UNIVERSITY OF SOUTHAMPTON

FACULTY OF ENGINEERING AND THE ENVIRONMENT

Civil, Maritime, and Environmental Engineering and Science Academic Unit

Quantifying the movement and behaviour of migratory European eel (*Anguilla anguilla*) in relation to physical and hydrodynamic conditions associated with riverine structures

by

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Thesis for the degree of Doctor of Philosophy

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ABSTRACT

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QUANTIFYING THE MOVEMENT AND BEHAVIOUR OF MIGRATORY EUROPEAN EEL (*ANGUILLA ANGUILLA*) IN RELATION TO PHYSICAL AND HYDRODYNAMIC CONDITIONS ASSOCIATED WITH RIVERINE STRUCTURES

By Adam Timothy Piper

Anthropogenic structures such as dams, weirs, sluices, and hydropower facilities fragment river networks and restrict the movement of aquatic biota. The critically endangered European eel (*Anguilla anguilla*) migrates between marine and freshwater habitats and has undergone severe population decline. Barriers to migration are one of the negative impacts to be addressed for compliance with the EC Council Regulation for recovery of eel stocks. This thesis examines measures to reduce the effects of riverine structures on eel and improve passage facilities for both juvenile upstream and adult downstream migrating lifestages of this comparatively understudied species.

The influence of turbulent attraction flow on eels ascending passage facilities was quantified at an intertidal weir. Plunging flow resulted in a two-fold increase in the number of eels using a pass. The behavioural mechanisms underlying this attraction, and wider questions of how eels respond to elevated water velocity and turbulent conditions found at barriers and fish passes were further investigated within a field flume. Eels showed a similarly strong attraction to turbulent areas, though adopted an energy conservation strategy by adjusting swim path to reduce the magnitude of velocity and turbulence encountered. Compensatory swimming speed was also used to reduce exposure to energetically expensive environments. Management recommendations are made to optimise the attraction of eels to pass facilities, yet ensure hydrodynamic conditions within the pass do not deter ascent.

Legislative drivers also stipulate targets for seaward escapement of adult spawner stock. The impacts of multiple low head barriers and water abstraction intakes on route choice, delay, entrainment and escapement were quantified in a heavily regulated sub-catchment using telemetry. Entrainment loss at a single abstraction point was the biggest cause of reduced escapement, and was influenced by pumping regimes and management of intertidal structures. Delays at some structures were substantial (up to 68.5days), and reflected water management practices and environmental conditions. Sub-metre positioning telemetry allowed detailed behaviour of adult eel to be further quantified in relation to physical and hydrodynamic features at a hydropower intake. There was predominance of milling and thigmotactic behaviours at lower velocities (0.15 – 0.71 m s^{-1}), whereas rejection occurred on encountering the higher water velocities and abrupt velocity gradients associated with flow constriction near the intake entrance.

Information presented has implications for wider catchment management and highlights the potential to reduce barrier impacts through manipulation of structures and abstraction regimes. Quantifying eel behaviour in response to physical and hydrodynamic environments will aid the development of attraction, guidance and passage technologies.

Keywords: fluvial connectivity; fishpass; behavioural guidance; attraction flow; fish telemetry

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Declaration of Authorship

I, Adam Timothy Piper, declare that the thesis entitled:

Quantifying the movement and behaviour of migratory European eel (*Anguilla anguilla*) in relation to physical and hydrodynamic conditions associated with riverine structures.

and the work presented in the thesis are both my own, and have been generated by me as the result of my own original research. I confirm that:

- this work was done wholly or mainly while in candidature for a research degree at this University;
- where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
- where I have consulted the published work of others, this is always clearly attributed;
- where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
- I have acknowledged all main sources of help;
- where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
- parts of this work have been published as:

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Glossary

Abiotic: Non-living components of the environment.

Accelerating velocity: The rate of increase in velocity over a defined distance (with particular reference to water velocity within this thesis)

Acclimation: The adjustment of an organism to altered environment.

Anadromous: lifecycle in which most feeding and growth occur in marine environments followed by migration of adults into freshwater to reproduce

Anguilliform locomotion: a sinusoidal swimming motioning using the entire body length utilised by eel-like fish.

Anthropogenic: Relates to a human driven/derived impact.

Benthic: lowest section within the water column; benthic organisms are associated with or inhabit the bottom substrate within a water body such as a lake or river.

Bernoulli's Principle: The total energy (H) at a given point in a fluid is the energy associated with the movement of the fluid (kinetic energy), plus energy from pressure in the fluid, plus energy from the height of the fluid. This is most simply described by the equation:

$$H = z + \frac{p}{\rho g} + \frac{v^2}{2g}$$

where, z = elevation above an arbitrary datum, p = pressure at the point, ρ = density of the fluid, v = fluid velocity, g = acceleration due to gravity.

Biotic: Biological or living components of an environment.

Blade strike: When a fish is struck by a rotating propeller/impeller.

Boundary layer: The thin layer of fluid in the immediate vicinity of a solid surface where the effects of viscosity are significant and fluid molecules closest to the solid are therefore stationary.

Bypass: An alternate route for fish to move downstream when main river flow is passing via a deleterious route such a hydropower facility or pumping station.

Catadromous: lifecycle in which most feeding and growth occur in freshwater environments followed by migration of adults to sea to reproduce

Cavitation: The rapid formation and collapse of low-pressure bubbles in liquids by means of mechanical forces.

Chaotic flow: Flow with properties that are neither constant in time nor presenting any regular periodicity. Fluid turbulence is generally chaotic.

Continuity of Flow: A principle describing the conservation of mass in a fluid system. For example, as water passes through a channel that varies in cross-section between points 1 and 2, the volumetric flow rate (Q) may be calculated as:

$$Q = A_1V_1 = A_2V_2$$

where A is cross-sectional area of flow, and V is the mean flow velocity.

Diadromous: migration occurring between freshwater and marine environments.

Discharge: See flow

Entrainment: fish passage through a physical screen, intake structure, hydropower or pumping facility, typically non-volitionally.

Escapement: Within the context of this thesis is defined as passage from freshwater to marine environments of adult seaward migrating eel for the purpose of reproduction.

Fishpass: A structure designed to facilitate the movement of fish past a natural or anthropogenic barrier or obstruction, usually within lotic systems, by conveying flow over a head drop, typically through a series of weirs, orifices or baffles.

Fish passage facility: See fishpass, though can encompass any device that facilitates fish passage past a barrier.

Fishway: See fishpass

Flow: The rate at which a volume of water moves per unit of time, commonly measured in units of m^3 s^{-1} or L s^{-1}. River flow (Q) is calculated in its simplest form as Q = water velocity x cross-sectional area of wetted river channel.

Forebay: The widening of a natural river channel directly upstream of an impoundment.

Habitat connectivity: A measure of the size, distribution and interaction between habitat patches.

Habitat fragmentation: The natural or anthropogenic subdivision of habitat of a similar type.

Habituation: A decrease in an elicited behaviour as a result of repeated exposure to a stimuli.

Head: The potential energy of an incompressible fluid (e.g. water) due to its height above an arbitrary datum and its pressure (see Bernoulli's Principle).

Hydraulics: The study of the movement and characteristics of fluids in pipes and channels.

Hydrodynamics: The study of liquids in motion.

Impingement: The non-volitional entrapment of a fish against a structure.

Kinetic energy: The energy possessed by a moving body. It is described by the equation: $kinetic\ energy = \frac{1}{2}mv^2$, where m is mass of the body and v is its velocity.

Laminar flow: Streamline flow of a fluid in which the fluid moves in layers without fluctuations or turbulence so that successive particles passing the same point have the same velocity. It occurs at low Reynolds numbers ($Re<500$ in open channels) where viscous forces are dominant, and is characterised by smooth, constant fluid motion.

Lotic: Flowing water environments

Milling: Within the context of this thesis is defined as a behaviour during which a fish makes repeated, multidirectional movements within the same area, apparently searching or foraging.

Potadromous: Lifecycle which involves considerable migration exclusively within freshwater systems, typically to access spawning, residential and feeding habitats.

Potential energy: The latent energy an object possesses due to its position or configuration. For example, the potential energy (see head) held by water upstream of a barrier due to its position (height) within the gravitational field. It is described by the equation: $potential\ energy = Mgz$, where M is mass of the body, g is the acceleration due to gravity and z is elevation of the body above an arbitrary datum.

Recurrence: within the context of this thesis, is defined as a behaviour during which a fish leaves and subsequently revisits a specific area.

Rejection behaviour: A behaviour during which a fish abruptly switches from positive to negative, or from negative to positive, rheotaxis, in response to a stimulus.

Reynolds number (Re): A dimensionless number that gives a measure of the ratio of inertial forces to viscous forces and consequently is used in fluid dynamics to quantify the relative importance of these two types of forces for given flow conditions. It is the ratio $\rho VD/\mu$, where ρ is the fluid density, V is the flow velocity, D is the characteristic linear dimension such as the depth of water in an open channel, and μ is the dynamic viscosity.

Rheotaxis: The behavioural orientation of an organism to water current

Smolt: The juvenile life-stage of an anadromous salmonid that has undergone physiological adaptation for saline environments.

Thigmotatic: Directed response of an organism to maintain physical contact with a solid structure.

Tortuosity: A measure of the departure of an animal movement path from straightness i.e. degree of sinuosity

Trashrack: A structure typically consisting of a panel of vertical bars placed over the entrance of hydropower and pumping station intakes to prevent the ingress of large material such as woody plant matter.

Turbulence: A flow pattern characterised by chaotic and stochastic property changes. Within this thesis, turbulence is primarily considered in terms of velocity variation, and is measured as a time-averaged fluctuation in velocity magnitude around a mean. For flowing water in open channels, turbulent flow occurs where Re > 2000.

