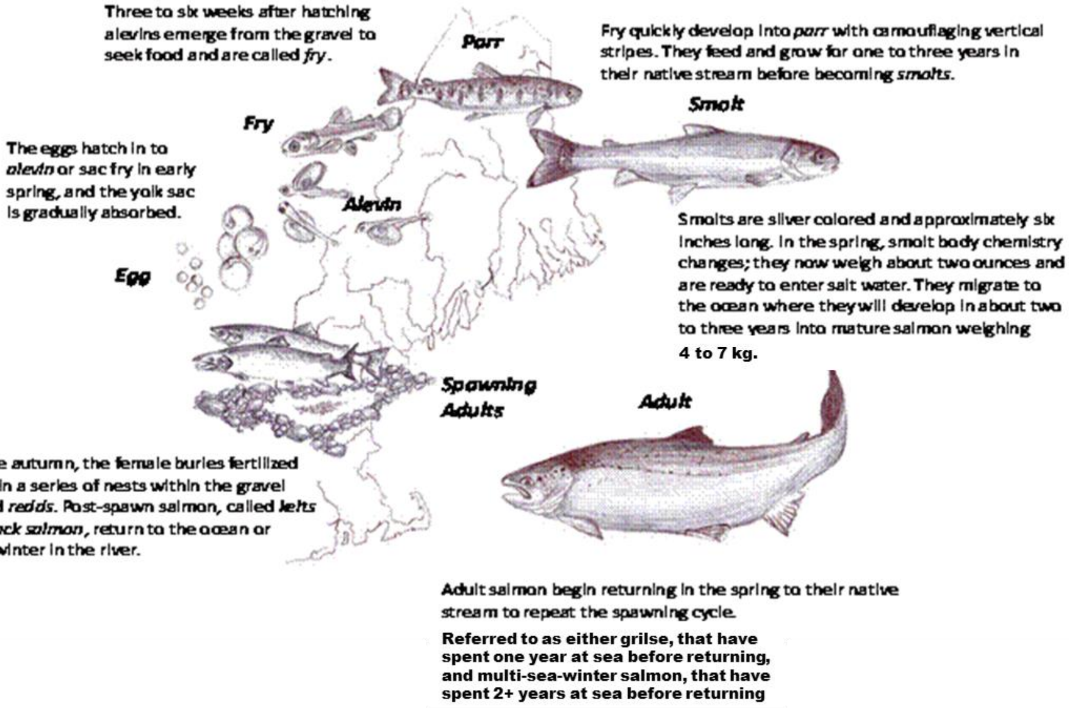


Figure 2.4. Life cycle of the Atlantic salmon. Artwork by Katrina Mueller, USFWS and Project SHARE. Adapted from U.S. Fish and Wildlife Service, 2017 and Miramichi Salmon Association, 2018. Figure available online at https://www.fws.gov/mainefieldoffice/Atlantic_salmon.html

Current status and reasons for decline

The conservation status is available for 48% of the 175 anadromous species. Of these, 30.9% are extinct or threatened (critically endangered, endangered or vulnerable) (Banbury & O’Meara, 2014). Due to having a specific life history requiring access to habitats over a large range, modification of the natural flow regime (Rolls *et al*., 2013) and barriers obstructing access to spawning grounds (Zhou *et al*., 2014) are recognised as some of the main reasons that this group of fishes are at risk. For example, wild Atlantic salmon are hugely important to the economy in recreational, commercial and subsistence fisheries (TEEB, 2009; NASCO, 2018). They have been prized for their migratory ability to return to pristine rivers and indicate a healthy ecosystem, passing seemingly impassable weirs; they are also culturally important Mawle & Peirson, 2009). They have declined throughout their range and have been lost from many areas of Europe (WWF, 2001), with a reported 90% fall in nominal catch in the past 40 years (ICES, 2017) (Figure 2.5). An anadromous life cycle requires great energy expenditure and high swimming performance, as adult migrants are required to swim against the flow in order to reach upstream spawning locations (Morais & Deverat, 2016). Hence, barriers to the migration that cause delays cause more energy to be expended and have a negative impact on populations. High market value can also lead to overfishing and destruction of populations (Morais & Deverat, 2016). The global supply of seafood is shifting from fisheries to aquaculture (FAO, 2007) and salmon in fish farms become infested with lice. Wild salmon are recognised to have declined from infestation of salmon lice from salmon farms, with an over 80% louse-induced mortality found in pink salmon (*Oncorhynchus gorbuscha* (W)) by Krkošek *et al*., 2007). Activities such as pollution, which can cause direct mortality, affect behaviour and degrade habitat; reduction in genetic diversity through anthropogenic activities, intended or unintended (farm escapes) (WWF, 2001; Vasemägi *et al*., 2005) as well as fisheries and global warming (Nicola *et al*., 2018) pose threat to salmonids.

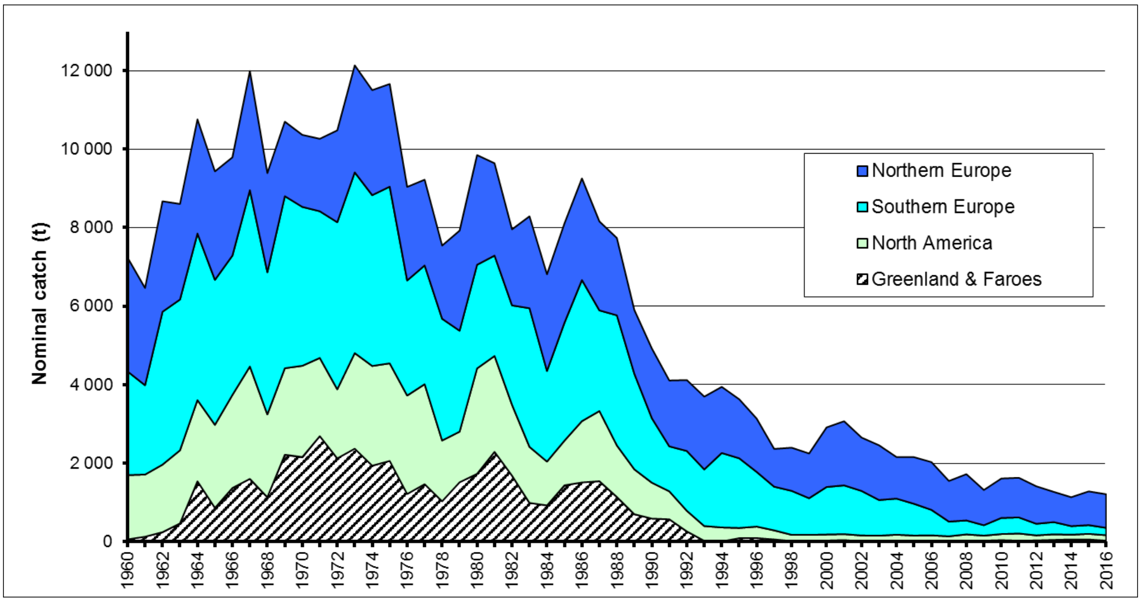


Figure 2.5. Total reported nominal catch of Atlantic salmon (tonnes round fresh weight) in four North Atlantic regions, 1960–2016. Taken from ICES, 2017).

2.4.3 Catadromy

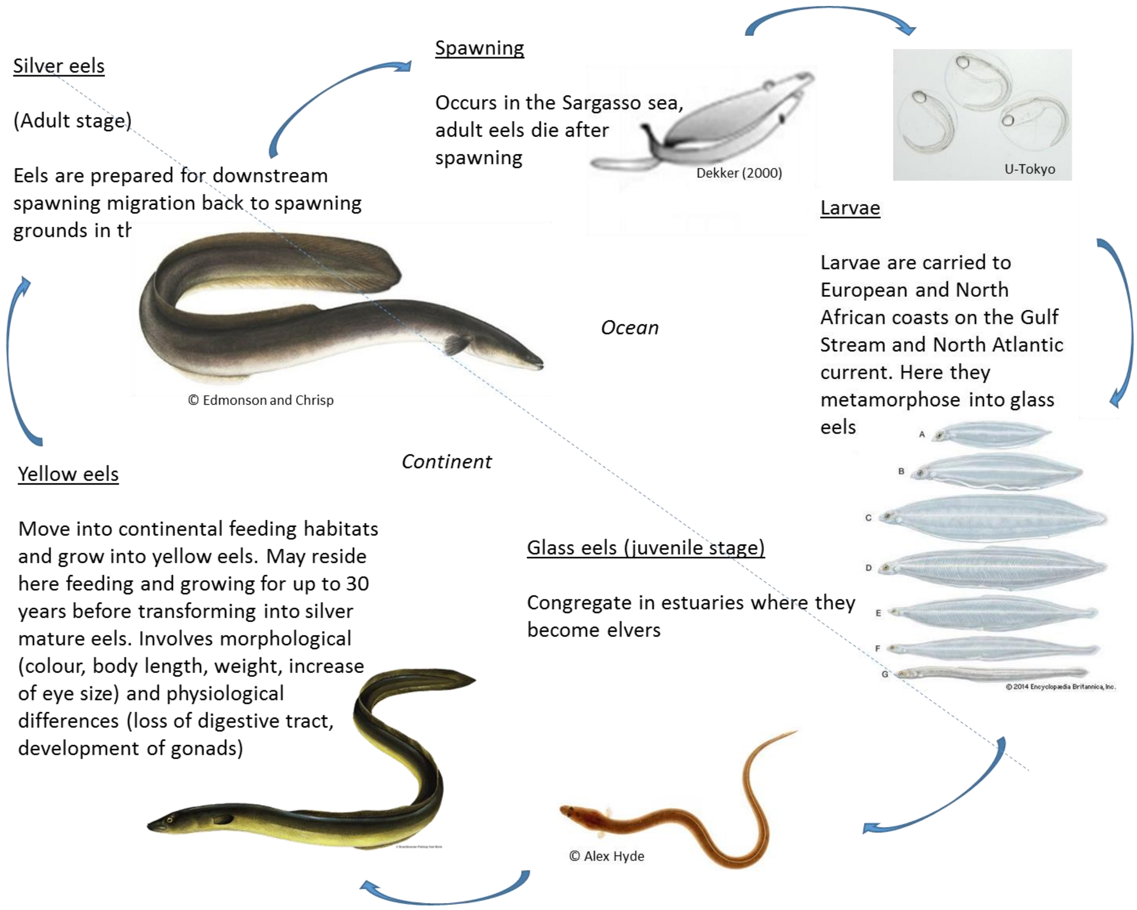
Information and distribution

Catadromous fishes are a unique subset of diadromous fishes because despite decades of research, there are less than 50 species reported (McDowall, 1987; Watanabe *et al*., 2009; Feutry *et al*., 2013). Other than eels, these species mostly contain a range of mullets, kuhliids and flatfishes; of catadromous species identified, 16 are anguillid eels, ~12 are mullets and five are kuhliids (McDowall, 1987; Watene *et al*., 2009; Feutry *et al*., 2013). Catadromous species are distributed at temperate to tropical latitudes, and the greatest are found at tropical to subtropical latitudes as a larger proportion of anugillid eels are found there (McDowall, 1997). Spawning and larval development occur in the marine environment, before migration to the freshwater habitat for feeding and growth. The spawning migration is in a downstream direction, exiting freshwater feeding grounds and returning to the oceanic spawning grounds as adults. Many catadromous species also display plasticity in the life history, particularly in terms of how much they use the pure freshwater environment (Tsukamoto *et al*., 2001). Anguillid eels can also display facultative catadromy, where some individuals remain in the ocean for juvenile growth (e.g. Tsukamoto & Arai, 2001; Daverat *et al*., 2006). Distance of migrations into the ocean varies widely, with anguillid eels being the most distinct and iconic, covering distances of up to 6,000 km (van den Thillart, Palstra & van Ginneken, 2009) to spawn. Other catadromous fishes differ to anugillid eels in that they migrate to just the nearshore waters where the water body becomes saline within estuaries (McDowall, 1988) and there is little evidence of any spawning areas far out in the ocean like anguillid eels (McDowall, 1987; 1988; 1997; Lucas & Baras, 2001). This makes the catadromous anguillid life history unique (Morais & Deverat, 2016).

Globally, there are 19 species of freshwater eel in the genus *Anguilla*, which are often cited as examples of large–scale migration; anguillid eels will be used as an example here. Eels, as well as other catadromous species, are highly valuable commercially (Tsukamoto 2001; Ringuet *et al*., 2002; Morais & Deverat, 2016) and are ecologically important as they are considered to be good ecological indicators of water quality due to their longevity, relatively sedentary lifestyle in catchments, and the fact that they are a key species in many aquatic food webs, feeding on a wide variety of prey and providing food to other species (e.g. Ruddock *et al*., 2003). All anguillid eels are thought to be semelparous and die after spawning (Tesch, 2003). Other species have apparently overall larger variation in life history patterns than anguillid eels (McDowall, 1988)

Species example and information

Although anguillid eels breed in a number of areas, they all carry out the same life cycle as the European eel (Figure 2.6). Eels metamorphose from the larval planktonic ‘leptocephalus’ into transparent ‘glass eel when nearing the continent and are called ‘elvers’ once the skin develops pigmentation. Juvenile eels reach the continent as either glass eels or elvers depending on the time taken for the journey and enter rivers where they will reside and feed as ‘yellow eels’ until it is time to return to the ocean spawning grounds. Accumulation of enough fat for the migration, gonadal development (Tesch, 2003) and appropriate environmental conditions (Brujis & Durif, 2009) trigger the onset of sexual maturity. During this process, eels transform from yellow eels into migratory ‘silver eels’. This transformation has been described as a second metamorphosis. However, Aroua *et al*., (2005) found that due to significant hormonal changes, silvering should be considered as an onset of puberty. Nevertheless, the transformation encompasses many significant changes that result in remarkable functional and ecological changes for the eel (Lokman, 2016) to prepare for survival during the oceanic migration. The body colour becomes silver due to differentiation of pigment cells (Pankhurst & Lythgoe, 1982) which increases countershading (Han *et al*., 2003). Eyes also increase in size, gonads develop and there are changes to the gut, muscle, heart, swimbladder (Lokman, 2016) and stomach (Tsukamoto *et al*., 2014). Having already acquired tolerance to salinity whilst in freshwater, behaviour also changes as feeding ceases and eels move downstream (Brujis & Durif, 2009). The most significant influence on eel movements during the downstream migration has been reported to be high flow but also hours of darkness and the dark moon, which is hypothesized to be an anti-predator mechanism (Sandlund *et al*., 2017; Huisman *et al*., 2016). Water level and temperature are also contributing factors (Vollestad *et al*., 1994; Durif & Elie, 2008) and all of these factors may interact (Sandlund *et al*., 2017).



Silver eels

(Adult stage)

Eels are prepared for downstream spawning migration back to spawning grounds in th

Spawning

Occurs in the Sargasso sea, adult eels die after spawning

Larvae

Larvae are carried to European and North African coasts on the Gulf Stream and North Atlantic current. Here they metamorphose into glass eels

Glass eels (juvenile stage)

Congregate in estuaries where they become elvers

Yellow eels

Move into continental feeding habitats and grow into yellow eels. May reside here feeding and growing for up to 30 years before transforming into silver mature eels. Involves morphological (colour, body length, weight, increase of eye size) and physiological differences (loss of digestive tract, development of gonads)

Figure 2.6. The life cycle and habitat use of the European eel, adapted from Jacoby & Gollack, (2014); Pujolar *et al*., (2015).

The mysterious life cycle of eels has fascinated biologists for many generations, and numerous studies have been conducted to better understand the specifics of the spawning migration. Eels may exclusively inhabit the marine environment (Tsukamoto *et al*., 2001); this would mean that they performed an oceanodromous migration. Marine resident eels may be explained by interspecific competition for resources in freshwater habitats leading to more resources being provided as a result of residing in the marine environment (Moriarty, 1978). Despite this plasticity, it is recognised that a catadromous life history is probably dominant in anguillid eels (Lucas & Baras, 2001). Tsukamoto *et al*., (2001) discuss whether entering rivers for the feeding stage is determined by genetics or behavioural plasticity, as the marine breeding habitats are probably a traditional trait from the marine ancestor from which anguillid eels orginate (Tsukamoto & Aoyama, 1998). Despite this variability, generally for fish to be considered catadromous they must migrate to the brackish or marine environment to spawn, with larvae feeding and growing in these habitats before entering estuaries or freshwater as juveniles for growth until maturity (Morais & Deverat, 2016).

Current status and reasons for decline

The decline of temperate species of eel is perhaps one of the most evident examples in recent years of the negative impact that humans have on a freshwater resource. Several species are now listed on the International Union for the Conservation of Nature (IUCN) Red List as endangered; American and Japanese ((*Anguilla japonica* (Temminck & Schlegel)) or critically endangered (European eel) (IUCN, 2014) after the decline in stocks of juveniles (Figure 2.7). For European eel, numbers have drastically dropped to just 5% of what they were in the 1960s and 1970s. ICES also advise that the stock is outside safe biological limits and that current fisheries are not sustainable (ICES, 2017). Although the species found in New Zealand (Shortfinned and Longfinned eel ((*Anguilla dieffenbachii* (Gray)) have not yet been evaluated by IUCN, the threats to eels of the Southern hemisphere are said to be the same as proposed for European eels and other temperate species (Feunteun, 2002; Lokman, 2016). Further, it is recognised in New Zealand that eel habitat loss is occurring and there has been a decline in glass eel and elver recruitment (Jellyman *et al*., 2002). A catadromous life history covering vast distances and a broad range of habitats makes eels particularly vulnerable to anthropogenic pressures that create barriers and affect movement between habitats (Bruijs & Durif, 2009; Calles *et al*., 2010; Marohn, Prigge & Hanel, 2014).

Barriers, particularly to adult downstream migrants attempting to exit the freshwater catchment, are recognised as being a major contributing factor to global eel declines (Dekker *et al*., 2016). They are sometimes in the form of turbines that must be safely navigated in order to exit the catchment but that can cause mortality associated with passage (Jansen *et al*., 2007). For example, a study on eel mortality in Canadian waters estimated that 75% of all anthropogenic American eel mortality is caused by hydroelectric dams (COSEWIC, 2012). Further, such infrastructure causes long delays to the migration (Winter *et al*., 2006) which could deplete fat reserves and consequently reduce chances of successfully reaching spawning grounds (Acou *et al*., 2008; Piper *et al*., 2013; Eyler *et al*., 2016; Dainys *et al*., 2017) as eels require enough fat reserves for oocyte development before spawning, and to travel the distance of the migration without feeding, as they are not fully developed at the time of maturation (Lokman *et al*., 1998) after an already energetically costly silvering transformation (Crook *et al*., 2014). There are multiple studies that generally accept that silver eels exit rivers in autumn to spawn as a single reproductive cohort the following spring (e.g. Vøllestad *et al*., 1986; Tesch, 2003; Miller *et al*., 2015; Capoccioni *et al*., 2014). However, findings from eel migrations leaving from several European coastlines using satellite telemetry demonstrated that many eels undertake a slower paced migration than that generally accepted in the literature, which enables them to reach the Sargasso spawning area before spawning begins again the following December (Righton *et al*., 2016) Durif *et al*., (2005) also discusses that the silvering process is actually more flexible than it was thought. This complicates management, but it is known that mature silver eels can revert back to yellow eels in response to delays (Svedang & Wickstrom, 1997). Despite this flexibility, multiple eel species are threatened worldwide, indirect impacts of delays at barriers such as increased predation risk and the worsening of diseases (if present) due to stress make this process potentially unfavourable (e.g. Garcia De Leaniz, 2008; Forty *et al*., 2016) and may further contribute to their decline. In terms of efficient passage (see section 2.6.1), it would obviously be best if eels, when mature, could exit the catchment without long delays and complete their spawning migration.

Other factors contributing to the worldwide decline of eels are climate change, changes in oceanic currents disease and parasites, exploitation at every phase of the life cycle, habitat loss, pollutants, predation and depleted body condition (e.g. Dekker *et al*., 2014), causing reduction of fitness (Tsukamoto *et al*., 2001; Baltazar-Soares *et al*., 2014; Hanel *et al*., 2014; Dainys *et al*., 2017). For European eel reduction of fitness can be caused by the swimbladder parasite *Anguillicola crassus* (Newbold *et al*., 2015), which reduces swimming performance and is proposed to consequently affect likelihood of reaching the spawning grounds (Barry *et al*., 2014).

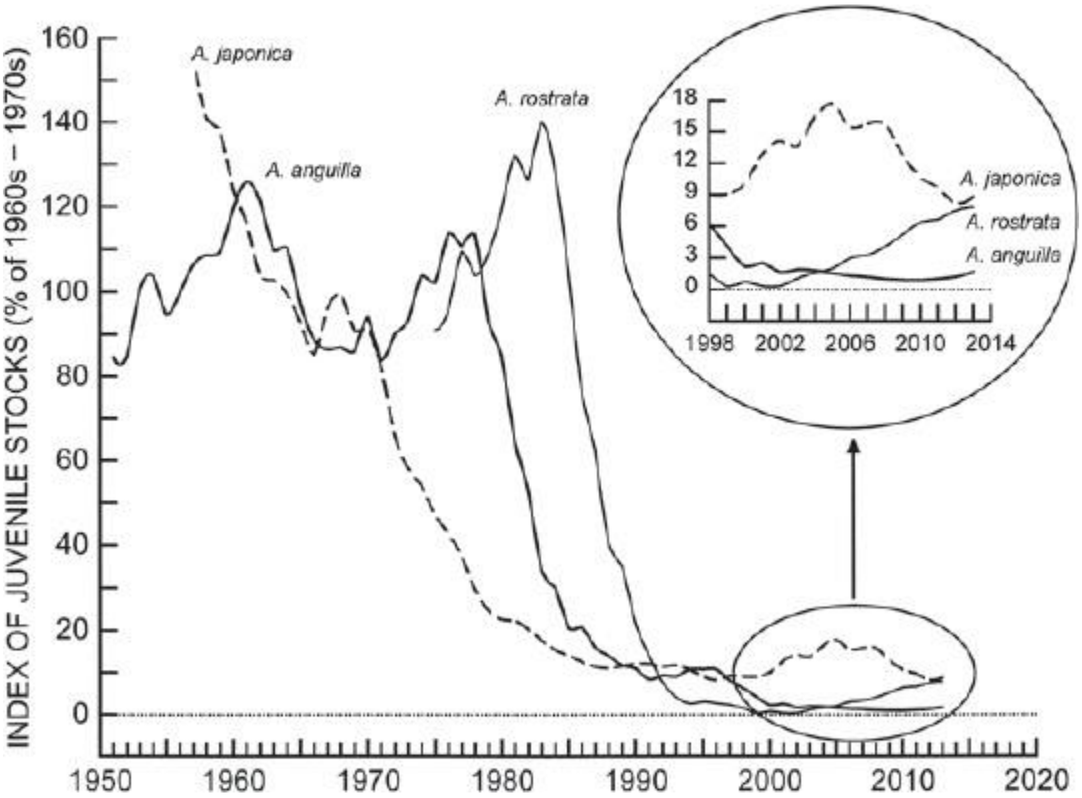


Figure 2.7. Time trends in abundance of major juvenile eel stocks of the world. Taken from Dekker & Casselman, (2014).

2.4.4 Summary

This section overviewed three of the main types of migration, with particular emphasis on spawning migrations and related environmental factors that allow habitats required for different life stage to be exploited. Although the spawning migrations of potadromous fish species within freshwater such as brown trout, are small in distance when compared to the transoceanic migrations of catadromous species such as the European eel, these migrations are just as important to enable completion of life cycles (Lucas & Baras, 2001) and all migratory fish require free movement between habitats throughout their ontogeny. The increasing demands on rivers as a result of climate change, the growing human population and resultant increase in anthropogenic pressures makes migratory species especially vulnerable to extinction or decline as they are affected by changes in inhabited ecosystems and consequently along migration routes (Runge *et al*., 2014), with barriers to the migration being particularly impactful. Research to better understand the behaviour of migratory fish in modified rivers is required in order to alleviate the pressure of barriers to spawning migrations of fish.

2.5 River modification and its effect on spawning migrations

Importance of rivers for humans and consequent modifications

As well as supporting fish to carry out complex life histories, rivers have been integral to the growth of society and the human population, with almost the whole population relying on freshwater sources for the variety of services they provide (Vorosmarty *et al.,* 2010). Historically, water was one of the first methods for driving machinery and transporting goods that did not involve the use of animals (Cowx & Welcomme, 1998). Through modification of waterways throughout the catchment, different areas have been utilized to meet water, energy and transportation needs for centuries, resulting in many anthropogenic pressures and alterations to freshwater systems (Nilsson *et al.,* 2005). Industrial processes have required on a reliable source of water, and society requires water for drinking and hygiene. Humans have accessed, exploited and inhabited areas that were once inaccessible such as those below sea level. In order to utilise rivers and flow for these uses, weirs and dams are often installed to divert the flow or hold back water and are increasingly installed in response to urbanization, rapid agricultural and economic development coupled with an unpredictable climate (World Commission on Dams, 2000; Lucas & Baras, 2001). This considerably reduces riverine flows (Cowx & Welcomme, 1998) and consequently removes or alters the natural flow regime. Free-flowing rivers are vital for people in developing areas where millions of tons of fish are harvested (Opperman, *et al*., 2015), yet only 36% of the world's rivers longer than 1,000 km are free-flowing. The rest (and majority) of the world's rivers are extensively modified or fragmented for anthropogenic benefit, with plans for more than 3,500 new dams in Asia, Africa and South America as the human population grows and the socio-economic status shifts (Brink *et al*., 2018). Many migratory freshwater fish are now endangered or nearly extinct (IUCN, 2017) with a major well accepted cause being threats from increasing human activities that create barriers to migration that make access to spawning grounds increasingly difficult. This has resulted in increasing controversy over construction of dams in developed countries (Jellyman & Harding, 2012, and references therein).

Impact of river modification on fish spawning migrations

As well as aforementioned endogenous (genetic, physiological, metabolic) factors determining the evolution and ability of fish to migrate (Foreseth *et al*., 1999; Acolas *et al*., 2012), migratory behaviour is intrinsically linked to the environment that fish have adapted to survive in. Migratory fish need longitudinal connectivity throughout the range of habitats required in order to complete their life cycles. Many migratory species are adapted to synchronize their behaviour with specific flow patterns such as peak floods in spring/winter or low flows in summer, with patterns providing cues for dispersal, migration and reproduction, feeding and predator avoidance as resources become available (Lehner *et al*., 2011) and all are recognised as being necessary for ecosystem functioning (Junk, Bayley & Sparks, 1989; Richter *et al*., 1996; Poff *et al*., 1997). In temperate regions there is a distinct seasonality in photoperiod and temperature which provides seasonal peaks in productivity; these seasons are much more extreme in arctic regions which results in highly distinct migratory patterns. In tropical and subtropical regions there is less seasonality, so required resources such as floods are less available to fish (Lucas & Baras, 2001). In a review by Poff *et al*., (2010) on the ecological responses to flow regime change, 17 papers reported negative responses of fish. These all reported disruption of fish spawning cues, in response to a shift in timing of peak flows (n = 12) and to increased predictability of flows (n = 5). Similar findings were found in a review by Webb *et al*., (2013). This highlights the complex relationship between spawning fish and the flow regime, and the need for flows to be available that provide the cues and opportunities for spawning. Thus, the potential for negative impacts of alterations to flow patterns on fish are obvious, through disruption of life cycles and ecological processes (Lehner *et al*., 2011).

Considering this, barriers to migration created by lack of flow or physical barriers in the form of weirs, dams and associated infrastructure upset the delicate, vital balance between fish and their ecosystems. Barriers in any form cause significant delays to migrating fish. This can worsen the onset of diseases (if present) due to stress (Garcia De Leaniz, 2008), increase predation risk (Forty *et al*., 2016), and ultimately prevent fish from reaching spawning grounds or cause fish to arrive at spawning grounds at unfavourable times (Eyler *et al*., 2016). Despite migration barriers often being thought of as localised structures (Silva *et al*., 2018), the concept can be extended to anything that causes a reduction in fitness both during and after passage (Castro-Santos, Cotel, & Webb, 2009).

The current situation leaves water resource managers today in a difficult position when attempting to balance the complex needs of the riverine ecosystem with those of society. In order to alleviate the pressures of barriers to fish migration, the behaviour of the species in question needs to be understood so that mitigation measures can be targeted. Those significant modifications to waterways and impacts of associated barriers that are relevant to the thesis will be discussed throughout this section, namely impoundments, particularly reservoirs, dams, hydropower stations and pumping stations.

2.5.1 Impoundments and dams

Impoundments are large bodies of water constructed by dams that impound or divert part or all of riverine flow, consequently also eliminating peak flows and stabilizing low flows (Lehner *et al*., 2011). A dam is defined as a concrete or earthen barrier constructed across a river and designed to control water flow or to create an impoundment, where a weir is a dam on a river to stop and raise the water level for the purpose of conveying it to a mill, forming a fish pond, or similar (IFC, 2018). One type of impoundment is a reservoir, which will be used as an example here. Reservoirs are constructed for potable, agricultural or industrial supply; flood control, irrigation, generation of electricity, recreation, navigation and development (Avakyan & Lakovleva, 1998; WCD, 2000; British Dam Society, 2018). There are 16.7 million reservoirs worldwide larger than 10 km^2 and estimated to be ~2.8 million larger than 0.001 km^2 (Lehner *et al*., 2011). Reservoirs are most commonly constructed by damming the natural watercourse, created between hills or mountains that act as walls to hold the water; the second method is created by draining a lake using a dam on a stream to allow water to collect at a different location and create a reservoir-lake; the third being a pumped-storage reservoir located in a geomorphological depression which also requires a dam to retain water (Avakyan & Lakovleva, 1998). Reservoirs exist on all continents, all altitudes and range in size, with the total capacity of stored water behind dams in Africa being 997.2 km^3 compared 95.5 km^3 in Australia (See Lehner *et al*., 2011 for a detailed review) (Figure 2.8).

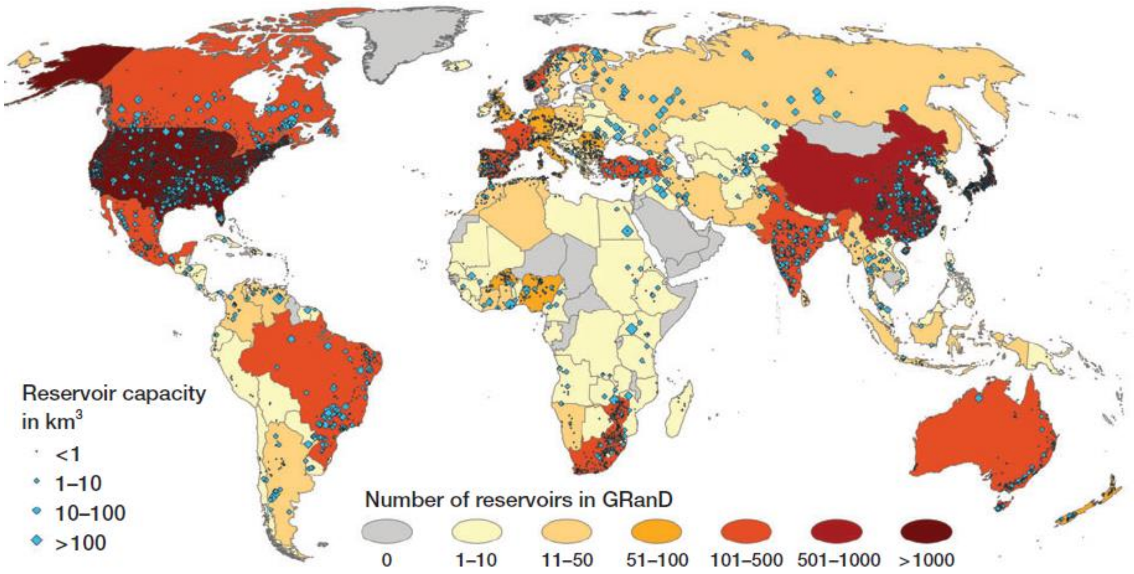


Figure 2.8. Global distribution (by country) of large reservoirs included in the Global Reservoir and Dam database (GRanD). Taken from Lehner *et al*., (2011).

Barriers created by dams and impoundments

Dams and impoundments (including reservoirs) create barriers to migratory fish by physically obstructing the river and consequently blocking longitudinal connectivity. This impedes upstream movement of anadromous and potamodromous species and downstream movement of catadromous species, both juveniles and adults by preventing them from completing life cycles when habitat required for different life stages is either side of the barrier. Impoundments, including reservoirs extend longitudinally and horizontally over a far greater distance than dams (Pelicice *et al*., 2015). This creates a behavioural barrier to juvenile and adult fish requiring downstream passage, as they likely lack the required orientation for downstream migration across the long stretch of water between upper areas of reservoirs and the dam in the lower area (Thornton *et al*., 1990; Pelicice *et al*., 2015). Juvenile fish may be prevented from dispersing and colonising new patches, which is essential for populations to persist in habitats (Nilsson *et al*., 2005; Travis and Dytham, 1999). Adult potamodromous and diadromous fish that do successfully ascend dams and enter a reservoir must also exit in order to migrate either up or downstream for feeding or reproduction. During seasonal migration periods, large numbers of juvenile fish have been reported to be pumped into reservoirs as a result of impingement (e.g. Ketelaars *et al*., 1998) Young fish that drift downstream to disperse and find appropriate habitat for feeding and growth as part of the life cycle, such as cyprinids in Europe (Reichard *et al*., 2001) and Atlantic salmon, white sucker ((*Catostomus commersoni* (Lacepède, 1803), Cyprinidae, and sea lamprey (*Petromyzon marinus* L.) in North America (Johnston, 1997) may be prevented from doing so due to the absence of the natural flow regime and infrequency of suitable flows (Pelicice *et al*., 2015). If fish are not aiming to drift downstream due to the risk associated with dispersing to new habitats, e.g. if there is a low amount of suitable habitat (e.g. Bowler *et al*., 2005), unnatural flows could cause fish to be washed out and/ or stranded (e.g. Greimel *et al*., 2015). If the reservoir operates using turbines to move water from one place to another, this may result in fish being impinged or entrained into turbines when searching for an exit, which can cause injury or direct mortality (see sections 2.5.2 and 2.5.3). Fish passes, or ‘fishways’ may facilitate up and downstream passage yet many are ineffective (Noonan *et al*., 2012; Brown *et al*., 2013) (see section 2.6).

If efficient passage solutions are not in place and fish are trapped in the reservoir or above/ below dams, migrations can be delayed, which can result in cessation of migration in adults (Aarestrup & Koed, 2003; Bolland *et al*., 2018) and cause aforementioned negative impacts from delays (see previous section). For juveniles, they can be prevented from accessing areas required for growth, which may increase predation risk and result in competition for resources (Freeman *et al*., 2001). Further, juvenile young-of-year fishes depend on stable habitat conditions for survival, and have previously been found to have reduced habitat persistence downstream of a hydropower dam which can reduce the persistence of native fishes in systems where flow is regulated (Freeman *et al*., 2001). Sometimes, reservoirs such as those associated with hydropower genration have spillways that can provide downstream passage; these have higher survival rates than exiting reservoirs via moving parts, i.e. turbines, or deep-water regulating outlets due to associated risk of injury or mortality (Cowx & Welcomme, 1998; Coutant & Whitney, 2000; Keefer *et al*., 2011). However, adult upstream migrants can repeatedly fall back over spillways, which in itself can result in injury or death and migration delays (Boggs *et al*., 2011).

Considering the aforementioned impacts, species can be lost from areas upstream of the dam / impoundment unless passage is provided (Cowx & Welcomme, 1998) as access to feeding and spawning grounds is prevented (Anderson *et al*., 2015). Longitudinal connectivity is required to facilitate ecological processes such as dispersal, migration and energy transfer along river networks, making freshwater biodiversity dependent on the capacity to maintain all such processes (Hermoso *et al*., 2018). Hence, fragmentation or disruption of longitudinal connectivity caused by dams and reservoirs has been responsible for significant declines in biodiversity (Vörösmarty *et al*., 2010) due to a number of contributing factors (

Table 2.1; McAllister *et al*., 2001).

Table 2.1. Impacts to freshwater biodiversity that are caused by dams and their associated reservoirs

• Blocking movement of migratory species up and down rivers, causing extirpation or extinction of genetically distinct stocks or species
• Changing riverine turbidity/sediment levels that species/ecosystems are adapted to affects species adapted to natural levels. Trapping silt in reservoirs deprives downstream deltas/estuaries of maintenance materials/nutrients that productive ecosystems require
• Filtering out of woody debris which provides habitat and sustains a food chain
• Changing conditions in rivers flooded by reservoirs: running water becomes still, silt is deposited, deepwater zones, temperature and oxygen conditions are created that are unsuitable for riverine species
• Providing new habitats for waterfowl in particular for overwintering or in arid regions which may increase their populations
• Possibly fostering exotic species. Exotic species tend to displace indigenous biodiversity
• Reservoirs may be colonised by species which are vectors of human and animal diseases
• Flood plains provide vital habitat to diverse river biotas during highwater periods in many river basins. Dam management that diminishes or stops normal river flooding of these plains will impact diversity and fisheries
• Changing the normal seasonal estuarine discharge which can reduce the supply of entrained nutrients, impacting the food chains that sustain fisheries in inland and estuarine deltas
• The cumulative effects of a series of dams, especially where the impact footprint of one dam overlaps with that of the next downstream dam(s)
• Modifying water quality and flow patterns downstream
• Other human activities, including agriculture, forestry, urbanisation and fishing, although these are primarily land-based.

Modification or removal of the natural flow regime

Flow regulation is one of the main ecological impacts caused by dams (Poff *et al*., 1997; Bunn & Arthington, 2002). Dams can hold back a high proportion if not all of the flow in a catchment for prolonged periods of time (Acreman *et al*., 2010) causing absence of or reduced frequency of flows than what would be experienced in the natural river. Consequently, floods and inter-annual, seasonal, weekly and hourly runoff flow redistribution are decreased or completely removed, which significantly transforms the river (Avakyan & Lakovleva, 1998). Often the water is managed in terms of minimum needs to meet ecological objectives which will vary site-by-site, i.e. the minimum flows required to keep water flowing over habitat (Acreman & Ferguson, 2010). In these cases, a uniform, ‘flatline’ compensation flow which does not replicate the natural flow regime (Figure 2.9) or a very small constant flow is all that is provided to rivers. In some cases, the only flow received may be to meet the needs of specific species of faunal groups, which is not suitable for all flora and fauna and hence does not maintain ecological integrity. Apart from this or if mitigation is in place that aims to replicate the natural flow regime to maintain ecological integrity (see section 2.6.5), the only other flow received by rivers downstream results from reservoirs overspilling if they are at capacity during high flow events. Removal of the flow regime also prevents associated habitat from receiving necessary flows for habitat maintenance and other functions, whilst allowing opportunistic vegetation to flourish; this in turn creates slower flow conditions, decreases the scouring action of the flow and encourages deposition of finer sediment due to inhibition of bed material movement (Cowx & Welcomme, 1998; Lucas & Baras, 2001).

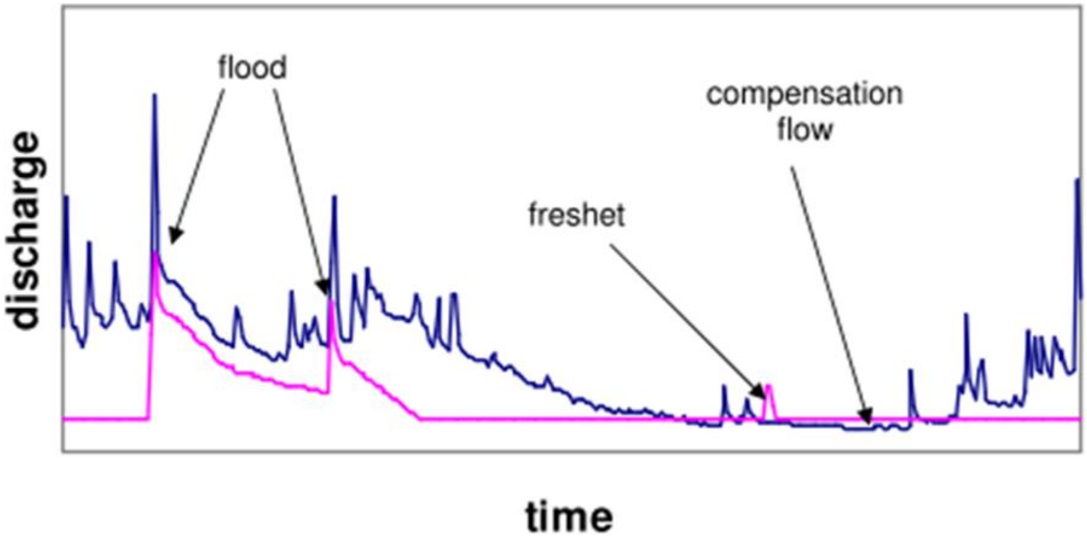


Figure 2.9. Hypothetical flow regime including natural flows (blue) and flow experienced in a regulated (pink) regime where the compensation flow and freshet releases are managed,that would typically be experienced downstream of a water supply reservoir (taken from Dunbar *et al*., 2008).

Other negative effects on migratory fish

The water released from reservoirs can be cooler than that in the river, if they are constructed in deep valleys. This can result in reduced species diversity and replacement of fish communities if the new temperatures are different to those required by inhabiting species (Lucas & Baras, 2001). Such temperature shifts reduce the naturally high degree of seasonal and temporal variation in rivers, with stream temperatures downstream of reservoirs being higher in winter and lower in summer

(Cowx & Welcomme, 1998; Lucas & Baras, 2001). These changes can also remove thermal signals that are essential for certain behaviours such as spawning, swimming ability and fish growth in different species (Cowx & Welcomme, 1998; Lucas & Baras, 2001). Further, gravels are trapped in reservoirs; this is particularly detrimental for species that require them for spawning such as salmonids and barbel (Cowx & Welcomme, 1998) when they are removed and the reservoir prevents them from being replenished.

2.5.2 Hydropower generation

Hydroelectric power, where power is generated by using the energy from falling water to drive water turbines that in turn drive electric generators, provides almost one-fifth of the world's electricity (Paish, 2002) and has risen steadily over the past 10 years but has always contributed the most renewable power capacity. Being a renewable energy source, it is rapidly gaining importance (Zarfl *et al*., 2015) and is considered the most important renewable electricity source worldwide (Bratrich *et al*., 2004) as global targets for renewable energy increase. Under the United Nations Sustainable Development Goals 7: affordable and clean energy, the global targets for achievement by 2030 include "universal access to affordable, reliable and modern energy services, a substantial increase in the share of renewable energy in the global energy mix and to enhance international cooperation to facilitate access to clean energy research and technology, including renewable energy, energy efficiency and advanced and cleaner fossil-fuel technology, and promote investment in energy infrastructure and clean energy technology" (UNDP, 2018). In the EU, legislation requires 20% of energy production to be from renewable sources by 2020, which further increases the interest in hydropower (EPCEU, 2009).

Of 37,600 dams higher than 15 m reported worldwide in 2011, more than 8,600 were primarily for hydropower generation (International Commission on Large Dams, 2011). There are plans to build many more, especially in the Amazon, Congo and Mekong, which are the world's most biodiverse river basins (Winemiller *et al*., 2016) as well as on other continents (Figure 2.10).

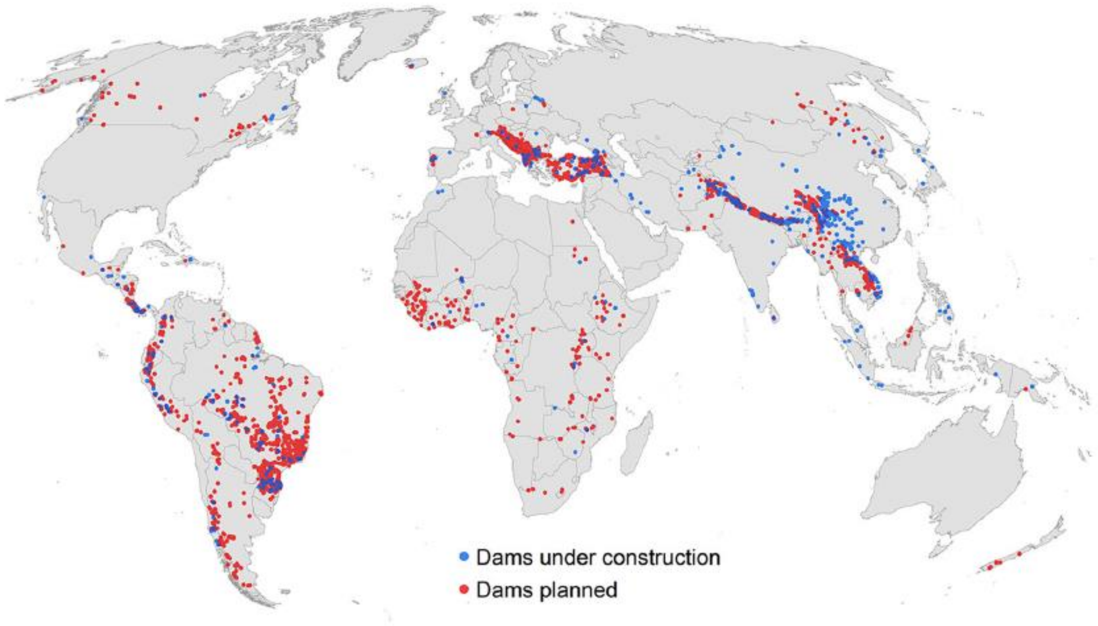


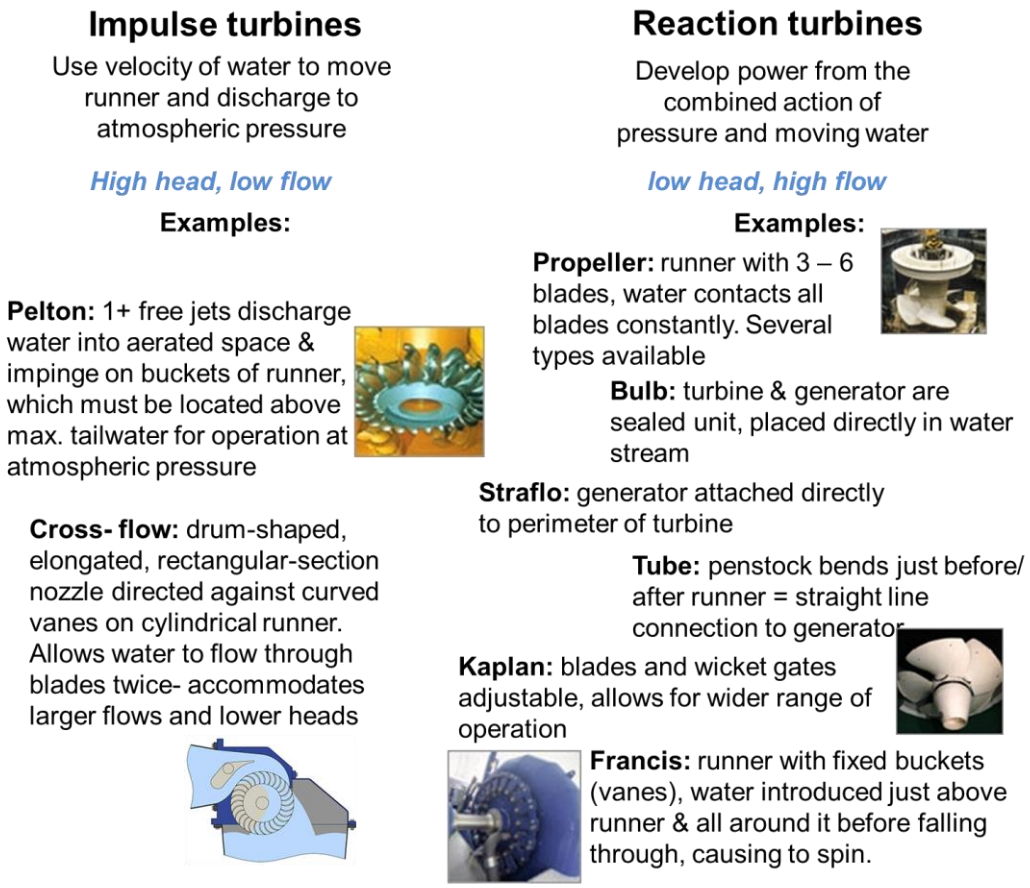
Figure 2.10. Global spatial distribution of future hydropower dams, either under construction (blue dots 17 %) or planned (red dots 83 %). Taken from Zarfl *et al*., (2015). Full details of data collection and processing on hydropower dams available in the reference.

Being renewable, hydropower is often environmentally preferred over fossil fuels or nuclear power (Renofault *et al.,* 2010). However, there are still significant environmental impacts that must be taken into consideration for it to be considered carbon-neutral, including construction costs and loss of terrestrial vegetation, fuel types used, average consumption and emission loads from equipment and machinery and emissions and CO2 (IFC, 2018). After construction, impacts to fish and other biota must also be considered, as potential impacts include changes in stream water flow, velocity and depth, timing, duration, abruptness of transition and predictability of flow regimes due to project activities; habitat fragmentation in watersheds; aggravation of existing soil erosion rates due to project activities; modification of quality of water in streams; changes in pH and elevated levels of turbidity, total suspended and dissolved solids, potentially causing fish kills and depletion of species richness and infrastructure creating barriers to fish migration (see IFC, 2018). As a result of these potential impacts, it may not be considered green energy in terms of the health of rivers and inhabiting biota (e.g. Rosenberg *et al*., 1995; Ausubel, 2007).

Large hydropower schemes are generally coupled with large impoundments whereas small scale schemes are ‘run-of-river’ (Robson, 2013) and do not require water to be stored but a weir or dam is installed to divert some of the flow to drive turbine(s) before water is returned downstream (Robson, 2013; Anderston *et al.*, 2015). Run-of-river schemes vary in design as they are tailored to the geography, historical use and modification of the water body (Anderson *et al.*, 2015). They are recognised as being one of the most cost-effective and the main prospect for future developments in Europe after recognition that large-scale opportunities have already been exploited or would no longer be deemed environmentally acceptable (Paish, 2002). Run-of-river schemes can utilise a low, medium or high head of water in order to power turbines. Low head schemes have been defined as using a head of water between 5-25 m but also less than 10 m and are said to vary with turbine size (Paish, 2002), and occur in lower gradient river reaches, medium-head use a head of water between 25-50 m and high-head 50 m+, the latter of which are limited to high-gradient, upland rivers (Anderson *et al.*, 2015). The head of water is the change in water levels between the intake and the discharge point of the hydropower scheme, and is a vertical height measured in metres, with more head meaning more water pressure across the turbine(s) and consequently more power being generated (Hogan, 2005; Renewables First, 2015).

Common turbine types

There are several turbine types, specifically designed for their application, i.e. impulse turbines are designed to operate at high head, low flow such as in large scale schemes, and reaction turbines that are designed for low-head, high flow application such as run-of-river schemes (Figure 2.11). Run-of-river schemes are generally said to generate power using ‘fast’ rotation impulse (high head) or reaction (low head) turbines (BHA, 2005).



Impulse turbines

Use velocity of water to move runner and discharge to atmospheric pressure

High head, low flow

Examples:

Pelton: 1+ free jets discharge water into aerated space & impinge on buckets of runner, which must be located above max. tailwater for operation at atmospheric pressure

Cross- flow: drum-shaped, elongated, rectangular-section nozzle directed against curved vanes on cylindrical runner. Allows water to flow through blades twice- accommodates larger flows and lower heads

Reaction turbines

Develop power from the combined action of pressure and moving water

low head, high flow

Examples:

Propeller: runner with 3 – 6 blades, water contacts all blades constantly. Several types available

Bulb: turbine & generator are sealed unit, placed directly in water stream

Straflo: generator attached directly to perimeter of turbine

Tube: penstock bends just before/ after runner = straight line connection to generator

Kaplan: blades and wicket gates adjustable, allows for wider range of operation

Francis: runner with fixed buckets (vanes), water introduced just above runner & all around it before falling through, causing to spin.

Figure 2.11. Types of typical Hydropower Turbines. Figure created from information in EERE, (2018), available online at https://www.energy.gov/eere/water/types-hydropower-turbines. Crossflow turbine diagram available from https://ossberger.de/en/hydropower-technology/ossbergerr-crossflow-turbine/.

Risk of entrainment or impingement

Despite intakes of hydropower turbines being screened to prevent debris being drawn in (Barnthouse, 2013), passage through turbines can potentially result in direct mortality (Larinier *et al*., 2008) or severe injury that will inhibit successful completion of the migration. Fish can be trapped or ‘impinged’ onto screens, or pulled or ‘entrained’ into turbines if the spacing of the bars on the screen are large enough to allow entry. Small diameter turbines are reported to be most damaging to downstream migrating fish (Watene & Boubee, 2005, and references therein). Injury and mortality rates vary from site to site, depending on turbine type, size, local hydraulic conditions, power station configuration, number and spacing of blades, rotation speed, water head and generation levels, and are also affected by fish size and behaviour, with downstream migrating eels being reported to have a higher mortality rate than juvenile salmonids due to their elongate body; this as well as low flow through turbines is recognised as the most damaging to eels (Larinier *et al*., 2008; Smith *et al*., 2017, and references therein; Yang *et al*, 2018). Damage during passage through turbines depends on the design of the turbine; typical hydropower turbines such as Kaplan or Franics have gaps between the blades and the turbine casing where fish can get caught, with small designs that spin fast to produce the most energy for the lowest cost being recognised as the most damaging (Spring, 2010). Kaplan turbines typically have five or six blades, Francis can have up to 18, which increases the risk of blade strike and injury to fish (Spring, 2010). Injuries can be caused by pressure increase or drop and effects to the swimbladder, cavitation, mechanical strike, scratch/ grinding, shear stress or turbulence (Figure 2.12), as well as potential damage caused in the outfall if it is not safe (i.e. too shallow) when fish exit (Lucas & Baras, 2001; Yang *et al*., 2018). Turbines are also used in some reservoirs so pose risks to migratory fish attempting to exit these impoundments (see section 2.4.1).

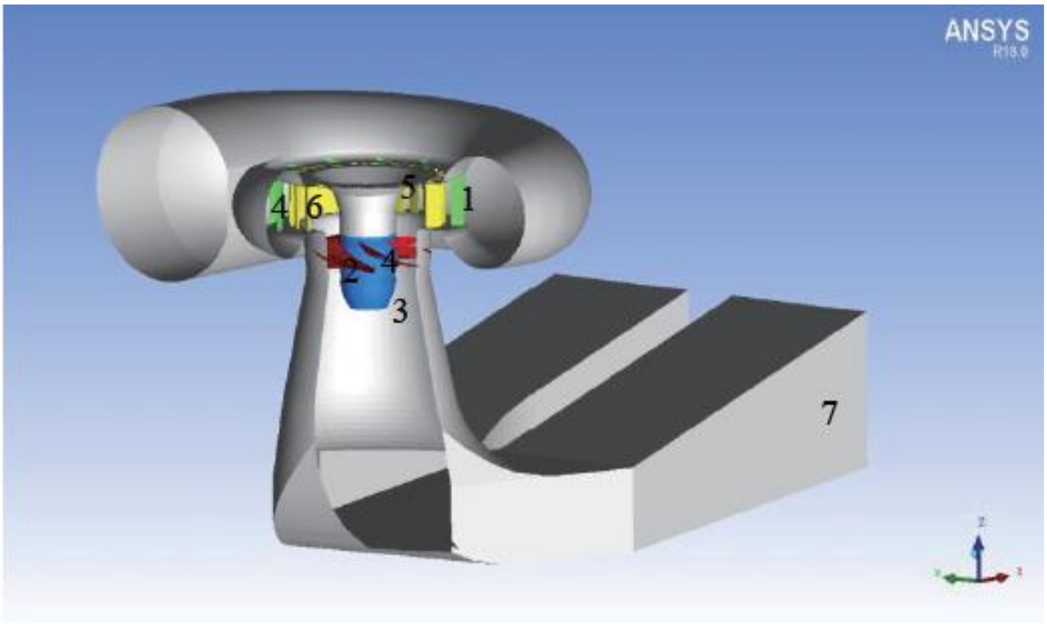


Figure 2.12. Mechanisms within a turbine that can injure fish. 1–Pressure increase; 2–Pressure drop; 3–Cavitation; 4–Strike;5– Scratch; 6–Shear stress; 7–Turbulence. Taken from Yang *et al*., (2018).

Studies on eels report wide variations in mortality during hydropower turbine passage i.e. 9 – 60% in European eels (Winter *et al*., 2006; Bruijs *et al*., 2009; Calles *et al*., 2010; Pedersen *et al*., 2012); 16 – 100% for American eels (Eyler *et al*., 2016; Carr & Whoriskey, 2008) and it is predicted to be 100% for large shortfins in New Zealand (Mitchell & Boubée, 1992), with risk of mortality increasing with size of eels and head height of the intake (see Beentjes *et al*., 2005). This has received increasing attention in recent years due to the aforementioned decline of eel species. Consequently, hydropower can only be considered as ‘green’ energy if environmental implications, specifically protection of fish and ecosystem services, are considered (BHA, 2008). There can be multiple hydroelectric dams along migratory pathways; for eels, cumulative mortality when multiple structures must be navigated can significantly reduce overall escapement of silver eels. Cumulative mortality rate was predicted to be 60% for female American eels leaving the Kennebec River basin, Maine, where there are 22 hydroelectric dams (McCleave, 2001) when presuming a very low (10%) mortality rate at each dam. However, it is likely survival at each structure will be lower; in the Ottawa River watershed, passage through five hydroelectric dams was estimated to be as low as 2.4% for American eels (MacGregor *et al*., 2015). For salmonids, 100% mortality was reported after passage through eight hydropower stations (Nyqvist *et al*., 2015). Replacing turbines with fish friendly ones (see section 2.6.42.6) are one mitigation measure that may reduce injury and mortality.

Modification or removal of the natural flow regime

Hydropower, regardless of head or whether water is stored, often diverts relatively large volumes of water which results in a stretch of river being depleted of flow while the station is operating (Anderson *et al*., 2015), except in the case of small run-of-river schemes. Hence, it poses many of the same aforementioned negative implications as large impoundment schemes, caused by separation of channel and diversion of flow (Robson, 2013). The amount of water available for hydropower generation depends on rainfall patterns, with more water available during wetter periods or high flows (Origin Energy Limited, 2017). During these times, power is generated when it is most cost – effective in response to fluctuating electrity rates, rather than to meet the needs of inhabiting fish, per se. This is usually at night, which is often when fish migrate due to the decreased predation risk during low light levels (e.g. Helfman, 1986). Despite more water passing the structure during these times, high flows associated with periods of rainfall provide a cue to diadromous and potamodromous species that follow the major flow during downstream migration (Anderson *et al*., 2015). Consequently, fish are attracted to hydropower intakes and unless there is a safe passage route, injury or mortality could result from impingement or entrainment, or delays to the migration and associated risks (Larinier *et al*., 2008).

In order to satisfy peaks in electricity demand, plants work intermittently; this creates periodic flow fluctuations in the receiving water body known known as hydropeaking (Valentin *et al*., 1996). These fluctuations generally have a more rapid start/stop than natural flow regimes, have more frequent changes and their maximum value is much lower than a natural high flow event for example, as they are driven by factors such as generation costs, turbine regulation and gate manipulation (e.g. Schmutz *et al*., 2015; Greimel *et al*., 2015). This has been found to have negative impacts on spawning behaviour in migrant fish; only 5% of adult lake sturgeon (*Acipenser fulvescens* Rafinesque) were in ripe-running condition in hydropeaking years compared with 79% of males and 39% of females in non-hydropeaking years (Lucas & Baras, 2001). Hydropeaking may be required in some years and not others, i.e. in years with more rainfall it may not be necessary and depending on demand. Hydropeaking can also wash juveniles further downstream, requiring a longer spawning migration as adults if the species homes (Lucas & Baras, 2001) and requiring significant energy expenditure to avoid downstream displacement (Griemel *et al*., 2015). It can also cause behavioural changes and loss of habitat (Vehanen *et al*., 2000, Flodmark *et al*., 2002). Further, rapid release of water from storage reservoirs could put fish inhabiting the donor water body at risk of impingement or entrainment.

Other negative impacts on migratory fish

The aforementioned impacts from impoundments associated with large schemes also apply here. Also, hydropeaking can also cause fluctuations in temperature if temperature of water released from upstream of the dam is different from that in the receiving water, known as thermopeaking (e.g. Choi & Choi, 2018). Flow regulation as a result of hydroelectric projects has been suggested to reduce normal turbulence, which can lead to disorientation and consequent slowing of migration (Odeh *et al*., 2002, and references therein).

2.5.3 Pumping stations

Another major impact to freshwater ecosystems and inhabiting migratory fish is through land drainage from pumping stations, which typically divert all water through pumps and represent a complete barrier to migratory species that must pass through these structures in order to exit the catchment. The land that pumping stations drain is often below sea level as it has been reclaimed from the sea for uses such as agriculture, flood protection, water level management, sewage control and to feed canals for navigation (Buysse *et al*., 2014). Consequently, water has to be pumped out of the catchment to a higher level in order for these areas to be inhabited and exploited (Figure 2.13). Wetland areas have been increasingly reclaimed in response to an increase in population and a decrease in the productive capacity of over-used farmland (Cowx & Welcomme, 1998). This has required an increase also in irrigation works that are regulated by pumping stations in order to supply the reclaimed areas, which increased exponentially between the years 1950 – 2000 (Fernando & Halwart, 2000). The worldwide distribution of pumping stations is poorly quantified (Buysse *et al*., 2014); notwithstanding, they are widely used in Europe; in England and Wales, Northern Ireland, Belgium and the Netherlands alone there are ~946, 335, 150 and 3000, respectively (Solomon & Wright, 2012; Buysse *et al*., 2014, and references therein; DEFRA, 2015; 2018; NI Water, 2019). There have been numerous studies to determine the impact of pumping stations on passing fish, (mainly salmonids) in Canada, France, Denmark, the U.S., New Zealand and Sweden (see Buysse *et al*., 2014, and references therein), highlighting the impact globally.

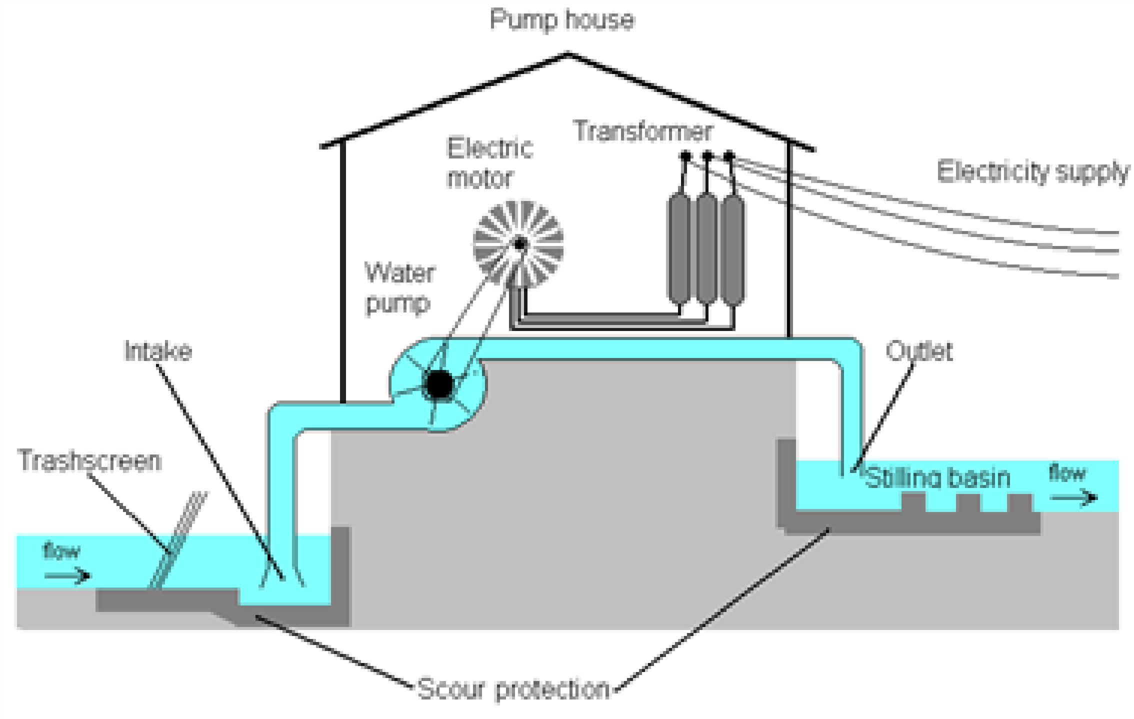
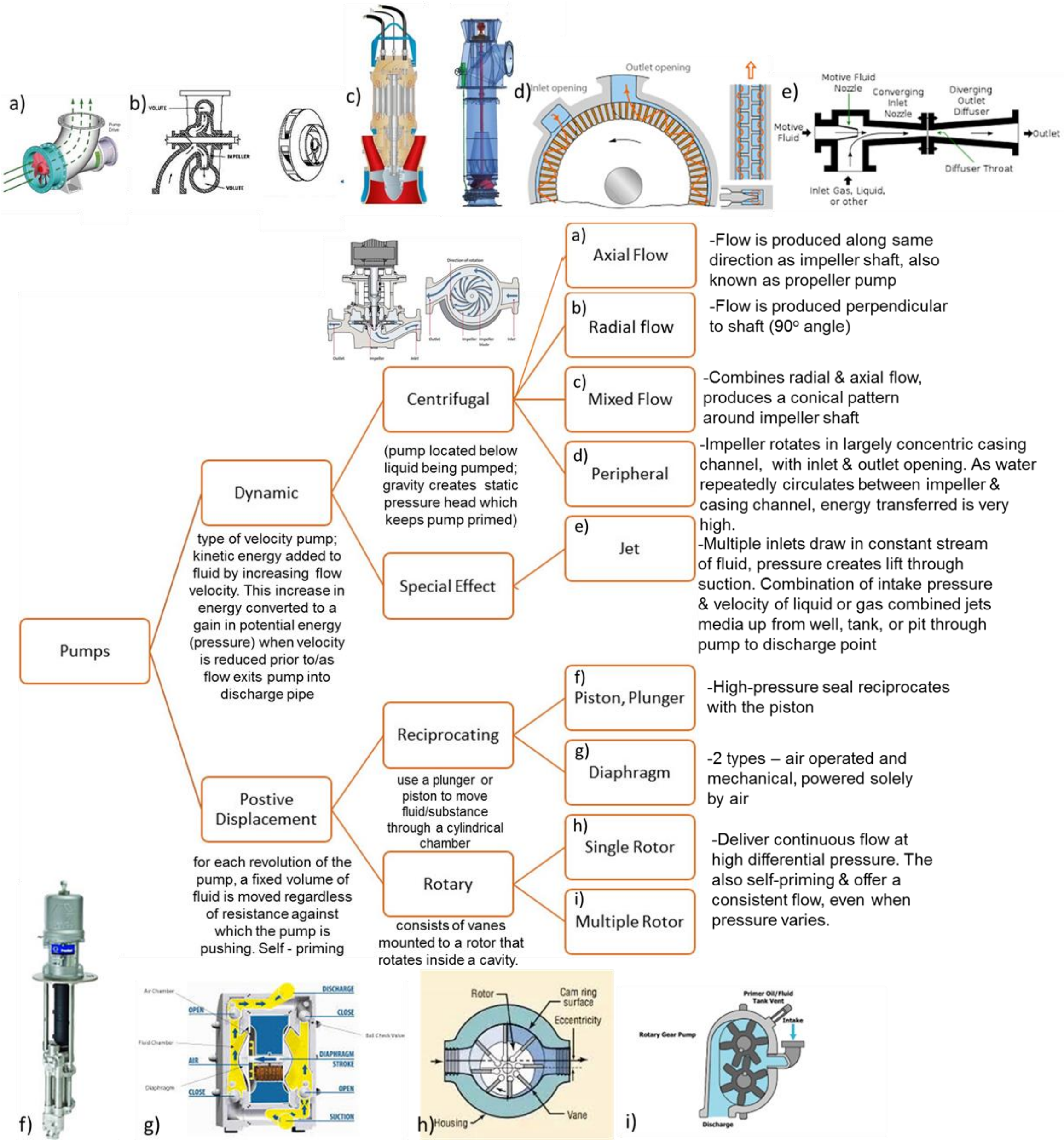


Figure 2.13. Major components in a pumping station. Taken from Environment Agency, (2010).

Risk of entrainment or impingement

The same risks of impingement, entrainment and damage caused by passage created by hydropower turbines apply to fish at pumping stations, and the impact is considered comparable (Brink *et al*., 2018). During passage through a pump, fish can be damaged by grinding, impeller strike, shear stress, or in the turbulence, as seen in hydropower (Figure 2.12), and/or surroundings in the outfall (e.g. Bolland *et al*., 2018). The risk of these, as with hydropower, is dependent on the pump type and the size of the fish. Cumulative mortality is also an issue after passage through multiple pumping stations (e.g. Buysse *et al*., 2014). The most common pumps used in the UK and Europe are axial flow pumps, which due to their design have 3 or 4 blades in front of a diffuser or guide- vane casing with 5 – 7 guide vanes to turn the flow in an axial direction. These are the most cost- effective method for land drainage as they are easy to install and as typically the discharge side is tidal or influenced by tidal conditions, resulting in large variation in head.

It has been found that small, axial flow pumps that are common in the UK and Europe (Bolland *et al*., 2018; Moria, 2008) can cause high rate of mortality, before centrifugal pumps, and that the high rotation speed of such pumps enhances injury and mortality preventing them from being 'fish – friendly' (see section 2.6.4). These types are amongst others such as mixed flow pumps, where both radial and axial flow methods are combined (Figure 2.14). All eels (*n* = 56) passing through a large (2.23 m diameter) mixed flow pump with a low rotational speed (100 rpm) in the UK were found to survive passage 96.5% had minor injuries, reduced physical condition or abnormal behaviour (Bolland *et al*., 2018). However, it is emphasized that fish friendliness can vary site to site depending on rotation speed (Rodgers & Patrick, 1985), pump diameter (Van Esch, 2012), number of blades (Pracheil *et al*., 2016) and other site features, i.e. associated pipework, flow guide veins, pump chamber walls and the outfall, and further research is required to quantify the impact of such pumps (e.g. Bolland *et al*., 2018). Also, post- passage fish injury and mortality studies are limited and require further research in order to fully understand the impact (e.g. Baumgartner *et al*., 2009; Buysse *et al*., 2014). Replacing pumps with fish friendly ones (see section 2.6.42.6) are one mitigation measure that may reduce injury and mortality.



type of velocity pump; kinetic energy added to fluid by increasing flow velocity. This increase in energy converted to a gain in potential energy (pressure) when velocity is reduced prior to/as flow exits pump into discharge pipe

for each revolution of the pump, a fixed volume of fluid is moved regardless of resistance against which the pump is pushing. Self - priming

(pump located below liquid being pumped; gravity creates static pressure head which keeps pump primed)

use a plunger or piston to move fluid/substance through a cylindrical chamber

consists of vanes mounted to a rotor that rotates inside a cavity.

-Flow is produced along same direction as impeller shaft, also known as propeller pump

-Flow is produced perpendicular to shaft (90° angle)

-Combines radial & axial flow, produces a conical pattern around impeller shaft

-Impeller rotates in largely concentric casing channel, with inlet & outlet opening. As water repeatedly circulates between impeller & casing channel, energy transferred is very high.

-Multiple inlets draw in constant stream of fluid, pressure creates lift through suction. Combination of intake pressure & velocity of liquid or gas combined jets media up from well, tank, or pit through pump to discharge point

-High-pressure seal reciprocates with the piston

-2 types – air operated and mechanical, powered solely by air

-Deliver continuous flow at high differential pressure. The also self-priming & offer a consistent flow, even when pressure varies.

Figure 2.14. Different pump types, modified from information available at All Pumps, (2016), available online at https://www.allpumps.com.au/blog/2016/01/25/classification-of-pumps/. Additional information and diagrams avalaible from Boilers Info, (2019), available online at https://boilersinfo.com/classification-of-centrifugal-pump/; Engineering 360 (2019), and references therein, available online at https://www.globalspec.com/learnmore/flow_transfer_control/pumps/jet_pumps; Houston Dynamic Service, Inc (2019), avaialable online at https://houstondynamic.com/main-pump-types-rotary/ and Tapflo Pumps (2018), available online at https://www.tapflopumps.co.uk/blog/ultimate-guide-to-diaphragm-pumps/. Barriers created to migratory fish

The intake and pumps of pumping stations are in most cases directly within the migration path of downstream migrants as the areas reclaimed and drained by pumping stations were once wetland feeding areas of migratory species. The same impacts as those created by aforementioned barriers are therefore present, as migrating fish requiring an exit route may experience significant delays and associated impacts, i.e. increased predation risk, worsening of diseases if present due to stress and depletion of fat reserves hence reducing the likelihood of successful spawning (e.g. Garcia de Leaniz, 2008; Eyler *et al*., 2016; Forty *et al*., 2016; Dainys *et al*., 2017). This also poses risks to juvenile life stages, as entry into large areas of feeding habitat is prevented by pumping stations acting as a barrier to upstream migration (Boogaard *et al*., 2015). This has resulted in the installation of elver passes at some pumping stations (Solomon and Wright, 2012; Griffioen *et al*., 2013) but importantly, restoration to improve upstream passage such as an elver ladder cannot be successful in terms of increasing the reproductive potential of the population until the impact to downstream migrants, namely mortality after passage through pumps, is reduced. In these circumstances, it has been discussed that discouraging rather than encouraging colonisation by elvers is favourable (Solomon & Wright, 2012).

Removal or modification of the flow regime

The natural flow regime in pumped catchments is modified because artificial high flows in response to high rainfall are experienced when pumps operate. This can provide spawning cues that attract downstream migrating fish into hazardous intakes. Further, flow modification can result in fish reaching potentially hazardous pumps when they are operational and pose risk of impingement or entrainment. Further, unless there is a gravity sluice or bypass available this is the only flow experienced, which may influence the timing and speed of downstream migrating fish that follow flow (e.g. Breukelaar *et al*., 2009). This can also result in delayed sexual maturation and small windows to exit the catchment due to no pumping activity (Buysse *et al*., 2014). However authors suggest that sampling at multiple times is advisable so as to avoid migrants leaving at other times, as the migration is recognised as being more flexible than first thought (e.g. Righton *et al*., 2016). Such research aids in planning future projects to inform management decisions.

2.5.4 Summary

Riverine modifications that create migration barriers in the form of dams, reservoirs, hydropower and pumping stations have contributed to many migratory fishes becoming endangered (Vorosmarty *et al*., 2010). The associated interruption to longitudinal connectivity and migratory pathways as well as flooding or depletion of the quality of spawning and nursery areas has reduced species diversity, abundance and mixing of the gene pool (Philipart & Baras, 1996) which has contributed to this endangerment. More barriers are being constructed than removed in response to global reliance on dams for flood control, irrigation, potable water and hydropower (Silva *et al*., 2018) and these pressures on water resources and flood protection will continue to increase with the increasing human population, climate change and the consequent sea level rise (Buysse *et al*., 2014). These issues warrant the need for research to aid in the understanding of the impact that these structures have on migratory fish behaviour so that mitigation measures can be put in place, to conserve migratory species.

2.6 Mitigating the impacts of flow regulation and barriers to migrations

In order to decrease the impacts of anthropogenic modification to migratory fish, passage solutions at barriers need to be provided so that spawning grounds can be reached efficiently, i.e. without significant delays that impair fitness and ability to complete the onward migration and reproduce. Understanding how fish use flow regimes is essential so that flows can be preserved or replicated to aid in fish passage. It is necessary to provide fish with the conditions they have evolved to depend upon, and an increasing major goal of river restoration is longitudinal reconnection. Fish not only require passage past barriers, but hazardous intakes need to be screened to prevent entrainment unless it is possible to replace pumps and turbines with fish-friendly ones (Moria, 2008) (see section 2.6.4) and ensure that the whole site is fish-friendly.

2.6.1 Provision of bypass solutions at migration barriers

The construction of migration pathways or fishways is a common management strategy to mitigate the impact of barriers to migration in rivers (Pelicice *et al*., 2015; Brink *et al*., 2018). That said, to date, overemphasis on economically important migratory fish species that must migrate long distances has been top priority and rendered species such as upstream migrating anadromous salmonids and their swimming ability the focus of research; this has mostly informed flow requirements in fish passage design, rather than using the behaviour of the target species (Clay, 1995; Rodriguez *et al*., 2006; USBR, 2006; Russon & Kemp, 2010; Kemp *et al*., 2011; Silva *et al*., 2018, and references therein). Such previous research biases have meant that fish passage solutions, despite being installed in catchments where catadromous and potamodromous species are present, do little to facilitate passage of these species (Lucas & Baras, 2001). In recent decades, the construction of fishways has increased, but in many regions thier performance remains low, likely due to factors such as a lack of biological knowledge and flaws in construction and/ or operation (Bunt, Castro-Santos & Haro, 2016; Nieminen *et al*., 2016; Kemp, 2016; reviewed in Silva *et al*., 2018, and references therein). In the U.S., despite emphasis on bypasses for downstream movement, particularly in North America (Anderson *et al*., 2015) there are still large variations in the availability of downstream passage solutions in large river systems (see Williams *et al*., 2005; Keefer *et al*., 2012), highlighting the complexity of the situation. It is recognised that improved international collaboration, information sharing, method standardization and multidisciplinary training are required, particularly in regions where hydropower dams are currently being planned and constructed (see Silva *et al*., 2018). In order to design fish passes that are suitable for multiple species and a wide range of sizes, as well as meeting the demands of the infrastructure that is creating a barrier (i.e. a hydropower station), innovative thinking and engineering design are required (Silva *et al*., 2018).

As the value of migratory species is increasingly recognised in response to human population growth and requirement for food sources, organisations such as the IUCN are recommending mitigation. In order to integrate policy, institutional, economic, social, environmental and legal issues into river management plans that consider the full range of ecosystem services required for both humans and the environment, the IUCN developed the ‘River Basin Approach’ (Gough *et al*., 2012; Brink *et al*., 2018). This is a strategy for ecosystem and social basin management that forms the scientific basis for many river management programmes, and it is key in finding solutions to resolve barriers and threats to migratory fish in a whole river context (Brink *et al*., 2018). Such plans have significantly contributed to restoring fish populations and their habitats in countries such as America and Spain (Silva *et al*., 2018 and references therein).

2.6.2 Legislation

Effective solutions to the issue of barriers to fish migration cannot be implemented without legislation, and the general requirement of legislation in many countries is for developers to provide fish passage at any new structures or substantially modified existing structures (Kemp, 2016; Silva *et al*., 2018). There is specific legislation in Europe to minimise the potential impacts of river engineering in the form of the Water Framework Directive (WFD; 2000/60/EEC) which was established in 2000 as “a framework for community action in the field of water policy”; to protect both ecosystems and water needs of inland, estuarine and coastal water. In 2003, this was transposed into UK law under the Water Environment (Water Framework Directive) (England and

Wales) Regulations 2003 and the Water Environment and Water Services (Scotland) Act 2003 and states that all heavily modified water bodies, such as those impounded by dams, must reach Good Ecological Potential (GEP), or the ecological quality that can be achieved in the affected water bodies without significant adverse impacts to the societal benefits, by 2027 (WFD; 2000/60/EEC). This aims to reach a balance between the societal benefits that water bodies provide whilst allowing ecosystem services to be delivered (Elliott & Whitfield, 2011). Good Ecological Status goals of the WFD (defined as a slight variation from undisturbed riverine conditions; ECRR, 2014) need to be met relative to reference assemblage conditions of populations, so require understanding of poorly dispersing fish as well as classing migrant species and strong dispersers in order to improve barrier passage (Silva, 2018, and references therein). In Europe, biodiversity is further protected by the Habitats Directive 92/43/EEC. In other countries, migratiory fish are protected by specific legislation, e.g. in New Zealand (Freshwater Fisheries Regulations (1983), America (Anadromous Fish Conservation Act (1965), Canada (Fisheries Act (1985), China (Article 27 Law of the People's Republic of China on Water (Shi *et al*., 2015) and Thailand (Fisheries Act, B.E. 2490 (TFA, 1947).

Barrier removal has been recognised as the best solution in the UK in ecological terms (Cowx & Welcomme, 1998) and is also being implemented in other countries such as Denmark (Candee, 2016), and the U.S. (Brown *et al*., 2013). A long term study found that removal of dams, in this instance removal of a small-scale hydropower dam, resulted in dramatic increase in trout density over 30 years (Birnie-Gauvin *et al*., 2017). This is an option especially if removal costs are less than those of the future benefits of a dam (Pejchar & Warner, 2001). That said, dam removal is often not possible at infrastructure such as water storage reservoirs, hydropower and pumping stations due to societal requirements for water, renewable energy and to mitigate flood risk (Silva *et al*., 2018). Thus, integral to improving barriers to migratory fish is to provide alternative routes of passage and prevent injury or mortality at hazardous intakes. The Salmon and Freshwater Fisheries Act (1975) accommodates the need to enhance fish passage when migration pathways are impaired, and is required in waters inhabited by salmon and sea trout if: a new impoundment is constructed, or

- if an impoundment is rebuilt or reinstated over half its length, or
- if an existing impoundment is altered physically, or
- as a result of flow reduction so as to create an increased obstruction (Environment Agency's Good Practice Guidelines, 2009).

Appropriate passage solutions are required to be implemented at a broad range of river structures that pose barriers to eel migration. The understanding of the impact of barriers on downstream migrating eel species has been complicated by their highly variable life history traits and habitat use (Daveret et al., 2016). It is recognised that an improved understanding of underlying processes of eel migration is needed (e.g. Piper et al., 2013) in order to design and implement suitable passage solutions, which applies to other temperate eel species that are recognised as being at risk of the same threats posed for European eels (Feunteun, 2002; Lokman, 2016).

In response to the rapid decline of the now critically endangered European eel in the past few decades, more of a focus has moved to downstream passage in the UK (Environment Agency, 2013a) and Europe where the focus was previously on upstream passage for resident and anadromous salmonid species (Lucas & Baras, 2001). The European Commission (1100/2007) legislation has employed specific Eel Management Plans (EMPs) for the European Eel in national territories and trans-boundary river systems (McCarthy *et al*., 2014), in Water Framework Directive river basin districts. The EU eel regulation strives for each Eel Management Plan to “reduce anthropogenic mortalities so as to permit with high probability the escapement to the sea of at least 40% of the silver eel biomass relative to the best estimate of escapement that would have existed if no anthropogenic influences had impacted the stock... the Eel Management Plan shall be prepared with the purpose of achieving this objective in the long term” (Council Regulation (EC) No. 1100/2007). Providing physical screening is strictly enforced under specific legislation in the UK; the Eels Regulations (England and Wales) 2009 Statutory Instrument calls for measures to improve eel passage and for any water intakes (including pumping stations) abstracting more than 20 m^3 a day to be screened, unless exempted by the Environment Agency. Parts of Europe (Anderson *et al*., 2015) and the U.S. also strictly enforce screening (e.g. USBR, 2006). In New Zealand, legislation making passage of eels and other indigenous fishes to be provided at instream barriers is mandatory (New Zealand Freshwater Fisheries Regulations, 1983) and management objectives also call for focus on increase in escapement of silver eels in response to reported reduced recruitment of longfinned eels, (Jellyman, 2007). Based on the aforementioned understanding of what constitutes a barrier to fish (namely physical and hydraulic barriers created by anthropogenic infrastructure), the main goals of improving fish passage are "to achieve diverse fisheries management objectives related to upstream–downstream connectivity that encompass biological, cultural and socioeconomic components” (Silva *et al*., 2018).

A common issue amongst water resource managers when mitigation requires changes to operational regimes is the loss of water that could be used for other means such as hydropower generation. This can be mitigated by water companies paying a levy that is used or can be invested in environmental protection, as is the case in the UK. The Environment Agency is involved in deciding how this fund should be invested. In the U.S. the rate paid by hydropower consumers includes the cost of actions to mitigate for resultant environmental damage (McFarland, 1966).

2.6.3 Overview of different fishway designs

Upstream fish passage can be provided by fishways of varying design, from nature-like bypass channels including rock-ramp types (Dodd *et al*., 2018) to highly engineered structures (Anderson *et al*., 2015) such as pool and weir or pool and slot fishways that achieve passage in stages, i.e. a series of small pools in steps requiring fish to swim over dividers from pool to pool, or with openings for fish to swim through dividers, respectively (Larinier, 2008). Passage can also be provided by the use of a mechanical lift (Armstrong *et al*., 2010) or by alteration of flows (Denil) (Beach, 1984). Downstream passes are typically highly engineered structures such as spillways or screened surface bypass collectors (Anderson *et al*., 2015) and natural bypass channels can also be suitable (IEA, 2000). In a review by Noonan *et al*., (2012), pool and weir, pool and slot and natural fishways had the highest passage efficiencies (Figure 2.15a) for species migrating both up and downstream, albeit there is a dearth of knowledge on non-salmonid species and downstream passage (Figure 2.15b). Further, upstream passage efficiency decreased significantly with fishway slope and increased with fishway length and water velocity (Figure 2.15c-e). The review highlighted the need for most passage facilities to be improved due to overall low efficiency (See Noonan *et al*., 2012).

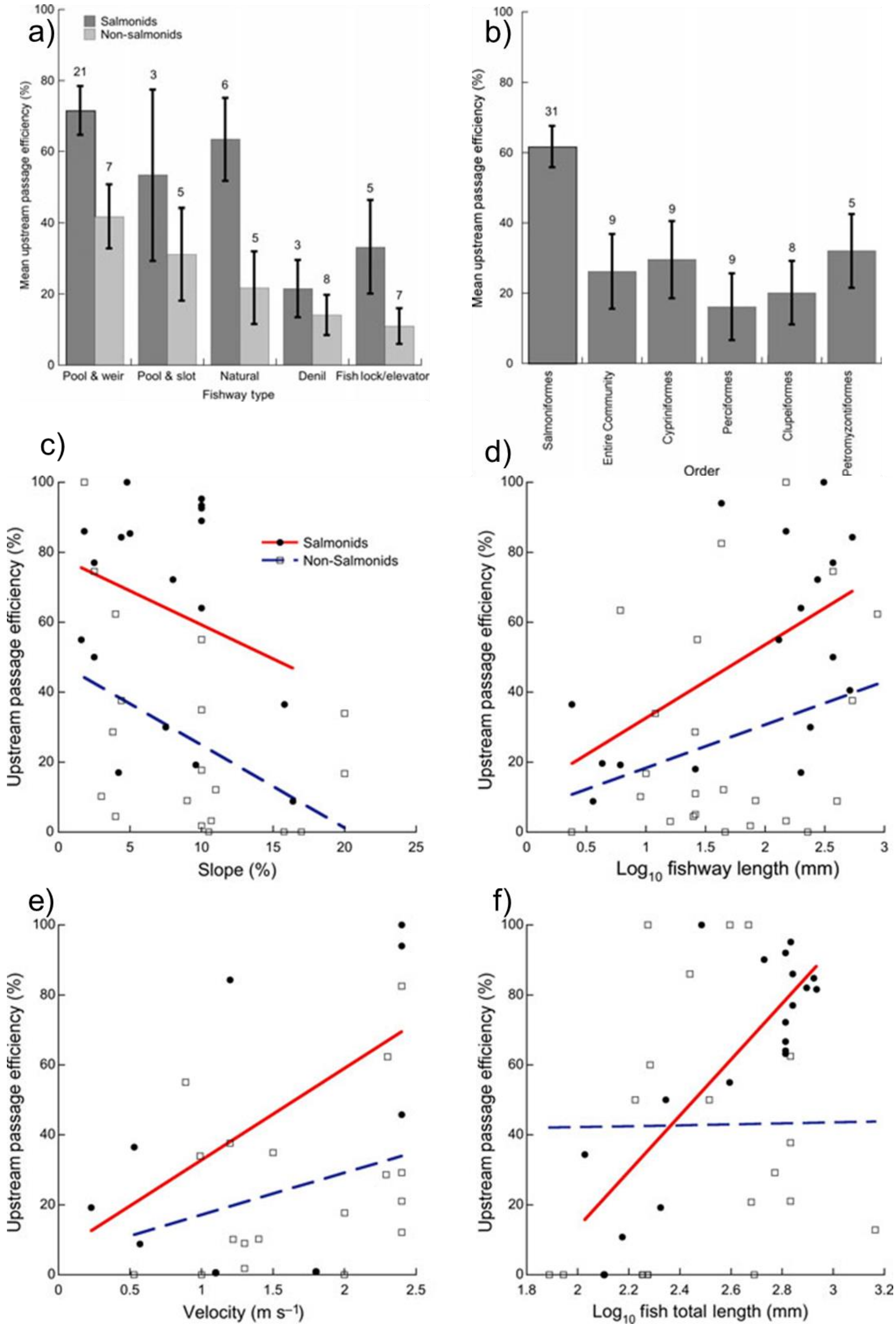


Figure 2.15. a) Mean (±SE) upstream passage efficiency for migration at five types of fish passage facility, for salmonid and non-salmonid fishes; b) Mean (±SE) upstream passage efficiency for all orders of fishes with N ‡ 5. Entire community refers to studies that measured the entire non-salmonid community with no distinction between orders. In all figures, numerals above the bars represent sample sizes; c- e) Upstream passage efficiency, for salmonid and non-salmonid fishes in relation to (c) fishway slope, (d) fishway length, (d) water velocity through the fishway and (e) total fish length. Lines represent least-squares regressions. Taken from Noonan *et al*., (2012) in a quantitative assessment of fish passage efficiency.

Regardless of design, an efficient fishway is one that can be readily located by the target species (attraction efficiency), including allowing for fish size variation; successful entrance into the fishway (entrance efficiency); and successful passage of the entire structure (passage efficiency) (Silva *et al*., 2018). Each metric used to measure fishway efficiency (attraction, entrance and passage) can be considered an individual state or phase associated with a distinct zone of the fishway (Silva *et al*., 2018). This needs to be achieved during the times of year (and associated flows) that the target species require passage, with emphasis on water velocity requirements of the target species, location at infrastructure and fishway design such as slope and length (Hadderingh *et al*., 1999; Noonan *et al*., 2012).

Maximising attraction efficiency

A fishway system must have a sufficient flow of water to attract the target species (Haro *et al.,* 2016). When installing fishways at sites where all discharge would otherwise pass through turbines or pumps, fish will encounter a high velocity environment at the intake to such infrastructure. Here, in the “approach” state, a fish will encounter physical signals to identify the location of the fishway (Silva *et al.,* 2018) that must be sufficient to attract fish away from other areas with higher, distracting discharge (Bunt *et al*., 2012, and references therein) such as the inflow caused by turbine/ pump operation, ecological flow or spilling discharge at the dam that may provide inescapable flows and result in impingement or entrainment.It has been reported that the flow at the intake to the fishway needs to be 2-5% of the competing flow (Larinier, 2008) to avoid the efficiency of the fishway being affected (Larinier *et al*., 2002; Ovidio & Philippart, 2002). Further, excessive turbulence and extreme water velocities in fishways have been interpreted by several authors to be factors that challenge upstream passage of migratory fish (see Bunt *et al*., 2012, and references therein), which warrants the need for adequate testing and monitoring.

The direction that fish are migrating in and the associated different requirements when locating a fishway needs to be considered. For example, upstream migrants are said to seek areas with higher velocities and on the edges where velocity gradients exist, whereas downstream migrants tend to avoid them, moving towards the area with the highest flow volume where velocity is highest but velocity gradient is lowest (Williams *et al*., 2012). For downstream passage, where all flow passes through turbines, it has been discussed by Lariniere, (2008) that due to fish being attracted to the turbine draft tubes (of a small hydropower station), the entrance to a fishway should be placed adjacent to the power (or pump) house, preferably in the river bank to maximise chance of fish locating it rather than being entrained with the turbine flow. Further, turbulence that disorientates fish may result in access to a fishway being blocked or restricted (Bunt, Katapodis & McKinley, 1990) which increases the need for a fishway entrance to be appropriately located. Further, when there is a diversion canal present, when deciding where to install a fishway, flow and operational regimes during the migration period need to be considered because fish can be attracted to continuous flow from operation or during low flow, but may congregate at dams during frequent spill or high flow (Lariniere, 2008). For upstream passage it has been found after research of two Denil fishways, that after fishway entrances were moved 2 m closer to the weir face in areas where fish were attracted by weir discharge, coupled with an increase in entrance size (removal of a 2 x 2 m block) there was a 2.6 – 3-fold increase in fishway use in pumpkinseed (*Lepomis gibbosus* (L.)) (Bunt, 2001). The author therefore recommends that fishway entrances be located as close to a dam or weir face as possible, whilst considering that velocity barriers resulting from spillway or tailrace discharge must not negate access (Bunt, 2001). This was discovered after a radio telemetry study revealed that several species were located in an area of high discharge upstream from the fishway (Bunt, 1999). This supports the value of monitoring studies and understanding site- by- site behaviour when maximising attraction efficiency.