Turbulent Kinetic Energy (TKE): TKE is a measure of the kinetic energy of velocity fluctuations, i.e. greater fluctuation from the mean velocity represents greater TKE. In this thesis TKE (J m^{-3}) was calculated as:

$$TKE = 0.5\rho(\sigma_u^2 + \sigma_v^2 + \sigma_w^2)$$

where ρ is water density (1000 kg m^{-3}) and σ_u , σ_v and σ_w are standard deviations of the longitudinal, lateral and vertical velocities.

Velocity gradient: The difference in velocity over a distance, i.e. v/x, where *v* is the velocity difference and *x* is the distance.

Water Velocity: The speed that water flows over a set distance for a period of time, commonly measured in cm s^{-1} or m s^{-1}

Chapter 1 Introduction

This research is concerned with quantifying the effect of key physical and hydrodynamic parameters on the behaviour, movement and swim capabilities of European eel. Gaining a better understanding of these relationships is important to develop effective management practices and mitigation technologies to facilitate eel migration through anthropogenically modified river systems. The negative impact of structures that delay or prevent eel migration within and between freshwater and marine environments is widely recognised. The direct damage and mortality caused when fish make physical contact with fixed and moving components of water control structures, screens, pumps and hydropower turbines has further potential to significantly reduce populations. Despite efforts to prevent these deleterious impacts and facilitate free passage at barriers, it is generally acknowledged that there remains a need to develop more effective methods to conserve this critically endangered species.

This thesis is composed of 9 chapters. The background and scope of this work will be provided in chapter 1, concluding with the broad study aims. In chapter 2, the trends, biases and knowledge gaps of current literature surrounding mitigation strategies for anthropogenic barriers to European eel migration are identified. This review was used to inform the specific study aims and objectives, outlined in chapter 3. Chapter 4 describes the main methodologies employed within investigations conducted to address the specific study aims, and discusses the principle benefits and limitations of each. Though the chapters of this thesis are intrinsically linked, the data chapters which follow (Chapters 5 – 8) are presented as standalone manuscripts. Chapters 5 and 6 use field and flume-based approaches, respectively, to quantify the influence of plunging and streaming attraction flow on the movement and behaviour of upstream migrating eel. The field-based studies presented in chapters 7 and 8 address the effect of key physical and hydrodynamic parameters associated with river infrastructure on downstream migrating adult eel. To conclude the thesis, a summary of the main findings are presented within the context of current knowledge, and their application for barrier mitigation discussed, along with future research opportunities (chapter 9).

1.1 Fragmentation of river systems

Fluvial ecosystems have been impacted globally by the construction of in-channel infrastructure such as sluices, weirs and dams for flood defence, abstraction for consumptive water, hydropower generation and navigation (Jungwirth, 1998; Nilsson *et al.*, 2005). Over 58% of the world's largest river systems have been dammed, and in Europe 74% of total river basin area is considered strongly impacted (Nilsson *et al.*, 2005). Structures reduce longitudinal, lateral and vertical fluvial connectivity, with consequences including disrupted flow regimes, changes to water chemistry, and altered geomorphology (Ward & Stanford, 1995; Poff *et al.*, 1997; Opperman *et al.*, 2010).

The impact of cross-channel structures on fish communities can be considerable. Obstructions hinder movement between the habitats required for different ontogenic stages (Werner & Gilliam, 1984; Northcote, 1998; Lucas & Baras, 2001), which has been directly linked to loss of populations and occasionally extirpation of species (Nilsson *et al.*, 2005). Fish accumulating at barriers are more vulnerable to harvest, predation and disease (Matthews *et al.*, 2001; Larinier & Travade, 2002; Briand *et al.*, 2003a; Garcia De Leaniz, 2008; Castro-Santos *et al.*, 2009); and may incur additional energetic costs (Nestler *et al.*, 2008a), particularly as fish display milling behaviour when delayed up- and downstream of barriers (Haro & Castro-Santos, 2000; Mueller *et al.*, 2008; Brown *et al.*, 2009). This loss of energy, and potentially body condition, will likely have the greatest impact on non-feeding migrants such as adult anadromous salmonids and catadromous eel. The impacts of smaller low-head features such as weirs, ramps, culverts and road bridges on fish populations are rarely considered by catchment managers although they comprise the majority of anthropogenic barriers. Such barriers are 2 to 4 orders of magnitude more numerous than large structures (>10 m head drop) (Lucas *et al.*, 2009), and may therefore have a greater influence on fish population dynamics (Katopodis, 2005; Roni *et al.*, 2008).

1.2 Decline of the European Eel

The European eel, *Anguilla anguilla* (Linnaeus, 1758) occurs in estuarine and inland waters throughout Europe with a range that extends from Iceland to the coasts of Morocco. This ecologically, culturally and commercially important species (Feunteun, 2002; Starkie, 2003) has decined markedly with estimated recruitment reduced in some catchments by 90 - 95% since the early 1980s (Moriarty, 2000; Dekker, 2003). As a result, in 2006 the European eel was designated as ‘critically endangered’ and the stock considered outside safe biological limits (ICES, 2006; Darwall *et al.*, 2009). Other anguillid species have experienced similar declines: American eel (*Anguilla rostrata*) (Haro *et al.*, 2000), Japanese eel (*Anguilla japonica*) (Han *et al.*, 2008), short-fin eel (*Anguilla australis)* (Glova *et al.*, 2001) and long-fin eel (*Anguilla dieffenbachia*) (Jellyman *et al.*, 2002). Exact causes of the decline of the European eel remain unclear, although suggested pressures include the swim-bladder parasite *Anguillicoloides crassus* (Kirk, 2003; Palstra *et al.*, 2007); bioaccumulation of PCBs and heavy metals (Palstra *et al.*, 2006); climate change and long-term shifts in oceanic currents including the North Atlantic Oscillation and the Gulf stream (Knights, 2003; Kettle *et al.*, 2008), and overfishing (Briand *et al.*, 2003a; ICES, 2006). The impact of anthropogenic barriers to migration and subsequent reduction in availability of accessible habitat has been identified as a contributory factor in local declines and the overall decline of the wider panmictic population (Moriarty & Dekker, 1997; White & Knights, 1997; Feunteun *et al.*, 2003).

1.2.1 Lifecycle of the European eel

The complex, highly variable and poorly understood life history traits of the European eel have exacerbated difficulties in identifying clear causes of the species decline. The European eel has a catadromous lifecycle whereby most feeding and growth occur in freshwater, after which fully grown adults migrate to sea to reproduce. Larval pre-leptocephali hatch at spawning grounds thought to be in the Sargasso sea, quickly developing into leptocephali which are carried for between 10 months to over 2 years on oceanic currents to the continental shelf

(Schmidt, 1923; Bonhommeau *et al.*, 2009) where they metamorphose into transparent glass eels. This lifestage moves up tidal estuaries and into rivers becoming pigmented glass eels, and then the larger ‘elvers’, before becoming yellow eels. This is the main growth phase which in freshwaters last 4 to 20 years (females) and 2 to 15 years (males) (Aprahamian, 1988; Tesch, 2003). At the end of the growth phase eels undergo a further metamorphosis (silvering). A number of reproductive and osmoregulatory changes occur in preparation for migration to the spawning grounds where the adults reproduce and are presumed to die (van den Thillart *et al.*, 2009) (Fig. 1.1).

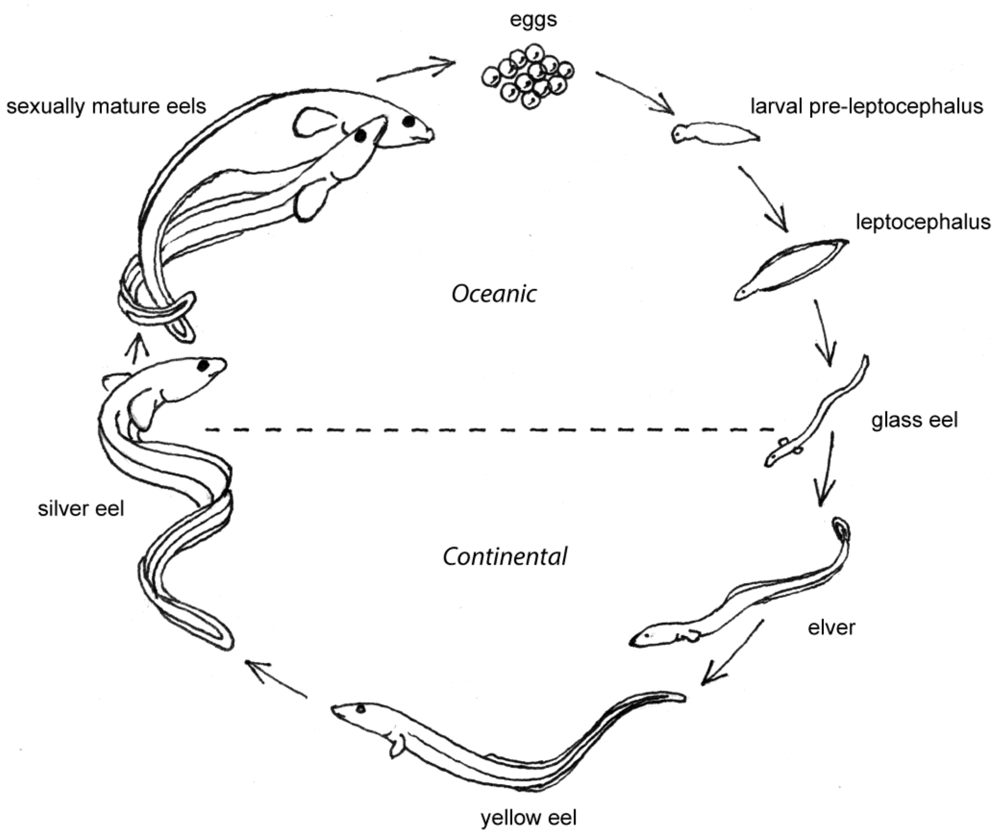


Figure 1.1 Lifecycle of the European eel (*Anguilla anguilla*)

1.2.2. Protection and Legislation

In response to the population decline, the European Union adopted Council Regulation 1100/2007/EC in 2007, establishing measures for the recovery of the stock of European eel. This legislation requires each member state to produce Eel Management Plans (EMP’s) outlining actions to achieve escapement to the sea of at least 40% of the silver eel biomass, relative to the best estimate of escapement prior to anthropogenic impact. Many member state’s EMPs highlight mitigation for the effects of riverine barriers by improving upstream and downstream passage as key means of achieving escapement targets (e.g. U.K., Denmark, Greece).