Entrance efficiency

During the “entry” state, a fish is able to detect and respond to the fishway entrance and a decision whether to enter the structure must be made; success or failure can be for reasons such as physical capability and behavioural rejection (Silva *et al*., 2018). In certain scenarios such as if the canal or river upstream is long or particularly wide, the chance of rapidly locating a single fishway is limited as the area is larger (Larinier, 2001; 2008). In such instances, multiple fishways or entrances may be required. Also, the depth and dimensions of the entrance of the bypass must be tailored to the position of the target species in the water column (Hadderingh *et al*., 1999). Both brown trout and European eel have previously been found to locate a channel-floor orifice rather than a mid-column one (e.g. Cotel *et al*., 2006; Russon & Kemp, 2011; Calles *et al*., 2013; Haro *et al*., 2016). Juvenile salmonids on the other hand have been found to be surface-oriented (e.g. Moulton *et al*., 1997; Coutant & Whitney, 2000; Johnson *et al*., 2005). Utilising this known behaviour of target species can be used to design effective bypass channels (e.g. Haro *et al*., 2016; Baker *et al*., 2018).

Passage efficiency

After entrance to a fishway, a fish occupies the “passage” state, where it must now pass through; this can also be affected by physical capability and/or behavioural rejection (Silva *et al*., 2018). Jumping ability and swimming endurance of the target species must also be considered. It has been recommended that water velocities in fishways exceed the aerobic swimming capacity of the target species and channel length be greater than the distance the species can cover in an anaerobic burst so that once fish enter the fishway they cannot reverse course and exit the bypass through the entrance rather than passing the entire structure. The average cross-section velocity of flow should also be less than the sustained swimming speed of the smallest fish to use the fishway, for both downstream and upstream migrating species (Evans and Johnston, 1980; Haro *et al*., 2004) to allow fish to move through the fishway without resistance.

Fishway efficiency, in order to encompass approach, entry and passage efficiency, should measure the encounter and path of individual fish relative to reference conditions, whether subsequent passage is successful or not and time elapsed to each event for each fish, (Castro-Santos & Haro, 2003; Castro-Santos & Perry, 2012; Cooke & Hinch, 2013). Designing an attractive fishway that minimises time spent searching is desirable, to minimise fitness cost (Johnson & Miehls, 2014, and references therein). Due to the different physiological characteristics, swimming abilities, body size and behaviours of species potentially requiring passage at a structure, there is no scientific basis to assume that a single fishway design will be appropriate for multiple species (Bunt *et al*., 2012, 2016) and two or more fishways of differing size and hydraulic conditions may therefore be required (Silva *et al*., 2018). Lucas & Baras (2001) recommended 90-100% attraction and passage efficiency targets for effective restoration or maintenance of diadromous and strongly potamodromous populations, due to recognition that the cumulative impact of barriers to migration through reduced net passage across multiple sites (see Anderson *et al*., 2015, and references therein; Silva *et al*., 2018).

Several authors have highlighted that due to a wealth of research to re-establish lonigtuidnal connectivity for upstream migrating fish in previous years, there is strong evidence evidence to help provide efficient upstream passage for salmonids, shad and possibly pacific lamprey ((*Lampetra tridentata* (Richardson)) (Clay, 1995; Larinier, 2002c; Armstrong *et al*., 2004; Williams *et al*., 2012; Calles *et al*., 2012). Despite this being the research bias for decades, authors such as Bunt, Castros-Santos and Haro

(2012) in a review of the performance of 19 different upstream fish passes including pool-and-weir, Denil, vertical-slot and nature-like fishways, report highly variable attraction performance for all designs. Mean passage efficiency was found to be inversely related to mean attraction efficiency by fishway structure type, with nature-like passes having the highest passage followed by Denil, vertical slot and pool and weir (see Bunt, Castros-Santos and Haro, 2012 for full results). Interestingly, their analysis revealed that the biological characteristics of studied fish were responsible for the variation in fish attraction, whereas variation in fish passage was related to fishway type, slope and elevation. They concluded that in most cases, existing data are not sufficient to support design recommendations. This considered, it is recognised as being “even more difficult for biologists/ engineers to determine a location for a fishway for downstream migrating species at large obstructions”, and despite research into physical and behavioural deterrents (see sections 2.6.2 and 2.6.3) most attempts to re-establish longitudinal connectivity have targeted upstream migrants and the majority of fish actively migrating downstream through fishways rely on finding acceptable hydraulic conditions (Williams *et al*., 2012, and references therein). This highlights the need for research aiming to utilise the knowledge of known behaviour of downstream migrants such as providing attractive flows, as has been successfully trialled in two studies in American eels using two different types of fishway (Haro *et al*., 2016; Baker *et al*., 2018; see chapter 6).

2.6.4 Reduction of impingement and entrainment

Current situation

Due to the increase in dam construction globally for hydropower, impingement and entrainment at hydropower intakes is increasingly recognised as a threat to downstream migrating species that must pass through infrastructure to reach spawning grounds. Research into the impacts of impingement and entrainment at pumping stations is receiving increasing attention, with recognition that the most frequently utilised pumps (axial and centrifugal) are known to result in extensive damage if fish pass through (Moria, 2008). Hydropower has been said to be responsible for up to 100% of eel mortality (Boubee, Jellyman & Sinclair, 2008; Carr & Whoriskey, 2008) and research on downstream passage is growing in Europe and North America especially for eels and sturgeon as they are of conservation interest (e.g. Rytwinski *et al*., 2017). Mitigating injury and mortality from impingement and entrainment is challenging as different species migrate at different times, and there has been minimal research on downstream passage and entrainment risk of resident species (Lariniere, 2002).

Despite a wealth of solutions to prevent entrainment, they are not equally effective (Lariniere, 2002).

Fishways can reduce the impacts of barriers to longitudinal connectivity created by infrastructure such as hydropower and pumping stations, but additional measures are required to remediate the risk of impingement on screens or entrainment into turbines and pumps at hydropower sites and pumping stations. Recognising the impact of hydropower on fish, particularly downstream migrating species, the number of sites worldwide providing passage solutions at hydropower dams is increasing (see Rytwinksi *et al*., 2017).

Physical screening

Hazardous intakes have physical barriers or screens to prevent debris or weed (trash) getting pulled into infrastructure, referred to hereon as trash screen, but often the bar spacing is wider than the width of target fish species so fish can enter intakes. Using physical screening to prevent fish passing through the trash screen to intakes involves using sufficiently small mesh (Lariniere, 2002; Solomon & Wright, 2012) which will vary depending on the size of the target species. If screening can be installed to prevent entrainment, impingement can still be a risk if flows at the intake exceed fishes swimming ability, hence preventing escapement from the intake. As discussed for providing an alternative passage route, flow requirements are integral to preventing impingement and entrainment. Thus the limited swimming ability and behaviour of the target species as well as the physical and hydraulic conditions at the water intake must be considered (Lariniere, 2002). Considering this, a sufficient screen area must be provided in order to create approach velocities that are adapted to the swimming ability of the target species (Lariniere, 2002). Such physical screens prevent fish entering, but a passage solution needs to be provided so fish must also be guided fish to a fishway. As downstream fish move with the flow, they potentially have less time to assess cues at entrances to fishways, which must be considered when designing solutions to bypass barriers (Williams *et al*., 2012). Uniform velocities with eddy-free currents are required for effective guidance, which biologists and hydraulic engineers with considerable experience with site placement of upstream fishways (Williams *et al*., 2012) report can be achieved by placing screens diagonally to the flow with the fishway in the downstream area of the screen and recommend it guidelines for hydropower screening provided by the American Society of Civil Engineers (ASCE, 1995), evaluated in Lariniere & Travade, 1999; 2002). For example, screening that diverts fish away from turbines and into bypass chutes have been used for eels (EPRI, 1999;

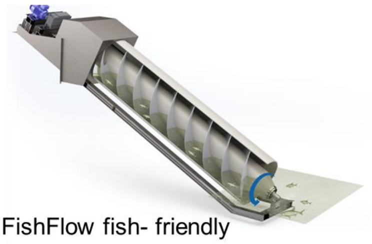
Gosset *et al*., 2005). However in order to develop effective fishways, biological knowledge and expertise of fish behaviour when encountering variable flows, velocity and turbulence needs to be applied in combination with that of hydraulic and civil engineering if appropriate hydraulic conditions are to be provided (Williams *et al*., 2012).

Fish-friendly turbines and pumps

As recognition of the impacts of hydropower generation on fish increases, research is focusing on developing ‘fish-friendly’ turbines and pumps. A ‘fish-friendly’ turbine or pump is defined as a pump that is passable and where fish survive after passing through without incurring any external or internal damage or loss of scale (Moria, 2008; Hidrostal, 2010). Screw pumps are one of the designs that can be used to safely transfer fish (Spring, 2010) and all have a ‘corkscrew’ design. Design principles to make these designs fish friendly aim to reduce the damage caused by blades as blades rotate slower which reduces blade strike and, to minimise the risk of sheer stress (Moria, 2008). Pumps that claim to be fish friendly include the De Wit adapted Archimedes screw (Figure 2.16), Hidrostal pumps, the FishFlow screw pump and an adaptation to the fan in axial screw pumps (Helfrinch *et al*., 2004; Moria, 2008, and references therein). This is achieved by blades having curved edges so that they move more smoothly (Archimedes), the width gradually increasing in radial direction (Hidrostal), the width gradually decreases from the middle outwards during the last few windings until they merge with the housing of the screw (FishFlow) (Moria, 2008; Hidrostal, 2010; Bedford, 2016). These methods prevent fish getting trapped between the blade and the pump casing as there is no gap. It is important to still consider the speed of these blades and that noise can deter fish, so their effectiveness depends on willingness of fish to pass through, as well as safe passage; however, as mentioned in sections 2.5.2 and 2.5.3, for a site to be truly fish friendly, site-specific features need to also be considered such as whether the outfall is safe for fish (Sheridan *et al*., 2014). Also a combination of measures needs to be employed (Moria, 2008), not only to allow passage past the barrier but also to mitigate the hazard, which is when other measures such as behavioural deterrents and guidance may be required.

The screw pump design has been adopted for application in hydropower developments (as opposed to use for pumping water) such as the Alden Turbine (Figure 2.16; Spring *et al*., 2010). The design allows fish to move down a smooth channel with a few blades that are turning more slowly than traditional hydro turbines, which decreases the aforementioned risks (Dixon, comms. *in* Spring *et al*., 2010). For example, an Alden turbine for a particular site would rotate at 120 revolutions per minute (rpm) whereas using a conventional 13- blade Francis turbine at the same site would rotate at 189.5 rpm and a five-bladed Kaplan would be 267.9 rpm (Perkins *et al*., 2013). By making a turbine rotate slower, the turbine size needs to be increased to compensate (Spring *et al*., 2010). This technology has been refined since research started in 1995 by using computational fluid dynamic and testing of a physical model of the turbine (Dixon, 2011), with the latest prototype survival being estimated to be 98.4% and application at two sites allowing 98.1% survival for fish up to 200 mm and at the other, ~99.9% for 200 mm smolts/ ~96% for 700 mm kelts, respectively (Allen *et al*., 2015).

Archimedes screw pump: a long worm wheel, diagonally placed in pipe or trough, creates upward displacement of water when driven. Conventional design - first winding scoops water from polder > lifted to downstream waters by subsequent windings. Often fish injured by first winding when it hits water, or due to entrapment between screw & trough. **FishFlow:** Screw enclosed in pipe attached to screw thus rotates together with it, preventing this damage.



FishFlow fish- friendly screw pump

Alden hydropower turbine: three blades. No clearances between blades & crown or housing (with exception of small areas around blade & leading edges), pressure and velocity (shear) gradients that meet established bio- criteria for safe passage (Perkins et al., 2013).

Alden fish- friendly turbine

Figure 2.16. FishFlow fish – friendly Archimedes screw pump and Alden hydropower turbine, adapted from principles of traditional screw pumps. Information and diagrams from Spring *et al*., (2010); Perkins *et al*., (2013); FishFlow Innovations, (2019).

In the UK and Europe, slower rotation devices, mainly reverse screws, at low head sites have increased significantly (Bracken & Lucas 2013; Lyons & Lubitz 2013). When applied for pumping, screw pumps such as Archimedes are generally considered to be less likely to cause damage. In fish trials through archimedian screws in the UK, no significant damage has been reported for fish entering and passing the turbines, in salmonids naturally passing through (Kiel, 2007), artificially introduced (Kibel & Coe, 2008), eels (Kibel & Coe, 2008), coarse fish (Kibel, Coe & Pike, 2009) and lampreys and there are over 100 in operation on the continent (Lucas & Bracken, 2010) none of which report fisheries issues (reviewed in FishTek consulting, 2011). Further, in a study of European eels, where a propeller pump caused 97 ± 5% mortality whereas a large Archimedes caused only 17 ± 7% and a small Archimedes caused 19 ± 11%. The earliest study in the UK on fish passing through an Archimedean screw turbine (1.4 m diameter, 615 L/s) was conducted by Spah (2001) and the majority of species did not have any injuries (Table 2.2). Those that did are thought to have come from the leading edge of blades being sharpened by stones over time. These findings led to the recommnedations by FishTek consulting to fit rubber bumpers on the leading edge of small Archimedean screws (under 2.5 m diameter) in order to reduce the force that fish are subjected to (Kibel, Coe & Pike, 2009). Despite promising results, only a limited range of pump sizes have been tested and further research is needed in order to determine whether results are transferable.

Table 2.2. Summary of results from Spah (2001), showing the number that passed through of each species and the lengths of fish affected

Species	No. Tested	Length Range (cm)	No. fish injured	Injuries
Eel	22	36-58	0	
Grayling	3	20-36	0	
Brown trout	31	8-35	0	
Perch	19	14-18	0	
Chub	63	8-43	5	Scale loss, haematoma
Gudgeon	8	12-14	0	
Bullhead	3	11-14	0	
Dace	1	21	0	
Roach	8	16-21	2	Scale loss, haematoma

Behavioural deterrents and guidance

If non-physical methods are to be used to deter or guide fish away from hazardous areas, provide a passage solution and reduce impingement and entrainment, it is desirable if they can operate without affecting water flow or navigation (Johnson & Miehls, 2014; Noatch & Suski, 2012) (and consequently the operation of the infrastructure). If effective, they are also generally cost-effective in comparison to physical screening or pump replacement. Such measures can therefore direct fish to fishways (push) as well as deterring them away from hazardous intakes (pull; Cook *et al*., 2007; Noatch & Suski, 2012). Applications include using flow to guide fish (Lariniere, 2002), bubble barriers (Dawson *et al*., 2006), electric barriers (Swink, 1999), sound (Popper & Carlson., 1998) and strobe lights (Sager *et al*., 2000). There are limitations to each measure, depending on prevailing environmental conditions such as competing flows in the area and presence of an alternative route; visibility of bubble barriers (Noatch & Suski, 2012), susceptibility to electrical fields and potential for injury if not used correctly (Reynolds, 1996), hearing ability of the target species (Schlit, 2007), turbidity of water affecting suitability of strobes (McIninch & Hocutt, 1987) and differences in individual species behaviour. Utilising the relationship between flow and migration, louver flow deflectors that compose an arrangement of vertical slats aligned across the channel at a specific angle to the flow direction (ACSE, 1995) have been successful to guide fish away from power turbines, especially when modifications were made to increase velocity and reduce turbulence for Atlantic salmon in the bypass (Ducharme, 1972). This measure has been found to succeed in areas of comparatively high approach velocities, shallow depths and uniform flow (Larinier, 2001) such as those of forebays to infrastructure. As with entrance to fish passes, the design should accommodate for the migratory behaviour of target species, such as considering orientation of fish in the water column. For example, for Atlantic salmon smolts that are observed to remain in the upper portion of the water column when migrating (Larinier, 2001) a partial depth system on the intake channel at Holyoake hydroelectric power station on the Connecticut River was effective for 97% of fish (Odeh & Orvis, 1998). However, in environments where fish are migrating over spill bays such as those at dams, there has been found to be no significant difference in survival with or without flow deflectors in yearling chinook salmon or steelhead (Muir *et al*., 2001).

Electrical stimuli are amongst the earliest methods for controlling fish movement. Their effectiveness is mainly due to behavioural response from the fish (Flammang *et al*., 2014), in this case avoidance behaviour (Katopodis *et al*., 1994). An electric field has been classified as a ‘fright stimulus’ (Bullen & Carlson, 2003). In order to create such stimuli, an electric field is passed through the water. When a fish enters this field, it becomes part of the circuit and has a current moving through its body.

Both alternating current (AC) and direct current (DC) have been studied. In an AC field, classical electrotaxis or full “stunning” does not occur and currents act only to mildly stun or frighten fish (Hocutt, 1980), but AC is known to be more stressful to fish and potentially more dangerous for human operators. When guiding or deterring fish, the aim is not to cause full electrotaxis or electronarcosis (where equilibrium is lost), as this would not allow fish time to escape from the electric field, especially during downstream migration when fish could be washed downstream and entrained. For this reason, pulsed DC is preferred as it permits fish time to escape (Boubee & Paterson, unpubl.).

Electric barriers have been most commonly used to deflect upstream migrating fish (Boubee & Paterson, unpubl.) including control of invasive species such as sea lamprey in the U.S. (Swink, 1999). Upon entering the field, the discomfort or aversive behaviour experienced causes them to be washed back downstream away from the hazardous area. For downstream migrating eels, they are thought to be particularly susceptive to electric fields, as their long length allows them to detect the repelling stimulus at low field strength; they have been observed to turn at a comparatively far distance from electrodes (Hadderingh & Jansen, 1990) - this coupled with their strong swimming ability is thought to assist in retreat from an electric screen. For downstream migrating European eels, a maximum approach velocity of 0.5 m/s was recommended to minimise entrainment (Adam & Schwevers, 1997) upon intake screens; this is also relevant for New Zealand eel species (Boubee & Paterson, unpubl). Electric barriers can be installed either in a horizontal or vertical orientation depending on the specific management application, both of which have greater intensity closer to the substrate; horizontal electrodes are suitable in areas of high debris, where they can be installed flush with the substrate (Swink, 1999; Ostrand *et al*., 2009). This would also be suitable in higher velocity, shallow streams, whereas vertical electrodes can be used in deep streams with lower velocity. Juvenile sea lamprey have been successfully guided to fishways using both vertical and horizontal pulsed DC electric fields, with medium (0.12 m/s) velocities correlating with the highest guidance rates (Johnson & Miehls, 2014). The authors highlighted the need for future research to determine the response of other species to non-uniform fields of pulsed DC.

Due to limitations of single non-physical measures, two are often used in conjunction to increase their success (Patrick *et al*., 1985; Sager *et al*., 1987; Flammang *et al*., 2014). For example, light has been used as an attractor to draw fish away from hydropower turbines in conjunction with sound and a bar-screen veneer installed on trash racks, and collectively reduced entrainment of blueback herring (Ploskey *et al*., 1995).

Operational changes

At reservoirs, hydropower and pumping stations with multiple downstream passage routes, operational changes to reduce the proportion of fish that pass through harmful intakes have been successful. These include intentional spill to allow movement through spill gates without passing through turbines (Boubee & Williams, 2006). Seasonal turbine shutdowns have also been successful in reducing the mortality of downstream migrating silver American eels by allowing passage via spillways or through bypass chutes (Smith *et al*., 2017) and have been recommended in France based on findings from a Bayesian model to track eel movements (e.g. Droineau *et al*., 2017). At pumping stations, if multiple pump types and/or sizes are available and one is less harmful to fish, this could be operated to provide downstream passage, probably coupled with operational changes to ensure only the safer pump operates when fish are known to migrate. When there is not an alternative route available, alternative solutions would need to be employed such as provision of an alternative bypass channel. Operational changes as a remediation measure require further research, in the interests of utilising existing site features to improve fish passage, and could negate the need for expensive refurbishment such as physical screening and turbine replacement at such structures. This will be explored further in chapters 4 and 5 of the thesis.

2.6.5 Replicate or preserve natural flows

Human water needs are often secured at the expense of the environment (e.g. Vörösmarty *et al*., 2010). In regulated rivers downsteam of infrastructure that do not receive a natural flow regime, the concept of “environmental flows”, or “eflows” is widely used (Acreman *et al*., 2014) to develop mitigation measures for impacts caused by impounding water and are defined as “the quantity, timing, duration, frequency and quality of water flows required to sustain freshwater, estuarine and near-shore ecosystems and the human livelihoods and well-being that depend on them” (Acreman & Ferguson, 2010). How much water to (re-)allocate to the environment and how to balance this with other demands is controversial (Pahl-Wostl *et al*., 2013). As a minimum, reservoir dams release a constant discharge throughout the year, also known as a compensation flow, which is used to describe a variety of low-flow releases including those for protection of river ecosystems. In the UK, 70% of reservoir dams release constant discharge throughout the year with the average compensation flow being 16% of the mean flow, similar to other countries such as France and Brazil; That said, some impoundments have no flow release structure so cannot release water back to the environment (Acreman *et al*., 2009). Using this concept and through recognition of the importance of the variability of flows in the natural flow regime, each flow is referred to as a ‘building block’. This is implemented in Europe by the WFD requirements and in the UK is recommended by the UK Technical Advisory Group (UKTAG) with information on why each one is ecologically beneficial. UKTAG provides guidance on why, how and when to implement flow ‘building blocks’ (UKTAG, 2013) (Figure 2.17) to meet GEP. However, generally it is only when there is a lot of interest in commercial or recreational fishing that flows are varied seasonally and only a few are recorded to release short-duration higher flows, or freshets, one of the motivations being to trigger fish migration (Acreman *et al*., 2009). For example, for salmonid species that must migrate to upstream spawning grounds (anadromous and potamodromous), UKTAG guidance states that freshets intended to simulate floods to promote upstream spawning migrations should be released. This is through implementation of flows in the autumn/ winter flow building block for dispersal and fish migration. Under this guidance, artificial flow releases should also be performed to move sediment downstream, clean spawning gravels and provide the flow required to trigger migration (UKTAG, 2013).

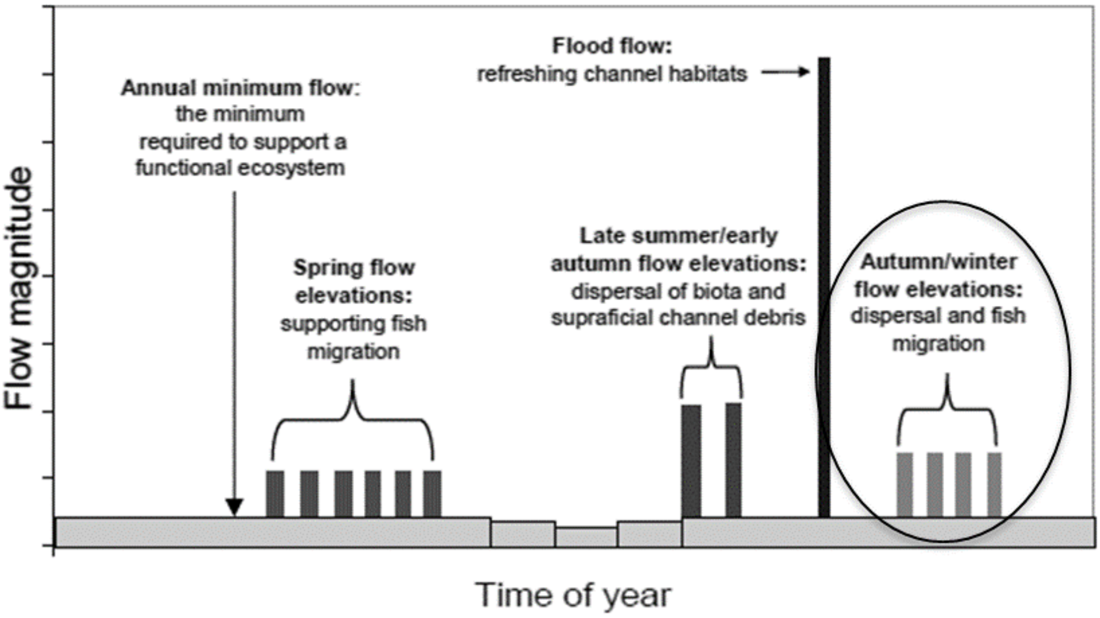


Figure 2.17. Schematic representation of a mitigation flow regime based on the recommended flow 'building blocks' (from UKTAG, 2013), including autumn/winter flow elevations for fish dispersal and migration (black circle).

Eflows science has progressed remarkably since its' declaration in 2007 (the Brisbane Declaration). It is recognised that developing new tools, models and integrated implementation frameworks in response to research is the way forward (Arthington *et al*., 2018) in order to sustain diverse aquatic ecosystems in a dynamic and uncertain future (Poff & Matthews, 2013; Rockstrom *et al*., 2014). Freshet research, as with passage research, has predominantly focussed on the response of upstream migrating salmonids moving from the sea into, and through, freshwater to spawn and has reported variable results over the years. Despite the number of weirs passed and distance moved during freshets being greater than during residual flow (Thorstad and Heggberget, 1998; Thorstad *et al*., 2005b), due to low migration speeds and erratic movements it was concluded that short and small artificial freshet releases in large regulated rivers may be a waste of money (Thorstad *et al*., 2005b). Lundqvist *et al*., (2007) demonstrated that larger freshets may be more useful in facilitating salmon passed a power station. Others reported successes (Heggenes *et al*., 2007) and stated that duration should be 2 – 3 days with a mixture of discharges (Archer *et al*., 2008) but it is recognised that further research (Hasler *et al*., 2014) particularly into the influence of larger and longer lasting freshets on upstream migration are required (Thorstad *et al*., 2008). That said, there is a dearth of knowledge about the migration of salmonids to their spawning grounds during artificial freshets in regulated rivers (see chapter 3).

For rivers regulated by hydropower, the WFD implements minimum flow requirements for the depleted stretch of river (Anderson *et al*., 2015). These requirements drive UK policy to maintain a 'hands off' flow in depleted stretches, i.e. the hydropower scheme can only operate when the flow in the river exceeds a threshold, i.e. there is enough flow to warrant hydropower generation whilst not removing more than is needed by the water body. There is variation in Europe between what constitutes a suitable threshold (ESHA, 2008) and studies have questioned whether this as an adequate mitigation measure for fish (Robson, 2013). Alternatively, 'flow splitting' of the flow above implemented hands off levels, or proportionally splitting this flow between the channel and the scheme in order to promote a more natural flow regime, or stopping operation during key fish life cycle stages may be implemented (Anderson *et al*., 2015). Legislation to protect flows does not exist for catchments that are drained by pumping stations.

2.7 Conclusion

Migratory fish in free-flowing rivers perform incredible journeys to spawning grounds sometimes thousands of kilometres from their feeding grounds. The remarkable life histories of migratory fish have evolved in direct response to the flow regime provided in rivers where longitudinal connectivity is uninterrupted. Globally, rivers have been increasingly impounded by dams and reservoirs, hydropower and/or pumping stations in response to the requirements of society as the human population grows and the climate changes. As evidence for the negative impacts these impoundments are having on migratory fish increases, so does the challenge of balancing societal benefits with those of the environment. Mitigating the impacts on fish is challenging because the priorities of infrastructure take priority from a societal, water-security and flood protection perspective, but cost-effective remediation measures are required at a vast amount of sites worldwide. It is therefore essential to understand the behaviour of the study species in response to measures to reduce mortality and damage around potentially hazardous intakes. This includes providing operational changes to replicate natural flows or provide attractive flows through alternative routes, and when providing alternative passage solutions. This is a knowledge gap that needs to be filled, ultimately to conserve populations of migratory fish by allowing access spawning grounds.

3 THE EFFICACY OF RESERVOIR FRESHET RELEASES OF VARYING PROFILES TO FACILITATE THE SPAWNING MIGRATION OF RIVER-RESIDENT TROUT

3.1 Introduction

River ecosystems are hydrological networks structured by the flow of water, sediment and nutrients, which may facilitate the movement and migration of inhabiting fauna (McCluney *et al*., 2014). All elements of the natural flow regime (Poff *et al*., 1997), including the quantity, timing and variability of flows, are considered ecologically important drivers for riverine ecosystem functioning (Enders *et al*., 2009; Nislow & Armstrong, 2012). Fish populations rely on a variety of flows to migrate between and exploit a diversity of habitats (feeding, spawning and refuge) and complete their life cycles (Cowx & Welcomme, 1998; Nislow & Armstrong, 2012). The majority of rivers in the developed world are impounded in some way, often by water-storage reservoirs for potable supply, flood control or hydropower (Vörösmarty *et al*., 2010; Gillespie *et al*., 2015). Impoundments alter the magnitude, timing and duration of ecologically important natural flood flow characteristics which should typically facilitate spawning migrations (by providing the cue and opportunity), with subsequent impacts on the downstream fish communities (Nilson *et al.*, 2005).

The European Union Water Framework Directive states that all heavily modified water bodies, such as those impounded by dams, must reach Good Ecological Potential (GEP) by 2027 (WFD; 2000/60/EEC). GEP is the ecological quality that can be achieved in the affected water bodies without significant adverse impacts to the societal benefits provided. In an attempt to comply with this, the UK Technical Advisory Group (UKTAG, 2013) provided recommendations, using the application of “environmental flows” or eflows, to identify a number of ecologically important components of river flows. The application of environmental flows is widely used (Acreman *et al*., 2014) as a mitigation measure in regulated rivers around the world and is defined as “the quantity, timing, duration, frequency and quality of water flows required to sustain freshwater, estuarine and near-shore ecosystems and the human livelihoods and well-being that depend on them” (Acreman & Ferguson, 2010). Regulated rivers receive these flows through artificial freshet releases of appropriate magnitude, duration, timing and frequency. These aforementioned ‘building blocks’ (Figure 2.17) provide guidance to identify which are likely to be ecologically beneficial in a particular river, at a particular time of year. The methodology aims to find the most efficient flow regime that conserves ecosystem functioning whilst preserving water for potable supply.

Research into the impacts of reservoir releases on downstream biota and the importance of sustainable water management is increasing worldwide (Vörösmarty *et al*., 2010; Pahl-Wostl *et al*., 2013; Chen & Olden, 2017; Sabo *et al*., 2017). Research into fish migration during freshets has predominantly focused on anadromous salmonids, which move from the sea into fresh water to spawn (e.g. Hawkins & Smith, 1986; Hawkins, 1989; Webb & Hawkins, 1989; Laughton, 1991; Smith *et al*., 1994; Aprahamian *et al*., 1998; Solomon *et al*., 1999). In unregulated rivers, potamodromous brown trout undertake spawning migrations over many kilometres (Arnekleiv & Kraabøl, 1996; Ovidio *et al*., 1998). Notwithstanding, there is currently a dearth of knowledge about the migration of brown trout to their spawning grounds during artificial freshets in regulated rivers, despite explicit recommendations for the timing, frequency, magnitude and duration of the autumn/winter flow elevation building block to reach good ecological potential in UKTAG guidance (UKTAG, 2013; Table 3.1). Further studies are hence required to develop evidence-based mitigation guidance to provide suitable freshet reservoir-release in rivers downstream of reservoirs in order to maintain ecological integrity. Brown trout are often the dominant fish species in upland rivers where reservoirs are prevalent in many regions, making them a suitable study species.

Table 3.1. UKTAG recommendations for autumn and winter flow elevations to support brown trout in rivers to their spawning grounds and the migration of adult salmon, sea trout, river and sea lamprey, in order to reach good ecological potential (UKTAG, 2013).

Building block	Description
Timing	October, November, December and, where possible, synchronised with catchment rainfall events.
Frequency	Once per week at night.
Magnitude	6x Qn95. Ascending and descending limbs of flow rise to mimic those of comparable natural flow rises.
Duration	12 hours if no obstacles to migration are present. If a number of obstacles are present, two to three days.

During this empirical investigation, the influence of the timing, magnitude and duration of autumn/winter freshet releases from two impounding water-storage reservoirs on brown trout movements over multiple years was assessed. The UKTAG recommendations for the autumn/winter flow building block for dispersal and fish migration were used to guide freshet releases (Figure 3.1). The study also incorporated days (the same fish) and reaches (different fish) that fish were not exposed to freshet releases to 'control' for fish movements under 'normal' conditions. This iterative and adaptive approach that was designed based on previous knowledge and adapted year on year based on findings uniquely attempted to robustly quantify the autumn/winter flow building block required to stimulate and facilitate brown trout spawning migrations by using multiple years of research and a control reach, and thus inform practical and evidence-based guidance on environmental flows from reservoirs operated by the water industry.

3.2 Material and methods

3.2.1 Study area

The impact of reservoir freshet releases, intended to simulate natural high-flow events, on brown trout spawning migrations was assessed in the River Holme catchment in northern England. Thie aim wasto find the most efficient flow regime that provides the conditions required by inhabiting fish in order for them to complete their life cycles, whilst conserving water for potable supply. Brownhill and Digley water storage reservoirs on Ramsden Clough and Marsden Clough, respectively, are located approx. 4km southwest of Holmfirth, West Yorkshire (Figure 3.1) The study was performed in three reaches in October and November 2012 (a, b and c; Figure 3.1) and two reaches further downstream were added to the investigation in October to February 2013/14 and 2014/15 (d and e; Figure 3.1). The experimental design allowed the movements of fish in response to freshets (in impact reaches) to be compared with those in a reach unaffected by the release (control reaches), as only one reservoir released water at any one time; i.e. when a freshet was released from Digley Reservoir, fish in Ramsden Clough were used as controls and Marsden Clough for Brownhill Reservoir (Figure 3.1). If fish were encouraged to migrate upstream in response to freshet releases, it was expected that they would congregate in weir pools of impassable weirs, as is common for migratory species when reaching an impassable barrier (e.g. Schlit, 2007; Wright *et al*., 2016). Reservoir overtopping was logged but ungauged, and did not coincide with any freshet releases. Brown trout spawning habitat was identified throughout the 3-km study reach using qualitative walkover survey, Wolman pebble count (*Wolman*, 1954) and quantitative assessment of depth, flow and substrate size (Armstrong *et al*., 2003).

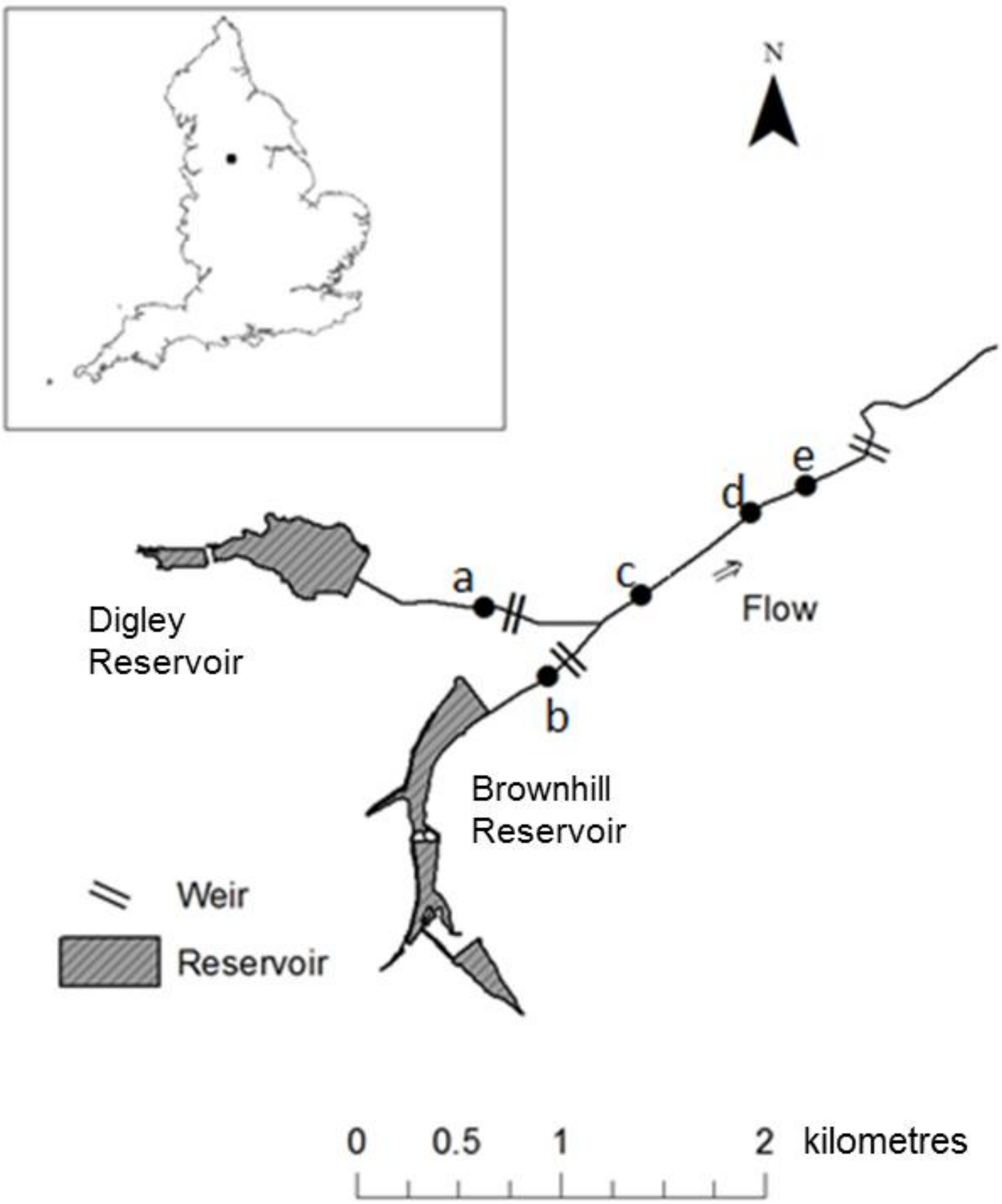


Figure 3.1. The release locations of radio tagged brown trout in (a) Marsden Clough (downstream of Digley Reservoir), (b) Ramsden Clough (downstream of Brownhill Reservoir), and the River Holme at (c) Co-op Lane, (d) Mill Pond and (e) Old Mill. Sites a – c studied in 2012 and sites a – e studied in 2013 and 2014. Three impassable weirs constructed at the same time as the reservoirs are displayed using parallel lines.

3.2.2 Freshet design

Eleven freshets (09:00 am release start) of contrasting timing, magnitude and duration were investigated during three study years, i.e. 2012, 2013 and 2014, using an iterative process based on direct observation of river flow and fish movements in previous years (Figure 3.2), whilst complying with the licensing restrictions and health and safety regulations of the water managers. Specifically, a single small-magnitude (peak = 17.3 × Qn95; 69.0 ML/d) and short-duration (10-hours) freshet was released in November 2012 (Figure 3.2). The profile was comparable to freshets released for ecological reasons, i.e. to maintain and refresh channel habitat and spawning gravels since 2004. In 2013, freshets of differing timing and magnitude were released: i.e. freshets were released in October, November and December, alternating between small- and large-magnitude (peak = 122.4 × Qn95; 465.0 ML/d) (Figure 3.2). In 2014, the magnitude and duration of freshets released were medium-magnitude (peak = 43.1 × Qn95; 163.9 Ml/d) and long-duration (28-hours) in October, November and December, but a small-magnitude and long-duration freshet was released in December (Figure 3.2).

Table 3.2. Freshet number, date, reservoir, magnitude, duration, timing and year trialled.

Freshet	Date	Reservoir	Magnitude	Duration	Timing	Year	Code
1	15/11/12	Brownhill	Small	Short	November	2012	SSN12
2	16/10/13	Brownhill	Small	Short	October	2013	SS013
3	11/11/13	Brownhill	Small	Short	November	2013	SSN13
4	11/12/13	Brownhill	Small	Short	December	2013	SSD13
5	17/10/13	Digley	Large	Short	October	2013	LSO13
6	19/11/13	Digley	Large	Short	November	2013	LSN13
7	12/12/13	Digley	Large	Short	December	2013	LSD13
8	22-23/10/14	Digley	Medium	Long	October	2014	MLO14
9	25-26/11/14	Digley	Medium	Long	November	2014	MLN14
10	9-10/12/14	Digley	Medium	Long	December	2014	MLD14
11	3-4/12/14	Brownhill	Small	Long	December	2014	SLD14

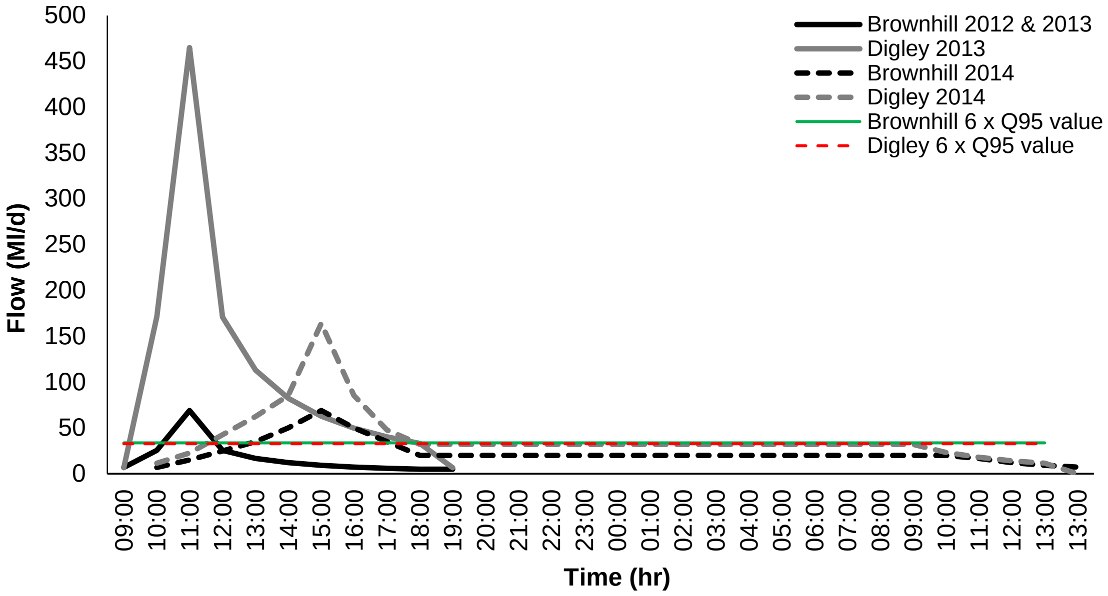


Figure 3.2. The magnitude (small, medium and large) and duration (short and long) of freshets released during the study from Digley (grey lines) and Brownhill (black lines) reservoirs, solid lines indicate freshet profiles in 2012 and 2013 with dashed lines indicating modifications made in 2014. 6 x Q95 value calculated for each reservoir indicated using red dashed (Digley; 32.7) and green solid (Brownhill; 33.8) lines).

During the investigation, UKTAG released guidance (UKTAG, 2013) stating autumn and winter flow elevations should have a 6 × Qn95 magnitude, 12-hour duration and occur once per week at night in October, November and December, “to support the migration of brown trout… to their spawning grounds” (UKTAG, 2013). Freshets were designed and implemented by the water company to best meet the criteria recommended by UKTAG, but due to operational constraints and reservoir licensing restrictions a magnitude of exactly 6 × Qn95 could not be achieved at night during small and medium magnitude, long duration releases in 2014, i.e. 5.0 (20.0 ML/d) and 8.4 (32.1 ML/d) × Qn95 were released, respectively.

3.2.3 Sampling, tagging and tracking procedure

The largest available brown trout, i.e. the adults in the population, were caught by electric fishing, anaesthetised using buffered tricaine methanesulphonate (MS-222, 0.08 g L^{-1}), weighed (g) and measured (fork length, mm) (Table 3.3). Trout had to be 50 x the tag weight in order to be implanted with tags so that any negative effects on the fish were minimised. If individuals had visible signs of milt, they were noted to be male. Prior to surgery, the unique frequency (between 173.000 and 173.999 MHz, with a nominal spacing of 10 kHz) of each tag was verified and logged using a hand-operated receiver. Radio transmitters were sterilised with diluted iodine solution and rinsed with distilled water prior to use. An 8-10 mm long, ventro-lateral incision was made anterior to the muscle bed of the pelvic fins and the whip antenna was run via the incision in the body cavity to the exterior, posterior to the pelvic fins using a shielded needle. The transmitter was then inserted into the body cavity, i.e. not obstructing in a way that would affect gonads and the incision closed with an absorbable suture. Gills were irrigated with a diluted dose (0.04 g/L^{-1}) of anaesthetic throughout the tagging procedure, which lasted between 3-4 min. Each fish was released at the approximate site of capture when fully recovered from the anaesthetic. All fish were treated in compliance with the UK Animals (Scientific Procedures) Act 1986 (Home Office licence number PPL 60/4400). The radio transmitters used in 2012 (type PIP, 20 × 10 × 5 mm, 15 cm × 0.1 mm whip antenna, potted in medical-grade silicone, 0.96 g weight in air; Biotrack, UK) had an expected life of 56 days. In the 2013/14 and 2014/15 study years, radio transmitters (type Crystal controlled 2-stage, 15 × 7 × 4 mm, 12 cm × 0.1 mm whip antenna, potted in medical-grade silicone, 0.90 g weight in air; Advanced Telemetry Systems, USA) with a longer life expectancy of 135 days were used.

Table 3.3. Number (*n*), tagging date, fork length, mass, tag-body mass ratio and release location of brown trout in the River Holme catchment, northern England.

Study year	Site code	n	Date	Length (mean ± SD (range), mm)	Mass (mean ± SD (range), g)	Tag-body mass ratio (mean (range), %)
2012	a	15	7/10/12	185.8 ± 19.8 (164 – 238)	76.9 ± 29.0 (51 – 162)	1.4 (0.6 – 1.9)
	b	15	7/10/12	198.5 ± 27.9 (163 – 256)	92.0 ± 41.4 (51 – 190)	1.2 (0.5 – 1.9)
	c	15	8/10/12	199.5 ± 21.5 (163 – 240)	96.3 ± 32.9 (53 – 167)	1.1 (0.6 – 1.8)
2013	a	10	2/10/13	179.2 ± 7.7 (169 – 196)	64.3 ± 8.2 (55 – 81.2)	1.5 (1.2 – 1.8)
	b	10	2/10/13	189.4 ± 14.5 (171 – 222)	76.7 ± 21.7 (54 – 129)	1.3 (0.7 – 1.8)
	c	10	3/10/13	208.7 ± 16.7 (191 – 241)	102.3 ± 22.3 (76 – 150)	1.0 (0.6 – 1.3)
	d	10	3/10/13	202.4 ± 29.9 (164 – 241)	99.6 ± 40.3 (49 – 148)	1.1 (0.6 – 2.0)
	e	10	3/10/13	203.3 ± 23.0 (168 – 239)	93.4 ± 27.6 (52 – 141)	1.1 (0.7 – 1.9)
2014	a	10	1/10/14	176.0 ± 10.3 (166 – 197)	65.0 ± 10.2 (54 – 84)	1.5 (1.1 – 1.8)
	b	10	1/10/14	214.1 ± 20.3 (184 – 247)	117.9 ± 32.3 (65 – 175)	0.9 (0.5 – 1.5)
	c	10	30/9/14	192.6 ± 30.6 (166 – 269)	94.2 ± 43.3 (59 – 205)	1.1 (0.5 – 1.6)
	d	10	30/9/14	198.5 ± 33.5 (170 – 282)	88.1 ± 25.5 (61 – 147)	1.2 (0.7 – 1.6)
	e	10	30/9/14	219.1 ± 23.4 (182 – 258)	130.8 ± 40.7 (77 – 203)	0.8 (0.5 – 1.2)

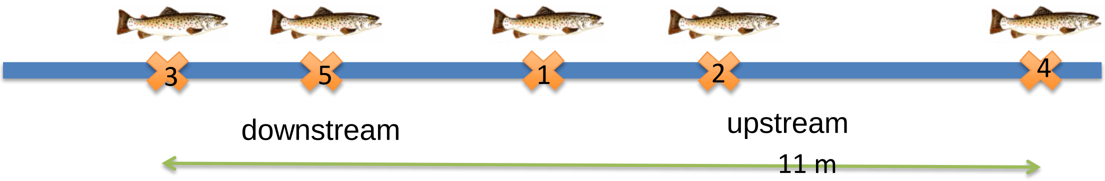
Radio tagged brown trout were located manually using a hand-operated receiver (Sika model, Biotrack, Wareham, UK) and a three-element Yagi antenna daily in 2012 and weekly in 2013 and 2014 once the study was over a longer period and a larger area, apart from for the three days before and after freshets where fish were located daily, and every 30-minutes, 1-hour and 4-hours during freshets in 2012, 2013 and 2014, respectively. When a fish changed location, the longitudinal distance moved was measured (to the nearest metre) using a tape measure for specific short distances to be accurately recorded. At most sites, fish were tracked from ~2 m from the bank so as to minimise disturbance.

3.2.4 Brown trout movement data analysis

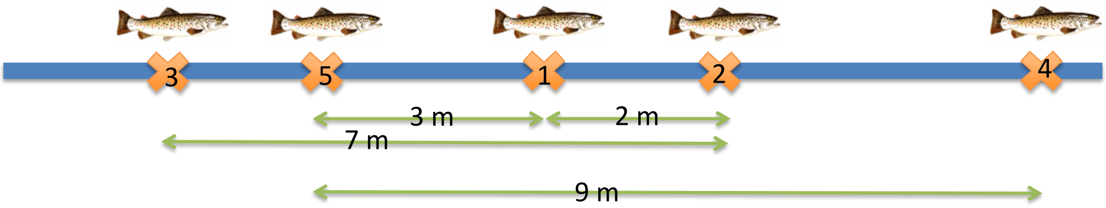
Fish move for a large spectrum of fundamental behavioural and ecological reasons, including spawning migrations, habitat exploration, for feeding and/or predator avoidance. The intention of freshet releases during this investigation was to initiate and facilitate a spawning migration, therefore the analysis performed was tailored to identify whether such a migration occurred. Movement for reasons other than migration inevitably occurred and were also explored, although this was not the primary focus of the analysis. There is no universally accepted definition of migration, but fish movement during a spawning migration is thought to be persistent, undistracted and straightened-out (Dingle, 1996; 2006), and between separate habitats (Northcote, 1984), discrete sites (Baras & Lucas, 2001) or localities (Shaw & Couzin, 2012). Migrations are also thought to involve a substantial proportion of the population (Northcote, 1984; Shaw & Couzin, 2012) moving with predictability or synchronicity in time (Baras & Lucas, 2001; Shaw & Couzin, 2012; Brönmark *et al*., 2013). Therefore, if a freshet release facilitated a spawning migration during this investigation it was anticipated that a large proportion of radio tagged brown trout would have performed a unidirectional movement to a new location, i.e. a discrete patch of spawning habitat.

The spawning location fish are migrating towards, in theory, will be a different finite distance from the starting point of each individual and thus path length will vary between individuals (unless trout were moving from exactly the same position to exactly the same spawning area, which is unlikely due to the territorial nature of the species (Johnson & Forser, 2002). Therefore, the pattern and extent of movement were analysed to deduce whether a spawning migration occurred. Crucially, it was assumed that a fish performing a spawning migration would be at the extremities of the range occupied during a freshet, after the freshet subsided, either because it reached a spawning location or because the freshet ended prior to reaching the spawning location it was travelling towards. Three metrics were used to quantify the extent of fish movement during a freshet: viz. range, total distance moved and beeline distance (Figure 3.3). The range during a freshet was calculated as the longitudinal distance between the furthest upstream and downstream position recorded for each individual. The total distance moved during a freshet was the sum of the longitudinal distance moved by an individual between each occasion it was located during the freshet. The beeline distance was distance between locations occupied immediately before and after a freshet (Bovet & Benhamou, 1988) (Figure 3.3).

Range during freshet release (11 m)



Total distance moved during freshet release (2+7+11+9 = 29 m)



Beeline distance (-3 m)

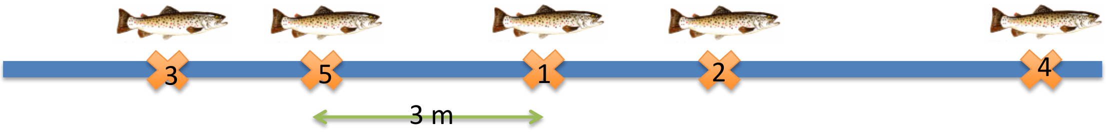


Figure 3.3. Hypothetical scenario of fish movement during a freshet release to demonstrate descriptors of movements during freshet releases.

Two indices were used to quantify the pattern of fish movement during a freshet, viz. directionality and relocation. The directionality index, also referred to as straightness or tortuosity by others (Fritz *et al*., 2002; Morales & Ellner, 2002), was the ratio between the beeline distance and the total distance moved during the freshet, ranging between 0 and 1, 1 being a completely directional movement to the final position after the freshet, therefore a higher value indicated fish performed more unidirectional movements during freshets. The relocation index was the ratio between beeline distance and the range during a freshet, ranging between 0 and 1, with a higher value indicating the fish relocated closer to the extremity of the range occupied during a freshet release. Beeline distance and total distance moved, and beeline distance and range were plotted, i.e. directionality and relocation indices, respectively, including a dashed line which indicated a score of 1 for each index.

Daily beeline distances of individual fish were calculated as the distance between locations occupied on consecutive days for fish in the impact reach in the three days before and two days after a freshet, thus enabling comparison to beeline distance during a freshet. In addition, the home range during the entire tracking period for each individual and range per day tracked were calculated as general descriptors of the extent of movements. Home range was determined by the longitudinal distance between the furthest upstream and downstream position recorded for each individual during the entire tracking period (Hojesjo *et al*., 2007). Range per day tracked for individual fish was calculated by dividing the home range by the number of days over which the individual was tracked, which describes the extent of river used, standardised for the period of tracking (Ovidio, 2002). The range during a freshet was calculated as a percentage of the home range occupied during the whole study period for each individual, to quantify the extent of movement by an individual during a freshet, and is referred to as relative range during release.

Data for flow in the catchment was available in 15 min intervals from a gauging weir at Queen’s Mill (~11 km downstream of Digley and Brownhill reservoirs), and data were provided by Yorkshire Water for the period 2004 – 2015, for comparison between brown trout movements and flow experienced in addition to compensation flow and freshet releases. Compensation flow data from each reservoir were also available in 1-day intervals, and were used to compare the flow experienced in each tributary throughout the study.

3.2.5 Statistical analysis

As there were no pairwise significant differences in home range between sites, data for fish inhabiting all reaches impacted by a freshet release, ,i.e. not the control reaches, were pooled for analysis. In order to predict the freshet characteristics that may influence whether brown trout move and what characteristics affected how far fish moved, general linear (zero inflated) models were conducted (to account for the large amount of zero values as a result of fish that performed no movement). Maximum likelihood estimation of these models were analysed using the R package ‘pscl’ (Jackman, 2017).

For comparisons between two groups (within individual freshets, between control and impact reaches for directionality and relocation indices; range, relative range during release, total distance moved and beeline distance), data were first tested for normality of variance using Shapiro-Wilk Normality tests. For comparisons between two groups (within individual freshets, between control and impact reaches for range, total distance moved and beeline distance as well as directionality and relocation indices and relative range during each release), as data were non- normally distributed and due to presence of many ties in the data, in order to obtain exact *P*-values, permutation tests were conducted using the ‘coin’ r package (Hothorn et al., 2006). For comparisons between multiple groups (i.e. of directionality and relocation indices in impact reaches between all freshets, overall range and range tracked per day between all three study years and beeline distances between the three days before, day during and two days following each freshet release), Kruskal- Wallis tests (referred to as KW- test) were used with a Dunn non-parametric pairwise multiple comparisons post-hoc test (referred to as post-hoc test). Compensation flow data (daily resolution) was provided by Yorkshire Water and compared between reservoirs in years that both released freshets (i.e. 2013/14 and 2014/15) (independence-test), All statistics were carried out in R studio v 3.3.0 and packages coin (Hothorn et al., 2006), dunn.test (Dinno, 2017) ggplot2 (Wickham, 2016) gridExtra (Auguie & Antonov, 2017); median and interquartile ranges were extracted from data in tables using the r package 'purrr' (Henry & Wickham, 2018).

3.3 Results

3.3.1 Movements during freshet releases, in comparison to control reaches

Likelihood of movement

Results of a generalized linear model to predict the freshet characteristics that may influence whether brown trout move indicated that fish in both impact and control reaches were less likely to move in November (estimate = -0.731, std. error = 0.362, Z = -2.019, probability = 0.044). When analysing what characteristics affected how far fish moved using the same method, fish were more likely to move further in October (estimate = 0.675, std. error = 0.265, t = 2.546, probability = 0.012). For fish in impact reaches only, the most important factor influencing movement was duration of freshets, with shorter duration being likely to result in less movement (estimate = -1.451, std. error = 0.394, Z = -3.679, probability = 0.0002).

Extent of movement (range, total distance moved and beeline distance)

The distance fish moved during freshets was generally small. The total distance moved during a freshet was less than 20 m for the majority of fish in impact (68.1%) and control (86.8%) reaches (Figure 3.4). The beeline distance for most (83.3%) brown trout in impact reaches during freshet releases was less than 10 m upstream or downstream from the location they occupied at the start of the release, whereas in control reaches this was true for all but one (98.9%) brown trout (Figure 3.4). Further, the range occupied by the majority of fish was smaller than 20 m in impact (84.3%) and control (90.1%) reaches (Figure 3.5). Brown trout were, however, more active (total distance moved) and occupied a larger extent of river (range) in impact than control reaches during all short-duration freshets, significantly so during small-magnitude releases in November 2012, October 2013 and December 2013 and large-magnitude releases in October and November 2013 (see Table 3.4 for statistics). Total distance moved and range were all larger during/after long rather than short-duration freshet releases in impact reaches, but were always comparable to control reaches (Table 3.4). Beeline distance, however, was comparable between impact and control reaches after all freshets (Table 3.4).

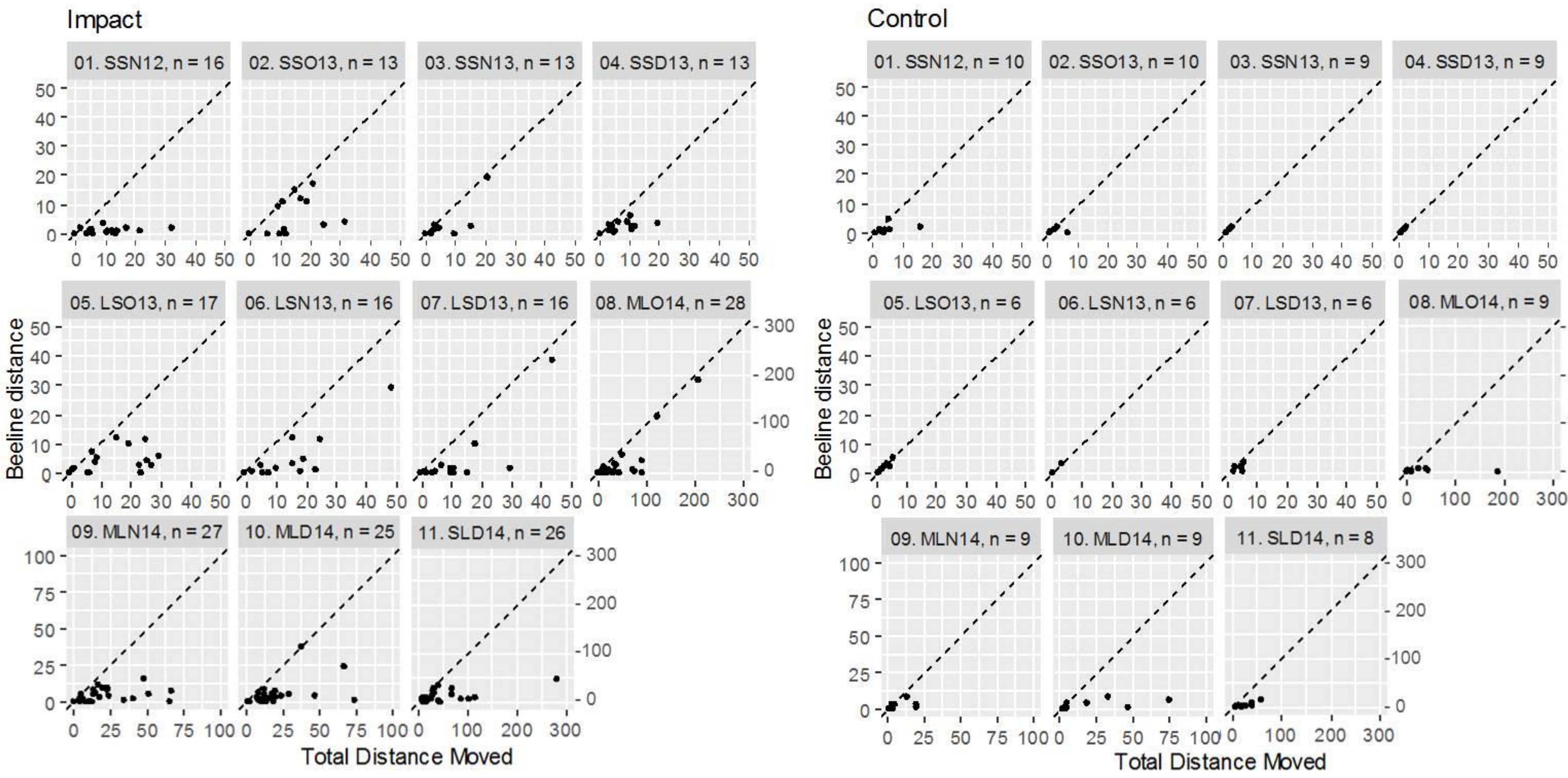


Figure 3.4. Total distance moved in relation to beeline distance for brown trout in impact (left) and control (right) reaches during freshets (code = 1st letter: magnitude (S=small, M=medium, L=large), 2nd letter: duration (S=short, L=long), 3rd letter = month (O=October, N=November, D=December), number code = year (12=2012, 13=2013, 14=2014); freshet code in Table 3.1) dashed line equivalent to directionality index = 1.

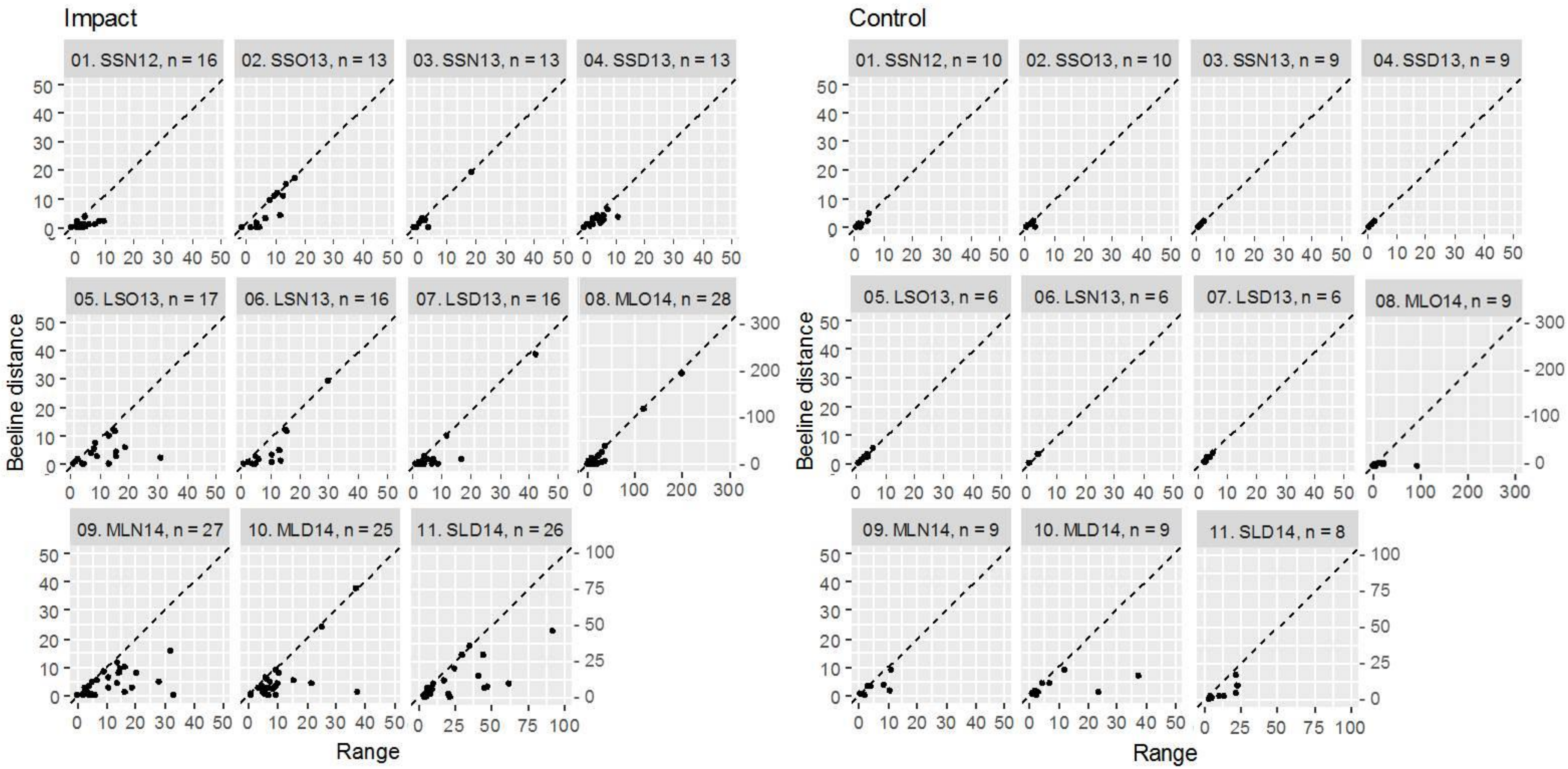


Figure 3.5. Range in relation to beeline distance for brown trout in impact (left) and control (right) reaches during freshets (code = 1st letter: magnitude (S=small, M=medium, L=large), 2nd letter: duration (S=short, L=long), 3rd letter = month (O=October, N=November, D=December), number code = year (12=2012, 13=2013, 14=2014); freshet code in Table 3.1); dashed line equivalent to relocation index = 1.

Table 3.4. Total distance moved, beeline distance and range (all median, interquartile range) of brown trout in control and impact reaches during freshets of differing magnitude (M), duration (D), timing (T), year (Y). Permutation test significance indicated by * = $P < 0.05$, ** = $P < 0.02$ and *** = $P < 0.01$.

Freshet features				Total Distance moved			Beeline distance			Range		
M	D	T	Y	Control	Impact	Statistics	Control	Impact	Statistics	Control	Impact	Statistics
Small	Short	Nov	2012	2.7, 2.9	11, 8.7	$Z = -2.401$, $n = 26$, $P = 0.016$**	0.05, 1.5	0.5, 1	$Z = 0.126$, $n = 26$, $P = 0.900$	1.5, 1.1	4, 2.9	$Z = -2.387$, $n = 26$, $P = 0.017$**
Small	Short	Oct	2013	0.2, 1.1	12, 9	$Z = -3.451$, $n = 23$, $P = <0.001$***	0, 0.6	3, 11	$Z = -1.673$, $n = 23$, $P = 0.094$	0.2, 1.1	9.5, 8	$Z = -3.456$, $n = 23$, $P = <0.001$***
Small	Short	Nov	2013	0, 1	2, 4.5	$Z = -1.668$, $n = 22$, $P = 0.095$	0, 0	0, 0	$Z = 0.516$, $n = 22$, $P = 0.606$	0, 1	1, 3	$Z = -1.266$, $n = 22$, $P = 0.206$
Small	Short	Dec	2013	0, 1	6.2, 6.7	$Z = -3.046$, $n = 22$, $P = 0.002$**	0, 0	-1.5, 4	$Z = 1.627$, $n = 22$, $P = 0.104$	0, 1	4.7, 3.7	$Z = -2.955$, $n = 22$, $P = 0.003$***
Large	Short	Oct	2013	2.5, 2.5	16, 18.9	$Z = -2.067$, $n = 23$, $P = 0.039$*	0.5, 3.3	0, 7.5	$Z = -0.471$, $n = 23$, $P = 0.638$	2.5, 1.8	8, 11.1	$Z = -2.149$, $n = 23$, $P = 0.032$*
Large	Short	Nov	2013	0, 0	9.3, 14	$Z = -2.122$, $n = 22$, $P = 0.039$*	0, 0	0, 1	$Z = 0.566$, $n = 22$, $P = 0.572$	0, 0	4.5, 9.5	$Z = -2.039$, $n = 22$, $P = 0.042$*
Large	Short	Dec	2013	4, 1.9	8.9, 10.8	$Z = -1.405$, $n = 22$, $P = 0.16$	-0.5, 3	0.2, 1.6	$Z = -0.935$, $n = 22$, $P = 0.35$	2.3, 1.3	3, 5.9	$Z = -1.001$, $n = 22$, $P = 0.317$
Med	Long	Oct	2014	11.5, 37.4	29.8, 31.5	$Z = -0.331$, $n = 37$, $P = 0.741$	-0.2, 3.4	-0.5, 8.3	$Z = 0.575$, $n = 37$, $P = 0.566$	6.5, 19.5	14.5, 16.3	$Z = -0.485$, $n = 37$, $P = 0.628$
Med	Long	Nov	2014	5, 16.5	13.5, 15.5	$Z = 0.851$, $n = 36$, $P = 0.395$	-0.5, 3	-0.2, 6.3	$Z = 0.618$, $n = 36$, $P = 0.537$	4, 7.6	9, 11.6	$Z = 0.694$, $n = 36$, $P = 0.488$
Med	Long	Dec	2014	5, 28.7	14, 10.3	$Z = 0.134$, $n = 34$, $P = 0.894$	1, 1.2	-0.5, -2	$Z = 0.251$, $n = 34$, $P = 0.80$	4.5, 9.7	7.5, 4.5	$Z = -0.109$, $n = 34$, $P = 0.913$
Small	Long	Dec	2014	22.8, 23.9	20.8, 34	$Z = -0.712$, $n = 34$, $P = 0.477$	-2.5, 5.3	0, 12.3	$Z = -0.800$, $n = 34$, $P = 0.423$	12, 16.8	10, 27.4	$Z = -1.202$, $n = 34$, $P = 0.230$

Pattern of movement (directionality and relocation indices)

The directionality and relocation indices for fish in impact and control reaches were not significantly different during individual freshet releases (permutation-tests P>0.05) (Table 3.5), except during the large-magnitude, short-duration freshet in December 2013, when both indices were significantly larger in the control than the impact reach (Table 3.5). Indeed, the beeline distance and range relative to the total distance moved by individual fish during freshet releases were highly variable during all releases, as indicated by the spread of data between the x-axis and the dashed line in Figure 3.4 and Figure 3.5. Fish rarely performed exclusively directional movements (i.e. directionality index = 1; impact = 7.1% and control = 25.3%), indicated by the distance between data points and the dashed line that represents directionality index = 1 (Figure 3.4) but a higher proportion relocated to the extremities of their range after freshet releases (i.e. relocation index = 1; impact = 31.0 % and control = 47.3 %) (Figure 3.5). In impact reaches, 20.5% of fish returned to their start point (directionality and relocation index = 0); of these, 41.9% did not move during the release and 58.1% homed to the previous location, with the latter occupying a range of as little as 1 m and up to 33 m. In control reaches, 3.3% had a directionality and relocation score of 0, all of which homed but occupied small ranges (i.e. 1 – 3 m).

Table 3.5. Directionality and relocation index (median, interquartile range) in control and impact reaches during freshets of differing magnitude (M), duration (D), timing (T) and year (Y). Permutation independence test significance indicated by indicated by * = $P < 0.05$, ** = $P < 0.02$ and *** = $P < 0.01$.

Freshet features				Directionality index			Relocation index		
M	D	T	Y	Control	Impact	Stats	Control	Impact	Stats
Small	Short	Nov	2012	0.2, 0.4	0.1, 0.1	Z = 1.389, n = 26, P = 0.165	0.5, 0.8	0.2, 0.2	Z = 1.436, n = 26, P = 0.151
Small	Short	Oct	2013	0, 1	0.1, 0.8	Z = -0.107, n = 23, P = 0.914	0, 1	0.4, 1	Z = -0.590, n = 23, P = 0.556
Small	Short	Nov	2013	0, 1	0, 0.4	Z = 0.607, n = 22, P = 0.544	0, 1	0, 0.7	Z = 0.147, n = 22, P = 0.883
Small	Short	Dec	2013	0, 1	0, 0.4	Z = -0.211, n = 22, P = 0.833	0, 1	0.5, 0.4	Z = -1.158, n = 22, P = 0.247
Large	Short	Oct	2013	1, 0.4	0.2, 0.5	Z = 1.931, n = 23, P = 0.054	1, 0.25	0.3, 0.8	Z = 1.576, n = 23, P = 0.115
Large	Short	Nov	2013	0, 0	0.1, 0.3	Z = -0.187, n = 22, P = 0.8514	0, 0	0.2, 0.4	Z = -0.750, n = 22, P = 0.453
Large	Short	Dec	2013	0.5, 0.2	0, 0.2	Z = 2.460, n = 22, P = 0.014*	0.7, 0.3	0.1, 0.4	Z = 2.436, n = 22, P = 0.015**
Medium	Long	Oct	2014	0.2, 0.2	0.1, 0.4	Z = 0.161, n =37, P = 0.872	0.3, 0.3	0.3, 0.7	Z = -0.41378, n = 37, P = 0.679
Medium	Long	Nov	2014	0.6, 0.9	0.2, 0.4	Z = 1.918, n = 36, P = 0.055	0.8, 0.8	0.3, 0.6	Z = 1.2355, n = 36, P = 0.217
Medium	Long	Dec	2014	0.3, 0.2	0.2, 0.2	Z = 0.144, n = 34, P = 0.886	0.5, 0.6	0.3, 0.5	Z = 0.25988, n = 34, P = 0.795
Small	Long	Dec	2014	0.1, 0.2	0.3, 0.6	Z = -1.898, n = 34, P = 0.058	0.2, 0.3	0.6, 0.7	Z = -1.480, n = 34, P = 0.139

The majority of fish in impact reaches with directionality (58.8%; (Figure 3.4) and relocation (67.6%; Figure 3.5) indices >0.9 moved a very short distance (beeline distance <10 m). Two fish were notable exceptions during the medium-magnitude, long-duration freshet release in October 2014; they moved a total distance of 121 and 198 m, had a beeline distance of -115.0 and -191.1 m, and a range of 118.0 m and 198.1 m, i.e. directionality index = 0.95 and 0.93, and relocation index = 0.97 and 0.96, respectively. The largest total distance moved by an individual fish during a single release was 282 m in an impact reach during the small-magnitude, long-duration freshet in December 2014, and had a 46 m beeline distance (directionality index = 0.16) and 92 m range (relocation index = 0.50). Only four other fish had a beeline distance larger than 30 m after a freshet, all of which scored high for directionality and relocation indices despite having relatively short beeline distances, i.e. the short movements were directional; 38.5 m (0.87 and 0.93), 37.5 m (0.76 and 1), 37.2 m (1 and 1) and 35.0 m (0.85 and 1).

3.3.2 Movement before, during and after freshet releases

There was no significant difference in the median daily brown trout movements (beeline distance between the fish locations each day) in the impact reach before (Days 1 – 3), during (Day 4) and after (Days 5 and 6) freshets for any of the releases studied (KW-tests; *P* > 0.05; Figure 3.6) except during the small magnitude, short duration freshet in October 2013 and the medium magnitude, long duration freshet in November 2014 when beeline distance during freshets was significantly different to before (post-hoc *P* = 0.020/ 0.008) and after freshets (post-hoc *P* = 0.004/ 0.007, respectively). In these instances, the majority of fish remained near to the start location with more outliers in the days before and after freshets, and during freshets more fish moved away from their start position but there were less outliers (Figure 3.6 a and b). The largest movements by individual fish did not exclusively coincide with freshet releases. For example, the largest movement in this time period was 554 m upstream three days before the medium-magnitude, long-duration freshet release in November 2014. There were the two aforementioned downstream relocations of 191 and 115 m during the medium-magnitude, long-duration freshet in October 2014. The only other movements that exceeded 50 m were 74 m downstream two days after the small-magnitude, long-duration freshet in December 2014 and 65.5 m downstream one day after the small-magnitude, short-duration freshet in October 2013 (Figure 3.6).

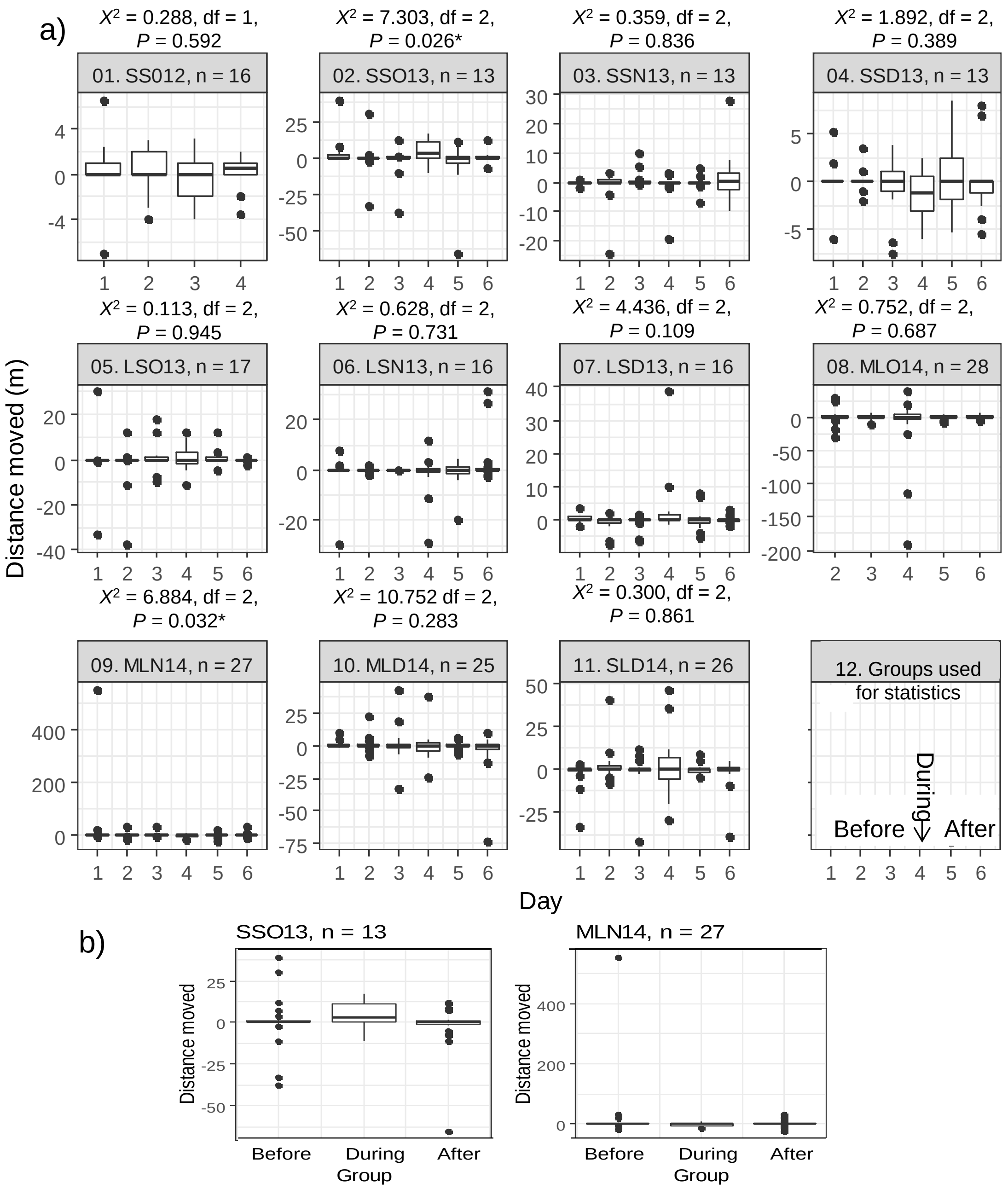


Figure 3.6 a) Daily brown trout beeline distance in impact reach before (days 1 – 3), during (day 4) and after (days 5 and 6) freshets (freshet code in Table 3.2), results of KW-tests (grouping method for statistics demonstrated in plot 12; b) Freshets that had significant differences in beeline distances during freshets compared with before and after (plots 2; left and 9; right).

3.3.3 Movements during freshets relative to the entire study

The overall range during the tracking period in 2012 was 67.3 ± 99.2 (5.8 – 525.3 m); in 2013 was 99.6 ± 77.2 (19.2 – 300.1 m), and in 2014 was 99.1 ± 128.2 (11.7 – 1090.5 m). Range per day tracked in 2012 (1.7 ± 2.5 (0.1 – 13.1)) and 2013 (1.8 ± 1.5 (0.3 –

8.3)) were significantly smaller than in 2014 (2.6 ± 6.7 (0.4 – 57.4)) (KW-tests; X^2= 7.887, df = 2, *P* = 0.019; 2012 Dunn test post-hoc *P* = 0.013 and 2013 post-hoc *P* = 0.012). The range during freshet releases was small relative to the range occupied at all other times, i.e. daily location during the whole tracking period (overall 18.4 ± 22.2), but it was larger in impact than control reaches during all releases except the small-magnitude, short-duration freshet in November 2012. The relative range was significantly larger in impact than control reaches during small-magnitude, short-duration releases in October and December 2013 (Table 3.6).

Table 3.6. Difference in relative range (median, interquartile range) of brown trout between control and impact reaches during freshets of differing magnitude (M), duration (D), timing (T) and year (Y). Permutation test significance indicated by * = P < 0.05, ** = P < 0.02 and *** = P < 0.01.

Freshet features				Relative range		Statistics
M	D	T	Y	Control	Impact	
Small	Short	Nov	2012	3.5, 16.9	9.7, 5.5	*Z* = 0.304, *n* = 16, *P* = 0.761
Small	Short	Oct	2013	0.2, 1.1	15.9, 20.3	*Z* = -3.377, *n* = 13, *P* = 0.0007***
Small	Short	Nov	2013	0.0, 0.5	0.9, 10.5	*Z* = -1.774, *n* = 13, *P* = 0.076
Small	Short	Dec	2013	0.0, 0.7	10.4, 8.2	*Z* = -2.399, *n* = 13, *P* = 0.016**
Large	Short	Oct	2013	5.4, 4.8	6.3, 16.3	*Z* = -1.338, *n* = 17, *P* = 0.181
Large	Short	Nov	2013	0.0, 0.0	5.7, 8.2	*Z* = -1.613, *n* = 16, *P* = 0.107
Large	Short	Dec	2013	4.4, 4.0	4.0, 8.9	*Z* = -0.722, *n* = 16, *P* = 0.470
Med	Long	Oct	2014	10.6, 19.2	20.2, 25.3	*Z* = -0.563, *n* = 28, *P* = 0.574
Med	Long	Nov	2014	6.7, 9.6	11.3, 19.1	*Z* = -0.593, *n* = 27, *P* = 0.553
Med	Long	Dec	2014	8.1, 16.9	9.4, 23.2	*Z* = -1.179, *n* = 26, *P* = 0.239
Small	Long	Dec	2014	9.1, 12.6	20.1, 38.0	*Z* = -1.827, *n* = 27, *P* = 0.068

The largest unidirectional movement during a freshet was 191 m. By contrast, there were six larger unidirectional movements at other times during the investigation in both directions; 2012 = 377 and 464 m downstream (Figure 3.7b and d), 2013/14 = 274 m upstream (Figure 3.7 g) and 2014/15 = 194, 324 and 1065 m upstream (Figure 3.7 m, n and o, the latter being a continuation of the previously reported 554 m upstream two days before the medium magnitude, long duration freshet in November 2014), although they rarely coincided with that of another fish (one occurrence in 2012 and 2013 and two in 2014). Three fish remained at the new location; one fish moved back downstream just under half the distance and two homed to a location previously occupied within four days. All six unidirectional movements larger than 191 m occurred at low flows (<5m^3/s), coinciding with the falling limb of periods of elevated flow in each year due to rainfall rather than freshet releases (Figure 3.7), and five also coincided with reservoir overtopping events (Figure 3.7 j and m). Two long-distance movements also occurred at low flows (< $5m^3/s$) and when the reservoir was not overtopping, i.e. 146 and 325 m upstream in 2014/15 (Figure 3.7 m and n, respectively).

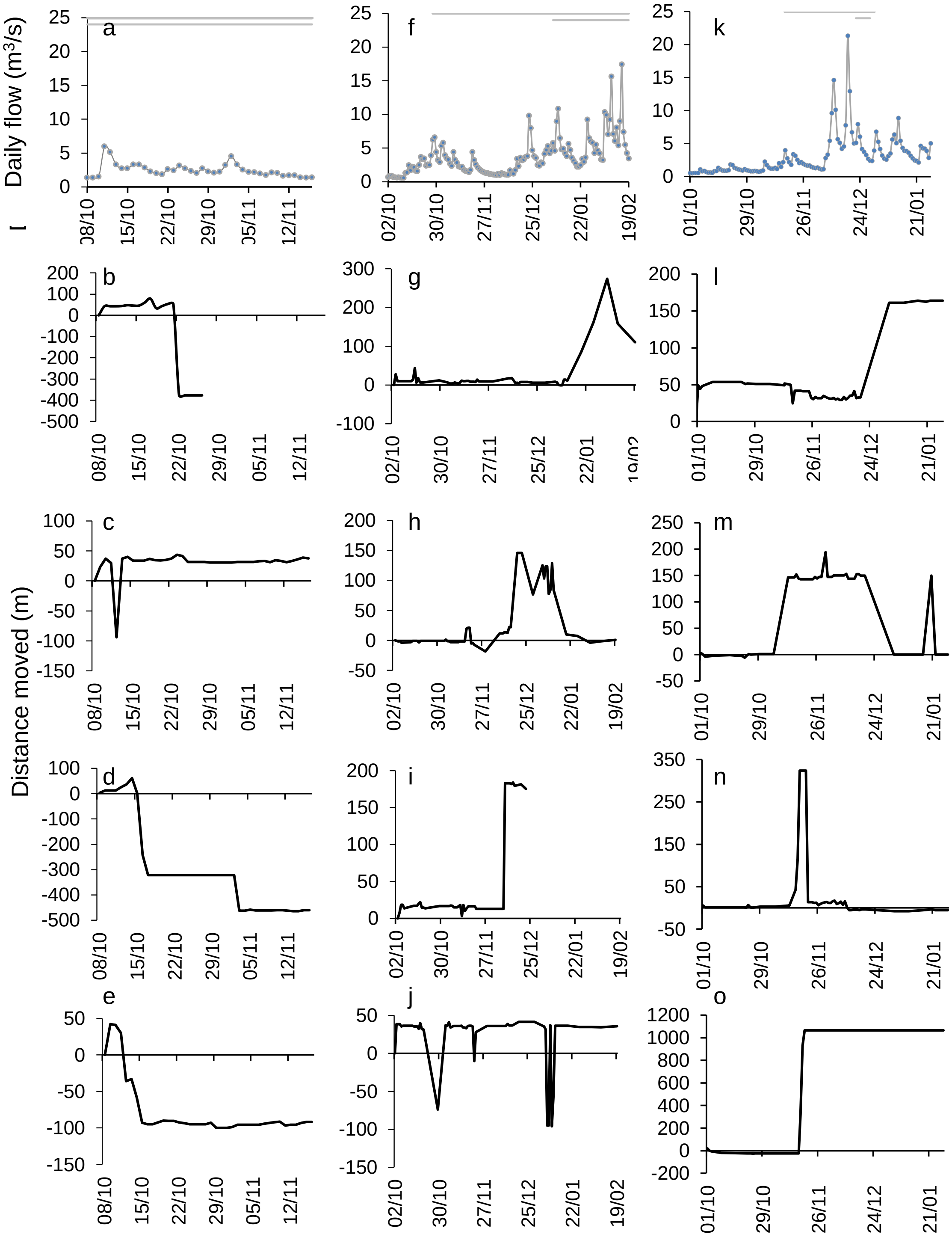


Figure 3.7. Daily flow in catchment (m^3/s) during tracking period in 2012, 2013/14 & 2014/15 (left - right; a, f & k, respectively) showing reservoir overtopping (grey lines) and largest unidirectional movements per study year (b - e = 2012; g - j = 2013/14 & l – o = 2014/15).

The compensation flow experienced downstream of each reservoir during freshet releases (Figure 3.8) was larger than that experienced at other times downstream of Brownhill reservoir in 2013/14 and 2014/15 (Figure 3.8c and e). In all other cases when there was a freshet released (a, d and f), peaks outside freshets that indicate reservoir overtopping events are larger in magnitude and duration than freshets. This is when large movements occurred. Compensation flow was comparable between the two reservoirs in 2013/14 (independence-test; $Z = -1.583$, $n = 201$, $P = 0.113$) and 2014/15 ($Z = 1.108$, $n = 205$, $P = 0.268$).

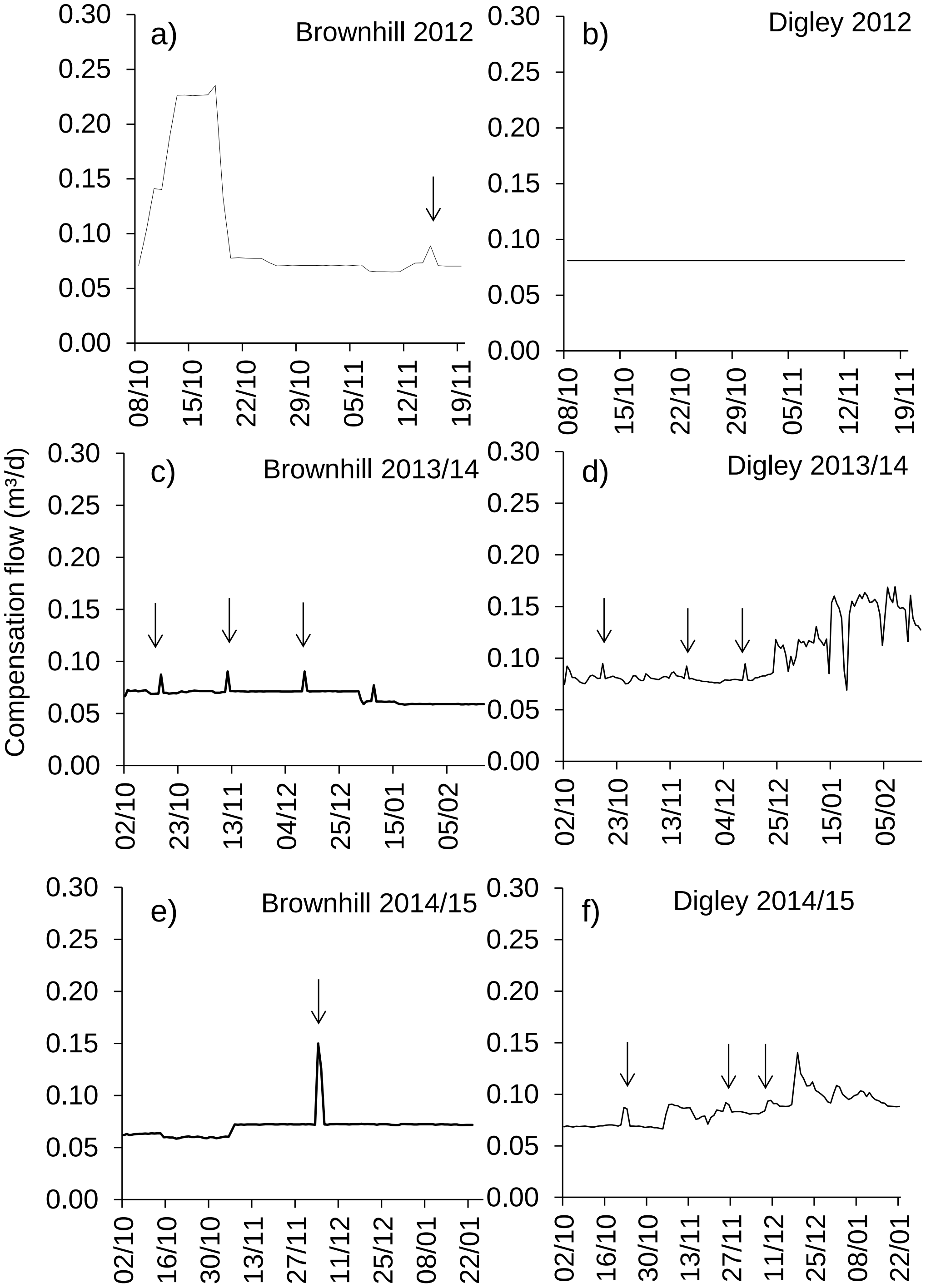


Figure 3.8. Daily compensation flow (m^3/d) from Brownhill (left) and Digley reservoirs (right) for the study period in 2012 (top), 2013/14 (middle) and 2014/15 (bottom). Freshet releases are indicated by black arrows.