In the UK, The Eels (England and Wales) Regulations 2009 Statutory Instrument came into force on 15th January 2010 for implementation of the EC council regulation. This requires owners of any structure capable of abstracting greater than 20 m^3 per day, or returning water to a river channel or the sea, to fit a suitable screen or equivalent eel exclusion measure, for all vulnerable lifestages at that location. This regulation also gives powers to insist appropriate passage be provided for eels at any structure where free passage is considered to be impeded. The UK EMPS were published in 2009 and the first progress report, three years on, indicates that 9 of the 11 River Basin Districts in England and Wales are failing to achieve the 40 % escapement target. The report highlights the need to reduce the impacts of tidal flaps, water supply intakes, barriers to migration and poor wetland habitats (Defra, 2012).

Additionally, the European Water Framework Directive (WFD) (2000/ 60/EC) requires that water bodies meet good ecological status, of which unobstructed passage for fish is a key component (Moss, 2004). The presence of eel, where expected, also contributes to fisheries classifications for assessing ecological status (APEM, 2012).

In 2007, the European eel was provided additional protection under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Appendix II (Annex B of Reg. (EC) 338/97). This requires that European member states exporting eels hold an export permit, which is only issued if the export is obtained legally and will not be detrimental to the survival of the species.

1.3 Impacts of anthropogenic structures on eel

Within Europe, it is estimated that of the 123 800 km^2 of potential eel habitat, 33%, is inaccessible due to man-made barriers (Moriarty & Dekker, 1997). Obstructions have been attributed as the cause of decreases, or even extinctions, of local populations in Europe (Legault & Porcher, 1990; Moriarty & Dekker, 1997; Feunteun, 2002). In the UK alone there are over 26 000 potential anthropogenic barriers to fish migration, approximately 500 of which are considered to severely restrict free passage (Environment Agency, 2011a). Structures such as dams weirs, and sluices may present a restriction to free fish migration in a number of ways. Structures may physically prevent fish passing by creating a height difference, thus a physical step, between water levels above and below the barrier that may exceed a fish's leaping capabilities. Steps as little as a few cm can prove impassable to upstream migrating eel, which unlike salmonid species, are unable to leap (Porcher, 1995) (Fig. 1.2). Additionally, by restricting free flow, structures convert the kinetic energy of flowing water to potential energy or 'head' due to both the water being held at greater elevation upstream than downstream of the impoundment, and increased water pressure. When water spills either over, under or through the structure, this potential energy is converted back to kinetic energy; as described by Bernoulli's principle (Vogel, 1994). Further, due to the principle of Continuity of Flow, as the cross sectional area of flow is reduced compared to that upstream of the structure, this results in increased water velocity at and directly downstream of the structure (Vogel, 1994) (Fig. 1.3). The velocities created within the tailwater at structures may therefore exceed the swimming capabilities of fish and render structures impassable under certain flow conditions.

Figure 1.2 A broadcrest weir with a large height difference or ‘step’ between upstream and downstream water levels.

Figure 1.3 Flow constricted at an undershot sluice creates high water velocity downstream of the structure.

A diadromous lifecycle requires double passage past structures, yet unlike the anadromous migration of salmonids which move upstream as adults, eels must ascend often significant head drops and high flow velocities as relatively weak-swimming juveniles. The challenges posed by anthropogenic structures are fundamentally different for juvenile and adult lifestages, and require separate consideration.

Structures such as sluices, weirs, flood gates and tidal flaps are commonly installed below the natural point of tidal influence to enable land drainage for agriculture, retain freshwater for abstraction, and protect conurbations from fluvial and tidal flooding. However, such intertidal barriers can severely limit eel recruitment, a crucial bottleneck in many populations (White & Knights, 1997; Feunteun *et al.*, 1998; Bult & Dekker, 2007). Foreshortening estuaries both limits the distance glass eels are able to move upstream using tidal transport (Briand *et al.*, 2003a; Bult & Dekker, 2007; Laffaille *et al.*, 2007), and restricts freshwater flow into the intertidal zone. Glass eel orientation and navigation are strongly influenced by salinity gradients, olfactory cues (Tosi *et al.*, 1990; Crivelli *et al.*, 2008), and the strength and direction of currents (Feunteun *et al.*, 2003); all produced as freshwater flows into estuaries. In obstructed systems, water velocities may be inadequate to stimulate the positive rheotactic behaviour required to progress upstream (Gascuel, 1986).

The accumulation of immigrants below barriers may incur density dependant mortality as a consequence of limited habitat and food resources, reduced water quality and increased prevalence of disease (Vollestad & Jonsson, 1988; Lucas & Baras, 2001; Costa *et al.*, 2008). Furthermore, disease and high densities both increase vulnerability to predation by piscivorous fish and avian predators (Peake *et al.*, 1997; Matthews *et al.*, 2001). Commercial fishing conducted downstream of barriers, even with relatively low effort, can significantly reduce total catchment recruitment (Briand *et al.*, 2003a; Briand *et al.*, 2003b; Beaulaton & Briand, 2007).

Sex determination in eel is believed to be strongly influenced by population density, whereby high densities result in a greater proportion of males (Roncarati *et al.*, 1997); though the underlying mechanisms are unclear (Côté *et al.*, 2009). In unobstructed systems population density decreases with distance from the sea, hence the sex ratio is typically male dominated in the lower reaches, countered by a higher proportion of females in the upper reaches (Feunteun *et al.*, 2003). In obstructed systems, the high densities found downstream of barriers may result in more males, skewing the overall sex ratio with potential population level consequences (Roncarati *et al.*, 1997; Tesch, 2003; Costa *et al.*, 2008).

The impact of water abstraction facilities on upstream migrating eels remains unclear. Immigrants are unlikely to be attracted to water abstraction points by hydrodynamic cues, principally because the direction of flow is contrary to that which elicits the positive rheotactic behaviour governing upstream movement. Nevertheless, the relatively weak swimming capabilities of juvenile lifestages may result in non-volitional entrainment at these facilities (Environment Agency, 2011b). Perhaps of greater concern are water discharge points, the flow of which may attract individuals away from natural channels and into harmful locations such as fish farms, waste water treatment works, and power stations (Turnpenny & O'Keefe, 2005).

For the adult downstream migrating lifestage, structures such as large dams may permanently prevent escapement from freshwater systems into the sea (Acou *et al.*, 2008), though a more common impact is migratory delay (Behrmann-Godel & Eckmann, 2003; Durif *et al.*, 2005). When delay persists beyond the migration window, sexually maturing individuals may revert to pre-maturation yellow eel phase until conditions allow passage (Durif *et al.*, 2003). As with juveniles, delay of adults at structures exacerbates predation and disease pressures (Lucas & Baras, 2001; Larinier & Travade, 2002), and increases susceptibility to fishing (Bruijs & Durif, 2009). Indeed, water control structures are frequently employed to divert flow and downstream migrants through capture facilities (Calles *et al.*, 2010; Brown, 2011).

The recurrent and exploratory behaviour exhibited by silver eels delayed upstream of structures (Haro & Castro-Santos, 2000; Behrmann-Godel & Eckmann, 2003; Brown *et al.*, 2009; Travade *et al.*, 2010), is presumed to incur greater energetic cost than direct passage (Acou *et al.*, 2008; Castro-Santos *et al.*, 2009; Calles *et al.*, 2010). As eels desist from feeding during the silvering process, it is likely that the long-term viability of spawners is impaired through depletion of finite energy reserves required for successful oocyte production and an oceanic migration of 5000-6000 km; though the energetic consequences of delayed migration have not yet been quantified. Finally, in heavily obstructed systems, the environmental cues that stimulate downstream migration may be disrupted. Whether due to the loss of natural cues or accumulative delay, migration in heavily obstructed systems is less associated with strong peaks of movement (Haro *et al.*, 2003), and is more likely to extend into the spring (Feunteun *et al.*, 2000; Acou *et al.*, 2008).

Silver eel typically migrate downstream following the principle route of flow (Jansen *et al.*, 2007) which frequently brings them into contact with intake screens, pumps and turbines. Their elongated morphology and relatively poor burst swimming capabilities makes them susceptible to entrainment at such facilities (Calles *et al.*, 2010). Direct contact with rotating turbines or pumps, shear stress, cavitation and pressure differences may all induce mortality (Turnpenny *et al.*, 1998; Bruijs & Durif, 2009). A study which assessed fish damage and mortality at 14 water pumping stations in the Netherlands, a country with over 4600 such facilities, demonstrated that of the 91 tonnes of fish damaged or killed annually, approximately one third were eels (Kunst *et al.*, 2008). Typical hydropower mortality rate has been estimated at between 15 and 38% per turbine encountered (Hadderingh & Bakker, 1998; ICES, 2007; Winter *et al.*, 2007), though may be as high 100% in some cases (Carr & Whoriskey, 2008). Impingement at screens and contact with hard structures in the tail water region also results in abrasion and damage which may be lethal or render the fish more susceptible to predation and disease (Bruijs & Durif, 2009).