3.4 Discussion

Understanding the influence of flow on fish movement is invaluable when designing environmental flow regimes, also known as eflows, for efficient water resource management and to conserve fish populations. This real-world and adaptive trial attempted to identify the capacity of artificial freshets to stimulate and facilitate potamodromous brown trout spawning migrations using the building-block approach (UKTAG, 2013). Freshets of differing timing (October, November and December), magnitude (small, medium and large) and duration (short and long) over multiple years (2012, 2013 and 2014) did not result in brown trout performing movements that were characteristic of a spawning migration, i.e. unidirectional movements to a new location with high synchronicity in time.

In theory, reservoir releases should simulate the range of natural intra- and inter-annual variation of hydrological regimes to produce “naturalized” flows in regulated rivers (sensu Poff *et al.,* 1997). Timing, frequency, magnitude and duration are key flow characteristics when designing an ecologically beneficial autumn flow building block (Acreman & Ferguson, 2010; UKTAG, 2013; Figure 2.17). Based on comparing brown trout movement data during the study to that in the literature for spawning migrations, it does not appear that brown trout performed a spawning migration during any combination of flow characteristics tested during this investigation. It is possible that the freshets trialled in this investigation did not provide the combination of flow characteristics required for fish to perform a spawning migration. However, by comparing fish movements during a freshet release with flows in control reaches, and with other releases and movements at other times, it appears that this population of river-resident fish studied do not perform spawning migrations. This possibly arises because there are areas of suitable spawning habitat throughout the reach studied, which were discovered in 2014, and more localised brown trout movements have been found where spawning, nursery and adult habitat are in close proximity (Solomon & Templeton*,* 1976). Further, although not tested here, Heggenes *et al*., (1999) reported competition and trophic interactions (predation risk) affect habitat selection while Johnsson & Forser (2002) found increased residence duration increased perceived territory value in brown trout, which may help explain lack of movement in the present study.

In this study, as predicted by models, brown trout did move further during freshets of longer duration, however this was always comparable to the control reach so is likely due to the increased opportunity for movement rather than more favourable conditions as a result of the freshet release. Fish were however more active (i.e. total distance moved) and had a greater extent of movement (range during freshet) relative to the control reaches, during short duration freshets. Therefore, while not the objective of the freshets released, short duration freshets may have benefitted individual fish by providing a short opportunity to search to gain knowledge (Gowan & Fausch, 2002) or find superior habitat (Gowan *et al*., 1994; Smithson & Johnston, 1999; Crook, 2004). Gillespie *et al*., (2015) performed a critical analysis of regulated river ecosystem responses to managed environmental flows from reservoirs and found only three out of 76 studies investigated how freshet duration affected downstream biota and none specifically investigated fish, with the majority focusing on the influence of flow magnitude (69 out of 76 assessed). The ecological responses to increased flow magnitude were inconsistent, with 38% reporting an increase, 25% had no change and 21% had a decrease, possibly due to variation in location and climate (Gillespie *et al*., 2015).

The largest unidirectional movements mostly occurred during periods of elevated river level due to rainfall and reservoir overtopping events which had far greater magnitude and duration than freshet releases in some cases, although the extent of longitudinal fish movements varied considerably between individuals. Such observations have been found previously for brown trout (Heggenes *et al*., 2007; Bunnell *et al*., 1998; Ovidio *et al*., 2002). Ovidio *et al*., (1998) also reported large movements occurred in response to reservoir overtopping events rather than freshets of comparable timing, suggesting that the unpredictable nature of such events as a result of varied temperature over consecutive days is what was responsible for initiating migration (Ovidio et al., 1998); a characteristic that may not result from artificial freshet releases. The largest unidirectional movements rarely coincided with that of another fish or in response to a particular flow, and thus were probably not a spawning migration. Some individuals homed to the location previously occupied, as reported for other freshwater fish after diel feeding (Clough & Ladle*,* 1997), spawning (Fredrich *et al*., 2003) and displacement by high flows (Lucas, 2000). More importantly, in the context of freshet releases, fish performed long-distance movements during periods of low flow when a freshet was not being released from the reservoir, and thus were not reliant on freshets for the opportunity to perform a long-distance spawning migration.

Despite this study finding little evidence to support the use of freshets for potamodromous fish to perform spawning migrations, it is widely accepted that understanding the natural flow regime has played a large part in the development of environmental flows science and application in the past two decades (Poff, 2017). Since the 2007 Brisbane Declaration which proposed the aforementioned definition of eflows, there was a call for global research to quantify ecological goods and services in rivers worldwide, through development and assessment of ecological models (Arthington *et al.,* 2018). Research conducted therein (see Kennen, Stein, & Webb, 2018) has seen implementation of new frameworks that have advanced implementation of alternative environmental water hypotheses and management schemes (Arthington *et al*., 2018). Frameworks include the Ecological Limits of Hydrologic Alteration framework (ELOHA, Poff *et al.,*2010) which paves the way for holistic flow–ecological models to be developed for rivers of a particular hydrological nature through flow regime classification (Arthington *et al.,* 2018). Arthington *et al.,* (2018) provide a review of how this, along with associated derivative frameworks, have been implemented in the U.S.A (Buchanan, *et al.,* 2013; Kendy & Blan 2012; Reidy Liermann *et al*., 2012; Sanderson *et al.,* 2012), Spain (Belmar, Velasco, & Martinez-Capel, 2011), China (Zhang *et al.,* 2012), Australia (Arthington *et al.,* 2012; James *et al.,* 2016; Mackay, Arthington, & James, 2014) and Africa (O'Brien *et al.,* 2017).

3.4.1 Recommendations

The impact that water resources management policy has on downstream biological and ecological processes is poorly understood. This investigation used telemetry techniques over multiple years to gain an understanding of how individual, potamodromous adult brown trout responded to anthropogenic alterations to river level downstream of potable water supply reservoirs. Fish did not perform a spawning migration during freshets of differing timing, magnitude and duration, thus raising doubts over the efficacy of artificial freshets as a mitigation measure in regulated rivers, to achieve, for example, Good Ecological Potential (GEP) (WFD*;* 2000/60/EEC). The majority of greatest fish movements in this investigation occurred during extended periods of reservoir overtopping, which were also largrer in magnitude than freshet releases. This indicates that despite following recommendations as far as possible within licensing restrictions, brown trout in this study may have been more influenced by the larger flows from rainfall causing reservoirs to overtop, than by the variey of freshets released from each reservoir. Considering this, and in the interests of conserving water, measures to promote overtopping could be pursued by water companies. During years when overtopping events are unlikely to occur such as when there has been little recorded rainfall, discharge regimes could focus on small-magnitude releases to maximise benefits to downstream fish communities while minimising the total amount of water released. This case-study demonstrates the importance of robustly quantifying flow characteristics for specific downstream biota at potable water supply reservoirs, and findings should inform evidence-based guidance on environmental flows for water resource managers globally.

4 THE IMPACT OF A HIGH-HEAD HYDROPOWER STATION ON DOWNSTREAM MIGRATING SHORTFINNED SILVER EELS

4.1 Introduction

Hydropower, which utilises natural river flow for power generation, contributes 80% of the electricity generated from renewable sources worldwide (World Bank, 2014 c). This causes negative environmental impacts hydropower such as associated infrastructure creating barriers to migratory fish (See Brink et al., 2018). Despite this, it is becoming increasingly popular as a renewable energy source globally, and there are plans to build new schemes on most continents, particularly in Central and South America, Europe and Asia (see Zarfl et al., 2015). Aside from creating barriers, despite intakes of hydropower turbines being screened to prevent debris being drawn in (Barnthouse, 2013), fish can be trapped or 'impinged' onto screens, or pulled or 'entrained' into turbines if the spacing of the bars on the screen are large enough to allow entry. High mortality of migratory temperate eels after passage through turbines, partly due to their elongate body shape, has been more widely reported since the 1980's (Lucas and Baras, 2001; Larinier & Travade 2002; Calles *et al.,* 2010) and has received increasing attention in recent years due to the decline of freshwater eels worldwide (Dekker & Casselman, 2014). Hydropower can be especially hazardous for adult eels inhabiting upstream catchments because generation occurs during periods of elevated flows that are also the cue for eel seaward spawning migrations (Anderson et al., 2015). It is of global interest to find cost-effective solutions to eel passage but a more comprehensive understanding of the migratory behaviour of eels in catchments with hydropower is required to achieve this.

In New Zealand, hydropower is responsible for producing greater than half of the country's electricity (MBIE, 2018). Native shortfinned eel (*Anguilla australis*) and longfinned eel (*A. diefenbachii*) are commercially (Boubée *et al.,* 2001) ecologically (Booker & Graynoth, 2013) and culturally significant (McDowall, 2013) species. They both have a complex catadromous life cycle and despite numbers of both being reported to be increasing (APO 2017; Dunn et al., 2018) they are susceptible to many of the same anthropogenic disturbances proposed for European (*Anguilla anguilla)* and other temperate eels, namely overexploitation, habitat loss and barriers to the downstream spawning migration (see Feunteun, 2002; Lokman, 2016). Due to these species' larger size in comparison to other freshwater eels, so are at particular risk from risks associated with turbine passage (Beentjes et al., 2005) due to greater likelihood of collision with internal structures. A third species that has recently colonised in New Zealand, *Anguilla reinhardtii*, would also be at risk of the same impacts from

Hydropower. Mortality or damage caused by turbines can have long lasting negative effects on eel populations, particularly long lived species such as shortfinned and longfinned eels that can inhabit freshwater for more than 60 and 100 years, respectively, before reaching maturity (Boubée *et al.,* 2008) as recovery of long-lived species can take decades (Musick, 1999).

The risks posed to New Zealand eel species when attempting to exit the freshwater catchment is recognised amongst traditional and commercial eel fishers and dam operators, and trap and transfer programmes are implemented at numerous sites (MPI, 2016). Despite this, there is no programme for monitoring escapement of migrant eels in New Zealand (Haro, Dekker & Bentley, 2015) and although the New Zealand Freshwater Fisheries Regulations 1983 requires that fish passage be provided at barriers, the regulation came into effect after many barriers were already installed so conflict arises around when and where the protective measures need to be implemented (Boubée & Williams, 2006). Management objectives for New Zealand eel species strive for high levels of recruitment and conservation, preservation and improvement of eel habitats in order for societal and economic benefits to be reached.

By employing acoustic telemetry, the migratory route and behaviour of downstream migrating shortfinned eels upon reaching barriers to the downstream spawning migration can be quantified. Therefore, in this study, timing of arrival, route selection, migration delay and escapement of silver shortfinned eels during their downstream migration were evaluated at Wairua Power Station (referred to hereon as WPS); a high-head, run-of-river hydropower station and associated diversion weir in Northland, New Zealand. It was hypothesized that eels with higher hormone levels, or more mature eels, may exhibit behaviour that demonstrated stronger drive to migrate, such as faster migration speeds. Therefore, the study aimed to understand the full extent of WPS influence on downstream migrating silver shortfinned eels, including their maturation level through analysis of sex steroid levels. Specifically, the objectives were to:

1. Assess whether downstream migrating eels were able to migrate over the diversion weir and proceed to migrate through the natural river course, or if they entered WPS forebay and under what conditions, including gate opening and flow in the catchment
2. Assess whether eels passed over the spillway at the intake of WPS or were impinged/entrained, under what conditions and quantify the delay experienced by eels at both the diversion weir and WPS

3. Assess the areas occupied within 10 m of WPS intake chamber under differing power generation and spill level
4. Determine the final detectable location of tagged eels and whether eels that passed the weir or spillway were detected on the final receiver
5. Assess the speed and timing of eel downstream migration through the catchment in relation to flow and lunar cycle
6. Assess whether there were correlations between eel speed of migration, length and level of reproductive hormones 11-ketotestosterone or estradiol- 17β; two of the main reproductive hormones responsible for inducing silvering in eels (Lokman, 2016; Thomson-Laing *et al*., 2017).

4.2 Methods

4.2.1 Study catchment

The Wairua River drains the north-eastern part of the northern Wairoa catchment through the Hikurangi Repo (swamp) and flows out to sea via the Wairoa River and upper Kaipara Harbour (Figure 4.1). The catchment is the sixth largest in the North Island of New Zealand and covers approximately 567 km^2. Major tributaries of the Wairua River include the Whakapara, Waiotu and Mangere. In the early 1970s the Hikurangi Swamp Land Drainage and Flood Protection Scheme was constructed by the Northland Catchment Commission to control floodwaters within the Hikurangi valley and to increase production from farmland in the Hikurangi floodplain. The Scheme consists of stop banks, drainage channels, flood gates and at least seven pumping stations. The Hikurangi Swamp Scheme is currently operated by the Whangārei District Council under a resource consent granted by the Northland Regional Council in May 2012. It is recognised that flow regulation in this catchment poses the greatest risk to downstream migrating eels due to non-fish-friendly pump stations and aforementioned risks posed by power station operation (Williams *et al*., 2013) such as delays to the migration and reduced fitness or mortality caused by impingement or entrainment.

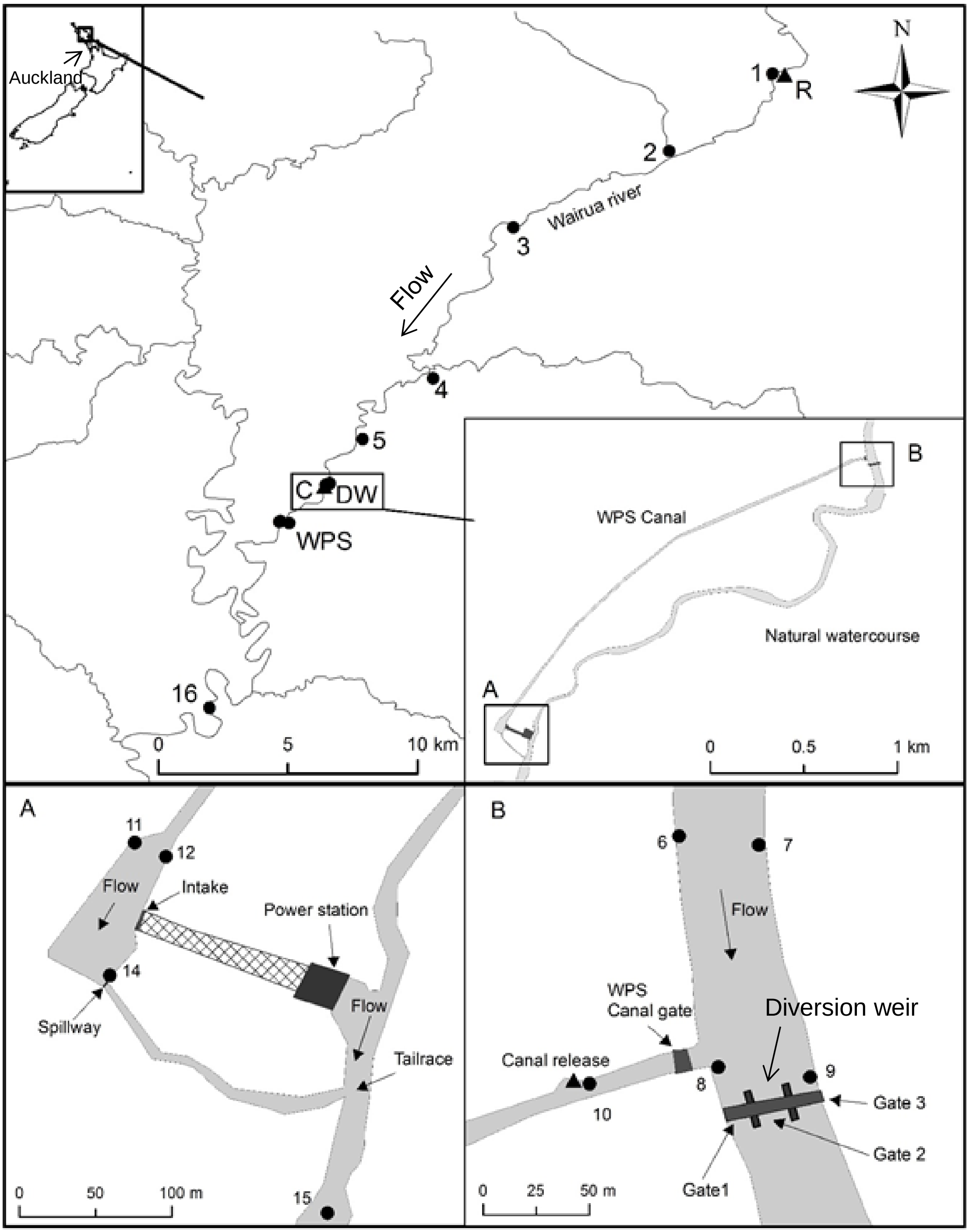


Figure 4.1. Map of study catchment showing receiver locations, river (R) and canal (C) release site locations and location of arrays of receivers at A. WPS (3 receivers) and B. the weir (4 receivers); Schematic of the WPS, showing receivers (6 – 9) and gate locations (1, 2 and 3) at the diversion weir that lead to Wairua falls, and the canal gate that leads down the canal to WPS; receiver locations in the WPS forebay area (11 – 13), location of intake, spillway, the power station and receiver 15 in the tailrace. Natural watercourse and power station canal and tailrace are indicated.

4.2.2 Wairua Power Station (WPS)

Wairua run-of-river hydropower station (-35.757444°, 174.067728°) was commissioned in 1915 and utilises the natural head over the Omiru Falls (-35.746151°, 174.084229°) to generate up to 4 MW (Figure 4.1). The station has four Francis turbines, three with 18 blades, 840 mm (*n* = 2) and 760 mm (*n* = 1) and one 880 mm with 13 blades, and a surface spillway. The turbines are protected with a vertical trash screen with 23-25 mm spacing which impinges eels though some of the bars are bent so eels can also become entrained. Upstream of WPS (2.5 km) the river can either flow through or over a diversion weir (-35.744347°, 174.084521°) with a series of gates (gate 1; vertical gate and gates 2 and 3, tip gates; referred to hereon as gate 1, 2 and 3, respectively) and follow the natural watercourse or be diverted to WPS through vertical, bottom opening canal gates (Figure 4.1). Gate 2 was not open when tagged eels were detected upstream so will not be discussed further.

4.3 Tagging and tracking methods

4.3.1 Animal collection, tagging and blood sampling

Eels were captured by fishermen in a trap upstream of WPS during a forebay and canal dewatering event (*n* = 13) and released at the head of the ‘Canal’ release site (hereon referred to as C). In addition, eels were collected from the trash pile after removal from the WPS forebay (*n* = 2) or caught in fyke nets elsewhere in the catchment (see appendix 1; *n* = 10) and released 33-km upstream at ‘River’ release site (hereon referred to as R) (Figure 4.1). Prior to tagging in the field, the maturity status of migrant eels (*n* = 25) was visually determined (Todd, 1981; Thomson-Laing et al., 2017). Eels were then anaesthetised using Aqueous solution of AQUI-S® at a dose rate of 15-20 mg/L for 10 – 15 minutes before they were weighed and total length (775 – 1033 mm), horizontal (7.3 – 10.6 mm) and vertical (7.2 – 11.8 mm eye diameters were recorded. A 10 – 15 mm long, ventro-lateral incision was made and an acoustic transmitter was implanted into the body cavity. The incision was closed with absorbable sutures. A total of 23 x V13 (36 mm long x 13 mm diameter, 11-g weight in air, 198 days expected life) and 2 x V9 (21 mm long x 9 mm diameter, 4.7-g weight in air, 271 days expected life) acoustic transmitters were implanted (Vemco, Halifax, Canada; https://vemco.com/). This practiced method, including in this river system, shows little to no scarring after two weeks nor does any suture remain (Boubee, pers.comm.) Transmitters had a 15 – 45 second coded ping delay that was emitted at 69 kHz. A blood sample (no more than 0.1% of eels’ body weight) was taken from the caudal vein using a hypodermic needle, distributed into a labelled Eppendorf tube (5 ml) containing

50 µl of 200 mg/ml ethylenediamine tetracetic acid and stored on ice to prevent blood clotting until the sampling process was finished. Samples were transported to a laboratory where they were centrifuged at 4^{o}c for 10 minutes for plasma collection. Plasma was aspirated and stored at -80^{o}c until sex steroid (11-ketotestosterone and estradiol- 17β) levels were assayed using radioimmunoassay. Eels were held in aerated tanks until visual observation confirmed full recovery (swimming around, alert) before being released. During the study WPS was visited monthly to check equipment; during these visits two tagged eels (one live and one dead) were found on the trash pile after being impinged onto intake trash screens. It is possible that eels impinged at other times may not have been observed and members of the public may have harvested them from the trash screen or trash pile, as this is a common occurrence at this site. Eels handled in this study were captured under the Fisheries Act 1996 with the number and fate of the eels reported to the New Zealand Ministry of Fisheries. All operations were carried out under NIWA's standard fish tagging protocols that were devised to ensure animal behaviour was unaffected.

4.3.2 Tracking methods

Acoustic transmissions were recorded using 15 x VR2W receivers (69 KHz; Vemco, Halifax, Canada; https://vemco.com/) strategically located throughout the catchment from 1 April to 16 June 2016. Receivers were bottom mounted, each attached to a line that was attached to a breeze block using plastic-coated metal wire, with the receiver attached using cable ties approximately 1 m from the bottom, facing upwards. Each had an individual code from R1 (first receiver downstream from R release) to R16 (most downstream receiver) (Figure 4.1). Of these, four (R11-R14) were installed in an autonomous underwater acoustic telemetry array system ((Vemco Positioning System (VPS), Vemco, Halifax, Canada)) in the immediate vicinity of the forebay of WPS. R13 malfunctioned early into the study; hence the array was only made up of three receivers. Receivers with known detection ranges were arranged in a formation that maximised coverage of the required study area as these ranges overlapped. In order for eel positions to be generated, tag transmissions must be 'heard' by three or more receivers. Transmitter location in such a system is calculated by hyperbolic positioning using delays in time of arrival of acoustic signals between receivers in differing locations around the transmitter. Each receiver was installed with a co-located synchronization or 'sync' tag (V8, 69 kHz transmitter, 386 days expected life) approximately 30 cm from the top of the receiver using cable ties, which synchronises the time between all of the receivers and measures positioning error by comparing 'predicted distance' to the actual distance between pairs of receivers. GPS positions of receivers were taken during installation to enable real error to be calculated. The data were offloaded from each receiver at the end of the study and initial processing was conducted by Vemco. The first step involves a process of time synchronizing the data as precisely as possible using time of arrival signals from neighbouring receivers. When the study is setup each receiver is programmed to transmit a unique identification code on a pseudo random schedule, typically 500-700 seconds. Vemco’s synchronization software aligns the pseudo random patterns of each self transmissions at each receiver to generate time corrections for each receiver. Once all receivers are time synched, Vemco’s VPS software uses closed form quadratic equations to calculate a position from each group of 3 receivers that detected a fish tag transmission. When multiple groups of receivers are used a relative error estimate is computed. The final position is derived using a weighted average approach where solutions with the lowest error have the greatest contribution to the final position (Webber, pers. comm.).

VPS provides position data for individual tagged eels in the acoustic receiver array, and a relative, unitless estimate of the accuracy of this position; this is referred to as horizontal position error (HPE) (Smith, 2013). Data exploration, as described by Smedbol *et al.*, (2014), demonstrated that position error in the downstream section of the array (i.e. between receivers 13 and 14) at WPS was greater than for the rest of the array Figure 4.2a) hence a tag detected in the upstream section of the array (Figure 4.2b) would be more accurately positioned than one further downstream (Figure 4.2c). The array would have benefitted from the fourth receiver (R13) or even more receivers being installed, had they been available. That said, in terms of analysing fine- scale behaviour at WPS intake, it was determined that all records in the vicinity of the intake chamber were retained if a HPE filter of 5 or less when evaluating eel locations within 10 m of the intake chamber (analysed in ArcGIS). The number of eel detections (HPE <5) in 1 m zones within 10 m of the intake were analysed in relation to power generation (i.e. 0 – 0.1, 0.1 – 1, 1 – 2, 2 – 3, 3 – 4 and 4 – 5 MW).

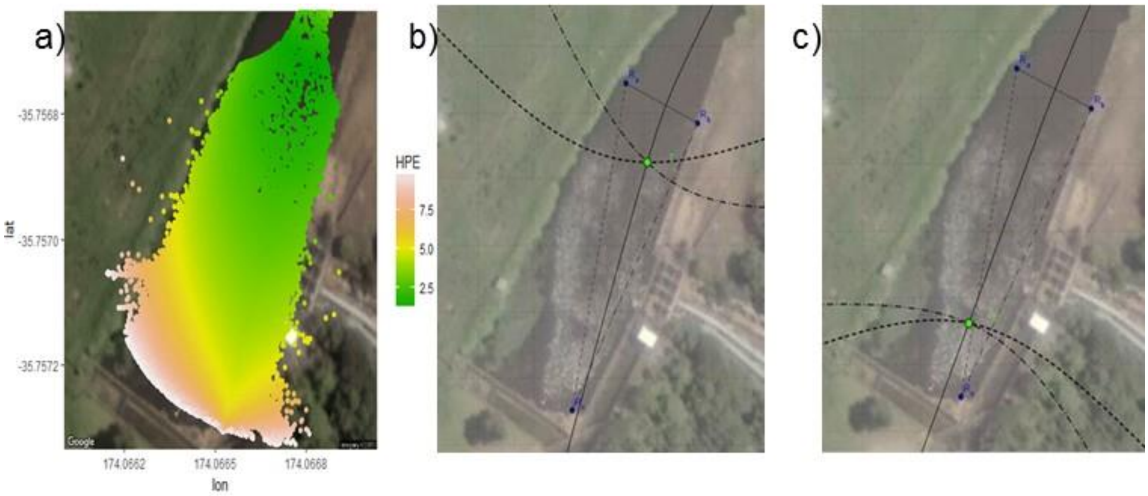


Figure 4.2. a) HPE error ranging from a score of 0 – 10 for all eel tags in the array at WPS forebay and b/c) detection triangle created by the three receivers (fainter black dotted lines) with examples of two intersecting range hyperbolas (curved black dotted lines) that identify the location (green dot) of a hypothetical transmitter.

4.3.3 Flows in the catchment and power generation

Flow data for the catchment were recorded at Purua (-35.652708°, 174.152150°), 20-km upstream of the diversion weir, and provided by the Northland Regional Council. Power generation data (MW at 30 minute intervals) during the study period (mean = 2.78 MW (range = 0 – 4.75 MW)) were provided by Northpower, owners of the WPS. The canal and power station intake forebay was dewatered for maintenance between 4/04/16 and 13/04/16 which facilitated the deployment of the acoustic receivers at these locations. There was a strong positive correlation between canal flow and power generation (Pearson Product-Moment correlation, $t = 155.62$, $df = 3104$, $P < 0.001$, $cor = 0.94$), so power generation data were used for analysis when comparing conditions experienced with eel passage. Forebay level (MV) throughout the period eels were detected in the array (13/04/2016 – 15/06/2016) was used as a measure of spill-over. A flow exceedance curve (Q values; referred to hereon as Q) was calculated for both river flow (when eels passed through the diversion weir) and power generation (when eels passed through WPS during the study period (release date to final eel detection).

4.3.4 Data analysis

Timing of all eel movements were cross-compared to sunrise and sunset hours for Auckland (~160 km distance) for the relevant dates (Time and Date, 2018) in order to determine whether movements occurred in hours of daylight or darkness. For statistical comparisons between two variables, data were first tested for normality of variance using a Shapiro-Wilk normality test and a T-test was used (referred to as t-test) if data were found to be parametric or a Wilcoxon Signed-Rank test was used (referred to as Wilcox-test) for non-parametric data. For small sample sizes, i.e. when comparing conditions experienced when eels passed over the diversion weir (*n* = 3) to when eels entered WPS canal (*n* = 8), speed of eels released at R that passed each of these routes and reached the final receiver (R16) (WPS *n* = 3, diversion weir *n* = 3) between R15 and R16 and the flow when each of these groups of eels were last detected, independence permutation tests were used (referred to as independence-test) (see Hothorn *et al*., 2008, and references therein). For correlations between two factors, a Pearson Product-Moment correlation was used (referred to as cor-test). To compare the distribution of eel detections in the area upstream of WPS intake, Komolgrov-Smirnov tests were used (referred to as KS-test). Significance levels are given to three decimal places. All statistical analyses were carried out in R studio v 3.3.0 including the use of packages data.table (Dowle & Srinivasan., 2018), ggplot2 (Wickham, 2016), ggmap (Kahle & Wickham, 2013), gridExtra (Baptiste, 2017), lubridate (Grolemund & Wickham, 2011), fasttime (Urbanek, 2016) and coin (Hothorn *et al*., 2006).

Migration speed of eels through an unobstructed 33 km reach upstream of the diversion weir was calculated from the final detection on R2 to the first detection on one of the four receivers at the weir (R6–R9), and correlated (cor-test) with flow and eel length. To explore the relationship between eel maturation stage and migration speed, speed and reproductive hormones were tested for correlations. Speed of migration from the diversion weir (last on R6–R9) to WPS tailrace (first on R15) and from WPS tailrace (first on R15) to the most downstream receiver (first on R16) were compared between eels released at R that passed through the diversion weir and WPS spillway (t-tests).

Time between first and last detection of individual eels at a) the diversion weir and b) WPS are referred to as ‘passage time’. WPS power generation and forebay level (used as a measure of spill-over, hereon referred to as ‘spill level’) Average power generation/spill level was tested for correlation with passage time for both impinged/entrained eels and those that passed downstream over the spillway (cor-tests). Wilcox-tests were used to investigate conditions experienced by eels during the last detection before impingement/entrainment compared to before passage over the spillway. Average power generation and spill level while tagged eels were in the WPS canal was compared between impinged/entrained eels and those that passed (t-test) and power generation/spill level when individual eels were last detected was calculated as a proportion of the maximum generation/spill level experienced per eel to allow analysis of conditions when the eels left relative to that experienced. This proportion was also compared between impinged/entrained and those that passed (Wilcox- test) as well as the proportion of detections in 1 m zones extending to 10 m upstream of the intake under different power generation (Wilcox-test) and between impinged/entrained and those that passed within power generation categories (t-tests) for impinged/entrained eels and those that passed, respectively, to assess whether power generation affected eel distribution in this area. Size of eels (t-test) and passage time at WPS (Wilcox-test) were also compared between impinged/entrained and those that passed. Reproductive hormone levels were compared between impinged/entrained eels and those that passed (t-test) and correlations between delay length and hormone levels were conducted for each group (cor-tests).

4.4 Results

4.4.1 Passage at the diversion weir or entry into WPS canal

Eleven of the 12 tagged migrant eels released at R were detected upstream of the diversion weir (33 km from R) in between ~2 – 38 days from release and the other eel was last detected at R4 (12.6-km from R) ~39 days after release. The mean ± S.D. migration speed was 0.18 ± 0.14 ms^{-1} (min – max = 0.01 – 0.34) and was positively correlated with flow (cor-test; $t = 2.2991$, $df = 9$, $P = 0.047$, $cor = 0.61$) (Figure 4.3). Estradiol-17β ranged from 466.24 - 1205.79 and 11-ketotestosterone from 10013.35 - 20615.037 pg/mL and was not correlated with speed of migration, eel length, eye diameter or eel total length, nor was there a correlation between speed and eel length (cor-tests; $P > 0.05$). Eels arrived at the diversion weir at river flows of 5.9 – 44.0 m^3/s ($Q_{5.4}$ – $Q_{99.7}$), with 63.6% arriving in hours of darkness (18:19 – 07:04) and 36.4% during daylight (07:35 – 16:45) (Figure 4.3; Table 4.1), on all states of lunar cycle.

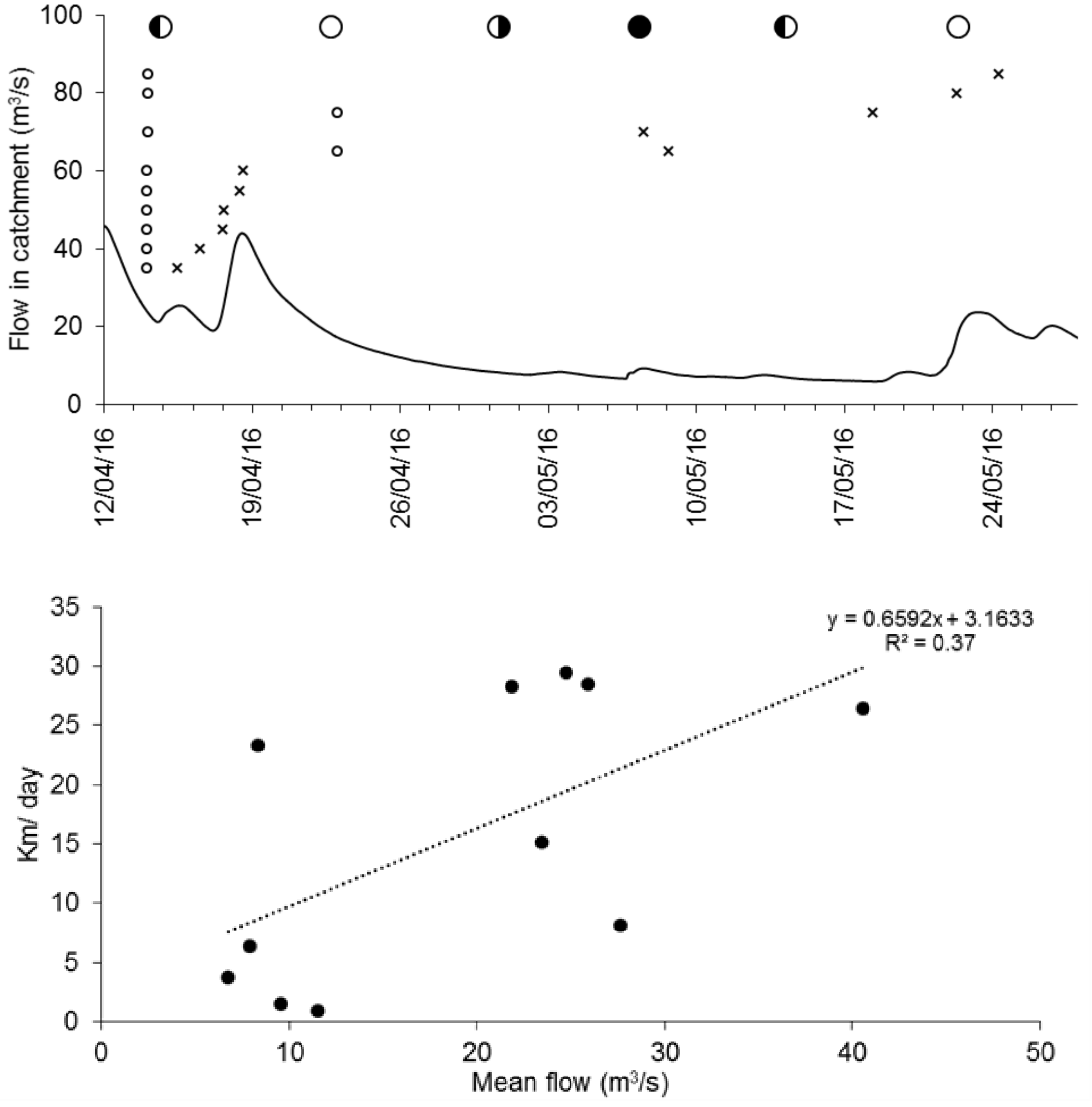


Figure 4.3. Timing of eel release (circle) and first detection at diversion weir (cross), flow in the catchment (m^3/s) and lunar cycle (top), and speed (Km/day) and mean flow (m^3/s) during each eel's movement from release to the diversion weir.

Table 4.1. Release date, date,time and flow (Q) on arrival at the diversion weir, passage route (DW = diversion weir; WPSC = WPS canal), time of passage, passage time, position Gates 1 and 2, and WPS generation at time of passage.

Eel	Release date	Time of arrival	Q on arrival	Passage route	Time of passage	Passage time (hh:mm:ss)	Gate 1 (cm)	Gate 3 (%)	Power generation (MW/day)
33888	14/04/16	18/04/2016 21:10	5.4	DW	21:12	00:02:13	22	61	4.6
33898	14/04/16	19/04/2016 01:08	6.3	DW	01:17	00:08:19	22	46	4.7
33889	23/04/2016	24/05/2016 18:19	38.4	DW	18:29	00:09:35	19	1	3.2
33880	23/04/2016	07/05/2016 23:57	67.3	WPSC	00:13	00:16:23	2	1	2.0
33883	14/04/16	17/04/2016 15:26	5.4	WPSC	15:28	00:01:42	11	1	4.2
33884	14/04/16	15/04/2016 22:34	21.4	WPSC	23:10	00:36:33	1	35	4.5
33899	14/04/16	17/04/2016 00:47	39.2	WPSC	00:55	00:07:46	2	14	4.7
33901	23/04/2016	18/05/2016 07:35	99.7	WPSC	07:49	00:13:12	1	1	1.1
33905	14/04/16	08/05/2016 16:45	74.6	WPSC	08:47	16:01:52	2	1	2.5
33906	14/04/16	22/05/2016 07:04	46.0	WPSC	07:17	00:12:37	1	1	2.7
33907	14/04/16	17/04/2016 13:50	23.1	WPSC	13:51	00:00:47	14	1	4.5

Three eels (27.2%; flow = $Q_{38.4} – Q_{5.4}$; power generation = 3.2 - 4.7 MW/day) passed downstream over gates at the diversion weir and eight (72.7%; $Q_{99.7} – Q_{18.6}$; 1.1 - 4.7 MW/day) entered the WPS canal (). During passage at the diversion weir, flow (independence-tests; Z = -1.5751, n = 11, P = 0.1152) and power generation (Z = 1.0311, n = 11, P = 0.303) was not significantly different between each of these routes. Nine of the 11 eels (81.8%) passed over the gates of the diversion weir or entered the WPS canal in less than 16 minutes, the remaining two eels took 36 minutes and just over 16 hours (Table 4.1). Three eels (33888, 33898 and 33889) passed over the diversion weir when Gate 3 was 61%, 46% and 1% open, Gate 1 was 22 cm, 22 cm and 19 cm open, and power generation was 4.6 MW/day, 4.7 MW/day and 3.2 MW/day, respectively. Two eels entered WPS canal when only Gate 3 at the diversion weir was open 14% (33899) and 35% (33884), and the other two passed when only Gate 1 at the diversion weir was open 11 cm (33883) and 14 cm (33907). Four eels entered WPS canal when all gates at the diversion weir were closed, i.e. all river water was diverted to WPS, which included the eel that took over 16 hours to pass.

4.4.2 Passage at WPS

All eels that entered (n = 8) or were released in (n = 13) the WPS canal entered the forebay, predominantly during hours of darkness (95.2%) except for one eel that arrived at 09:59 (33887). Power generation upon forebay entry ranged from 0.0 to 4.7 MW (Q_{100} – $Q_{4.0}$) and spill level ranged from -10.3 to 109.4 MV (Figure 4.4). One eel (33905) was detected on two occasions on the receiver at the head of the canal (2 km upstream) after being detected in WPS forebay, but subsequently returned to the forebay.

Based on tag detections on receivers upstream and downstream of the WPS, eleven tagged eels were impinged or entrained (52.4%), all when three or four turbines were in operation (turbine flow = $Q_{54.1} – Q_{3.9}$) with the minimum turbine flow that an eel was impinged on being 3.04 MW; (Figure 4.4) and ten passed downstream over the spillway (47.6%). There was no significant difference in eel total length between those that were impinged/entrained (mean ± SD = 918.4 ± 70.8 mm) and those that passed downstream over the spillway (884.8 ± 80.5 mm) (t-test; t = 1.2911, df = 17.569, P = 0.213). Two tagged eels impinged on the trash screen and were removed by automated mechanical cleaners and were found in trash during visits to service equipment; one (33880*) was last detected in the forebay two days earlier and was dead, whereas the other (33895) was last detected on the same day it was found alive.

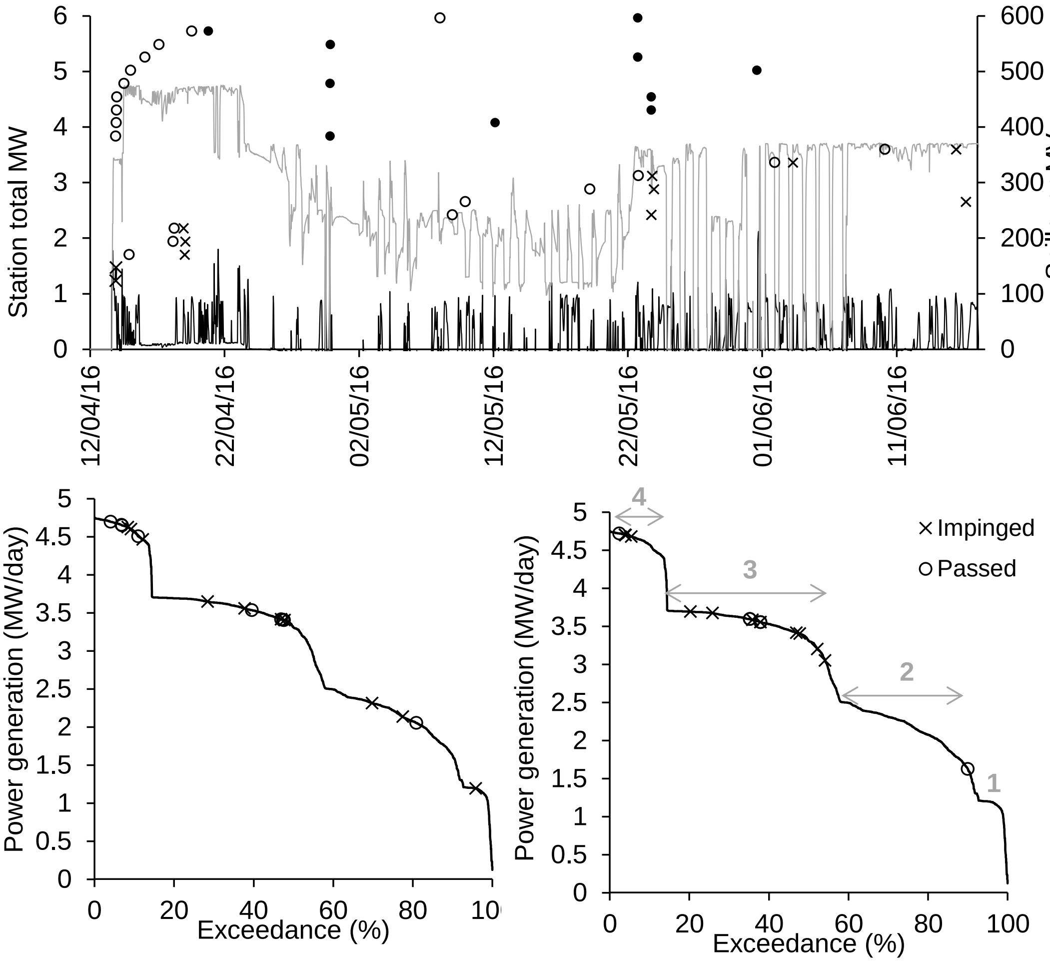


Figure 4.4. Top: Power generation (grey line) and spill level (black line) at WPS during the study showing eels first (white circle) and last detection in the array (black circles for eels that passed and crosses for eels that were impinged; crosses only indicate eel was impinged shortly after first detection). First (bottom left) and last detection (bottom right) in WPS forebay for eels that were impinged/entrained (cross) and passed (circle) in relation to power generation exceedance curve during the study period, grey numbers and arrows indicating number of turbines in operation (note: nil power generation not plotted).

All but three (21549, 33895 and 33896) of the 21 eels detected in WPS forebay were last detected in the forebay during hours of darkness (85.7%). Power generation when last detected did not differ between eels that were impinged/entrained (*n* = 11; 3.7 ± 0.6 MW; $Q_{54.1}$ – $Q_{3.9}$) and those that passed over the spillway (*n* = 6; 2.3 ± 2.0 MW; Q_{100} – $Q_{2.4}$) (Wilcox-test; *W* = 69, *n* = 21, *P* = 0.340) (Figure 4.5 a and b), though four eels passed downstream through the spillway when turbines were not operational. Likewise, one eel was impinged/entrained when no water was passing through the spillway and one when spill level was low (1.9 MV), and hence was not considered to be providing a downstream passage route. Further, eels that passed over the spillway experienced significantly higher spill level during last detection in the forebay (113.4 ± 61.0 MV) than eels that were impinged/entrained (46.1 ± 43.6 MV) (t-test; *t* = -2.9278, *df* = 18.055, *P* = 0.009). Average power generation while tagged eels were in the WPS canal also did not differ between eels that were impinged/entrained (3.2 ± 0.9 MW) and those that passed downstream through the spillway (3.3 ± 0.9 MW) (t-test; *t* = -0.279, *df* = 18.572, *P* = 0.783) (Figure 4.5 c and d). Similarly, there was no significant difference in average spill level between eels that were impinged/entrained (31.9 ± 32.2 MV) and those that passed over the spillway (15.1 ± 10.2 MV) (Wilcox-test; *W* = 75, *n* = 21, *P* = 0.173) However, power generation when the eels were last detected relative to maximum generation experienced prior to each eel passing was significantly larger for impinged/entrained eels (96.4 ± 5.5%) than for eels that passed over the spillway (49.8 ± 44.4%) (Wilcox-test; *W* = 93, *n* = 21, *P* = 0.008). Also, spill level when last detected relative to maximum spill level experienced prior to passage was also comparable for impinged/entrained eels (46.3 ± 44.2 MV) and eels that passed over the spillway (66.5 ± 29.3 MV) (Wilcox-test; *W* = 40, *P* = 0.304) (Figure 4.5 e and f).