1.4 Barrier mitigation

It is clear that anthropogenic structures have the potential to restrict or prevent access to habitat that may be important or essential for completion of the catadromous lifecycle of the European eel. In an attempt to restore fluvial connectivity and reverse the negative impacts of riverine structures on fish, complete barrier removal and large scale habitat restoration is frequently advocated (Graf, 2003; Kocovsky *et al.*, 2009), though not feasible in many situations (Doyle *et al.*, 2003). There are increasing demands on water for potable use, irrigation and power generation, hence new structures continue to be built and, additionally, many dilapidated existing structures are being restored for hydropower generation (Demirbas, 2007). Within Europe, the EC Renewables Directive 2009 (2009/28/EC) has defined the target that 20% of Europe’s gross energy consumption be derived from renewable sources, of which hydropower is projected to form the second largest source (10.5%), after wind power (14.1%) (European Renewable Energy Council, 2012). As the majority of viable large scale high head hydropower opportunities have already been exploited within Europe (Paish, 2002), recent targets have stimulated particularly rapid growth of low-head schemes. Conventional fish exclusion screening techniques, particularly when required to be fine enough to exclude juvenile life-stages, are considered economically unviable at many low head schemes due to associated loss of generation efficiency and cleaning regimes required to maintain screens free from blockage. In view of this, it is desirable to develop alternative strategies to ameliorate the negative impacts of barriers and restore fluvial connectivity for fish.

Provision of fish passage facilities is one of the principal strategies currently employed to restore migratory pathways for anadromous fish. A successful facility minimises both the time a fish takes to find or be diverted to the pass entrance, and the time taken to enter the pass. Furthermore, the physical and hydrodynamic conditions within the pass should encourage rapid passage of the fish through it, with minimal stress and energetic costs (Clay, 1995; Castro-Santos *et al.*, 2009). Many existing facilitates exclude or delay the passage of their target species, usually upstream migrating salmonids (Aarestrup *et al.*, 2009; Caudill & Peery, 2009), and demonstrate particularly poor efficiency for non-salmonid species (Bunt, 2001; Bunt *et al.,* 2001; Cooke *et al.,* 2005; Roscoe & Hinch, 2009; Noonan *et al.*, 2011). Salmonid species in general have a long held commercial and cultural importance, and as such have been the focus of fish passage research and development (Williams *et al.*, 2012). The European eel is comparatively understudied in this regard, despite its socio-economic importance. It is estimated that the number of commercial fishermen employed catching all lifestages is approximately 7750 throughout Europe which, combined with a considerable artisan fishery, landed approximately 4000 tonnes in 2011 (ICES, 2011). Though it is not possible to accurately estimate the total value of European eel fisheries (ICES, 2011a), it has been estimated as worth in excess of £8 million per annum in Britain alone (Anon, pers. comm).

The development of effective fish passage facilities depends on fundamental knowledge of swim capabilities, combined with an understanding of behavioural responses to environmental stimuli (Castro-Santos *et al.*, 2009; Kemp *et al.*, 2012; Williams *et al.*, 2012). Due to the salmocentric research legacy, much of this fundamental information is lacking for eel, though must be addressed if we are to restore fluvial connectivity for this critically endangered species, fulfil legislative requirements for unhindered passage for eel and other migratory freshwater fish, and concurrently meet increasing demands for consumptive water and power generation. A greater understanding of what structures constitute barriers for eel; how they behave in the vicinity of barriers, and their swim capabilities under the conditions synonymous with anthropogenic structures, including fish passes, are fundamental steps towards improving barrier mitigation measures for this species.

To address these knowledge gaps, this thesis will describe research conducted to meet two primary aims:

1) Assess the influence of physical and hydrodynamic parameters on eel movement and behaviour at riverine barriers and passage facilities

2) Aid the development of more effective upstream and downstream passage solutions for European eel

To meet these aims, an initial objective has been formulated:

1) Review current literature to highlight research trends and biases, and to identify knowledge gaps that may present opportunity to improve eel passage

Chapter 2 Literature review

2.1 Aims and Scope

The aim of this literature review is to synthesise knowledge on the current status of barrier mitigation strategies for eels; identify the key capabilities, sensory cues and behaviours important during passage at structures; and identify gaps in current knowledge which offer potential for improving passage facilities for this endangered species. It is comprised of two parts: a quantitative and a narrative review.

Systematic searches and quantitative review methods are increasingly used as a means to overcome the tendency for bias and lack of methodological transparency present in the standard "narrative review" which is commonly employed in ecology (Roberts *et al.*, 2006). Calls for the greater use of systematic review in ecology has led to the development of suitable review protocols (Pullin & Stewart, 2006). Further, this approach has been used in several recent reviews quantifying the impacts of barriers on fish passage and the success of mitigation methods (e.g. Roscoe & Hinch, 2009; Bunt *et al.*, 2012; Noonan *et al.*, 2012). Therefore, a systematic search and "vote-counting" approach was employed to quantify any methodological and species biases within the literature. It had 3 key objectives: 1) to identify current approaches to barrier mitigation for eel, 2) to determine how the success of mitigation strategies has been quantified, and 3) to identify the assessment methods used.

Further, a narrative review was employed to understand the key cues relevant to both upstream and downstream migrants around structures, and to identify gaps in knowledge surrounding current eel barrier mitigation strategies. A wide array of peer reviewed and grey literature was drawn on. Although this thesis is primarily concerned with European eel, literature concerning other anguillid species, for which findings are widely considered transferable (Tesch, 2003; Righton *et al.*, 2012), is included. Current barrier mitigation strategies for eel, and their deficiencies, are examined within the context of wider fish passage developments.

2.2 Barrier mitigation methods for eel- a quantitative review

2.2.1 Methods

The following search strings were used to retrieve literature from the bibliographic search engines Google Scholar and Web of Knowledge over the period August 18th – 20st 2010, and updated July 23rd to 24th 2012 to include studies published in the interim period:

eel OR elver OR anguill* AND

1) pass*; 2) ladder; 3) bypass; 4) fishway; 5) attraction; 6) guidance; 7) diversion

Pilot searches revealed that all relevant peer-reviewed studies were returned within the first 400 hits. When in excess of 400 articles were returned by a search string, only the first 400 were retained. All search hits were imported into a reference management program (Endnote X2, The Thomson Corporation, CA, USA) and duplicate articles removed. Titles were initially screened for relevance and only retained for review if they met re-defined criteria (Table 2.1). Due to similar life-history traits, and common impacts it was considered appropriate to consider literature covering all anguillid eels. For studies to be retained, the main focus must have been to assess a barrier mitigation method for eel, whether it be a physical structure e.g. fishway, or a behavioural guidance method e.g. sound or light. Positive exclusion mitigation methods (e.g. screens) and post-entrainment modifications (e.g. “fish friendly” turbine blade design) were excluded as volitional and behavioural mitigation methods (i.e. prior to physical contact or entrainment) were of principal interest for this review.

Table 2.1 Pre-defined selection criteria for literature to be retained for full review

Criterion	Priority within screening process
Reference made to anguillid eel either in title or abstract	1
Peer-reviewed literature	2
Full text attainable, with reasonable ease	3
Full text in English, unless detailed translation available	4
A key aim of the research was examining some aspect of a single or combination of mitigation measures for barrier(s) to migration	5
Not exclusively concerned with total exclusion methods (e.g. screens) or modification to facilities that reduce entrainment damage or mortality e.g. “fish friendly” turbines, blade spacing	6

Where papers dealt with both upstream and downstream lifestages, data and findings for each lifestage were extracted separately. After selection, the literature underwent full screening and information extracted to populate a database. The fields of enquiry included: lifestage(s); eel species; mitigation measure(s); type of study, e.g. laboratory or field; how the mitigation measure was quantified (quantification measure); and research methods applied.

Quantification measures included:

Presence/absence or count - whereby eels were either recorded using the applied mitigation approach, or were counted, with no measure of *passage efficiency.*

Passage efficiency - defined as having demonstrated a level of efficiency to pass a structure, i.e. passage rate in relation to available migrants, or fish attempting to pass; or provide a relative efficiency of marked groups; or relative efficiency between trials.

Attraction/guidance efficiency - studies within this group used the same efficiency metrics as described for *passage efficiency*, but specifically to assess some aspect of attraction or guidance.

Population recovery - measured population density before and after mitigation.

Behaviour (coarse) - measured behaviour at less than 1 m accuracy.

Behaviour (fine) - measured behaviour at greater than 1 m accuracy.

2.2.2 Results

A total of 914 studies were retrieved in the searches. Of the 94 studies that met the 6 selection criteria, 30% were primary research articles concerned with barrier mitigation strategies for upstream migrating eel, 38% for downstream migrants, and 12% addressed both upstream and downstream migrating lifestages. Studies covered 4 anguillid species: European eel (*A.anguilla*) (55%); long-fin eel (*A.dieffenbachii*) and/or short-fin eel (*A. australis*) (11%); and American eel (*A. rostrata*) (34%). Review articles, synthesising the findings of primary literature, comprised 20% of the total 94 and were not considered further. Studies dated from 1978 to 2012, with 74% published within the last 10 years.

A wide range of mitigation methods, which varied between upstream and downstream migrating lifestages, were addressed in the studies (Fig.2.1). Eel specific pass provision and adaptation were the predominant upstream mitigation measures (89%), most notably eel ladders. Only 2 upstream studies used methods that attempted to restore natural tidal ingress past intertidal structures, and 2 addressed mitigation through behavioural guidance. The focus of downstream mitigation methods was more evenly split between pass provision (40%) and assessing the potential of guidance devices (44%). The remaining studies predominantly addressed altered operation of hydropower facilities (e.g. non-generation) and weir spill; or methods to predict peaks in migrations for the purpose of scheduling altered operation (Fig.2.1).

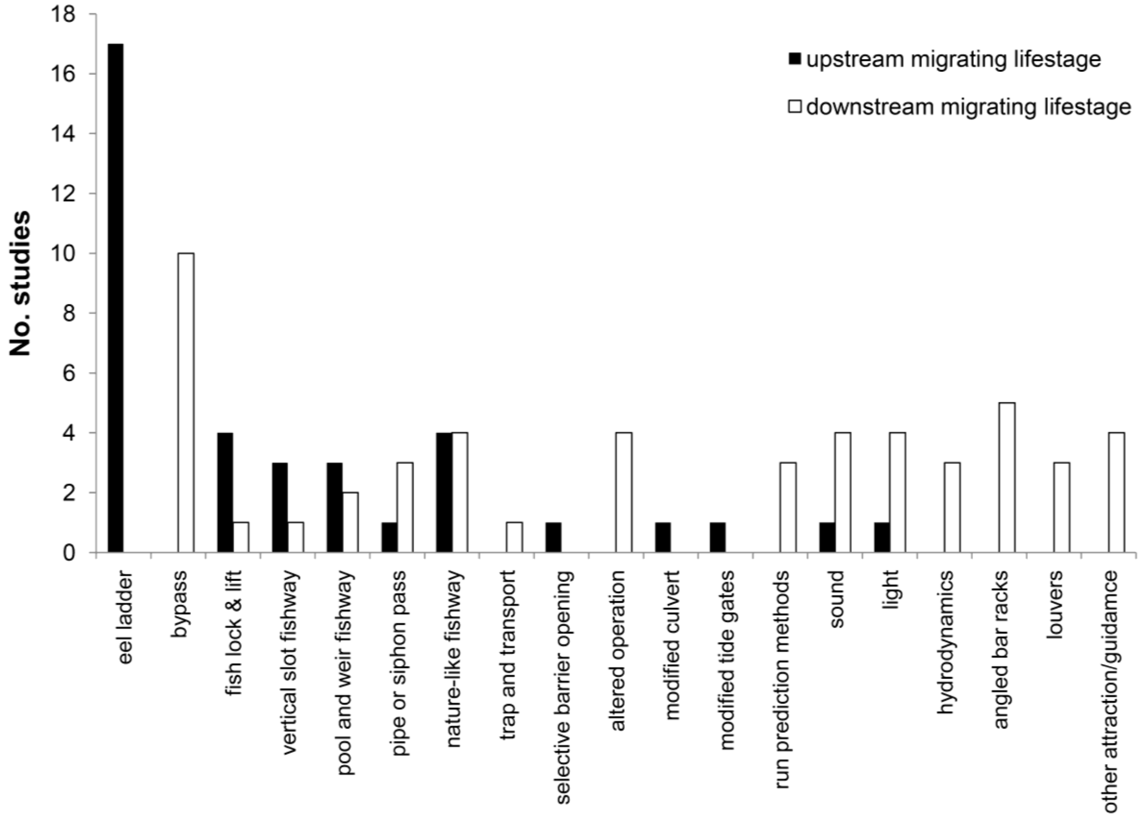


Figure 2.1 Number of primary research studies assessing various barrier mitigation strategies for upstream and downstream migrating lifestages of anguillid eels. Multiple mitigation strategies addressed within a single study are counted separately.

Presence/absence or count data were most common within upstream studies (56%), followed by the quantification of passage efficiency (36%) (Fig.2.2). Fewer upstream studies incorporated a behavioural component (15%), than downstream studies (28%), in which behaviour was quantified at either a coarse (26%), or fine (15%) scale. Attraction or guidance efficiency was rarely assessed in upstream compared to downstream studies, 8% and 51% respectively (Fig.2.2).

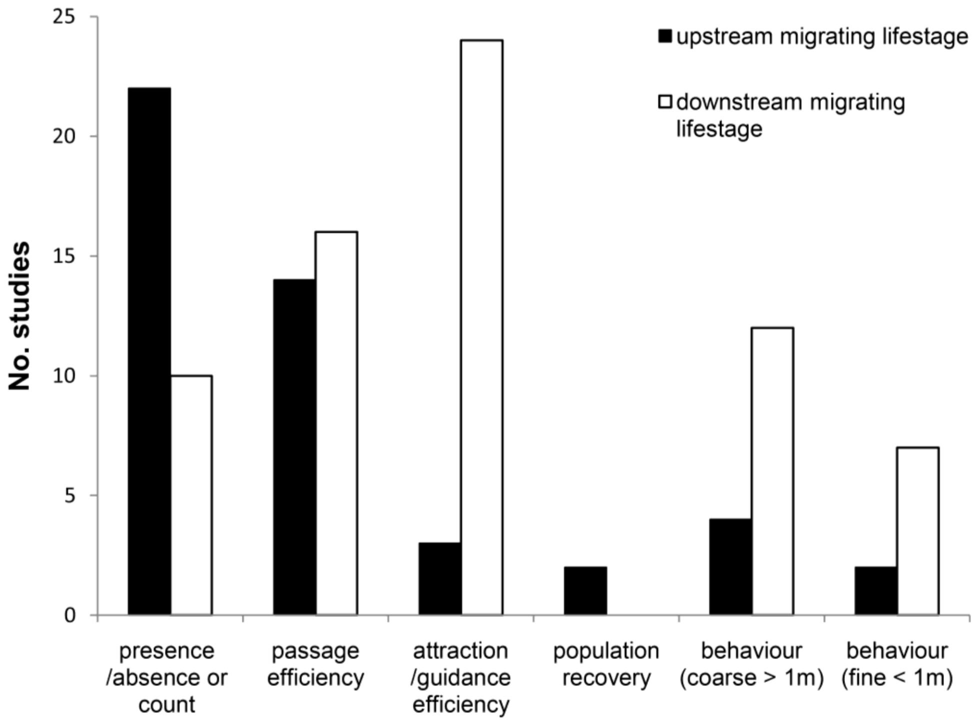


Figure 2.2 Approaches employed in primary research studies to quantify success of barrier mitigation strategies for upstream and downstream migrating lifestages of anguillid eels. Multiple approaches used within a single study are counted separately

Flume-based approaches were more commonly adopted to assess mitigation in downstream (17%) compared to upstream (5%) studies, though a field approach predominated across all studies. Capture methods, primarily trapping, were the most widely applied in the upstream studies (49 %), whereas telemetry methods predominated in downstream studies (49%) (Table 2.2).

Table 2.2 Assessment methods employed in primary research studies to quantify success of barrier mitigation strategies for upstream and downstream migrating lifestages of anguillid eels. Multiple methods used within a single study are counted separately

Method	**No. studies**	
	Upstream migrating lifestage	**Downstream migrating lifestage**
Flume	**2**	**8**
Capture data	0	2
Visual/video observation	2	6
Field	**37**	**39**
Capture data		
Trap	19	7
Netting	6	4
Electro-fishing	6	3
Telemetry		
PIT	2	8
Acoustic	0	7
Radio	0	8
Mark-recapture	3	2
Visual/video observation	5	2
Fish counter	2	0

2.2.3 Discussion

A quantitative examination of literature surrounding barrier mitigation strategies for eel revealed key research biases between lifestages. For upstream migrants, mitigation strategies focussed on the provision of fishways, whereas guidance measures were far more prominent within the literature on downstream passage. The research methods employed to quantify mitigation measures again varied markedly between the two migratory lifestages.

The species bias in research towards the European eel may reflect both the larger range of this species and greater economic value as a fishery, compared to the American and Australasian species. The mitigation strategies adopted, and methods used to assess them, varied greatly for up and downstream migrants, as might be expected for lifestages with such different physiological and behavioural characteristics.

There were large differences in the role of fishways, compared to physical/behavioural guidance, for the different lifestages. The success of upstream passage facilities has been described as principally reliant on attraction to and into the facility, along with swimming capability to pass it, primarily because migrants are moving against flow. In contrast, downstream migrants are moving with the direction of flow, so successful passage facilities often employ physical or behavioural, or combination techniques, to guide fish to benign routes such as bypasses (Katopodis & Williams, 2012; Kemp *et al.*, 2012; Williams *et al.*, 2012). This was clearly reflected in the findings with 89% of upstream studies addressing pass provision, and 44% of downstream studies addressing guidance.

Eel ladders dominated studies concerned with provision of upstream passage facilities. The installation of eel ladders is widespread across Europe and North America; in England and Wales alone, 265 passes have been installed at estuarine and riverine barriers (Andy Don, pers. comm.). Typically, eel passes comprise of a sloping channel (5˚- 45˚), furnished with mesh or bristle substrate to facilitate climbing, and supplied with water diverted from upstream, referred to as the conveyance flow (Knights & White, 1998; Porcher, 2002; Solomon & Beach, 2004). Estimates of passage efficacy were nearly a third less common than presence/absence or count data for mitigation assessment, which alludes to limitations for the transferability and wider application of findings. Due to the complexity and unpredictable temporal and spatial fluctuations that naturally occur in juvenile eel immigration, assessment of mitigation success through presence/absence or count data, irrespective to some relative measure of efficiency, offer limited and often site-specific knowledge. This deficiency was highlighted by Knights and White (1998), who in a UK-centric review of elver passage facilities criticised the lack of quantitative research into the efficiency of different systems. Quantitative or efficiency metrics are generally lacking in fish passage assessment throughout Europe (Roscoe & Hinch, 2009).