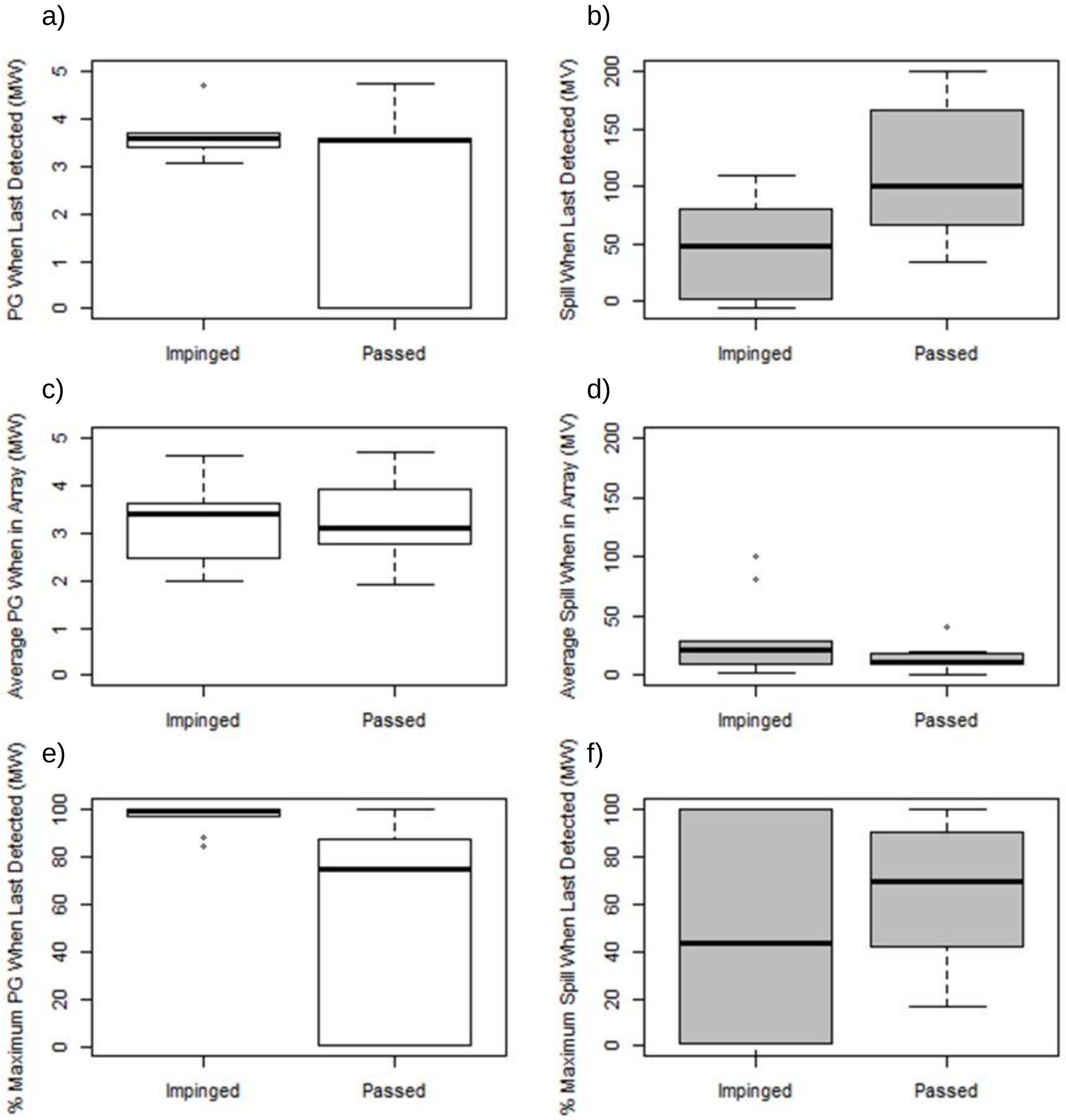


Figure 4.5. Boxplots of WPS power generation (PG, left) and spill level (right) when impinged/entrained eels and those that passed over the spillway were last detected (a and b), average while in canal (c and d) and last detected relative to maximum experienced (e and f).

Three eels (33888, 33889 and 33898) released at R passed downstream over gates at the diversion weir and travelled to WPS tailrace (R15; 2.95 km downstream) at a migration speed of 117.0 ± 36.0 (min – max = 75.9 – 142.9 km/day) . This migration speed was significantly faster than that of the two eels (33880 and 33884) that entered WPS canal and passed over the spillway to R15 (2.48 km; migration speed = 0.1 ± 0.1 (min – max = 0.1 – 0.2 km/day)) (t-test; *t* = 5.621, *df* = 2.000, *P* = 0.030). Eels were impinged/entrained at WPS after 06d 09:33:10 ± 11d 03:00:50 (min – max = 0d 00:03:07 – 37d 08:30:36) which was significantly less time than that of eels that passed downstream over the spillway (25d 04:09:50 ± 15d 02:53:47 (01d 05:53:14 - 46 d 18:00:21)) (Wilcox test; $W = 14$, $n = 21$, $P = 0.003$). Indeed, 82% of eels were impinged/entrained in less than 05 days 07:45:39 whereas for eels that passed over the spillway, 90% remained in the forebay for between 12 days 18:33:39 and 46 days 18:00:21 (Figure 4.6 top).

There was a negative correlation between mean power generation and passage time at WPS (Figure 4.6 bottom); which was significant for eels that passed over the weir (cor-tests; $t = -2.418$, $df = 8$, $P = 0.042$, $cor = -0.64$) but not for impinged/entrained eels (t = -1.629, df = 9, P = 0.138, cor = -0.48). There was also a significant negative correlation between mean spill level and passage time at WPS for eels that passed over the spillway (cor-tests; $t = -3.055$, $df = 9$, $P = 0.014$, $cor = -0.71$) but not for impinged/entrained eels ($t = -1.626$, $df = 9$, $P = 0.138$, $cor = -0.48$). Likewise, there was no significant correlation in passage time at WPS and reproductive hormones estradiol (122.48 - 1040.00 pg/mL) (cor-tests; $t = 1.714$, $df = 3$, $P = 0.185$, $cor = 0.7$; $t = -2.369$, $df = 3$, $P = 0.099$, $cor = -0.81$) or 11-ketotestosterone (10962.55 - 95408.82 pg/mL) ($t = -0.220$, $df = 3$, $P = 0.84$, $cor = -0.13$; $t = 0.556$, $df = 3$, $P = 0.617$, $cor = 0.31$) for impinged/entrained eels or eels that passed over the spillway, respectively, nor was there a significant difference in either hormone between impinged/entrained eels (estradiol; 292.92 - 913.03 pg/mL and 11-ketotestosterone; 14242.64 - 48941.47 pg/mL) and eels that passed over the spillway (estradiol; 122.48 - 1040.00 pg/mL and 11-ketotestosterone; 10962.55- 95408.82 pg/mL) (t-tests; estradiol; $t = -0.020$, $df = 6.794$, $P = 0.985$ and 11-ketotestosterone; $t = -1.301$, $df = 5.342$, $P = 0.246$).

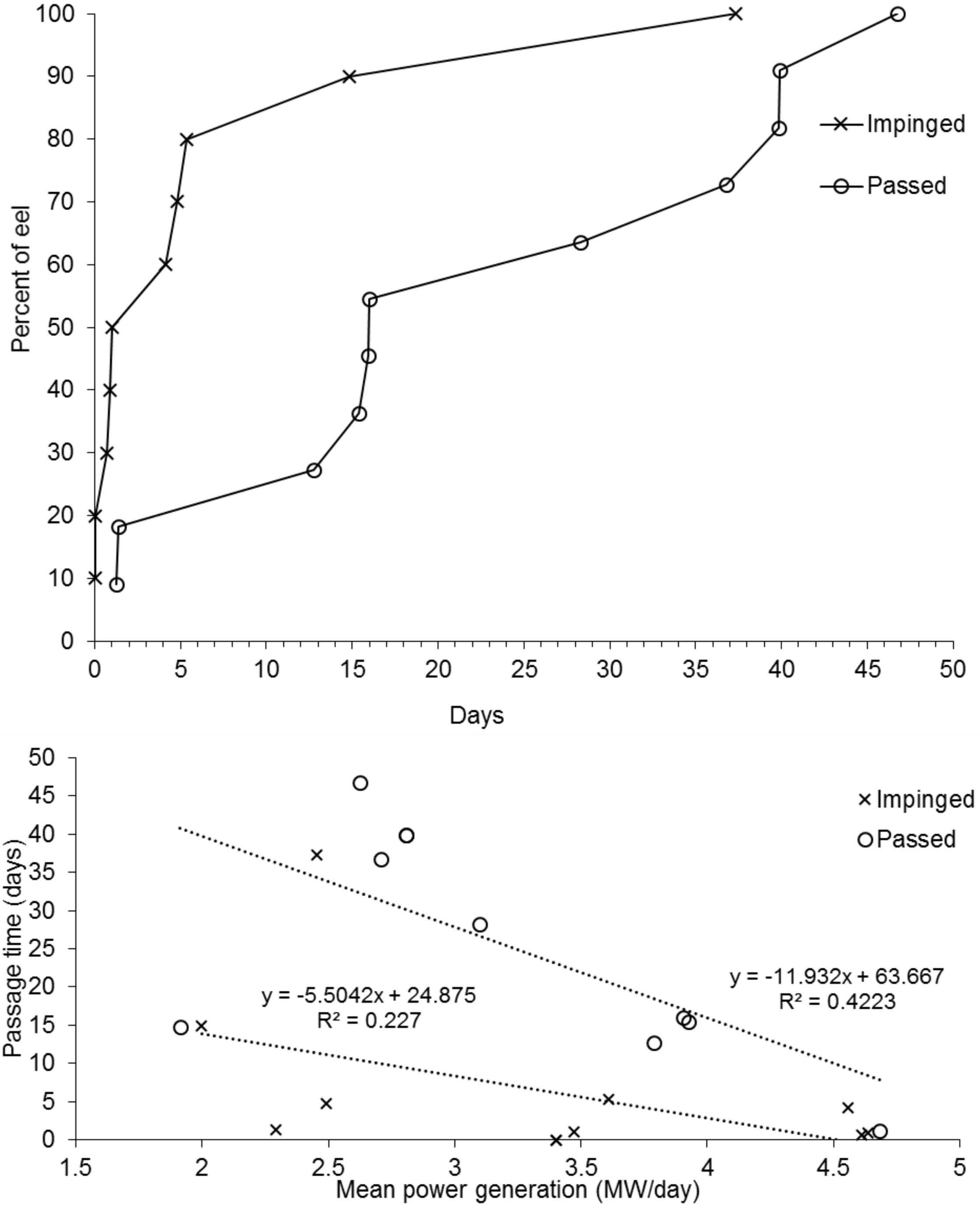
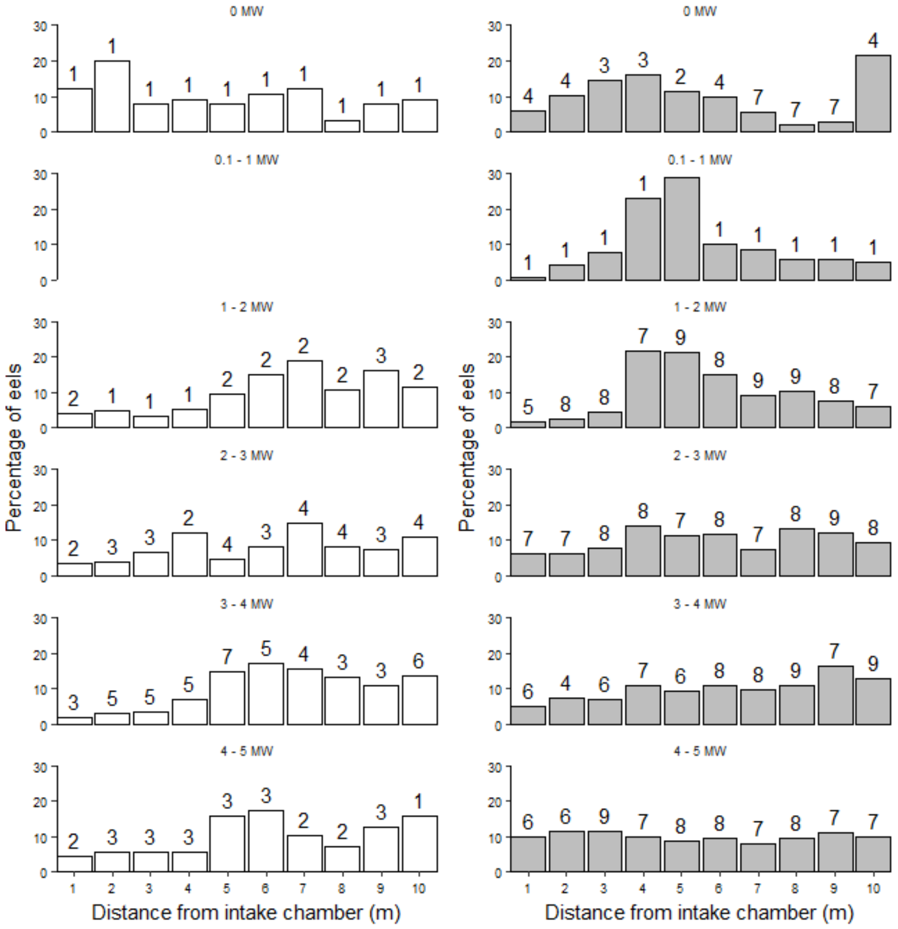


Figure 4.6. Cumulative proportions (%) (top) and mean power generation (MW/day) (bottom) for time (days) between first approach to WPS and subsequent impingement/entrainment (crosses) or spillway passage (circles).

4.4.3 Behaviour upstream of WPS intake chamber

Relatively few eel positions (<12%) were immediately upstream (within 1 m) of the intake chamber for eels that were impinged/entrained. For these eels, the majority of positions from power generation 1 – 2 MW and higher were from 6 – 8 m away from the intake chamber (1 – 2 MW = at 7m (19.0%), 2 – 3 MW = 7m (15.0%), 3 – 4 MW = 6m (17.0%) and 4 – 5 MW = 6m (17.4%). In contrast, for eels that passed the spillway, at 2 – 3 MW and higher, there were a large proportion of detections within 1 m of the intake chamber (2 – 3 MW = 70%; 3 – 4 and 4 – 5 = 60% of eels) (Figure 4.7). Essentially this means that a number of eels that did get close to the intake chamber escaped and passed downstream. Overall, there was no significant difference in eel positions upstream of the intake between impinged/entrained eels and those that passed downstream over the spillway (Wilcox-test; *W* = 1466, *P* = 0.841) nor was there any significant difference in the position of the eels between the six levels of power generation examined (ks-tests; P > 0.05) (Figure 4.7).



KS- test statistics

d = 0.3,
n = 20,
P = 0.760

n/a

d = 0.2,
n = 20,
P = 0.995

d = 0.3,
n = 20,
P = 0.760

d = 0.4,
n = 20,
P = 0.401

d = 0.5,
n = 20,
P = 0.164

Figure 4.7. Percentage of detections within 1m zones upstream of the intake chamber, for impinged/entrained eels (left) and eels that passed over the spillway (right) at differing power generation. Data labels = number of different eels in each group.

4.4.4 Onward migration

Fifty percent (*n* = 6) of eels released at R (*n* = 12) were detected on the most downstream receiver (R16); three passed over the diversion weir (50%) and three passed over the spillway at WPS (50%). Passage time at the diversion weir was between 2 and 36 minutes and passage time at WPS was 12 to 36 days, which equated to 0.01 – 0.02% and 47.62 – 92.17%, respectively of the total time individuals were detected in the river. Despite delays, eels that passed over the spillway at WPS were detected on R16 (08/05/2016 – 23/05/2016) during the same period as eels that passed over the diversion weir (30/04/2016 – 25/05/2016) (Figure 4.8 top). One eel arrived at R16 on a third quarter moon, two on a new moon and three on a full moon. Both groups of eels also migrated through the unobstructed reach downstream of WPS at a comparable speed (WPS eels = 0.41 ± 0.30 m/s^{-1} and diversion weir eels = 0.12 ± 0.22 m/s^{-1}; independence-tests; $Z = 1.344$, $n = 6$, $P = 0.179$). However, the flow when these eels passed R16 was higher for eels that passed through WPS ($Q_{42.7}$ – $Q_{26.6}$) compared with eels that passed over the diversion weir ($Q_{85.2}$ – $Q_{68.9}$) ($Z = -2.1295$, $n = 6$, $P = 0.033$) (Figure 4.8 bottom). In addition, the seven eels released at C that passed over the spillway were all detected on R16 in between 0d 08:31:25 and 06d 00:14:04 after last detection at WPS, but the eel (33895) found in trash removed from the screen and released downstream of the WPS was never detected again.

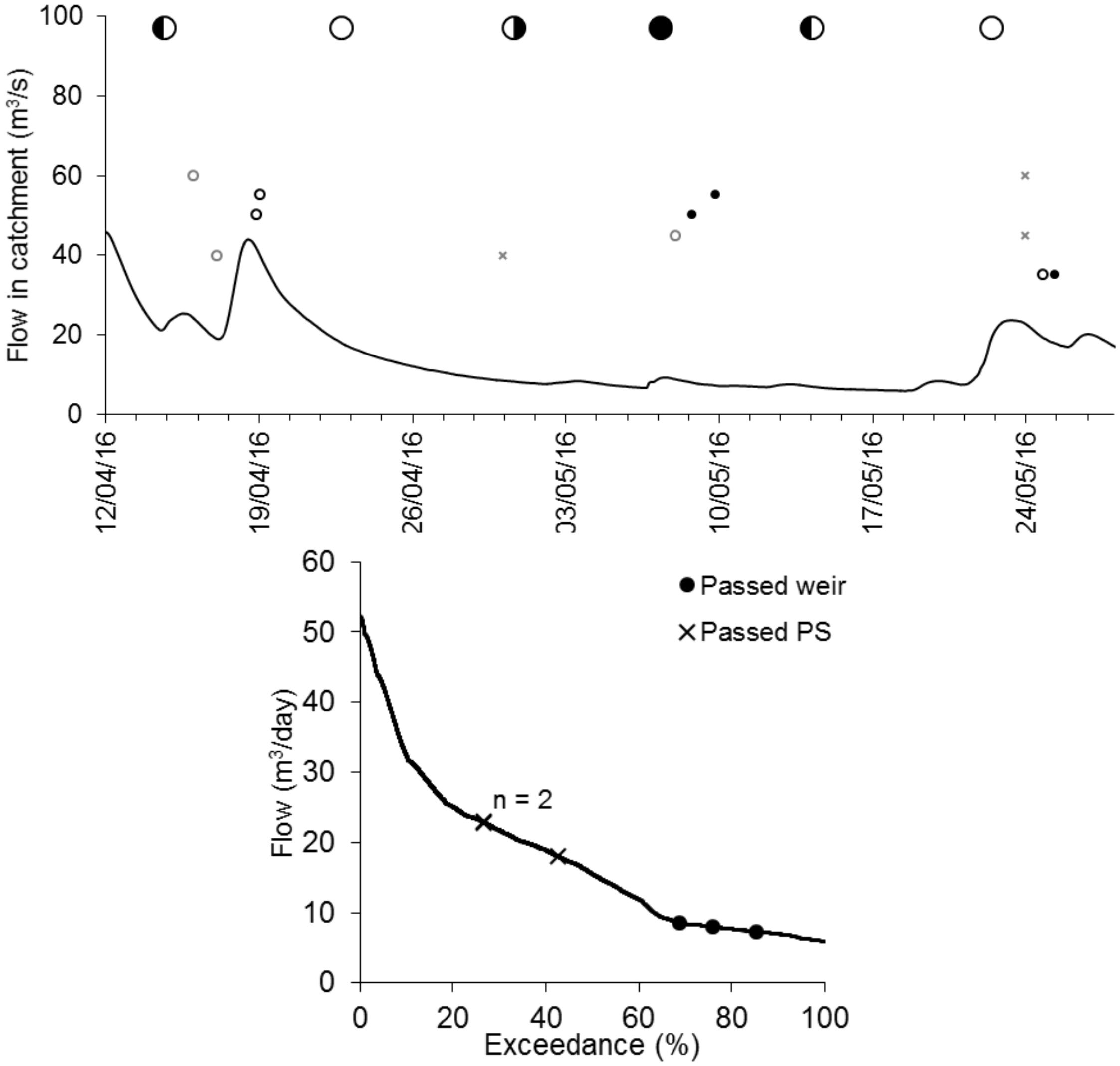


Figure 4.8. (top) Timing of eels arriving at Receiver 16 (last receiver in the catchment) after either passing through gates at the diversion weir (black symbols) or over the WPS spillway (grey symbols). River flow in the catchment (m^3/s) and lunar phase also shown. (Bottom) timing of last detection on Receiver 16 (last receiver in the catchment) in relation to flow exceedance curve of the catchment flow data. All records are for eels released at R1 that travelled via the diversion weir (*n* = 3) and power station spillway (PS; *n* = 3).

4.5 Discussion

Eels were caught, tagged and released during a period of elevated river discharge which probably triggered their downstream migration, as reported by Boubée *et al*., (2001) and Jansen *et al*., (2007). Eel movements in an unregulated reach of the Wairua River were quicker during higher river flow but arrival at the first barrier (the diversion weir) occurred across a wide range of flows ($Q_{5.4}$ – $Q_{99.7}$), both during the day (36.4%) and at night (63.6%) and on all states of the lunar cycle. A high proportion of eels (73%; $Q_{99.7}$ – $Q_{18.6}$) entered WPS canal, including two when diversion weir gates were open, allowing access to the natural river channel (Q_{39} and Q_{46}), which is in contrast to a previous study in this catchment which found the majority of eels passed through the diversion weir gates during flood flows (Boubée, NIWA, pers. comm.).

Minimising the proportion of migrants that enter the WPS intake canal and maximising the proportion that pass through diversion weir gates is considered the preferred option for minimising the impact of hydropower generation on shortfinned eel stocks in the Wairua River. Previous investigations have recommended hydropower stations should perform operational shutdowns during periods of elevated discharge at night and linked to environmental conditions such as during a dark moon when silver eels are known to migrate downstream (Eyler *et al*., 2016; Haro, 2003; McCarthy *et al*., 2008). Unfortunately, such a tailored approach would not be economically acceptable at this site given the broad range of flows, times of the day and lunar cycle that eels approached the diversion weir. It is hence recommended that a gate at the diversion weir should remain open by the minimum amount eels were observed passing during this study (i.e. i.e. gate 1 = >19 cm; Gate 3 = >46 %) throughout the autumn shortfin eel migration period, i.e. February – May (Boubée *et al*., 2001). Opening of weir gates has been successful in passing a large number (70%) of migrant eels at a hydropower station elsewhere in New Zealand (Watene & Boubée, 2005) and has influenced route choice and rate of eel migration in Europe (e.g. Breukelaar *et al*., 2009). That said, four eels entered the power canal when gates at the diversion weir were open and the time between arrival and passage was short (91% of eels passed downstream (either route) in less than 36 minutes). Therefore, it is recommended that attempts are made to deter eels from entering the WPS canal, possibly using physical screening (Gosset *et al*., 2005) or possibly behavioural deterrents such as strobe lights (Patrick *et al*., 2001; Brown., 2000), acoustics (Patrick *et al*., 2001; Deleau *et al*., 2016) or a graduated electric field (O’Farrell *et al.,* 2014).

A similar proportion of eels were impinged/entrained at WPS (52.4%) and were considered dead as none were detected further downstream, or passed over the spillway (47.6%) and were considered alive as they were detected further downstream. Turbine mortality rates in other studies vary widely but were comparable; 9 – 60% has been reported in European eels (Winter *et al*., 2006; Bruijs *et al*., 2009; Calles *et al*., 2010; Pedersen *et al*., 2012); 16 – 100% for American eels (Eyler *et al*., 2016; Carr & Whoriskey, 2008) and is predicted to be 100% for large shortfins in New Zealand (Mitchell & Boubée, 1992) with risk of mortality increasing with size of eels and head height of the intake (see Beentjes *et al*., 2005). In the current study, all tagged eels were impinged/entrained when three or four turbines were in operation (turbine flow = $Q_{54.1} – Q_{3.9}$) and impingement occurred when flow was significantly higher than for the rest of the time the eels were in the head race, indicating, as Calles *et al*., (2010) reported, that escapement is not possible when there are high flows through the intakes as eels are impinged and injured or killed before escapement is possible. Thus, at lower flows eels have the opportunity to reach the spillway. The relatively few positions within 1 m of the intake chamber is possibly due to eels either being impinged/entrained quickly or escaping when avoiding high flows at higher power generation. Avoidance behaviour upstream of hydropower and pumping station intakes and searching for a safe exit has been observed elsewhere (Behrmann-Godel & Eckmann, 2003; Jansen *et al.*, 2007; Brown *et al.,* 2009; Bolland *et al*., unpubl. data), potentially in response to changes in patterns of water flow (Jansen *et al*., 2007; *Piper et al*., 2012), noise or visual cues. Avoidance of screens has resulted in return upstream until the next migration trigger (Watene *et al*., 2003), however only one eel retreated upstream after arrival at WPS, emphasizing the need for an efficient bypass solution. Further study to investigate eel behaviour directly upstream of the intake screen using sonar imaging such as multi-beam sonar technology (e.g. ARIS or DIDSON) could help quantify behaviour in response to different flow fields at this site, coupled with flow profiling in this area. It would also be beneficial for further studies to include transmitters that have a higher transmission rate to make it possible for more detailed fine-scale behaviour directly upstream of intakes to be quantified.

Eels are particularly vulnerable at turbine and pump intake screens due to their elongate body length (Larinier, 2008) although fish length did not influence passage route during this investigation. A possible remediation measure would be to install an effective fish recovery and return (FRR) system (Turnpenny, 2011) which collects impinged eels and transports them downstream of WPS. However, an impinged eel recovered from trash at WPS and released downstream on the same day failed to complete its onward migration, thus suggesting it had reduced fitness or injuries from being impinged. Similar findings have been reported by Calles *et al*., (2010) for eels where all those impinged (18% of those that approached the bar rack) were dead and Pedersen *et al*., (2012) where they were dead or severely damaged, as is reported for other fish species (e.g. Rytwinski *et al*., 2017). That said, two eels that were retrieved from the WPS weed pile that appeared to be in good condition and were tagged early in the study, both migrated through the catchment after release at R but were impinged onto intake screens potentially because of reduced fitness that was not visible. Further, it is known that members of the public enter the forebay area to retrieve eels from WPS trash screen for consumption despite the fencing, signage and extensive consultation, and thus a FRR system would be ineffective if eels can be removed by members of the public.

Approximately half of the eels (47.6%) that entered WPS passed downstream through the spillway, all of which were detected within 3 m of the intake when three or four turbines were operating. Four of the ten eels that passed downstream did so when turbines were not operational, potentially because there were no competing flows, but the remaining seven eels passed through the spillway during almost the entire range of turbine flows ($Q_{100} – Q_{2.4}$) and turbine flow did not influence route choice. Spill occurred (>0 MV) for 52.8% of the time that turbines were operational during the study period, but two eels were impinged/entrained when there was no downstream passage route available, i.e. no water was passing through the spillway or spill was low (1.9 MV) compared with the range of spill when eels passed (33.9 – 201 MV). Based on six years of silver American eel catch data, Haro *et al*., (2003) simulated that mortality of the eel run decreased with increasing spill flow. It is therefore recommended that the water level in WPS forebay should be maintained at a higher level to ensure a minimum spill level (i.e. 33.9 MV based on present findings) at night throughout the shortfin eel migration, given 95.2% of tagged eels first approached and 85.7% passed during hours of darkness. This suggestion is in accordance with Boubée & Williams (2006) who suggested that at a small power station studied elsewhere in New Zealand, spilling could be implemented to allow downstream migrating eels to safely pass downstream. Also, an alternative, more easily implemented solution than a FRR system is to operate the turbines at a lower capacity (no more than 3.04 MW at any one time based on findings that this was the lowest turbine flow an eel was impinged on) during the eel migration window. This would reduce flows experienced and thus prevent the impingement of eels on the trash screen. Turbine shutdowns have been successful in the U.S. at hydroelectric dams to allow passage via spillways or through bypass chutes (Smith *et al*., 2017) and when employed on days of rainfall in Maine rivers was predicted to reduce mortality from 10.7 to 3.9% (Haro *et al*., 2003).

The onset of the spawning migration coincides with onset of puberty and an associated increase in sex steroid levels, principally estradiol-17β and 11-ketotestosterone (Lokman et al., 1998). Moreover, experimental exposure of yellow eels to 11-ketotestosterone results in many of the changes that are seen during the silvering transformation (Rohr et al., 2001), prompting the hypothesis that levels of both sex hormones could be indicative of migratory readiness. However, whilst morphology was indicative of and biochemical criteria (sex steroid levels) were within the range typical for migrant female shortfins (c.f., Lokman et al., 1998), there was no correlation between speed of eel movement or passage time at WPS in the present study, and thus all silver eels were considered to be equally motivated to migrate.

Eels that passed through the spillway were delayed for up to 47 days, despite spilling for 43.8% of the time turbines were not operational during the study period, and thus indicates that the spillway was either hard to find (i.e. low attraction efficiency) or eels were reluctant to pass over it (i.e. low entrance efficiency); both of which are important for bypass efficiency. This is further evidenced by spill being significantly higher when eels used this route. Reluctance to pass the spillway could also be due to the location of the spillway in the forebay, or that the spillway entrance was at the surface and thus bottom-orientated eels species do not readily pass through (Brown *et al.,* 2009; Haro *et al.,* 2000a). Delays in downstream migrating silver eels have been reported upstream of other hydropower, water abstraction and pump stations, ranging from 8 to 157 days (Behrmann-Godel & Eckmann, 2003 = 8 days; Verbiest 2012 = 28 days; Piper *et al*., 2013 = 68.5 days; Eyler et al., 2016 = 157 days). Consequently, it is recommended that a bespoke silver eel bypass channel be considered at this site with a bottom-orientated entrance and attractive flows at both the entrance and passing through pipework (e.g. Conte airlift bypass, Haro *et al.,* 2016). Previous eel bypasses at forebays have had variable success (Boubée & Williams, 2006; Gosset *et al.,* 2005) and thus further research is required to determine the optimum location and entrance flow under different scenarios to maximise eel passage. Crucially, from a hydropower generation/water resource management perspective, such an approach may demand less water than ensuring flows pass over the existing spillway.

It has been suggested that migration delays can influence time of arrival at spawning grounds (Eyler *et al*., 2016), deplete energy reserves of eels that cease feeding during their spawning migration (Dainys *et al*., 2017; Larsson *et al*., 1990), increase the risk of diseases due to stress and increase predation risk (Garcia De Leaniz, 2008). During this investigation, eels released at R that passed through the spillway at WPS were delayed for up to 37 days, though these eels were detected in the estuary (R16) at a comparable time to eels that passed through gates at the diversion weir. Five of six (83.3%) eels arrived on either new (*n* = 3) or full (*n* = 2) moons, which corresponds to when tide would be highest as the catchment is tidal below WPS, regardless of route taken. This indicates that route choice did affect delay length but not onward migration. Consequently, delays at WPS did not appear to impact on time to escape from the catchment, possibly because eels that did not pass through WPS paused their migration during either sub-optimal conditions, earlier stages of maturity or because of stress, (e.g. Durif *et al*., 2003, Tesch, 2003, Watene & Boubée, 2005, and Aoyama *et al*., 2002). Although silver eels generally perform directional movements during their migration, both silver and yellow eels have been found to seek refuge during the day, which is said to be essential for providing shelter in areas that potentially have rocks or debris for hiding or soft mud for burrowing (Aoyama *et al*., 2002). As forebays to intakes generally have reduced habitat and flow diversity (SEPA, 2008), eels that were delayed by WPS may have expended considerable energy avoiding impingement/entrainment and finding a safe downstream passage route and when eventually passing would have had depleted energy reserves. Further, eels delayed at WPS migrated faster which would be more energetically costly. While providing attractive safe downstream passage route for eels would reduce delays, it is recommended that artificial refuges be installed in forebays, to minimise indirect impacts on eels. Potentially, it may be possible to use these refuges as a way of catching migrant eels for safe manual transfer downstream of the station.

4.5.1 Summary of remediation measures and conclusions

Understanding eel downstream spawning migration in catchments with obstructions to longitudinal connectivity and around potentially hazardous intakes is essential to identify whether solutions for eel passage are required and ultimately to improve access to spawning grounds. During this study, a high proportion of downstream migrating eels entered the WPS Canal, approximately half of the eels that entered the forebay were unable to continue their seaward journey and those that passed through the spillway experienced long delays before passage. This knowledge led to the identification of following four potential remedial measures that could be implemented during the eel migration period:

(1) To improve passage at the diversion weir
    (a) Ensure that a gate is always open by a minimum amount (i.e. gate 1 = >19 cm; Gate 3 = >46 %)
    (b) Install a physical screen or behavioural deterrent on WPS canal intake
(2) To reduce the risk of impingement or entrainment
    (a) Generate no more than 3.04 MW at any one time during the eel migration window
(3) To increase the attractiveness of the spillway
    (a) Always maintain flow over the spillway, possibly coupled with turbine shutdown at night
(4) To improve safe passage, provide an additional bypass channel in the forebay tailored to eel behaviour

In addition, flow refuges could be provided in the forebay to reduce energy expenditure and reduce risk of impingement and entrainment. Combined with trap and transfer activities these refuges could provide an effective means of catching migrants for release below the power station.

While operational changes (i.e. measures 1, 2 and 3) and installing additional bypass channel are relatively inexpensive in comparison to engineered solutions, such as physical screening (fine-mesh and low through-screen velocities) and retrofitting fish-friendly turbines, they will potentially reduce the amount of power generation in order to reduce the impact to migratory eels and thus will incur indirect costs throughout the period of implementation. Such generation losses would certainly impact hydropower generation, which is a dilemma for New Zealand water resource managers (see Beentjes *et al*., 2005). However the increasing pressure on fish stocks worldwide calls for reassessment of legislative requirements in order to protect migratory fish. Utilising the natural conditions of the river and adapting management regimes (Haro *et al*., 2003) reduces the necessity for expensive structural changes to provide safe alternative routes. Therefore, a combination of approaches that demand the least amount of water could potentially be explored if it is not possible to implement all recommendations. These findings should be transferrable globally to water managers that are attempting to identify cost-effective solutions for remediating the impact of water intakes on the downstream migration of anguillid eels.

5 THE EFFICIENCY OF A GRAVITY SLUICE FOR DOWNSTREAM PASSAGE OF EUROPEAN SILVER EELS AT A PUMPING STATION

5.1 Introduction

Once mature, the European eel must exit their freshwater feeding grounds and migrate to oceanic spawning grounds ~6000km away in the Sargasso Sea. Barriers to adult mature downstream migrating silver eels, as well as climate change, changes in oceanic currents (Baltazar-Soares *et al*., 2014; Hanel *et al*., 2014), disease and parasites (Newbold *et al*., 2015), overexploitation, habitat loss, pollutants and predation (Piper *et al*., 2013) have contributed to a multi-decadal decline in European eel recruitment (ICES, 2017), to the point that the species was classified by the IUCN as critically endangered in 2008 (Jacoby & Gollock, IUCN, 2014). In response to this decline, the International Council for the Exploration of the Sea (ICES) advises that "all anthropogenic impacts (e.g. recreational and commercial fishing on all stages, hydropower, pumping stations, and pollution) that decrease production and escapement of silver eels should be reduced to – or kept as close to – zero as possible." The EU implemented a recovery plan in 2007 (Council Regulation (EC) No. 1100/2007). Under this, all member states are requird to develop their own Eel management plans (EMP) that primarily aim to ensure that 40% of the historical (when no anthropogenic impacts were acting on the species) biomass can safely exit the freshwater catchmen. This is in order to increase the number of mature adults that are able to hopefully undergo the full spawning migration and spawn in order to ultimately improve recruitment levels.

Globally, water levels in freshwater catchments are controlled by pumping stations, weirs, dams and sluices (Verhalst *et al*., 2018). Indeed, much of the UK and Europe rely on pumping stations for flood protection, which are located across the intertidal feeding grounds of eels, hence eels must safely navigate these structures in order to exit the catchment. Often, the only route out of the catchment is through turbines which can cause injury or direct mortality (Russon *et al*., 2010) from impingement or entrainment. That said, some (e.g. 44 of 125 in Anglian region of England) (Solomon & Wright, 2012) have gravity sluice doors, which are usually surface oriented and are used as the main drainage method, and pumps only operate when the level difference either side of the gate prevents gravity drainage, or in floods (Solomon, 2010). Eels must pass downstream of impoundments quickly to avoid negative impacts from delays such as increased predation risk, worsening onset of disesases (if present) due to stress (Garcia de Leaniz, 2008) and depletion of vital energy reserves (e.g. Dainys *et al*., 2017). There is potential for gravity sluice doors to provide a safe downstream passage route during periods when pumps aren't operational, which may reduce the delay caused by pumping stations. However, it is not known if eels approach pumping stations when gravity sluices are open, or what their behaviour is upon reaching these structures. If eels pass though gravity sluices, it may remove the need for the current expensive remediation measures such as screening or pump replacement, and will help prioritise sites for remediation.

5.1.1 Aims and objectives

This study aimed to understand the passage routes taken by downstream migrating European silver eels at a pumping station with a co-located gravity sluice door. Specific objectives were to:

1. Understand the timing of eel approach to a pumping station with a co-located gravity sluice in relation to route availability (pumps or sluice), time of day and lunar cycle
2. Quantify the fate of tagged eels and passage time
3. Determine the amount of time each route was available for each eel under the current operating regime
4. Compare fine-scale behaviour upstream of the pumps and the gravity sluice under different operating regimes and different fates of eels, including the backward beeline distance, backward path length and number of retreats during the final visit before passage through either route.

The applicability of the findings to other sites with a gravity sluice and additional measures required to improve eel passage, including operational changes will be discussed.

5.2 Materials and methods

5.2.1 Study site

Five Towns pumping station (52.871898, -0.044521) is responsible for drainage of the Five Towns Drain into the tidal River Welland. It was commissioned in 1962 to provide flood protection to the 32 km^2 catchment using three 1.07 m diameter, 1.7 cumec capacity mixed flow pumps. The upstream river level is primarily controlled by manually removing stop blocks from a surface-oriented gravity sluice and automated pointing doors (i.e. level sensor) further downstream prevent upstream ingress (Figure 5.1). The trash screen has 12 mm thick bars with 50 mm spaces and the upstream channel is ~1.5 m deep. During the study period (31 October 2016 – 24 November 2016), the gravity sluice was open for ~59 hours (daily average = 02:27 hours per day), though it varied considerably depending on downstream tide level (min-max = 00:18 – 12:45 hours per day). There were five pumping events during the study period which equated to 12:08 hours of pumping (min-max = 00:02 – 05:17), of which 11:59 hours were between 20:55 on 21 November and 20:10 on 23 November (25.4% of this time) and the remaining 9 minutes occurred on 14 (04:00) and 15 (05:00) November. As Five Towns pumping station is tidal, estuarine conditions directly downstream prevented a receiver from being safely installed to log eels passing through the infrastructure.

Figure 5.1. Location of Five Towns pumping station and location of the pumping station, gravity sluice and location of receivers 1 – 8.

5.2.2 Fish sampling and tagging

Actively seaward-migrating adult silver eels (*n* = 7) were caught by a commercial fisherman using fyke nets that were emptied weekly by the fishermen in the reach 100 m upstream of Five Towns pumping station (hereon referred to as FT pumping station). Two eels were caught between the 24 and 31 October, one between 31 October and 07 November and the remaining three between 14 and 21 November, tagged on the same day that nets were emptied (31 October, 07 and 21 November) and released back into the river ~200 m upstream of FT pumping station at dusk (16:30 onwards) after full recovery (regained balance and actively swimming). Throughout the study, there was an issue with eels caught for tagging being predated upon by otters before nets were emptied, also there were often no eels caught at this site, which prevented a larger sample size from being obtained. Only eels with no visible signs of injury and that were actively swimming and reactive were tagged.

Prior to tagging in the field, acoustic transmitters were activated and tested with a hand held receiver (Vemco VR100) to verify they were transmitting. Eels were visually assessed for signs of silvering (Durif *et al.,* 2009) and anaesthetised using buffered tricaine methanesulphonate (MS-222; 0.16 per 10 L of river water). Once anaesthetised, each eel was weighed (g) then placed in a clean V-shaped foam support and total length, left pectoral fin length, head width, left eye horizontal and vertical diameters (all in mm) were measured. Eels were required to have less than 2% tag to body weight ratio (ratio 0.6 – 1.3 %). Eels were placed ventral side up and a ventro-lateral incision was made with a scalpel anterior to the muscle bed of the anal fins. Acoustic tags (25 mm long x 9 mm diameter, 3.7 g weight in air, 180 kHz, High Residence (HR) and Pulse Position Modulation (PPM) nominal delay = 1 – 2 and 50 – 70 seconds, respectively, expected battery life 170 days; www.vemco.com were disinfected with providone-iodine and rinsed with saline solution before being implanted into the body cavity, which was closed with an absorbable monofilament suture. After surgery, fish were continuously monitored in a well-aerated tank of fresh river water. Maturation stage was later calculated following methods of Durif *et al.,* (2009), i.e. FII = 2, FIII = 2 and FV = 3; all eels were determined to be in the migratory phase. All fish were treated in compliance with the UK Animals (Scientific Procedures) Act 1986 Home Office licence number PPL 60/4400.

5.2.3 Tracking methods

An autonomous underwater acoustic telemetry array system (VPS, Vemco, Halifax, Canada) was installed in the forebay of FT pumping station (Figure 5.1). Vemco acoustic receivers (6 x HR1 and 2 x HR2) were arranged in a formation that maximised the overlapping detection ranges and thus coverage of the required study area. Each receiver was installed with a co-located synchronization or 'sync' tag. GPS positions of receivers were taken during installation to enable real error to be calculated by comparing real distances to those determined by sync tag detection, and a reference tag was installed at multiple locations during the study to further understand array performance and determine more accurate fish positioning. In such a system, transmitters are located by hyperbolic positioning using delays in time of arrival of acoustic signals between receivers in different locations around the transmitter. Using tags with a regular frequency of transmissions, or 'pings' allows near-continual location of the tagged animalas long as it is within the array. In order for eel tags to be positioned, they must be detected by three or more receivers at any one location. The data were periodically offloaded from each receiver and sent to Vemco, where initial processing was conducted.

5.2.4 Data analysis

Data for Five Towns pump and gravity sluice operation were provided by Welland and Deepings Internal Drainage Board, and were used to indicate when a pump was operational or the gravity sluice was open. Eel time of arrival at FT pumping station during the first approach was compared to lunar cycle and time of day in Boston, Lincolnshire (~14 km away, available at www.timeanddate.com). There were cases when eels 35825, 35826 and 35827 were recaptured in fisherman's nets during the study; the time and date of recapture were recorded and eels were re-released ~200 m upstream. When conducting data analysis, time in nets was determined by continual positions in one area (verified using GPS of net location in Google Earth (2018)) leading up to recorded time of recapture; these data were excluded from analysis so that only data containing free movement upstream of FT pumping station trash screen (referred to as trash screen) or gravity sluice was analysed. Due to eels being recaptured multiple times in the net, it did not appear that presence of the net affected eel behaviour in between recaptures, i.e. eels did not avoid the net. Downstream route (gravity sluice or pumps) was determined for each eel using the location of each eels' final position. Passage was determined when an eel was last detected upstream of FT pumping station trash screen when a pump was operational, or last detected upstream of the gravity sluice shortly before it was opened. For eels determined to have passed through the gravity sluice, although pointing doors were closed during their last detection, eels were considered to have passed over stop blocks into an enclosed area and were outside of the receiver array, before passage when routes became available.

VPS provides position data for individual tagged eels in the acoustic receiver array, and a relative, unitless estimate of the accuracy of this position; this is referred to as Horizontal Position Error (HPE), with lower values indicating more precise positions. To determine broad descriptors such as those in Table 5.1, all HPE data were used, which included both HR (High Residence), which allows frequent and precise positioning of multiple animals in a short time frame and a small area (VEMCO, 2018) and PPM (Pulse Position Modulation) which when used in isolation can achieve longer battery life; using the two together increases the likelihood of accurately recording animal positions at potentially high density and over a longer period. . For fine- scale analysis upstream of the trash screen and gravity sluice, a HPE <2 filter was applied after data exploration revealed that using this filter did not lose any of the positions available when applying HPE < 5, demonstrating the efficiency of the array, to determine the relevant metrics indicated in Table 5.2. The number of positions retained when applying this filter and proportion of records retains for fine-scale anaylsis are available in Table 1. Positions were not available within 5 m upstream of the gravity sluice due to limited receiver coverage in the narrow (~6 m wide) and shallow (~1 m deep) channel. For fine-scale plotting, HR data only were used due to the accuracy of this tag coding in displaying eel positions. One eel (35845) was only detected 9 times, always ~100 m upstream of the receiver array and did not pass downstream, so positions were instead used as a measure of presence/absence in the river and to indicate that this eel did not pass downstream.

Table 5.1. Number of eel positions detected on receivers upstream of FT pumping station when no HPE filter is applied compared with when a HPE filter of <2 is applied, and the number of positions retained when applying this filter.