Intertidal barriers impose a primary constraint on juvenile recruitment into freshwater systems, yet only 2 studies addressed partially restoring natural cycles of tidal ingress as a means to facilitate passage of glass eels; one through selective opening of the barrier on high tides, and one through a novel siphon pass (Bult & Dekker, 2007; Mouton *et al.*, 2011). This likely reflects the undesirability for water managers of creating a saline gradient upstream of the barrier, which may limit abstraction opportunities (Mouton *et al.*, 2011). However, Mouton *et al.* (2011) demonstrated that selective barrier opening could be managed in such a way so as to provide cost-effective and efficient barrier mitigation. Minimal barrier opening on rising tides caused a low level of saltwater intrusion (on average 2.8 % of freshwater flow), though a greater than 200 fold increase in glass eel numbers reaching the lower freshwater reaches on each tide.

For downstream mitigation types there was an approximately even spilt between pass provision, primarily via bypasses, but also using vertical slot, pool-and- weir types and nature-like passes; and a range of guidance technologies including sound, light, and louvers. Quantification measures included much greater use of methods permitting behaviour to be assessed than upstream studies. This was evident in the greater use of flumes, which enable fine scale observation of movements (e.g. Adam & Schwevers, 1997; Russon *et al.*, 2010), and also certain telemetry techniques in field studies (e.g. Brown *et al.*, 2009). The size of downstream migrants means direct observation or use of telemetry is more viable than for relatively small upstream migrating eels.

The principle aim of this systematic review was to identify and quantify the methodological and species biases within the published literature relating to eels and barriers. It was beyond the scope of this review to quantify the influence of economic, social and legislative drivers which may give rise to such biases; however as the majority of studies (74%) were published within the last 10 years, it is likely that the increasing focus on conservation for anguillid eels and technological advancements are important influences. Since the 2003 Quebec declaration of concern on eel stocks (Dekker *et al.*, 2003), there is increasingly legislative protection for eels within Europe (e.g. EU Council Regulation 1100/2007/EC) and North America (e.g. Ontario's Endangered Species Act, 2008), which in turn generates both research interest and funding. Recent technological advancements, for example fish positioning telemetry, high definition sonar imaging and underwater filming techniques, have increased the resolution at which migration and behaviour may be observed, thereby enabling researchers to address questions pertaining specifically to eel behaviour at barriers and responses to potential guidance devices within natural environments.

2.3 General literature review: Fish passage research, wider context and future directions

2.3.1 Introduction to fish passage facilities

In recognition of the multiple negative impacts of riverine barriers on fish, there are increasing legislative requirements that fluvial connectivity be restored. To this end, complete barrier removal represents an appealing panacea and may present both an ecologically effective and cost efficient method (Garcia De Leaniz, 2008; Kemp & O'Hanley, 2010). Among the many ecological benefits of this approach (Bednarek, 2001), significant and rapid increases in fish abundances have been reported (Scully *et al.*, 1990; Roni *et al.*, 2002). There are however often social, historic and biological reasons that make complete barrier removal undesirable or unfeasible at many locations (Doyle *et al.*, 2000; Stanley & Doyle, 2003). Alternatively, partial restoration of fish migratory pathways is frequently attempted through the provision of passage facilities at the structure.

Our current legacy of historic fishway design is beset by poorly operating facilities; particularly for potadromous and catadromous fish (Bunt, 2001; Cooke *et al.*, 2005; Roscoe & Hinch, 2009). Recent reviews of fish passage efficiency have demonstrated that the majority of fishways do not effectively mitigate the effect of barriers that block access to areas upstream (Noonan *et al.*, 2011; Bunt *et al.*, 2012). The causes of poorly functioning fishways are not fully understood (Castro-Santos *et al.*, 2009), though suggested reasons include a lack of understanding of the cues that drive motivation, biological constraints, and lack of meaningful post-build evaluation (Kemp, 2012).

2.3.2 Development of fish passage facilities

Technical fish passage facilities likely existed in Europe from as early as the mid 17th century (Clay, 1995); with provision for socially and economically important salmonids the principal driver in both Europe and North America (Williams *et al.*, 2012). The historic focus of fish passage development has consequently tended towards designs targeted at anadromous salmonids, in particular the upstream migrating lifestages which were perceived to be most impacted by barriers (Kemp *et al.*, 2008a; Larinier, 2008; Katopodis & Williams, 2012). Consequently, non-salmonid species and downstream migrating juvenile salmonids have been relatively neglected (Calles & Greenberg, 2005; Roscoe & Hinch, 2009).

It has long been recognised that information about swimming performance, energetics and biomechanics provide important baseline information for fishway design (Brett, 1964; Haro *et al.*, 2004; Liao, 2007; Castro-Santos *et al.*, 2009; Tritico, 2009). Fishways have improved incrementally through the last century, largely through the evolution of designs based on swimming capabilities combined with a 'build-and- try' approach (Anderson, 1988; Katopodis & Williams, 2012). Though more recent recognition of the failings of accepted designs, even for the target species, has instigated a change of focus from site-specific solutions to transferable designs that draw on a growing understanding of how fish behave in their hydrodynamic environment, combined with physical capabilities (Lucas *et al.*, 1999; Nestler *et al.*, 2008a; Castro-Santos *et al.*, 2009; Roscoe & Hinch, 2009).

2.3.3 Improving fish passage facilities

The theoretical optimum for any fish passage facility is to allow unhindered passage up and downstream for all lifestages of all fish species, and impose no physiological or biological costs (Castro-Santos *et al.*, 2009; Roscoe & Hinch, 2009). The three key components of successful passage facilities are first, attraction and/or guidance to the entrance of, and into, the facility; second, passage through the facility; while third, minimising delay, stress, injury and energetic cost (Clay, 1995; Lucas & Baras, 2001; Castro-Santos *et al.*, 2009; Williams *et al.*, 2012). Lack of attraction to pass facilities, perhaps due to poor positioning of the pass entrance or insufficient attraction flow, for example at low velocity nature-like passes, has been highlighted as a principal cause of poor passage efficiency (Moser *et al.*, 2000; Larinier, 2002a; Sprankle, 2005). Furthermore, the role of these and other elements in the attraction of migratory fish remains poorly understood (Castro-Santos *et al.*, 2009; Bunt *et al.*, 2012).

Once a fish has entered the pass, conditions should be such that the fish is physically able to rapidly ascend or descend; and is encouraged to do so by the physical and hydrodynamic characteristics within it. Furthermore, conditions should be compatible with the capabilities of the entire range of intended species and individuals, including both up and downstream lifestages, and not just the athletes (Clay, 1995; Larinier, 2002b; Castro-Santos *et al.*, 2009). Improvement in the design of passage facilities is therefore dependent on first, quantification of swimming performance to determine the pass velocities and other hydrodynamic parameters that fish are physically able to negotiate; and second, understanding of the fine-scale behavioural responses of target fish species and lifestages to the multiple environmental stimuli encountered at structures, so conditions around and within the pass can be optimised to encourage efficient attraction/guidance and passage (Kemp *et al.*, 2012).

2.3.4. Swimming capabilities

Knowledge of fish swimming capabilities has been fundamental to the development of passage facilities (Anderson, 1988). Early work focused on determining swimming thresholds and energetic costs at different velocity ranges under highly artificial test environments created within swim chambers and respirometers (e.g. Bainbridge & Brown, 1958; Beamish, 1966). Tests were conducted under forced rather than volitional swimming (e.g. Brett, 1964), with space restrictions within these facilities shown to exclude some swim behaviours, thereby potentially skewing measured capabilities of the test subjects (Peake, 2004; Tudorache *et al.*, 2007). For example, Peake (2004) showed that smallmouth bass *Micropterus dolomieu* were able to attain maximum critical swim speeds 22% higher in open channel flumes, compared to their counterparts subjected to forced swimming in a respirometers; this was principally due to adopting a burst and glide swimming gait, only possible within the space provided within the large flume facility. Flow characteristics within swim chambers are also unrealistically uniform, thereby lacking the heterogeneity that fish would experience in natural environments, which invariably contain turbulent elements. Enders *et al.* (2003) highlighted the effect of introducing hydraulic heterogeneity through turbulence, demonstrating a 1.9 to 4.2 fold greater overall swimming cost to fish swum in turbulent flows compared to the calculated costs in uniform flows.

Similarly, maximum burst swimming capability (< 20 seconds prior to fatigue (Beamish 1978)) for adult European eel (≥ 450 mm TL) was found to be 1 to 1.5 m s $^{-1}$ based on swim chamber work, (Clough *et al.*, 2002); lower than recent work in an open channel flume which showed eels volitionally burst swimming against velocities of 1.75 m s $^{-1}$ (Russon & Kemp, 2011a).

The catadromous life history of eel means their upstream migration is undertaken as juveniles and sub-adults. Actively upstream migrating lifestages may range in length from 60 to 300 mm, with typical burst swimming capabilities of 0.41 to 1.5 m s $^{-1}$ (Clough & Turnpenny, 2001; Clough *et al.*, 2004). The majority of existing fish passes have been designed to accommodate the swimming capabilities of upstream migrating adult salmonids, hence they often include physical and hydrodynamic features exceeding the capabilities of upstream migrating eel, such as steps greater than 30 cm height, and velocities of 2.5 to 3 m s^{-1} (Clay, 1995).

Numerous studies have also demonstrated the ability of elvers to climb up wetted, vertical surfaces including engineered materials such as the concrete commonly used to construct river infrastructure (Legault, 1988; Linton *et al.*, 2007; Imbert *et al.*, 2008). However, this is limited to fish below 10cm length (Legault, 1988), and only occurs above a temperature threshold of 12 to 14.5 ˚C, thus climbing ability cannot be relied on to negate requirements for passage facilities at engineered structures (Porcher, 2002). Eels exceeding 10 cm in length are able climb near-vertical surfaces if substrate is provided (Dahl, 1991; Knights & White, 1998), and this capability is exploited in the widely used ‘eel ladder’ passage facilities, though these more typically comprise slopes of 15 to 45° (Legault, 1992; Solomon & Beach, 2004).