Eel ID	Number of positions all HPE	Number of positions HPE <2	% of positions retained when applying HPE < 2 filter
35830	90	24	26.7
35828	581	195	33.6
35831	340	114	33.5
35827	4112	1698	41.3
35826	3230	625	19.3
35825	26073	895	3.4
35845	9	0	0

To analyse whether time from release to passage and passage time differed between route taken, independence permutation tests were used (referred to as independence-test) due to sample sizes being small (see Hothorn *et al*., 2008, and references therein). There were three operational scenarios during the study; 1) no pumps on, gravity sluice closed; 2) no pumps on, gravity sluice open and 3) a pump on, gravity sluice closed (i.e. the gravity sluice was never open when pumps were operational). The distances eel positions were from the trash screen and gravity sluice were measured by importing position data into ArcGIS and manually exporting 1 m zones at a distance from each exit (determined using Google Earth satellite imagery), up to 30 m upstream of the pump trash screen and 35 m of the sluice. Proportion of positions were compared between the three scenarios upstream of both the trash screen and the gravity sluice using non-parametric Kruskal-Wallis tests (referred to a KW-test), as the data violated the assumptions of the Levene's test for homogeneity of variance. A Dunn non-parametric pairwise multiple comparisons post-hoc test was used to determine specific differences between two scenarios. During the final visit of eels before passage, or 'passage track', the backwards beeline distance was plotted against the backward path length, so that the number of retreats before exit, the distance of the first and final retreat and the distance at which a directional movement was performed could be determined for each eel. All statistical analyses were carried out in R studio v 3.3.0 including the use of packages data.table (Dowle & Srinivasan., 2018), ggplot2 (Wickham, 2016), gridExtra (Baptiste, 2017), lubridate (Grolemund & Wickham, 2011), fasttime (Urbanek, 2016), Dunn.test (Dinno, 2017) and coin (Hothorn *et al*., 2006).

Table 5.2. Descriptors used to analyse eel behaviour at FT pumping station. Whether all HPE (and High Residence (HR) and Pulse Position Modulation (PPM) or HPE < 2 filter (using only HR positions).

Descriptor	Calculation/ reason
Broad descriptors	
Passage time	Time between first and last detection in the array (i.e. excluding time in nets)
Time of first/last detection	Compared to sunrise and sunset times for Boston at www.timeanddate.com to determine if during hours of light or dark
Time between release and first detection	Length of time, to determine how long eels took to arrive at FT pumping station after release
Time between release and passage	Length of time, to determine how long eels were detected in the study area
Proportion of time at liberty (TaL%) at FT pumping station	Passage time as a proportion of time between release to last detection, to determine how long eels were at FT pumping station compared to how long they were detected on receivers elsewhere
Time detected as a proportion of passage time	What proportion of passage time eels were detected in the array
Fine-scale behavioural analysis (HPE<2 filter applied)	
Number of visits to array	Separate visits determined when the interval between individual eel positions was greater than 30 minutes. Duration of visits also recorded.
Proportion of time pumps/gravity sluice open during time in array	Calculated by comparing operational schedule to times eels were detected in the array, to indicate route availability
Proportion of positions in array during day/night	Compared to sunrise and sunset times for Boston at www.timeanddate.com to determine if during hours of light or dark
Distance from last position to exit route (pumps or gravity sluice)	The beeline distance between the last detected position and the route taken by individual eels, calculated using measuring tool in Google Earth (2018).
Proportion of time upstream of each route	Calculated as a proportion of time in the array, compared to proportion pump or gravity sluice was available during these times
Last time eel detected within 1 m of trash screen	Compared to operational schedule to determine if pump available
Number of times eel detected within 10 m of trash screen or gravity sluice before passage track	Calculation of how many times each eel retreated from within close vicinity of trash screen (assigned as 10 m) before passage track, i.e. as an indicator of reluctance to pass
Passage track	Final visit to the array of each eel that passed through a pump or the gravity sluice.

5.3 Results

5.3.1 Summary of eel positions and delays experienced

All tagged eels (*n* = 7) approached FT pumping station; two (28.6%) passed through the gravity sluice, three (42.9%) passed through the pumping station and two (28.6%) did not pass, i.e. retreated upstream. Time of first detection for six (85.7%) eels at the pumping station was during hours of darkness (16:31 – 21:45) and one (14.3%) was during daylight (15:44) despite all eels being released at dusk. Time of first detection was across a range of lunar cycle; two during a dark moon that were released at dusk within ~2.5 hours earlier, one during first quarter moon after 6.11 days and the remaining four during a third quarter moon after 1.03 hours – 4.17 days. Eels took 3 hours and 2.35 days from release to pass through the gravity sluice and passage time was 00:05 and 00:38, respectively, which equated to 2.9 and 1.1% of the time at liberty upstream of FT pumping station. Eels took 10.04 hours, 16.02 days and 21.40 days from release to pass through pumps and passage time was 09:12, 9.91 days and 21.30 days respectively, which equated to 84.1, 61.9 and 99.5% of the time at liberty upstream of FT pumping station (Table 5.2; Figure 5.2). Time from release to passage (independence-tests; $Z = 1.2557$, $n = 5$, $P = 0.209$) and passage time ($Z = 1.228$, $n = 5$, $P = 0.2194$) were comparable for eels that passed through the gravity sluice and pumps. Time of last detection of eels that passed through the gravity was 17:04 and 22:22, compared to eels that passed through the pumps at 00:55, 16:27 and 23:40 i.e. all eels left during hours of darkness (Table 5.3; Figure 5.2). Two eels that did not exit the catchment were last detected upstream of FT pumping station 4.20 and 24.22 days after release on 25 and 24 November, respectively.

Table 5.3. Fate (G; passed gravity sluice, P; passed pumps, NP; no passage) of tagged European eels at FT pumping station, including time between release and first detection, moon upon arrival, time of first and last detection, time between release and passage, passage time and the passage time (all to the nearest minute) as a proportion of time at liberty (TaL; %).

Eel	Time of first detection	Time between release to first detection	Moon when arrived	Fate	Time last detection	Time between release and passage	Passage time	TaL (%)
35830	16:59	00d 02:59	3/4	G	17:04	00d 03:05	00 00:05	2.9
35828	21:45	02d 07:45	3/4	G	22:22	02d 08:23	00 00:38	1.1
35831	15:44	00d 01:44	3/4	P	00:55	00d 10:56	00 09:12	84.1
35827	18:35	06d 02:35	1/4	P	16:27	16d 00:28	09 21:53	61.9
35826	16:31	00d 02:3	Dark	P	23:40	21d 09:41	21 07:09	99.5
35825	16:35	00d 02:36	Dark	NP	19:18	24d 04:57	-	-
35845	18:02	04d 04:02	3/4	NP	18:45	04d 04:43	-	-

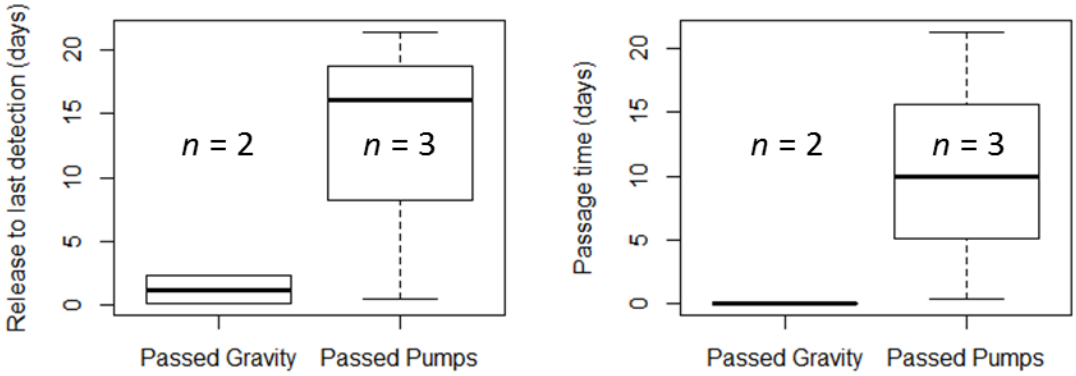


Figure 5.2. Passage time (top) from release to last detection (left) and passage time (right) for eels that passed through the gravity sluice and pumps.

5.3.2 Conditions experienced in the forebay

Overall, the gravity sluice was open for 6.0% of the time eels were detected in the array upstream of FT pumping station and the pumps even less; 3.9%. Eels that passed through the gravity sluice (*n* = 2) did so on 21 and 23 November during their first approach to the pumping station and experienced no pumping events between release and passage (Table 5.4. The gravity sluice was closed between release and 03.01 and 0.03 hours after each of the two eels were last detection in the array; these eels were last positioned 6 and 9 m upstream of the gravity sluice (position closer than this to the gravity sluice could not be determined) and thus were considered to have passed over stop blocks and were outside of the receiver array, despite pointing doors downstream being closed (see Methods). Eels passed through the pumps (*n* = 3) on 21, 22 and 23 November, after visiting the array two, eleven and six times and being detected at a single location in the array for up to a duration of 4.01 hours (mean ± S.D. = 00:58 ± 01:42) before passage. Pumps were operational for 100, 3.8 and 10.6 % and the gravity sluice was open for 0, 0 and 13.6% of the eels' time in array, respectively. For eels that did not pass, one approached FT pumping station on 29 separate occasions which equated to a total time of 01d 13:58:59 in the array, including 1 hour during pump operation and 02.03 hours during sluicing. The final eel was never detected within the receiver array and was detected on 9 occasions ~100 m upstream.

Table 5.4. Number of visits to the array, duration of visits (mean ± S.D. (min. – max.)), time in array as a proportion of passage time, total time, number of times and proportion of time both pumps and gravity sluice were operational during time in array.

Eel	Fate	N array visits	Duration of array visits (mean ± S.D. (min. – max.))	Time in array (proportion of passage time (%))	Total time pumps on when in array (number, %)	Total time gravity door open when in array (number, %)
35830	Gravity	1	00:03:13	0d 00:03:13 (59.4)	0	0
35828	Gravity	1	00:33:06	0d 00:33:06 (87.7)	0	0
35831	Pumped	2	00:09:15 ± 00:13:04 (00:00:00 – 00:18:29)	0d 00:18:29 (3.4)	00:18:29 (1, 100)	0
35827	Pumped	11	00:44:43 ± 01:20:20 (00:00:00 – 04:19:14)	0d 08:11:54 (3.5)	00:18:51 (2, 3.8)	0
35826	Pumped	6	00:23:14 ± 00:24:13 (00:02:00 – 01:07:39)	0d 02:19:26 (0.5)	00:14:43 (1, 10.6)	00:19:01 (2, 13.6)
35825	No pass	29	01:18:34 ± 01:36:09 (00:00:00 – 05:10:13)	01d 13:58:39 (6.6)	01:03:09 (3, 20.4)	02:38:42 (7, 7.0)
35845	No pass	-	-	0d 00:00:00	0	0

5.3.3 Fine-scale movement analysis

A total of 90.1% of eel positions (HPE <2) in the array upstream of FT pumping station were at night. Analysis of eel positions collected using VPS demonstrated that the number of eel positions in each 1 m zone in the array upstream of the trash screen in comparable locations during the three different operating scenarios, i.e. pumps off, gravity closed, pumps off, gravity open and pumps on, gravity closed (KW-test; X^2 = 2.1904, *df* = 2, *P* = 0.335) with the highest proportion of positions (17.3, 26.4 and 19.2%) being 15, 20 and 20 m away from the pumps under the three scenarios, respectively (Figure 5.3). Upstream of the gravity sluice, no eel positions were recorded within 15 m when it was open (Figure 5.3). Indeed, the number of eel positions in each 1 m zone upstream of the gravity sluice during the three different operating scenarios (i.e. pumps off, gravity closed, pumps off, gravity open and pumps on, gravity closed was significantly different (KW-test; X^2 = 6.2591, *df* = 2, *P* = 0.044); there were more positions closer to the gravity sluice (within 6 – 15 m) when a pump was the only route available than when the gravity was open (Dunn-test post hoc; *P* = 0.007). still, these positions only equated to 11.1% of positions recorded in this area under this scenario, compared with 27% when neither pumps nor gravity were on or open. Eels that passed through FT pumping station spent a higher proportion of time upstream of the trash screen (63.1, 67.7 and 72.1%) than the gravity sluice (36.9, 32.3 and 27.9%). When these eels were upstream of the trash screen, the pumps were operational for 100, 14.6 and 12.8% of the time, and the gravity sluice was open for 0, 0.75 and 12.2% of the time, with no route being available the rest of the time. They were also detected within 10 m of the trash screen twice, 17 and six times to a distance of 8, 1 and 4 m upstream before the passage track. Likewise, they were detected within 10 m of the gravity sluice once (closest = 8 m), 11 (to closest = 5 m) and four times (closest = 5 m), respectively, but it was closed, i.e. eels were detected within the near vicinity of each exit before passage. For the eels that passed through the gravity sluice, 95.8 and 44.0% of each eels' positions were upstream of this route, the rest being upstream of pumps when they were not operational. The eel that had entered the array but retreated upstream was detected within 8 m of the trash screen when pumps were not operational; it spent 50.4% of its total time in the array upstream of the pumps, and of this time a pump was operational for 2.5%, and 49.6% upstream of the gravity sluice, of this time it was open for 7.1%.

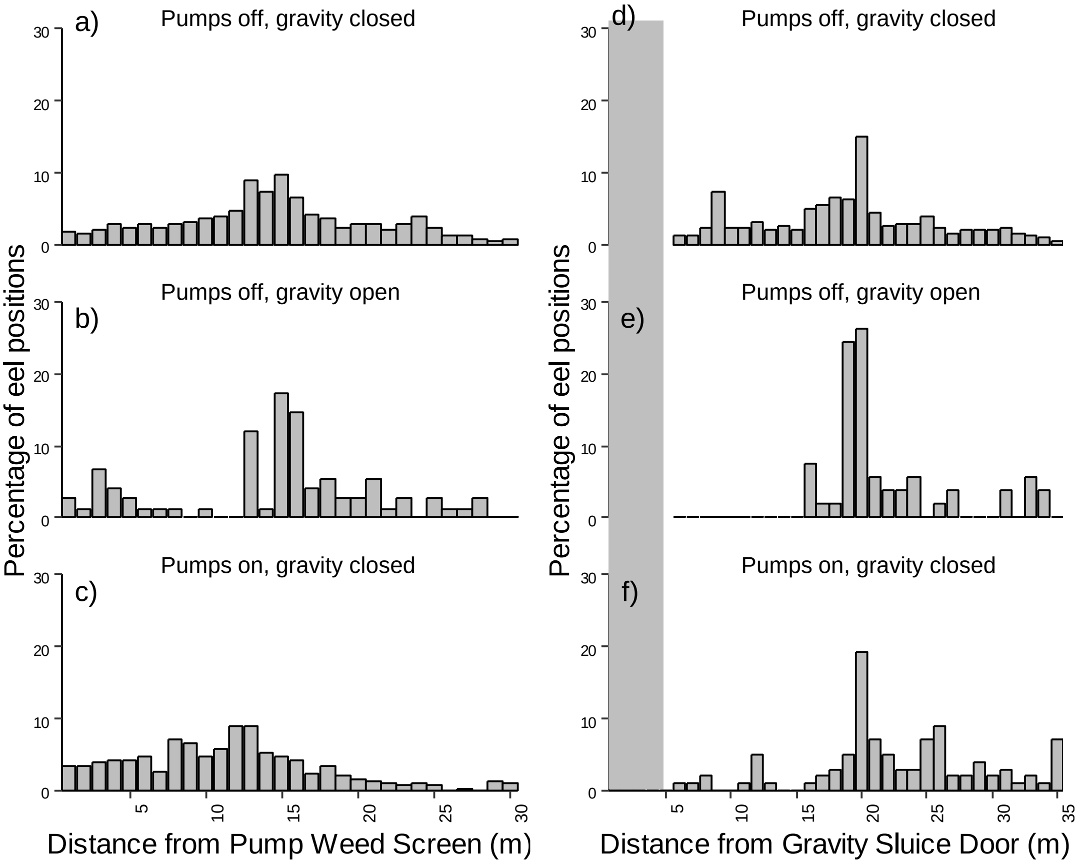


Figure 5.3. Proportion of eel positions HPE <2 in each 1 m zone upstream of the trash screen (left) and the gravity sluice (right) during each flow scenario (top to bottom). Shaded area indicates no positions recorded.

5.3.4 Behaviour of eels during passage track

The movements of two eels that passed through the gravity sluice during their first and only visit to FT pumping station differed markedly. One eel did not retreat before passage whereas the other retreated 15 times, first retreating from 6 m upstream of the gravity sluice before moving around the array and last retreating from 1 m from the trash screen when pumps were not operational; these were the closest approach distances to either exit. The last approach before passage was from 16 m upstream. For the three eels that passed through FT pumping station a pump was on for 100% of the final visit, i.e. eels were attracted to the array by the flow from the pumping event that they also exited on, and movements were highly variable. Eels retreated 1, 5 and 12 times with the first at a distance of 3, 27 and 8 m from the trash screen, respectively. The distances of each eels' final retreat before passage through pumps were 3, 1 and 19 m from the trash screen before directional movements towards the trash screen from 5, 5 and 20 m upstream, respectively (Figure 5.4).

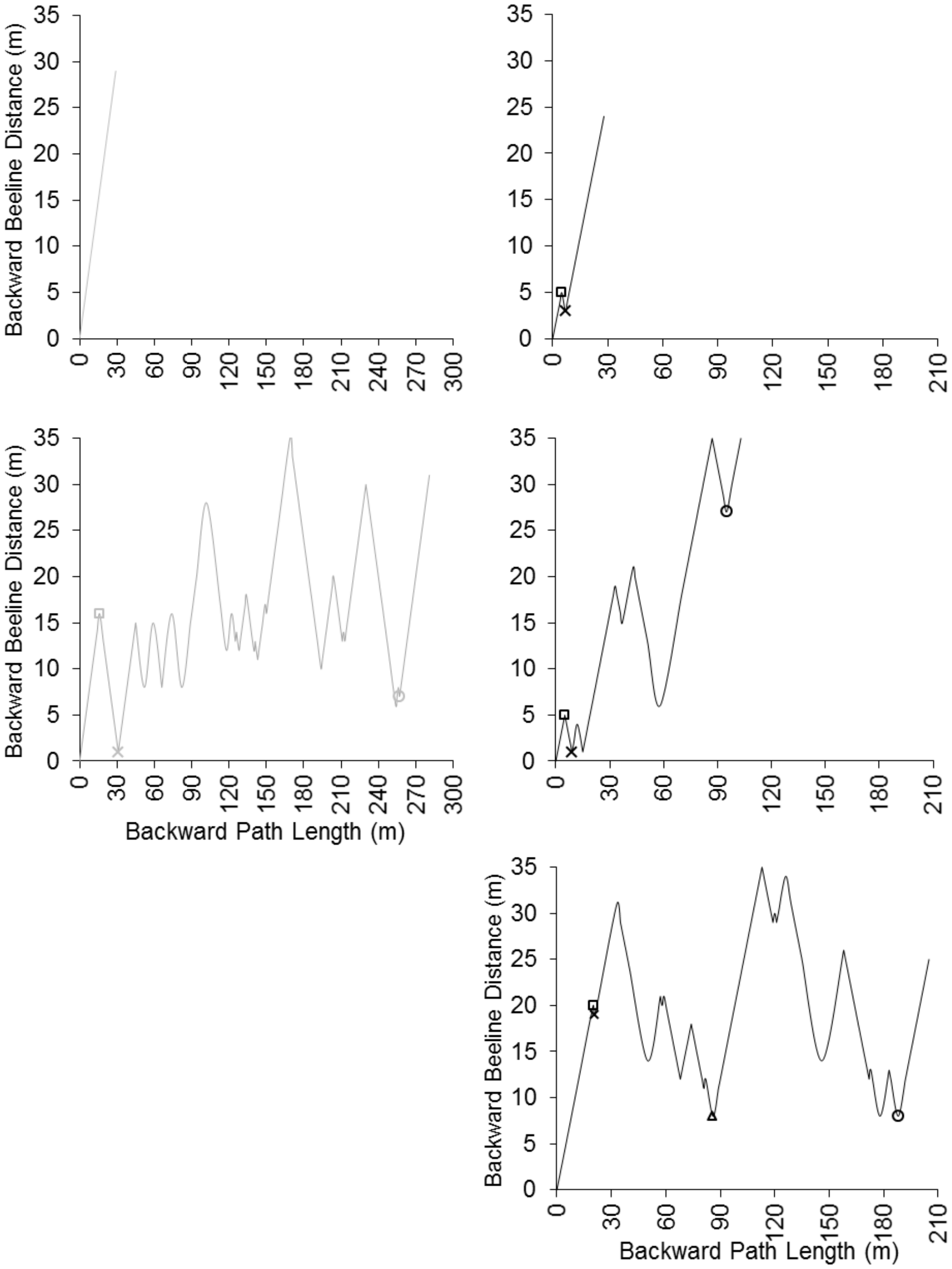


Figure 5.4. Backward beeline distance in relation to backward path length during eel passage tracks through the array (HPE < 2) that passed through the gravity sluice (n = 2; left) and through the pumps (n = 3; right), showing distance of first retreat (circles), final retreat distance (crosses), point before directional passage track (square) and

closest approach distance before passage on non- passage track (if closer than final retreat distance (triangle)).

5.4 Discussion

In this study, two of seven acoustic tagged eels (28.6%) passed through the gravity sluice at FT pumping station and are assumed to have continued their onward migration as this route provides an unobstructed passage route out of the catchment and into the estuary where there are no further barriers. Three eels passed through the trash screen and a pump (42.9%) and were assumed to have died as pumps of comparable size have been found to be particularly damaging to eels (Watene & Boubée, 2005; Bolland *et al*., 2018). Two eels retreated back upstream (28.6%) potentially resulting in reaching spawning grounds outside the spawning period if they were to pass through the gravity sluice at a later date. The two eels that passed through the gravity sluice approached and passed downstream over stop blocks in the gravity sluice chamber shortly prior to the pointing doors further downstream opening, i.e. they were not attracted to this route as a result of its' operation.

The low passage rate through the gravity sluice in this study could be attributed to associated flows during hours of opening not being strong enough or not occurring for long enough for migratory eels to be attracted, as is discussed by Verhalst *et al*., (2018). Also, traditional design bypasses with a surface orientated entrance are generally considered to be unsuitable for eels (see Baker *et al*., 2018). However, it is not feasible to change the gravity sluice at FT pumping station from surface to bottom orientated to maximise entrance efficiency because head difference would greatly reduce the number of sluicing opportunities. Travade *et al*., (2010) found that more migratory adult eels used a surface bypass designed for juvenile salmon than did a deep bypass, highlighting between-study variation. This, as well as the fact that all eels were detected upstream of the gravity sluice when it was closed regardless of route taken, is promising for eels to locate and pass the gravity sluice at FT pumping station and pumping stations of similar design, if flows are made more attractive. Otherwise, it may be necessary to implement an alternative passage route.

The operating regime during this investigation was tailored to regulated water level in the catchment upstream of FT pumping station by passing water over the gravity sluice when the water level downstream of the station permitted, not to provide downstream passage for eels, per se. The duration of sluicing ranged from 19 minutes to ~13 hours per day and represented a relatively small proportion of the time eels were detected in the forebay, i.e. 6%, and it was not possible to open the sluice at the same time as pumping occurred due to flood risk. As eels that passed the gravity sluice did not experience any pumping events and two eels that passed through a pump experienced no gravity sluicing, it would appear that eels exit the forebay via the first available route. This is unlikely to be the gravity sluice under the current operational regime as eels in the present study appeared to be attracted into the forebay as a result of flow experienced from pumping, and despite the sluice passing 28.6% of eels, passage did not occur in respose to a sluicing event. Other eels' behaviour upstream of the gravity sluice further supported this, as no other eels (including those that passed through pumps) were detected within 15 m upstream of the gravity sluice when it was open, despite being detected in the array during this time. This highlights that the current sluicing regime is not attractive to eels seeking exit from the catchment. Further, the third eel that exited via a pump experienced more sluicing (13.6%) than pumping (10.6%) during its' time in the array, indicating either that the flow from the gravity sluice is not attractive or the flows from pumping are potentially too strong to escape from, resulting in entrainment.

Previous investigations on European eel migrations in unregulated and regulated catchments have identified that eels migrate during periods of elevated river level in autumn and early winter, on a dark moon (Sandlund *et al*., 2017, and references therein; Tesch, 2003) and at night (Verhalst *et al*., 2018, and references therein). It is therefore recommended that the operating regime should be tailored to maximise silver eel escapement by sluicing as much water as possible at night (as 90.1% of positions in the array were at night) under high flows, as recommended by Verhalst *et al*., (2018) and on a dark moon. At this site, large wooden blocks or 'stop blocks' that are designed to fit in the gravity sluice chamber are removed gradually throughout the autumn in response to increasing river level, in order to allow more water to drain via this route. For example, additional stop blocks could be added to elevate upstream river level (without elevating flood risk) prior to sluicing to increase the duration of sluicing, and could be removed during sluicing to increase the total volumes of water sluiced. This would, in theory, maximise the amount of water passing through the gravity sluice when eels are actively migrating, increase the speed of water (head difference has a linear relationship with velocity (Solomon, 2010) to maximise attraction efficiency of this route and increase the depth of water over the stop-blocks to maximise entrance efficiency.

Altering the operating regime may maximise silver eel escapement but the gravity sluice will inevitably close when pump operation is required to mitigate flood risk and eels must avoid becoming entrained. During this study, five of seven acoustic tagged eels approached FT pumping station during the relatively small proportion of the study that a pump was operational (14 hours; 0.04% and 3.9% of the time eels were detected in the array). Fine-scale acoustic telemetry identified eels that passed through the pumps visited the array 2, 11 and 6 times, as did one of the eels that did not pass. Similar retreats were observed during the passage track through pumps with eels retreating 1, 5 and 12 times, from as close as 1 m from the trash screen. The repeated retreat behaviour, also described as highly tortuous movements by others (Nams, 1996; Morales & Elner, 2002), indicates unwillingness to pass through this route. The finding that eel 35825 that retreated upstream, had been upstream of both the gravity and the pumps when they were operational also supports this, and indicates that this eel managed to escape upstream. Brown *et al.,* (2009) reported similar milling behaviour by American silver eels in the forebay of a hydropower station. European eels have also been found to exhibit avoidance behaviour at water abstraction intakes, possibly in response to different flow fields (Behrmann-Godel and Eckmann, 2003; Jansen, 2007) or associated noise and turbulence (Sand *et al*., 2000). This is advantageous as it provides more of a window for a safe alternative passage route to be provided.

Long delays were observed for eels that passed through pumps during this study. Long delays upstream of pumping stations when eels were attempting to exit have been reported (Piper *et al.,* 2012) which can worsen the onset of diseases (if present) due to stress, increase predation risk (Garcia de Leaniz, 2008) and reduce fitness, potentially contributing to the decline of the species (Marmulla, 2001). Also, as feeding ceases once eels start the 6000 km migration to spawning grounds (Tesch, 2003) which can take six months, starting migration with full energy reserves is an optimum strategy (Lucas & Baras, 2001). Thus, delays can deplete energy reserves so much that arrest of the migration and the sexual maturation processes may occur so that feeding can resume until successful spawning is possible (Svedäng & Wickström, 1997). This would obviously cause further delays and may result in eels that have already undergone energetically costly silvering transformations (see Lokman et al., 2016) missing the opportunity to exit the catchment at the appropriate time when conditions are suitable, requiring them to revert back to yellow eels until conditions are again favourable, as discussed by Durif *et al*., (2005). This emphasizes the requirement for alternative downstream bypass solutions to be provided, to reduce the impact of delays. Ultimately, three of the five of eels that approached FT pumping station during operation were entrained (60%), and thus additional measures to prevent entrainment and improve the likelihood of eels passing through the gravity sluice are necessary. For example, the traditional trash screen with large spacing that allows eels to pass through could be replaced with one with appropriate bar spacing to prevent entrainment (see Sheridan *et al*., 2014) or behavioural deterrents could be employed such as strobes (Brown., 2000; Patrick *et al*., 2001), acoustics (Patrick *et al*., 2001; Deleau *et al*., 2016) or a graduated electric field (O'Farrell *et al*., 2014) to deter eels from entering hazardous intakes, but the cost implications could be significant for water resource managers.

Preventing entrainment and providing safe alternative downstream passage of critically endangered European eels is top priority for water resource managers, to maximise survival and production of remaining eel stocks. This study found a pumping station with an existing alternative downstream passage route, i.e. a gravity sluice, did not provide safe downstream passage for the majority of tagged eels (71.4%) and thus remediation measures are required in order for the site to meet the requirements of the Eel Management Plan of the member state and contribute to its' compliance with the Eel Regulations (1100/2007). It is recommended the upstream water level and gravity sluice should be managed to maximise silver eel escapement, though physical and/or non-physical measures may be required to prevent eels becoming entrained when the sluice is closed.

6 COMPARISON OF ATTRACTION, ENTRANCE AND PASSAGE OF DOWNSTREAM MIGRANT AMERICAN EELS THROUGH AIRLIFT AND SIPHON DEEP ENTRANCE BYPASS SYSTEMS

6.1 Introduction

Freshwater eels are of global concern following a 40 year drastic decline in recruitment of several eel species (Dekker & Casselman, 2014; Miller *et al*., 2015). They have a complex catadromous life cycle and must safely navigate to spawning groundsafter spending considerable time in freshwater (ranging from 6 – 60 years in for European eels (A. anguilla) (Tesch, 2003) and up to 40 years for American eels (Miller, 2005). During the downstream spawning migration they face riverine barriers from many anthropogenic influences, including hydropower and pumping station intakes. The direct mortality caused by passage through turbines and pumps (Coutant & Whitney, 2000), or indirect impacts caused by delays to migration and increased susceptibility to disease and predation (Garcia De Leaniz, 2008), have undoubtedly contributed to their decline (Feunteun, 2002). Guidelines to protect eel advise that such intakes are screened (U.S. Fish and Wildlife Service, 2017.), but this remediation measure is expensive (Electric Power Research Institute (EPRI), 2001) and there is still the requirement for a safe alternative downstream passage route in order for eels to exit the catchment. For these reasons, there is plentiful interest from environmental managers and engineers to find a cost–effective solution to downstream eel passage.

Flow is one of the key drivers during the eel downstream spawning migration (Stein *et al*., 2016); this cue can be exploited by providing an attractive entrance flow to a bypass channel and utilising the natural searching behaviour of eels. For such a bypass channel to be effective, the flow must not only attract eels but prevent them from leaving the pass in an upstream direction, whilst passing all eels with no mortality or visible signs of injury. In this study, two methods of producing flow within a bypass were investigated and compared, i.e. lifting water using air with using a siphon.

A typical airlift pump has a gas (usually air) injected at the base of a submerged riser tube. Gas bubbles suspended in the fluid cause the density of the fluid in the tube to be less than that of the surrounding fluid; the resulting buoyant force induces flow in the tube (Reinemann *et al*., 1990). Airlifts are used in wastewater treatment plants for low lift, high volume applications and have previously been used for transporting live fish in aquaculture (Summerfelt *et al*., 2009) and for sampling migrating juvenile salmonids (Brege *et al*., 1990). Haro *et al*., (2016) found that silver American eels readily located, entered, and passed through an airlift deep bypass system (the Conte airlift bypass) multiple times, with all eels passing through the bypass when the entrance velocity exceeded 1 m s^{-1}. A siphon requires a pipe or tube shaped as an inverted "U" placed between two fluids that have their surfaces at different heights, which continuously transfers fluid over the bend from the higher to the lower level through the combined effect of pressure and gravity (Richert and Binder, 2011). Siphons have been used as eel bypasses around the world. For example, Legault *et al*., (2003) reported 12% of the downstream migrating silver European eels passed through a siphon bypass in a reservoir in France. Boubée & Williams (2006) found a siphon used in conjunction with another free flowing bypass passed 79% of longfinned and shortfinned eels at a power station in New Zealand. However, Calles *et al*., (2012) found no tagged European eels passed through the siphon at a hydroelectric plant in Sweden due to failure of intake racks in preventing rapid entrainment of eels into turbines. These variable results highlight that eel bypasses require further research in order for effective designs to be developed.

6.1.1 Aims and Objectives

This study aimed to compare the performance of both airlift and siphon technologies under similar controlled laboratory conditions, with attraction hydraulics (flow and flow acceleration at the bypass entrance) held constant, and to test the repeatability of the Conte airlift deep bypass system experiment. Slip ratio, a metric to describe the measured velocity of the eel within the airlift or siphon pipe compared to the fluid velocity in the pipe, was also estimated. Analysis of slip ratio can be used to infer if eels are swimming with or against the flow within the pipe, or drifting passively.

Objectives of this study were to: 1) compare attraction, entry and passage rates of airlift and siphon bypasses; 2) quantify transit times, speed and slip ratio of eels passing through both bypasses; and 3) evaluate effects of both bypass designs on injury and mortality of passed eels.

6.2 Methods

6.2.1 Airlift and Siphon Design and Operation

A small diameter bypass system that could be configured as either an airlift or gravity siphon was designed to accommodate passage of large (approximately 100 cm total length) adult silver-phase eels and constructed in the U. S. Geological Survey S. O.

Conte Anadromous Fish Research Laboratory (CAFRL) Flume Facility (Turners Falls, Massachusetts, USA). Additional details of the operation of the airlift are given in Haro *et al*., (2016).

The bypass systems were constructed from steel and PVC pipe and fittings, and had a 30.5 cm diameter circular entrance (Figure 6.1), with the entrance invert located 11.4 cm above the floor of the flume. The entrance tapered to a 20.3 cm diameter horizontal section that transitioned to the 25.4 cm diameter vertical section via two 45° angle fittings. The vertical section of the airlift configuration extended 33.5 cm above the water surface with a total water depth of 3.84 m. For the airlift configuration, air was injected into the bottom of the vertical riser section to create a total vertical lift (from the invert of the bypass entrance) of approximately 4.5 m. Air was supplied to the bottom of the vertical riser section of the airlift from a portable rotary screw compressor powered by an internal combustion engine (Figure 6.1a). A valve was used to regulate the airflow from the compressor through the 2.5 cm diameter flexible airlines that terminated in a manifold consisting of four 2.5 cm diameter air injection pipes. The pipes were used to introduce air horizontally into an expansion fitting (Figure 6.1b).

The airlift pipe structure was modified to construct a closed-conduit, gravity siphon by connecting additional 25.4 cm diameter pipe to the top of the riser tube. The siphon extension consisted of a 90 degree elbow transitioning to a 21.8 m long horizontal section running above the water level of the containment area, passing over a bulkhead and descending vertically 4.4 m. A 90 degree elbow then transitioned horizontally from the vertical section to a gate valve and 1.5 m wide by 1.5 m high by 3 m long eel retention cage. The distances between antennas were identical in the airlift and siphon bypasses (A1 – A4), with the siphon having an additional 4 antennae (A5 – A8), Figure 6.1c.

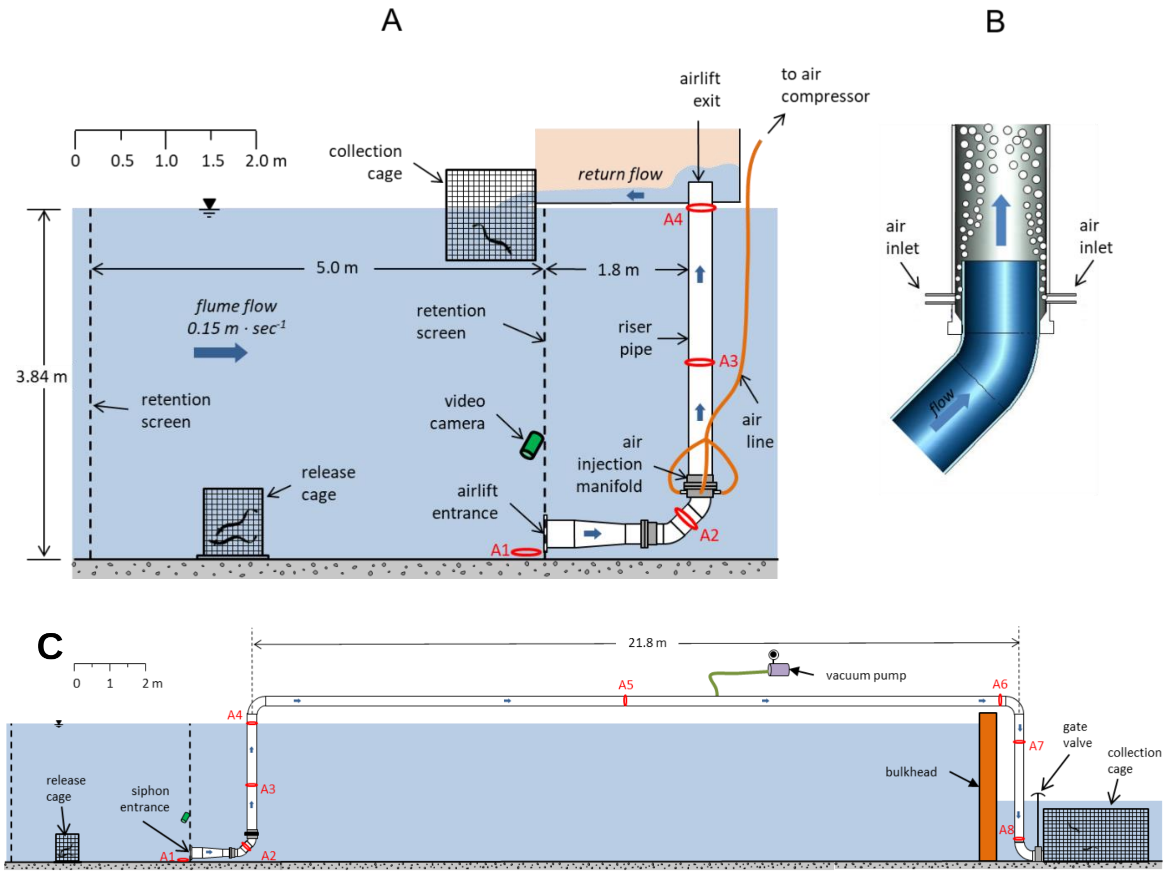


Figure 6.1.A). Elevation view of airlift test apparatus in the 6 m wide flume, approximately to scale. Blue arrows indicate direction of water flow. A1–A4: PIT antennas 1–4. B): cross-section of air injection manifold at base of riser pipe. C) Elevation view of siphon test apparatus in the 6 m wide flume, approximately to scale. Note modification of airlift riser pipe to extend pipe downstream and over a bulkhead, to a submerged collection cage, and addition of four PIT antennas (A5-A8) further down the pipe. Blue arrows indicate direction of water flow. The vacuum pump enabled evacuation of air from the pipe (with downstream gate valve closed) to initiate the siphon.

6.2.2 Bypass hydraulics

In the previous study of the Conte airlift (Haro *et al*., 2016), an entrance velocity of 1.2 m s^{-1} was associated with higher entry rates than lower tested velocities. Therefore a nominal cross-sectional water velocity of 1.2 m s^{-1} at the plane of the entrance was established for both the airlift and siphon bypasses in this study. Entrance velocity for the siphon bypass configuration was determined by measuring total flowrate through the siphon via a Signet Model 515 pipe-mounted flowmeter mounted at the centre of the horizontal section of the siphon, and calculating entrance velocity based on cross-sectional area of the entrance and flowrate. To establish a gravity siphon, the containment area was filled to the working depth (3.84 m), and the downstream gate valve was closed. Air within the siphon pipe was then evacuated using a vacuum pump, then the gate valve was opened to start the siphon flow.

6.2.3 Biological Test Conditions

An eel containment area was created in the 6.1 m wide CAFRL hydraulic flume by constructing two 3.9 m high retention screens (1 cm plastic mesh) oriented perpendicular to the flume flow (Fig. 1). The bypass system was installed 0.5 m away from one wall, with the entrance penetrating but flush with the downstream screen. A box made of wood at the exit of the airlift system was used to direct all flow and eel back into a collection cage (1 m wide by 1 m high by 1 m deep) within the containment area. For the siphon system, eels passing through the siphon were directed into a submerged collection cage (1 m wide by 1 m high by 2 m deep) located at the downstream end of the siphon pipe.

Passage of eels was monitored with four separate passive integrated transponder (PIT) coil antennas located at the entrance to the bypass and at several locations along the bypass pipe (A1-A4; Fig. 1A). Four additional coil antennas (A5-A8; Fig. 1B) were positioned on the horizontal and downstream vertical sections of the siphon. PIT receivers (Texas Instruments TIRIFD model S-2000) were interfaced to a computer that logged detections of individually tagged eel within 0.25 m of each antenna to the nearest 0.1 sec. The entrance was also continuously monitored with a downward-looking underwater video camera, with the viewing area illuminated by an infrared LED illuminator (Larson Electronics LEDLB-4R-IR-MSL, 850 nm cutoff wavelength; creating infrared illumination not visible to eels; Andjus *et al*., 1998) and a 1 m by 1 m retroreflective background (3M Diamond Grade 3990) placed on the flume floor. Ambient nighttime light levels inside the flume from outside sky illumination through skylights were approximately 0.0015 μW cm^{-1} or less, far below locomotor synchronization thresholds for eels of 20 μW cm^{-1} (van Veen & Andersson, 1982). Although these low ambient light levels may still have permitted eels to see structures within the test apparatus, the infrared illumination was considered to have no effect on attraction/repulsion to the bypass entrance, and behaviours were assumed to be representative of typical nocturnal behaviours of eels.

A cylindrical release cage (0.56 m diameter by 0.56 m high; constructed of aluminium perforated screen) which had no bottom screen was positioned in the centre of the containment area. The cage was magnetically attached to the bottom and could be lifted from the floor using an overhead hoist, allowing released eels to laterally disperse into the containment area without impediment.

Transit times of a passive particle moving through pairs of adjacent PIT antennas were calculated by dividing the calculated nominal water velocity through the pipe section between antennas (based on entrance velocity and pipe cross-sectional area and accounting for changes in pipe diameter) by the flow-path distance between PIT antennas.

6.2.4 Eel Collection, Holding, and Tagging

Adult, migratory American eels were collected from two sources: 1) the downstream bypass sampler at Hadley Station, Holyoke, Massachusetts (Connecticut River); and 2) commercial weirs in Newfoundland. Holyoke eels were collected on 1 and 29 October, 2015 between 19:00 and 23:00 h, and were immediately transported to the test facility in an aerated 500 l tank mounted in the back of a truck. Newfoundland eels were shipped by air freight for a separate telemetry study at a nearby hydro project, held in tanks at the hydro project (supplied with flow-through ambient Connecticut River water) for 1 week, and then transported by the truck tank to the test facility on 26 October. Handling, measurement, and tagging of eels followed protocols developed by Brown *et al*., (2009); eels were lightly anesthetized with a eugenol solution (Aqui-S 20E; Aqui-S New Zealand Ltd.), intraperitoneally tagged within 24 h of collection with 32 mm half-duplex glass-encapsulated passive integrated transponders (Texas Instruments TIRFID system; 3 mm diameter by 32 mm in length, weight 0.8 g, 134.2 kHz), and allowed to recover for at least 48 h before testing. During tagging, total length (nearest mm) and eye diameter (horizontal and vertical; nearest 0.1 mm) were measured. Eye and total length data were collected to calculate eye indices, a measure of developmental maturity to the downstream migratory silver phase (Pankhurst, 1982). Eels were held in 2 m diameter circular tanks supplied with open flow from the Connecticut River, and provided with hiding tubes and nylon netting for cover.

6.2.5 Test Protocol

Eels migrate downstream primarily at night, thus testing was initiated at dusk, with a 3 h trial from approximately 19:00 to 22:00; (ambient light levels within the flume facility <

0.1 lux and were presumed to be similar for all trials). Per night, only one trial was run; siphon tests took place on 3, 4 and 9 November and airlift trials took place on 5, 6 and 10 November 2015. A total of three trials were performed for each bypass with 14 eels per trial selected from both collection sites (9 Holyoke eels, 5 Newfoundland eels). To test for effect of sample size on bypass efficiency, all eels that had previously been introduced for passage through the airlift (three groups of 14) were tested in the siphon in one pooled group, (i.e., one run of n = 42) for eels first introduced for passage through in the siphon. Due to limited availability of wild silver eels, re-testing of these fish was necessary. Eels were tested in alternate bypasses to minimise potential influence of familiarity with the bypass as far as possible. Test eels ranged in size from 526 – 1005 mm TL (mean 755 mm). Eye indices ranged from 4.9 – 11.3 mm (mean 7.7) so all eels were deemed to be silver phase. Eels from Newfoundland and Holyoke collection sites were of comparable size (t-tests; t = -1.2842, *df* = 46.107, *P* = 0.206).

Eels were transported from the holding tank to the flume inside a dark, insulated 100 l cooler, and transferred to the release cage with the flume water depth approximately 0.5 m. Flows in the flume were then increased such that total depth was 3.84 m and velocity through the screened containment area was about 15 cm sec^{-1}. Air was then supplied to the airlift to establish the test airlift entrance velocity. Eels were allowed to acclimate to the release cage in the flume environment for 30 min and then released into the containment area by raising the release cage off the floor of the flume. Eels were allowed to explore the containment area for 3 h. At the end of the test period, the flume was drained and eels were collected using dipnets, for examination of any injuries or abnormal behaviours before being transported back to the holding tank. Post-test eels were inspected every 12 h over a 48 h period for mortality or evidence of developing injuries. Behaviour of individual eels was quantified by integrating PIT detection data at all antennas (4 in the airlift bypass and 8 in the siphon bypass) with behaviours recorded at the bypass entrance via the described underwater video camera.

Eels were removed from time, speed and slip velocity calculations when video footage analysis revealed missed detections at the entrance (airlift = 2 and siphon = 2). During siphon trials, twelve eels were not detected on A7 due to equipment failure and thus speed and slip ratio for A6>A7 and A7>A8 could not be calculated. There were 17 cases of crosstalk (detections of the same tag code at two antennas that were less than the antenna read rate [every 75 milliseconds]) between A6 and A7 and were removed from the dataset.

6.2.6 Fish pass efficiency metrics

A number of metrics were used to assess the behaviour of eels, the performance of each bypass and any difference between the bypasses (Table 6.1).