2.3.5. Eel behavioural responses to stimuli and opportunities for fish passage design

The way in which fish respond to stimuli is determined by complex interactions between internal factors such as motivation, and fitness, which may vary with individual life history traits (Lucas & Baras, 2001), fish species (Schilt, 2007), ontogenic stage (Lucas & Baras, 2001), motivation (Colgan, 1993), behavioural bias (Kemp *et al.* 2012), prior experience, learning and habituation (Odling-Smee & Braithwaite, 2003); coupled with external factors, i.e. the strength and nature of abiotic (e.g. water velocity) and biotic (e.g. presence of conspecifics) stimuli, and their relative magnitudes in the dynamic hierarchy of detection (Montgomery *et al.*, 1995; Nestler *et al.*, 2001; Kemp *et al.*, 2012).

To understand the behavioural responses of migrating eel to the dominant cues and stimuli encountered in the vicinity of structures, it is necessary to first understand the principal cues driving migration, the period during which eels are most likely to encounter structures.

2.3.6 Cues to upstream migration

Glass eels move from the continental shelf towards estuaries using coastal currents and Selective Tidal Stream Transport (STST), in which eels rise in the water column on flood tides, then either actively swim against currents of the ebb tide, or exploit velocity refuges at the channel bottom and edges (Wippelhauser & McCleave, 1988; Bolliet *et al.*, 2007). Flow direction and olfaction form the principal navigational cues for juvenile immigration into estuaries and rivers (Deelder, 1954; Crivelli *et al.*, 2008). Detection of a freshwater trace in the estuary is not only crucial for orientation, but also for migratory drive (Sola, 1995;

Briand *et al.*, 2002; Huertas *et al.*, 2007). Unlike anadromous salmonids which use olfactory cues to return to their natal river (Stabell, 1984), the immigrant juveniles of the catadromous eel have no previous experience of continental waters and thus there is no evidence of ‘homing’ to a specific river or area. Rather, dispersal throughout their range is considered to be predominantly determined by ocean currents (Kettle *et al.* 2008).

Fully active upstream migration, without the use of tide, occurs after glass eels commence feeding and undergo further metamorphosis into the active swimming and climbing juvenile lifestage (broadly termed ‘elvers’) (Sorensen & Bianchini, 1986). Elvers may either become sedentary over a small home range or continue to make multiple upstream movements during spring and summer months to the end of their adult growing (yellow) life-phase (Feunteun *et al.*, 2003).

2.3.7 Cues to downstream migration

Downstream migration of silver eel typically occurs in short peaks between autumn to early spring (Haro, 2003; Tesch, 2003). These movements are induced by a number of environmental cues, which may vary between systems. Migration peaks are strongly associated with increased flow and reduced water temperatures (Vollestad *et al.*, 1986; Haro, 2003; Tesch, 2003; Gosset *et al.*, 2005). Precipitation and low atmospheric pressure also seem important predictors in some systems (Lowe, 1952; Deelder, 1954; Okamura *et al.*, 2002); particularly so in lentic situations such as lakes (Bruijs & Durif, 2009). Silver eels are strongly photophobic (Lowe, 1952; Durif *et al.*, 2003); hence most migratory activity occurs in the first 6 hours after dusk (Behrmann-Godel & Eckmann, 2003; Travade *et al.*, 2006; Calles *et al.*, 2010), and is positively associated with high turbidity and dark phases of the moon (Haraldstad *et al.*, 1985; Bruijs & Durif, 2009). No literature to date suggests that there is a social component within downstream migration, with the apparently unified movement peaks most likely triggered by a complex, and often river-specific, combination of environmental factors, rather than social triggers.

2.3.8 Response to sound

Fish detect acoustic signals via the octavolateralis system comprising the ear and lateral line, with detection of sound pressure enhanced by the swimbladder (Hawkins, 1981). Sound has a dualistic nature, with both a pressure component and a kinetic component (Sand *et al.*, 2001). Fish are unable to 'hear', i.e. detect the pressure component, of sounds below 20-30 Hz, but can detect the kinetic component of infrasound, i.e. the vibrating movement of water particles in the sound field (Fay & Popper, 1999). Eels, seem insensitive to ultrasound (Turnpenny *et al.*, 1993), but have displayed reaction to low frequency infrasound (<20 Hz) (Sand *et al.*, 2000). This avoidance of infrasound has been suggested as a possible means to deflect downstream migrating silver eels from harmful areas and to safer passage routes (Sand *et al.*, 2000). The efficiency of infrasound at deterring silver eels at structures such as hydropower or water abstraction intakes is undetermined, though preliminary work on adult American eel has suggested that it may be inefficient in high water velocities >2m s^{-1} (Damien Sonny, pers. comm.).

2.3.9 Response to Light

Light avoidance by yellow eel has been demonstrated in the laboratory (Hadderingh *et al.*, 1999) and eels tend to avoid artificially lit areas during migration (Cullen & McCarthy, 2000). Strobe lights are suggested as a potential guidance technology, for example, to deter eels at hydropower facilities (Richkus & Dixon, 2002). They have been shown effective at deflecting silver eel, with a 10 fold reduction in eels entering a pumping station in the presence of a strobe (Keeken *et al.*, 2011); though in a flume test no reaction was observed (Adam *et al.*, 1999). For upstream migrating eels, a strobe light barrier tested in the field was 65 - 92% effective as a deterrent (Patrick *et al.*, 1982).

2.3.10. Olfactory cues

Olfaction plays an important role in juvenile eel navigation and upstream migratory drive. Freshwater trace in the estuary provides one of several cues that indicate upstream direction (Miles, 1968; Sola, 1995; Briand *et al.*, 2002; Huertas *et al.*, 2007). Manipulation of olfactory cues shows some potential for increasing attraction of juveniles to passage facilities. Briand *et al.* (2002) reported that trap catches at an eel ladder were 1.4 times higher when water from the catch pot containing eels was directed onto the pass; although the study design did not control for the possible attraction effect of the altered hydrodynamic conditions created by the additional flow in the vicinity of the pass.

Olfaction also plays an important role in the foraging behaviour of sub-adult yellow eels; however in the non-feeding silver eel stage, olfaction is thought to have little impact on behaviour (Tesch, 2003).

2.3.11 Tactile cues

It is unclear how important tactile cues are for juvenile lifestages. Juveniles do show a tendency to orientate along the edges of structures, and to remain in close proximity to river banks during upstream migration (Tesch, 2003; Bleistine, 2012). A laboratory study reported that juvenile American eel commonly moved in close proximity to the flume edges and bed substrate (Barbin & Krueger, 1994). The degree to which this behaviour reflects the use of physical structures as an aid to orientation and navigation (Tesch, 2003), or preference for reduced water velocities created at the fluid-structure interface (Barbin & Krueger, 1994), is unclear.

Adult lifestages appear highly tactile. Both laboratory and field studies report a strong propensity among adult eels to search along structures such as screens, bar racks and louvers, and that they appear motivated to explore openings, sometimes forcing their way through bar spacing significantly less than head diameter (Environment Agency, 2011b). Angled bar racks and louvers have shown potential to deflect eel in laboratory studies (Amaral *et al.*, 2003; Russon *et al.*, 2010). Eels frequently responded only after contact with the structures; either resulting in avoidance (Adam *et al.*, 1999; Russon *et al.*, 2010), or rejection upstream (Adam *et al.*, 1999). Racks of relatively shallow angles to flow, typically 15 – 30 °, were most effective at eliciting downstream guidance (61 to 98 %) (Amaral *et al.*, 2003; Russon *et al.*, 2010). Amaral *et al.* (2003) found guidance efficiency was improved by the addition of a solid bottom overlay (30 cm height), inferring that eels followed along the solid structure. Few studies have quantified the efficiency of angled bar racks and louvers for guiding eels in the field. In a notable exception Calles & Bergdahl (2009), demonstrated that a bar rack with a 35 ° vertical slope and 18 mm bar spacing prevented >90 % of downstream migrating eel from entering a hydropower intake in Ätran River, Sweden. Individuals subsequently entered one of six entrances to a submerged collection facility.

2.3.12 Hydrodynamic cues

Many advances in fish pass design have been derived from understanding how fish react to hydrodynamic features; both the ones they avoid, and the ones they seek (Williams *et al.*, 2012). The field of ecohydraulics, a sub-discipline of ecohydrology (Hannah *et al.*, 2004), evolved from increasing recognition of the importance to merge the disciplines of ecology and hydraulic engineering, integrating hydraulic and biological tools to better analyse and predict ecological responses of aquatic biota to physiochemical change (Nestler *et al.*, 2008a). Within the context of fish passage improvement, ecohydraulics integrates biological and ecological knowledge with hydraulic knowledge and innovations to mitigate for the impacts of anthropogenic structures and restore aquatic ecosystems (Rice *et al.*, 2010; Katopodis, 2012).

Fish exist in a complex hydrodynamic environment. The mechanosensory system, centred around the lateral line and the inner ear (Braun & Coombs, 2000), enables detection of direction and strength of flow, whole body acceleration and spatial velocity gradients (Kalmijn, 1989; Montgomery *et al.*, 2000; Nestler *et al.*, 2000; Goodwin *et al.*, 2007). Inanimate and stationary objects create distortion in the flow field that can be detected through the lateral line (Montgomery *et al.*, 1995). Detection range is a function of lateral line length, with near-field detection restricted to approximately 1 to 2 body lengths (Coombs, 1999); hence larger fish are able to generate a better hydrodynamic map of the surrounding environment (Nestler *et al.*, 2001). Kalmijn (2000) suggests that variations in salient features of the flow field underlie aquatic animal movements; particularly so in the hydrodynamically ‘noisy’ environments around structures where hydrodynamic parameters are likely to form the principal behavioural cues (Nestler *et al.*, 2000; Goodwin *et al.*, 2007).