Table 6.1. Fish passage efficiency metrics

Metric	Description
1) Attraction efficiency	Percentage of fish that are attracted to the bypass entrance (detected on A1)
2) Entrance efficiency	Percentage of fish attracted to the bypass that subsequently entered (detected on A2)
3) Passage efficiency	Percentage of fish that entered the bypass pipe (detected on A2) and successfully negotiated and exited the bypass (detected on A4 / A8)
4) Overall efficiency	Percentage of fish that were attracted to, entered and successfully negotiated the bypass (encompasses attraction, entrance and passage efficiency)
5) Number of approaches before passage / non-passage	Count of the number of times each fish was attracted to the bypass entrance, for detections greater than 15 seconds apart
6) Attraction time	Time from release to first detection at the bypass entrance (first detection on A1)
7) Entrance time	Time from release to entry (1st detection on A1 during last approach event)
8) Delay between first approach and entry	Time from arrival (first detection on A1) and entry (1st detection on A1 during last approach event)
9) Passage speed	Speed that eels travelled between each pair of antennae (distance between each antenna pair divided by difference in times of first detection on each antenna pair), and from bypass entrance (1st detection on A1 during last approach event) to exit (first detection on A4 / A8)

6.2.7 Effect of slip ratio

The airlift was designed to establish fluid (air +water) velocities within the riser sufficient to entrain, lift and transport eels of varying length, weight and cross-sectional area to target release points. Fluidization or lifting will occur when drag forces exerted on inanimate objects, by rising fluid velocities, reach an equilibrium with gravity forces including net buoyancy, e.g., minimum fluidization velocities of discrete particles are related to density of the solid, density and viscosity of the fluid, packing porosity, effective particle size and uniformity coefficient (Weber, 1971). In the case of eels, additional factors must be considered including potential for thrust development as well as induced drag related to bridging. Bridging is defined here as a deliberate or random change in the orientation of the eel relative to flow direction such that drag forces at the eel body-pipe wall interface increase over that expected with an eel oriented with the current and avoiding pipe wall contact. We calculated a dimensionless slip ratio (SR) to quantify the movement of eels (V_{eel}) relative to fluid movement (V_{fluids}): SR = $(V_{eel})/(V_{fluids})$ within various sections of the airlift and siphon. V_{eel} was derived from transit times of eels between PIT antennas A4 and A3 as well as the pairs A5, A6 and A7, A8 monitored during siphon tests. V_{fluids} was calculated based on pipe cross sectional area, water and air flow rate assuming (1), the two phase flow is homogeneous and (2), that gas absorption/desorption is negligible. Air flow rate was corrected for temperature and pressure using the Ideal Gas Law. Following the latter, air volume at the base of the riser (Antenna A3) is less than that present at the upper antenna A4. Therefore we used the log mean of V_{fluids} in our calculation of SR: $V_{fluids} = ((V_{fluids})_{A4} - (V_{fluids})_{A3}) / \ln((V_{fluids})_{A4} / (V_{fluids})_{A3})$. Slip ratio was also calculated for eels passing through the airlift bypass in the previous 2014 study at three different flows (Haro et al., 2016) for comparison between flows and between years (2014 compared to the present study) for eels passing at 1.2m s^{-1}.

6.2.8 Data analysis

Data from this study and from the 2014 airlift study (speed of passage and slip ratio data only) were analysed separately, but using similar techniques. All metrics used to assess performance of bypasses were comparable between runs within treatments ($P > 0.05$), so data were pooled among replicate runs for analysis. Data were tested for normality of variance using a Shapiro-Wilk Normality Test before using Welch Two Sample t-tests for normally distributed data (referred to as t-test) or Wilcoxon Signed-Rank tests for non-normally distributed data (referred to as Wilcox-test), to test for differences between two groups in metrics 5 – 9 and slip ratio (Table 6.1). When comparing eel orientation, passage speed between antennas and slip ratio, either one-way ANOVAs (normally distributed data) or Kruskal Wallis tests (KW-test) with a Pairwise Wilcoxon Rank Sum post-hoc test (post-hoc) (non-normally distributed data) were performed. Pearson product moment correlation was used to test for correlations between eel length, passage speed and slip ratio. Eel length and eye index were compared between collection sites and study years using t-tests.

Cox's proportional hazard regression (Allison, 1995) was used to test for differences in approach and passage rates (percentage of first approach and first pass events over time) under each of the treatments (airlift or siphon); dependent variables were time to approach and time to pass. Eels that failed to approach or pass during the trial were included as censored observations, with time set to trial duration (3 h). Proportional hazard regression was also used to compare approach and passage rates between the pooled *n* =14 trials and the *n* = 42 trails.

All statistical analyses were carried out in R studio v 3.3.0 and SigmaPlot v 12.0 including use of the package ggplot2 (Wickham, 2016).

6.3 Results

6.3.1 Fish pass efficiency summary metrics

The airlift had an attraction efficiency of 76.2% and the siphon 72.6% of the total number of eels released into the forebay. Of the eels attracted to the entrance, 85.9% successfully entered the airlift and 95.1% successfully entered the siphon, and all of these eels successfully passed through the whole bypass (100% pass efficiency) with none of the eels reversing course while passing through any section of the bypass. Eels usually passed after first investigating the entrance to either bypass, with mean number of attempts before passage (airlift = 1.18 and siphon = 1.21) (Wilcox-tests; *W* = 1529, *n* = 113, P = 0.544) or non-passage (airlift = 1.33 and siphon = 1.33) (*W* = 18, *n* = 12, *P* = 0.756) being comparable (Table 6.2).

Table 6.2. Summary of fish pass efficiency metrics between each bypass (three runs of *n* = 14 and one of *n* = 42, total 84 eels introduced for passage through each bypass).

Metric	Airlift	Siphon
Released (n)	84	84
Attraction efficiency (% (*n*))	76.2 (64)	72.6 (61)
Mean number of attempts before passage	1.18	1.21
Mean number of attempts before non-passage	1.33	1.33
Entrance efficiency (% (*n*))	85.9 (55)	95.1 (58)
Pass efficiency (% (*n*))	100 (55)	100 (58)
Overall efficiency (%)	65.5	69.0

6.3.2 Time from release to first approach, entry and passage

Eels behaved comparably after first release, upon first reaching and passing both bypasses; there was no significant difference in median bypass attraction time, median passage time or median delay time between first detection and first passage (Table 6.3; Figure 6.2).

Table 6.3. Attraction time, entrance time and delay time between first detection and passage (median ± SD, (range) and statistical analysis (Wilcox tests; W and P values). Time units are hour:minute:second.

	Attraction time	Entrance time	Delay between first detection and passage
Airlift	00:20:31 ± 00:42:48, (00:01:54 – 02:53:40)	00:21:12 ± 00:41:22, (00:01:54 – 02:53:40)	0 ± 00:10:26, (0 – 0:44:53)
Siphon	00:17:33 ± 00:40:00, (00:00:57 – 02:31:38)	00:27:01 ± 00:42:52, (00:00:57 – 02:51:17)	0 ± 00:24:05, (0 – 02:13:38)
Statistics	*W* = 2011, *n* = 121, *P* = 0.347	*W* = 1458, *n* = 109, *P* = 0.877	*W* = 1375, *n* = 109, *P* = 0.286

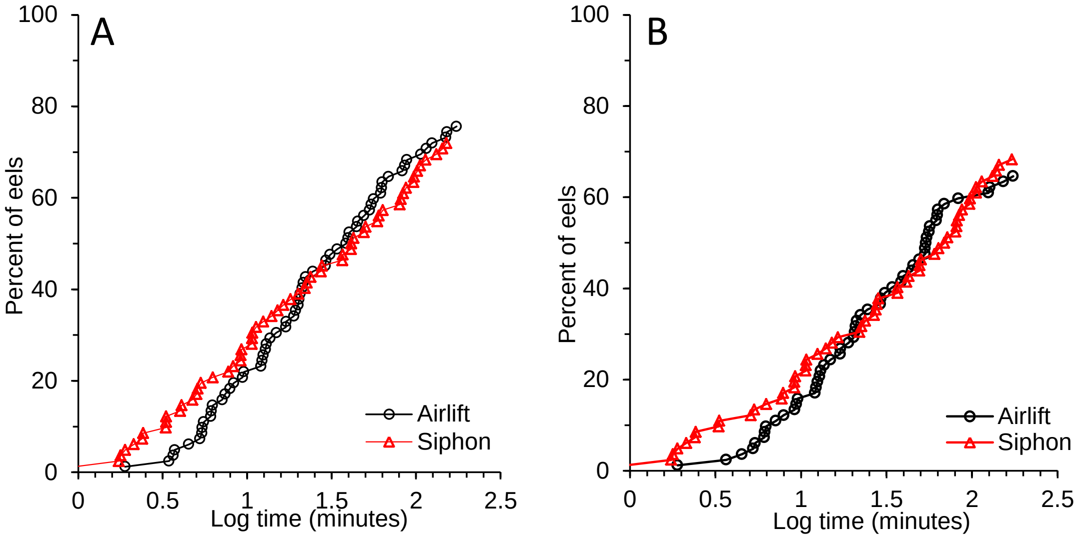


Figure 6.2. Cumulative time (log transformed data) eels took to a) first approach and b) first enter (expressed as percent of eels in each trial) for each airlift and siphon test.

There was also no significant difference in rates of approach between the siphon and airlift for either the pooled n = 14 (Cox's proportional hazard regression; P = 0.581) or n = 42 (P = 0.506) trials. Similarly, there was no significant difference in rates of passage between the siphon and airlift for either the pooled n = 14 (Cox's proportional hazard regression; P = 0.341) or n = 42 (P = 0.722) trials.

6.3.3 Orientation of passed eels

A comparable proportion of eels that approached the airlift (62%) and siphon (57%) in head first orientation rejected entry. A higher proportion of eels that passed through the airlift (63%) and siphon (74%) entered in a head first orientation. All eels that approached the airlift (21%) and siphon (19%) in tail first orientation rejected entry. There were fewer eels that were entrained in a tail first (airlift = 20.4% and siphon = 17.5%) or sideways (airlift = 13% and siphon = 3.5%) orientation (Table 6.4). Orientation of eels (head first, tail first or sideways) did not affect total passage time through the airlift (KW-tests; X^2 = 0.752, df = 2, P = 0.687) or the siphon (X^2= 3.998, df = 2, P = 0.136).

Table 6.4. Count and mean number of events per eel of orientation of eels rejecting and entering the airlift and siphon bypasses

	Reject tail first		Reject head first		Enter tail first		Enter head first		Enter sideways	
	Count	Mean	Count	Mean	Count	Mean	Count	Mean	Count	Mean
Airlift	11	1.1	18	1.29	13	0.2	35	0.6	7	0.1
Siphon	10	1.25	13	1.18	11	0.2	44	0.8	3	0.1
Total	**21**		**31**		**24**		**79**		**10**	

6.3.4 Passage speed

Speed of eel movement through the siphon was significantly faster than the airlift in sections A1>A2 (Wilcox-tests; W = 947, n = 109, P = 0.001), A2>A3 (W = 870, n = 109, P <0.001) but not A3>A4 (W = 1256, n = 109, P = 0.166) (Figure 6.3). The overall speed through sections A1>A4 in the siphon (mean ± S.D. = 1.04 ± 0.33 m s^{-1} (min – max = 0.41 – 1.86 m s^{-1}) was significantly faster than the airlift (0.82 ± 0.34 (0.18 – 1.79 m s^{-1}; W = 2117.5, n = 109, P = 0.001). As the siphon bypass had an extra 20.5 m of pipe (Figure 6.1), speed of eels moving through these additional sections was also investigated. Eels moved significantly faster through sections A5>A6 and A6>A7 of the siphon than all other sections (Kruskal-Wallis X^2 = 251.8, df = 147, $P < 0.001$; post-hoc $P < 0.001$) but were comparable to each other (post- hoc $P > 0.05$). Speed through the siphon was the most variable between antennas sections A2>A3 (0.2 – 2.7 m s^{-1}) and A6>A7 (1.4 – 4.8 m s^{-1}). There was no significant correlation between eel length and passage speed through any section in any of the trials in 2014 or 2015 ($P > 0.05$; Pearson product moment correlation).

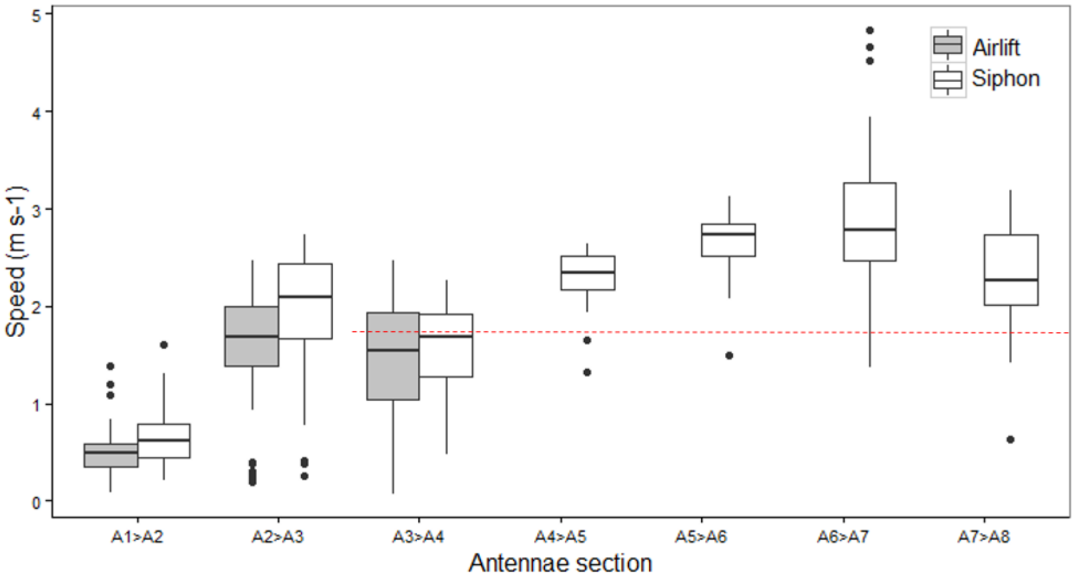


Figure 6.3. Speed (m s^{-1}) through each section of the airlift and siphon bypass (whiskers indicate range, midline indicates median, upper and lower limits of box indicate 75th and 25th percentiles, outliers indicated by black dots), dotted line indicates estimated water speed through each section of bypass.

6.3.5 Effect of different experimental designs on slip ratio

Slip ratio between bypasses and bypass sections

The siphon had significantly higher slip ratio (0.9 ± 0.2, 0.3 – 1.3) for vertically upward moving eels (A3>A4) than the airlift (0.6 ± 0.2, 0.0 – 1); (t-test; t = -8.10, df = 104, P <0.01), (Figure 6.4a). There was no significant correlation between eel length and slip ratio in this section of either bypass (Pearson product moment correlation, P >0.05).

The siphon bypass also included horizontal and vertically downward moving eels, thus slip ratio and the influence of gravity was also assessed. Slip ratio in the horizontal section (A5>A6; 1 ± 0.1, 0.5 – 1.2) was significantly higher than in the vertical downflow section section (1.0 ± 0.2, 0.2 – 1.2) (KW-test; $X^2 = 8.990$, df = 2, $P = 0.011$; post hoc $P = 0.002$) but the vertical upflow section (A3>A4; 0.9 ± 0.3, 0.3 – 1.3) was comparable to the horizontal and vertical downflow sections (post-hoc $P > 0.05$); Figure 6.4b). Again, there was no correlation between length and slip ratio in the horizontal or vertical downflow section of the siphon bypass (P >0.05; Pearson product moment correlation). There was no difference between slip ratio and different orientations of eels within each bypass (ANOVA; (F(1, 107) =2.914, $P = 0.091$)).

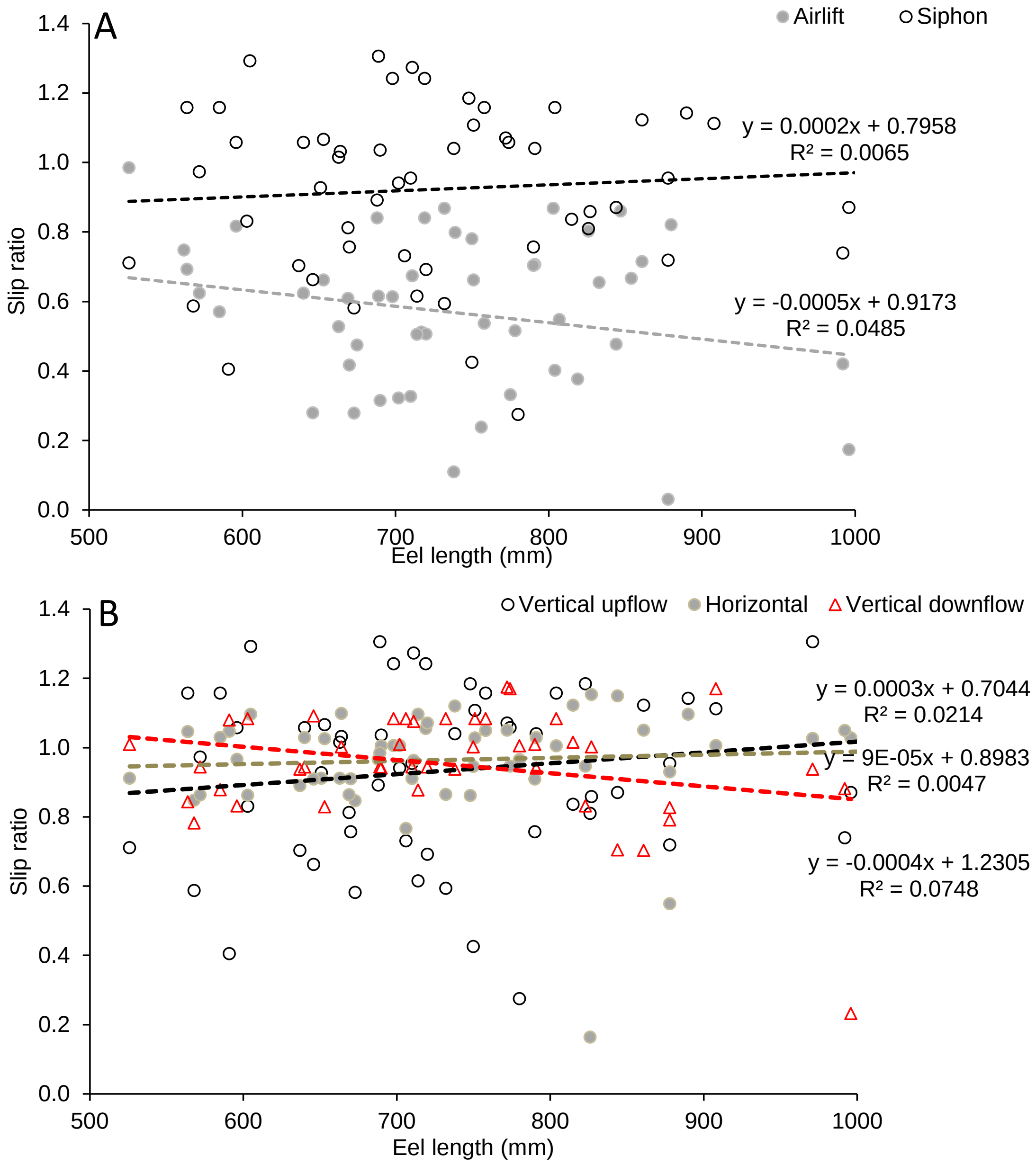


Figure 6.4 a) Slip ratio between the airlift and siphon bypass and b) between the horizontal and vertical sections of the siphon bypass. Colour of trendlines for data in each group corresponds to data points in that group. Intercept and R2 values displayed.

Slip ratio at different flows and between years

Slip ratio of eels tested at the three flows in 2014 did not differ significantly (KW-test; X^2= 2.333, df = 2, *P* = 0.312) but in 2015 eels had a significantly higher slip ratio (0.6 ± 0.2, 0 – 1) compared to eels at the same entrance velocity in 2014 (0.3 ± 0.3, 0 – 0.7 m

s^{-1}; Wilcox test; $W = 132$, $n = 41$, $P < 0.05$). There was no significant correlation between eel length and slip ratio in any of the flows in 2014 (Pearson product moment correlation, $P > 0.05$), and overall, eels in 2015 were significantly larger than those trialled in the previous study conducted in 2014 (Haro *et al*., 2016) ($t = -2.3748$, $df = 92.853$, $P = 0.022$) but eye index was significantly smaller ($t = 7.0691$, $df = 100.26$, $P < 0.001$).

6.3.6 Injury and mortality

All eels were alive, actively swimming and exhibited no external signs of injury or stress after the trials on the airlift and siphon bypasses. Latent mortality 48 h post-testing was zero, with no external evidence of developing injuries. Eels were released to the wild after the post-trial observation period.

6.4 Discussion

Addressing the issue of barriers to the downstream migration of *Anguilla* species is currently at the forefront of fish passage research. Types of barriers requiring remediation globally vary widely, warranting the need for bypass designs to be suitable for a broad range of installations. Results from eel bypass studies in the field have previously been inconclusive (Legault *et al*., 2003; Calles *et al*., (2012) or reported variable results (Boubée & Williams, 2006; Gosset *et al*., 2005). Controlled flume conditions make it possible to quantify and better understand eel behaviour around bypasses, which aids in determining the optimum settings for efficient passage before installation in the field. In this study, flows were generated in two different ways but attraction, entrance and passage rates were comparable; eels entered both the airlift and siphon bypasses quickly (typically in less than 2 hours), and all eels that entered successfully passed, mostly in headfirst orientation and on the first attempt. There was no mortality or visible signs of injury on any eels that passed. Hence there were no deleterious effects on eel health or survival from the way flows were generated. Further, all metrics used to assess performance in this study were comparable to a previous airlift study (Haro et al., 2016), and demonstrate the repeatability of the approach and thus confidence in its potential real-world application.

Extensive delays to eels at structures have been observed (Piper *et al*., 2013), with searching behaviour at intakes (Brown *et al*., 2009; Behrmann-Godel & Eckmann, 2003) and rejection of passage through bar racks (Russon *et al*., 2010) being exhibited.

These behaviours reduce the initial risk of eels being entrained into potentially hazardous intakes and provide an opportunity for them to find and enter safe downstream passage routes. Eels are known to actively search for a downstream passage route near the bottom of the water column in forebays of structures such as hydropower stations (Brown *et al*., 2009; Gosset *et al*., 2005) and navigate by following the walls and floor (Russon & Kemp, 2010); consequently bypass location will influence the ability of eels to find the bypass entrance, i.e. attraction efficiency.

Flow is one of the main drivers for the downstream spawning migration (Stein *et al*., 2016), and thus providing an attractive flow at the entrance to the bypass increases the likelihood of eels successfully locating the entrance and subsequently entering. Understanding the hydrodynamic cues used by outmigrating fishes is essential to ensure that fish are entrained in water velocities that exceed their burst speed, hence preventing failed passage (see Nestler *et al*., 2008). As most eels entered the first time they approached either bypass, and no eels exited either bypass after passing the first antenna, this would indicate that the flows and associated velocity gradients trialled in this study are attractive to eels. This is unlike findings from Piper *et al*., (2015) who reported avoidance of constricted, accelerating flow and changes in behaviour in these conditions by 95% of eels (n = 35) at lower flows than at the entrance to the bypasses trialled in this study; ranging from 0.14 to 0.67 m s^{-1}. In the field, bypass operation should coincide with other environmental factors known to be favourable to migrating eels such as lunar cycle and time of year (Tesch, 2003) to maximise downstream passage efficiency.

Eel orientation when entering the bypass did not affect speed through either bypass nor did result in any eels reversing course after entering the pipe. Fish orientation when passing through bypasses has previously been linked to diel cycle; shad orient visually into fast flows when using a bypass in the day (Kynard & Buerkett, 1997). In terms of bypass efficiency, it is felt that the focus should be on ensuring that fish cannot escape from the bypass once entrained, provided chosen flow settings result in safe passage for all test subjects, as found in the present study. Based on speed of movement through the bypasses, it is unlikely eels attempted to leave the pass in an upstream direction and thus eel energy reserves would not be depleted during passage. Eels readily passed through longer lengths of pipework during the siphon experiment; this is encouraging as real world bypass installations may require longer lengths of pipe.

Faster movement through the siphon bypass than the airlift bypass (A1>A2 and A2>A3) may indicate that either flows experienced in the siphon are easier to navigate or eels are more reluctant to move through flows created by the airlift, potentially due to reaction of eels to the injection of air (or associated sound/pressure changes) at the manifold. As speed was most variable between A2>A3 and A6>A7 in the siphon, this may indicate that eels were reluctant to move around bends during passage. This may be further evidenced by eels having a significantly higher slip ratio in the horizontal section of the siphon than the vertical downflow, however slip ratio between other sections was comparable and all eels that entered passed so this is not thought to affect probability of eels passing through the entire siphon bypass. Further, slip ratios were comparable between the three flows tested during the 2014 airlift bypass trial. It is also advantageous in terms of safe exit that the speed through the final section of the siphon was significantly lower than the previous two sections; this is difficult to explain. However longer pipework may affect speed and field trials will help understand this relationship in order to ensure safe exit from the bypass. In the field, locating the outfall of any bypass appropriately is also essential to overall success; if there is a large fall required by fish to re-enter the water, a reception pool can be used (Gosset et al., 2005) to reduce the impact of the fall on the fish. An outfall should be located where depth of the river is great enough to avoid injury upon exit resulting from collision with the river bed; ; a submerged outfall can be used to avoid the risk of avian predation (Congress, U.S., 1995).Outfalls should also be located away from the shoreline (Ferguson *et al*., 2007).

As sexual dimorphism exists in eels (Oliviera & McCleave, 2002) and the majority of migratory eels often move simultaneously in response to an increase in rainfall and flow (Boubée *et al*., 2001), mature eels of a range of sizes will require a downstream passage solution at similar times. As there was no influence of sample size or eel size on the attraction time, passage speed or slip ratio of either bypass, this indicates that both bypasses were attractive to and suitable for migratory eels with a range of biological features, regardless of number of eels in the forebay; these results are favourable in terms of maximising passage in real-world scenarios. Research could aim to quantify the passage behaviour of smaller, male eels to further support this. Further, the findings are applicable to other Anguillid species as both American and European eel species have been reported to have similar swimming abilities and behaviour

(Clough *et al*., 2002; Solomon & Beach, 2004). As eel passage is a worldwide issue affecting multiple species, this is advantageous.

As the method of flow generation did not influence bypass efficiency, this broadens the real-world applicability of the findings presented here; airlift and siphon bypasses have differing installation and operational requirements. For example, siphon bypasses require the water level downstream of the barrier to be lower than the upstream water level, but this is not a prerequisite of airlift bypass operation, so such a measure may be suitable at pum ping stations that transfer water to a higher level. Airlift bypasses require at least a 4 m riser pipe in order to generate the entrance velocity trialled in this investigation and thus the installation location must exceed this depth unless the bypass is excavated into the river bed. A limitation of airlifts is that they lift water a relatively short distance, 33.5 cm during this investigation, and thus an open channel sluiceway or collection device may be required with an airlift. A collection device may have problems with respect to debris loading and eels may need to be manually sorted from debris and transported downstream. Siphons do not require a water pump once they are operational, and fish are not subject to any pumping action (Bethune *et al.,* 1997).

It is clear from aforementioned previous research on this topic that the success of bypass systems for eels is not only affected by the design of the bypass, but also the nature of the site. As mentioned, variable results have been found in forebays of power stations, reservoirs and over spillways. This highlights the need to implement what has been determined so far in the field so that optimum settings can be adapted accordingly on a site-by-site basis.

6.4.1 Conclusion

The findings of this study support that an attractive bypass channel holds promise for providing a safe alternative route for downstream migrating eels. It was determined that two bypasses with flows being generated by air injection and siphon design both performed comparably, with most eels being attracted to the bypasses and passing quickly on the first attempt. All eels that passed did so efficiently and safely, with no mortality or visible signs of injury upon exit, and no evidence of energy depletion during passage. These findings and those in the previous study (Haro *et al*., 2016) add to the knowledge base for determining what an effective downstream route for eels is, of which there is currently a lack of knowledge despite the need globally to solve this problem. Further research into entrance velocities, size and shape are required along with field studies to demonstrate real-world effectiveness, especially in scenarios where intakes generate competing flows. Regardless, the novel findings presented are encouraging for improving downstream passage for anguillid species.

7 GENERAL DISCUSSION

7.1 Introduction

Spawning migrations of fish are intrinsically linked to the natural flow regime. High flows provide cues and opportunities for fish to access spawning grounds, but the natural flow regime is often removed or heavily regulated by anthropogenic influences that disrupt longitudinal connectivity (Chapter 2). For rivers downstream of reservoirs, artificial freshet releases may be released to replicate the natural flow regime and promote spawning migrations of potamodromous salmonids. This does not always result in movements that are characteristic of spawning migrations and fish may still perform large movements outside of freshets (Chapter 3). Catadromous fish such as eels require exit from the catchment in order to reach spawning grounds, but migration routes can be disrupted by infrastructure such as hydropower stations, which abstract some of the flow and result in a large proportion of migrant eels being impinged or entrained at hazardous intakes (Chapter 4). Likewise, eels inhabiting catchments where the flow is regulated by pumping stations may have an unobstructed downstream passage route available through a gravity sluice. However this is not operated for fish passage, per se, and may not attract any eels at required times, which can result in the majority being entrained into hazardous pumps during high flows (Chapter 5). Thus, there is a need to understand migratory behaviour of fishes so that safe, attractive passage routes that utilise this behaviour can be provided, where necessary (Chapter 6). The overall aim of the study was to investigate the impact of river regulation on migratory fish access to spawning grounds, and to understand the behaviour of migratory fish in regulated systems when reaching barriers, in the interests of utilising this behaviour to design and implement passage solutions, or recommend when operational changes could be put in place to improve access to spawning grounds. The study was divided into key topics that are addressed in Chapters 2 to 6. This Chapter discusses the knowledge gained throughout the previous Chapters in order to draw conclusions and recommend further study.

7.1.1 Modification of flow to improve fish access to spawning grounds

Chapter 2 provided a review of how spawning migrations of fish are diverse and depend on the complex riverine ecosystem in free-flowing rivers with longitudinal connectivity, and the associated range of flow, habitats and conditions provided. This is reflected in the evolution of different life history strategies in response to changing environment, classified by the habitat used for spawning and the direction of spawning migrations. Specific conditions are needed for different fish life stages, which must be exploited at appropriate times. The plethora of human modifications to rivers has resulted in widespread flow regulation and barriers to spawning migrations, which have had significant consequences for migratory fish. Global legislation now aims to restore longitudinal connectivity through measures such as replicating flows required by fish, reducing risk of mortality at infrastructure or providing passage solutions to migratory fish, but there is still a dearth of thorough, transferable information on the efficacy of such measures, particularly for downstream migrating species.

*Operational changes to **replicate** the natural flow regime*

Downstream of impoundments such as reservoirs, the natural flow regime is removed and water is instead stored for anthropogenic purposes such as potable supply. This can prevent fish from accessing areas required for spawning as they do not receive cues to spawn or opportunities to access these areas. Ecologically beneficial components of the natural flow regime are classified as ‘building blocks’, which can provide guidance for particular functions, such as provision of flow elevations for dispersal and fish migration under the autumn/winter flow building block. Radio telemetry was used to provide fine-scale movement data of individual potamodromous adult brown trout, in five regulated upland reaches of the River Holme downstream of two water storage reservoirs, in response to eleven freshets under this building block of differing timing, magnitude and duration over three study years (Chapter 3). However, potamodromous brown trout did not perform movement patterns that were indicative of upstream spawning migrations in response to freshets. Further, large fish movements occurred outside of these freshet releases, both during reservoir overtopping in response to natural high flows and in periods of low flow, suggesting fish were not dependent on the recommended freshet profile to migrate (Chapter 3). For this particular population, movements characteristic of spawning migrations were not performed but it was important to quantify the movements that were performed in order for suitable mitigation measures to be recommended.

Rehabilitation efforts in regulated rivers downstream of reservoirs need to focus on providing fish with the necessary conditions for spawning grounds to be maintained. Flows from reservoirs should be provided to refresh and maintain channel habitat and refresh spawning gravels that are required by both potamodromous and anadromous fish. Further research is required in order to assess if and when the fish populations downstream of reservoirs require artificial freshets to access spawning grounds, i.e. flow releases may be required in other scenarios. In these cases, to make freshets the most suitableto promote spawning migrations they should coincide with natural overtopping events, as fish were found to respond to overtopping events in Chapter 3; this will also help to conserve water.

*Operational changes to **utilise** the natural flow regime and provide attractive flows*

Despite finding that potamodromous fish may not rely on operational changes to perform spawning migrations in the aforementioned scenario, anadromous and catadromous species do require passage over barriers in order to reach spawning grounds. Acoustic telemetry helped understand the timing of catadromous eel movements during the downstream spawning migration through a regulated catchment (Chapter 4) and when passing impoundments for hydropower (Chapter 4) and a pumping station for water level regulation (Chapter 5). Despite there being alternative downstream passage routes available, eels responded to natural high flow events which resulted in greater operation of hazardous routes, demonstrating the well-documented influence of flow in attracting migratory eels. This often resulted in impingement or entrainment at the intakes to infrastructure. Such barriers are recognised as being one of the factors contributing to the decline of eels worldwide as heavy modification (and multiple barriers) are common in rivers globally, with increasing plans to build further dams on many continents (Chapter 2). Consequently, providing cost-effective solutions are of interest to water resource managers as there are often multiple sites requiring remediation.

Fine-scale behaviour of eels using acoustic telemetry demonstrated several important findings, including that passage time at a diversion weir upstream of a hydropower station was short and that eels were entrained in a pumping station when a gravity sluice was not available or could not be located (Chapters 4 and 5, respectively). It is essential that an alternative route is available at the appropriate times, i.e. during the autumn spawning season and during high flows. It is also essential that eels are attracted to such a route, i.e. by ensuring there is an attractive flow at the entrance. Further, eels at a hydropower intake experienced long delays but were not always impinged after spending time close to the intake chamber (Chapter 4), and at a pumping station exhibited avoidance behaviour upstream of operational pumps

(Chapter 5). This increases the likelihood of a safe alternative route being located when eels search for an exit. This could be through operational changes to increase the likelihood of eel using existing infrastructure, as 47.6% of eels were found to use an existing spillway (Chapter 4), or the installation of an eel-specific bypass channel (chapter 6).

Provision of an attractive bypass channel

An alternative and safe bypass channel can be installed in the forebay of hazardous infrastructure, though it must be approached, entered and passed quickly by the target species. A bypass channel designed to utilise the documented migratory behaviour of eels, i.e. with a bottom entrance and an attractive flow, was successful in passing migrant American eels whether flow was created by airlift technology (induction of air into a riser pipe) or a siphon (utilise the head difference to move water using gravity) (Chapter 6). Such a measure holds promise for providing a cost-effective solution for eel passage worldwide, especially as there are two different ways of creating flow which are suitable in different depth and gradient scenarios. Whilst these findings are beneficial in terms of reducing eel passage through hazardous intakes, mortality or reduced fitness through injury or energy depletion are still possible after interaction with intake screens. It would therefore be beneficial to take further measures to reduce the number of eels entering forebays to intakes, such as through the use of physical or behavioural deterrents.

7.2 Conclusions and recommendations

7.2.1 Modification of flow to improve fish access to spawning grounds

Rivers downstream of reservoirs are deprived of the natural flow regime. In response to freshet releases aiming to replicate flows required to promote spawning migrations, radio tracked brown trout did not display movement patterns that were characteristic of spawning migrations and the largest movements occurred outside of freshets. **It is recommended that reservoir overtopping is promoted during the spawning season, and that further research into the response of potamodromous species to freshet releases that coincide with overtopping is conducted.** This is recommended by UKTAG, but is not always possible due to flood risk, which calls for more research into the ideal freshet profile that best replicates the natural flow regime for migratory fish.

Radio telemetry gave insights into how a river-resident population of brown trout in headwaters respond to freshet releases, including comparisons to a control reach. **It is recommended that further research is conducted on the response of potamodromous species to freshet releases of differing timing, magnitude and duration, and quantify movements of fish inhabiting reaches further downstream in such catchments.** Specifically, studying fish from further downstream would help determine whether fish travel upstream into the headwaters for spawning in response to freshets. There is still a dearth of knowledge on the response of river-resident species to freshet releases, and such information is important for water resource managers in order to maximise benefits to downstream biota whilst conserving water.

When designing mitigation for migratory fish inhabiting rivers downstream of reservoirs, it is important to quantify where spawning habitat occurs so that it can be determined whether it is accessible by migratory fish, as small patches of spawning habitat were available to radio-tracked brown trout, which has been found to result in smaller movements. **It is recommended that future studies also determine whether spawning habitat is present and accessible by the population in question before deciding whether flow releases are necessary to ensure the life cycle can be completed.** It is important to recognize the importance of all required habitats being accessible to potamodromous species that must carry out the entire life cycle in the streams inhabited. This will help determine whether mitigation to allow access to spawning grounds is necessary.

Safe downstream passage of silver eels is a global issue, with many sites requiring remediation. Although some hydropower and pumping stations have existing alternative passage routes, such as spillway and gravity sluices, they were principally designed to pass water and a small proportion of eels pass through them, often after long delays. These findings should be considered when attempting to improve passage of downstream migrating eels in catchments where there is an alternative route available. **It is recommended that when this is the case, operational changes to maximise availability of alternative routes and hence improve passage through the safe route are put in place.** Specifically, opening the safe route during the eel spawning migration, during high flows and at night, before water is abstracted for other purposes, and determining the minimum amount that gates need to be open to keep these routes available for the duration of the spawning season.

Shortfinned eels entered a power station forebay when gates to the alternative route were open and approximately half passed over the spillway but experienced long delays, and no migrant European eels were detected within 15 m of a gravity sluice adjacent to a pumping station when it was open. **It is recommended that further research into flows required to attract eels to such routes is conducted to enable alternative routes to be more suitable for providing passage to eels.** This could be achieved by measures such as holding back water to increase the flow available to pass through alternative routes during the spawning season, potentially coupled with flow guidance to guide eels away from hazardous intakes. If passage through existing infrastructures is found to be successful, it may negate the need for expensive alternative remediation measures, and utilize the advantage of alternative routes being available. Flow refuge may also be provided to eels to reduce the energy expenditure when delayed in impoundment forebays.

A large proportion of both shortfinned and European eels became impinged or entrained at hydropower and pumping station intakes, and were believed to have died. **It is recommended that further research focuses on the efficacy of physical and behavioural deterrents to reduce the number of eels entering hazardous intakes.** Specifically, research into physical screening such as fine-mesh, flow guidance away from hazardous intakes or behavioural deterrents such as strobes, acoustics or an electric barrier at the head of diversion canals or in front of hazardous intakes is required under a range of scenarios including depth, competing flows, conductivity, debris load and turbidity of the area to determine their suitability and efficacy. This would increase the measures available to reduce impingement and entrainment at hazardous intakes.

Acoustic telemetry offered a broad spatio-temporal understanding of shortfinned eel movement both through a catchment regulated by a hydropower station, and fine-scale position data upon reaching the infrastructure. This provided insights into areas occupied under differing power generation scenarios. **It is recommended that future studies implement the use of transmitters that have a higher transmission rate in order for fine-scale behaviour directly upstream of intakes to be quantified.** Multi-beam sonar technology or using 3D acoustic transmitters would improve our understanding of fine- scale behaviour as well as positioning in the forebays of such infrastructure.

Sites with multiple routes available may be considered to not pose as much of a threat to downstream migrating eels as those where the only route of passage is through pumps or turbines associated with infrastructure. The findings of this study highlight the need for the behaviour of migrant eels around sites to be quantified before management decisions are made, as both shortfinned and European eels were found to be heavily impacted by both a hydropower and pump station despite an alternative route being available in these catchments. **It is recommended that further research into eel migratory behaviour and escapement from other catchments is conducted**, to further quantify the impact of hydropower and pumping stations with differing characteristics on migrant eels.

Both New Zealand shortfinned and European eels were negatively impacted by river regulation and associated infrastructure in this study. Legislation in Europe is more advanced than in New Zealand in response to the European eel being classed as critically endangered. As temperate eel species are in decline worldwide (Dekker & Casselman, 2014) this calls for legislation in countries where the situation is not as advanced to be updated so as to fill knowledge gaps more quickly. Considering this, **it is recommended that international collaborations continue to ensure knowledge exchange of this global issue.** This will also help ensure research and knowledge gaps are filled more quickly.

Despite this research providing insights into downstream passage of migratory eels through existing infrastructure, many sites do not have alternative routes available. **It is recommended that future research quantifies migratory behaviour of eels at sites without an alternative route so that informed decisions on passage solutions can be made.** Specifically, research should focus on the locations that migratory eels occupy upstream of impoundments with differing depth and flow profiles to inform the design of an alternative efficient bypass solutions.

In this study, no eels were detected upstream of a surface-oriented gravity sluice when it was open. **It is recommended that research is conducted around gravity sluices of different depths and entrance heights.** The efficiency of gravity sluices with different entrance heights (i.e. bottom and mid-channel instead of surface) and in different depths and locations in the catchment (as this will affect operational regime) is required to fill knowledge gaps of the potential for these routes to provide safe passage to eels.

7.2.2 Alternative downstream passage solutions

Both shortfinned and European eels in the forebay of a hydropower and pump station, respectively, were delayed for considerable periods of time and approached hazardous intakes multiple times. This reluctance to pass through turbines and pumps is advantageous as it reduces the risk of severe injury or mortality from passage and it increases the time period for eels to locate a safe alternative route. As well as aforementioned measures to improve eel passage through alternative routes, **it is recommended that an alternative bypass channel is installed in the forebay of such infrastructure.** Such a bypass must be tailored to eel behaviour so as to allow efficient passage and reduce the negative impact of delays to the migration.

Both an airlift and a siphon bypass successfully passed migrant American eels when trialled in a simulated forebay environment, with video footage and PIT telemetry quantifying that the majority of eels passed through the entire bypass and all eels that entered the bypass successfully passed. **It is recommended that such bypasses are tested in the field to fully quantify attraction, entrance and passage efficiency and optimal bypass flows.** Specifically, further research should be performed into the efficacy of such measures in shallow forebays, the influence of competing flows form hazardous intakes and the effect of forebay sizes is needed. This will help evaluate the attractiveness of these bypass solutions in a larger area and behaviour upon approach, the flows required to avoid eel escapement after entrance and ultimately will increase the transferability of such a measure to other sites and eel species, hence increasing the global suitability of such a measure in improving eel passage.

Despite providing important insights into how flows can be generated in a bypass channel, limitations are present with each technology; airlift design requires at least a 4 m deep intake and siphon relies on gravity so is only suitable when water is not being pumped downstream. Interesting insights into how the mechanisms driving creation of flow influence eel behaviour were found in the siphon bypass such as eels in the vertically upward portion of the siphon had a higher slip velocity than those in this section of the airlift. **It is recommended that research into eel responses to different ways of generating flow using other methods such as pumps continues in order to make such a measure more broadly applicable to different sites requiring remediation.** Specifically, pumping stations pump water upstream so a siphon is not suitable, and forebays are often shallower than 4 m.

7.2.3 Conclusion

In response to a 40% global decline in migratory fishes, it is essential to understand the behaviour during their remarkable spawning migrations in order to improve access to spawning grounds. Potamodromous brown trout downstream of two water storage reservoirs did not perform spawning migrations in response to freshets of differing timing, magnitude or duration. **Further research is needed to aid in best replicating the natural flow regime and the necessity of such measures for potamodromous species**. Catadromous New Zealand shortfinned and European eel in two catchments regulated by hydropower and a pumping station, respectively, were often impinged or entrained into hazardous intakes despite there being an alternative route available, i.e. a diversion weir and a gravity sluice. Utilising the existing features and the relationship between migratory behaviour and flow holds promise to provide passage solutions in regulated catchments, and operational changes are recommended to increase the attractiveness of alternative routes**. Further research is needed on eel responses to such operational changes**. A bypass that utilises this relationship was found to be successful in passing catadromous American eels, and holds promise for installation in the field to improve passage at infrastructure. **Further research is needed to quantify the applicability of such a measure in-situ at sites with a range of characteristics, and for other eel species.** The findings of this study provide insight into the potential for utilising understanding of fish migratory behaviour to inform operational changes and design alternative bypass routes, to improve access to spawning grounds for migratory fish inhabiting regulated river systems.

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APPENDICES

Appendix 1. Summary of where eels were sourced from for the study; when the canal was dewatered for equipment setup, a trap was set on the spill-over to collect any eels that were later used for tagging; some eels were also supplied by a local and a commercial fisherman that had caught them from elsewhere in the catchment.

Eel ID	Source	Release location	Total length (mm)
33889	Wairua catchment - Dargaville wetlands & lakes	R	880
33900	Wairua catchment - Dargaville wetlands & lakes	R	840
33901	Wairua catchment - Dargaville wetlands & lakes	R	855
33880 (2)	Wairua catchment - Dargaville wetlands & lakes	R	815
33883	Wairua catchment- Hikurangi- Waipuakahau stream	R	1033
33884	Wairua catchment- Hikurangi- Waipuakahau stream	R	1010
33888	Wairua catchment- Hikurangi- Waipuakahau stream	R	1031
33898	Wairua catchment- Hikurangi- Waipuakahau stream	R	950
33899	Wairua catchment- Hikurangi- Waipuakahau stream	R	880
33907	Wairua catchment- Hikurangi- Waipuakahau stream	R	910
33905	WPS trash pile	R	938
33906	WPS trash pile	R	880
21549	WPS dewatering trap	C	810
21551	WPS dewatering trap	C	775
33878	WPS dewatering trap	C	1020
33879	WPS dewatering trap	C	840
33881	WPS dewatering trap	C	825
33882	WPS dewatering trap	C	965
33885	WPS dewatering trap	C	900
33886	WPS dewatering trap	C	875
33887	WPS dewatering trap	C	880
33895	WPS dewatering trap	C	900
33896	WPS dewatering trap	C	1130
33904	WPS dewatering trap	C	1030
33880 (1)	WPS dewatering trap	C	860