It has been proposed that hydraulic based navigation is a dominant factor guiding outmigration of juvenile salmonids (Nestler *et al.*, 2000). Salmonid behaviour and movement is influenced by a number of hydrodynamic factors including: turbulence (Liao, 2007, Tritico, 2009), and accelerating flow (Haro *et al.*, 1998; Kemp *et al.*, 2008a; Enders *et al.*, 2009a; Vowles & Kemp, 2012). Studies that examine eel behaviour in response to the aforementioned hydrodynamic components are severely lacking, with one notable exception. In a study investigating the efficacy of bar rack and louver guidance devices in an open channel flume Russon *et al.* (2010) present evidence that downstream migrating silver eels predominantly followed routes of high turbulence intensity. More commonly, eel behaviours are reported in the context of broad conditions such as mean channel flow or turbine and pumping rate (Brown *et al.*, 2003, Spierts and Kemper, 2008, Gosset *et al.*, 2005).

The entrances to downstream fish passage facilities typically require a constriction of flow, which creates abrupt velocity gradients immediately upstream. Several studies have demonstrated that salmonids reject areas of rapidly accelerating velocity (Haro *et al.*, 1998; Kemp *et al.*, 2008a; Enders *et al.*, 2009a; Vowles & Kemp, 2012), which is thought to explain why fish frequently reject the entrances of passage facilities (Nestler *et al.*, 2001; Haro, 2003).

While increased velocities in front of intakes may act as an attraction flow for downstream migrating eel (Bruijs & Durif, 2009), rejection behaviours have also commonly been observed directly upstream of intakes; inferring that eels may, like salmonids, be reluctant to enter routes with rapid accelerating velocities (Jansen *et al.*, 2007; Calles *et al.*, 2010). There is some evidence that the intensity of recurrent and milling behaviours also increases with both water velocity and proximity to structures (Gosset *et al.*, 2005; Spierts & Kemper, 2008; Brown *et* *al.*, 2009); and that eels reject at structures prior to collision (Keeken *et al.*, 2011), presumably deterred by some environmental cue on the approach.

The degree to which eels respond to accelerating flow requires elucidation. If eels do reject rapid accelerating velocities, it may offer an explanation for the rejection behaviour exhibited at some bypasses (Calles *et al.*, 2012). Behavioural responses to velocity gradients may offer potential to deter fish from harmful areas towards more benign passage routes; as indicated by the quantitative review (section 2.2), guidance to safe passage routes is the principal goal of barrier mitigation technologies for silver eel.

Turbulence, inherent in lotic systems, describes stochastic or chaotic flow patterns and can simplistically be considered as a time-averaged fluctuation in velocity magnitude around a mean (Odeh *et al.*, 2002). It is another flow characteristic that has received attention for its potential to increase attraction and passage efficiency at fish passes. Indeed, upstream fish passes fundamentally work by the dissipation of the energy generated by head through turbulence (Castro-Santos *et al.*, 2009). Fish responses to turbulence appear complex. Swimming in turbulent as opposed to uniform flow conditions may incur greater energetic cost (Pavlov *et al.*, 2000; Enders *et al.*, 2005; Lupandin, 2005), perhaps due to the increased movements required to maintain stability under turbulent conditions (Enders *et al.*, 2005; Lupandin, 2005). Other work has suggested possible benefits to fish encountering turbulent factors. Liao *et al.* (2003; 2004) demonstrate reduced muscle activity and energetic costs for rainbow trout (*Oncorhynchus mykiss*) which used features of von Karman vortex streets to hold position in the turbulent conditions created downstream of cylinder arrays. Sockeye salmon (*Oncorhynchus nerka*) have been observed to exploit small reverse flow vortices to aid upstream migration (Hinch & Rand, 2000). Several researchers have suggested that quantifying eddy size and orientation in relation to fish length is important for understanding the effect of turbulence on swimming performance (Pavlov *et al.*, 2000; Odeh *et al.*, 2002; Tritico, 2009).

Upstream migrating eel seek low velocity areas and commonly exploit boundary layers close to structures (Barbin & Krueger, 1994); hence provision of low velocity areas within passage facilities should be a fundamental aim to aid upstream passage for eel. Eels are often unable to pass culverts and weirs, even under low velocities, due to the uniform laminar flow associated with such structures (Porcher, 2002). Creation of heterogeneity within flow fields has been suggested as a method to enable eels to pass high velocity ranges (Coutant, 2001; Porcher, 2002), and eels have been observed ascending the high velocities within upstream salmonid passes by utilising routes associated with heterogeneous flow (Clay, 1995; Porcher, 2002). The success of some facilities shown to pass multiple species and lifestages e.g. Larinier and nature-like fish passes, is in part attributed to the heterogeneity of hydrodynamic conditions produced within them (Calles & Greenberg, 2007; Williams *et al.*, 2012). Although it is recognised that such passes are typically built with a lower slope, and therefore present lower flow velocities, than most technical fishways (Bunt *et al.*, 2012).

Similarly, increasing turbulence may offer potential to attract downstream migrating eel and improve passage facilities. The reduction in turbulence as the result of flow regulation at hydropower facilities is considered to hinder migration as fish entering dammed forebays, lose directional cues, and take longer to find passage routes (Coutant & Whitney, 2000; Coutant, 2001). The preliminary evidence that silver eels may seek areas of high turbulence intensity (Russon *et al.*, 2010), suggests the potential for manipulating flow fields to create increased attraction at the entrance to downstream passage facilities.

2.3.13 Modelling fish responses to hydrodynamics

Recent modelling techniques such as The Numerical Fish Surrogate (NFS) aim to predict fish movement and behaviour in complex hydrodynamic environments such as those around river infrastructure. The NFS uses statistically derived behaviour rules generated from empirical swimming capability and behavioural data to inform the movements and behaviours of theoretical fish, combined with Computational Fluid Dynamic modelling (CFD) models of hydrodynamic environments. These methods are proposed to enable multiple scenario testing of pass designs prior to construction (Goodwin *et al.*, 2006; Goodwin *et al.*, 2007), offering potential advantages in accuracy, cost efficiency and transferability compared to treatment-based, ‘build-and-try’ techniques (Nestler *et al.*, 2000). However, the predominant focus of these models has been to predict the movement and passage of juvenile salmonids at large hydropower facilities. Knowledge of salmonid responses to hydrodynamic parameters such as velocity gradients, turbulence and shear factors required for accurate model predictions are relatively advanced compared to that of most other species. The current dearth of knowledge regarding the fine-scale movement and behavioural responses of anguillid eel to hydraulic parameters must be addressed before the NFS can be applied to eel.

2.4 Summary

Restoring fluvial connectivity is important for all migratory fish, not least the European eel which has undergone a substantial decline in recruitment in part due to the negative effects of river infrastructure. The upstream migration of juvenile lifestages with relatively poor swim capabilities present challenges for providing effective barrier mitigation at structures. Similarly, downstream migrating adult lifestages appear particularly vulnerable to impingement, entrainment and mortality at intakes, screens, hydropower turbines and pumps. This review has highlighted key biases and gaps in current knowledge surrounding barrier mitigation measures for eel. The importance of taking an interdisciplinary ecohydraulic approach has been identified as offering great potential for improving the design of fish passage facilities for all species and lifestages. There is a strong historic research bias towards salmonids, for which many improvements in upstream passage facilities have been gained through quantifying swim capabilities, movements and behaviours of actively migrating fish in response to hydrodynamic features. Non-anadromous species such as the European eel have been largely neglected within ecohydraulic studies to date, and there is a lack of knowledge regarding the swim capabilities and behaviours of both up- and downstream migrating lifestages in relation to hydrodynamic features ubiquitous at river infrastructure (including fish passes), yet the same fundamental approaches are advocated.

As highlighted by the quantitative review, the focus of current barrier mitigation research for eel is considerably different for the two migratory lifestages. There is a bias within upstream studies towards pass provision measures, with little attention on attraction to facilities. Poor attraction is cited as a primary constraint of many existing passes; hence this lack of understanding of how hydrodynamic parameters may be used to attract upstream migrating eel is identified as the first key knowledge gap (Table 2.3).

Table 2.3 Summary of key knowledge gaps identified through the literature review.

Life-stage	Knowledge Gaps
Upstream	Detailed understanding of the conditions required for successful passage in non-salmonids
	How to create efficient attraction to upstream pass entrances
	Alternative mitigation methods to eel ladders at riverine structures
	Behavioural responses to hydrodynamic parameters ubiquitous at riverine structures and passes
Downstream	Swim capabilities under hydrodynamic parameters ubiquitous at riverine structures and passes
	Understanding of fine-scale behaviour around riverine structures
	Behavioural responses to hydrodynamic parameters ubiquitous at riverine structures and passes; particularly at fine scale in field environments

It is clear from the literature that guidance of eels away from deleterious routes and provision of safe downstream passage are considered of equal importance for silver eel. It is likely that the behaviour of adult migrants approaching structures is influenced by multiple cues, many of which have been tested for their guidance potential e.g. sound, visual and tactile. Despite recognition of the fundamental role hydrodynamics have in the behaviour of many fish species and importance for attraction, guidance and overall passage at facilities, few studies quantify the responses of adult eel to hydrodynamic parameters. A lack of understanding of how silver eel behaviour is affected by the hydrodynamic conditions associated with structures is a second knowledge gap identified (Table 2.3).

Catchment managers seek clear guidance on effective and economically viable methods to meet legislative obligations to facilitate fish migration at structures, while still providing flood defence, freshwater abstraction and power generation. Barrier mitigation measures such as managed opening of structures or modified pumping or power generation may provide effective and economical alternatives to fish pass installation. However, the development of such management strategies is hindered by our limited understanding of how migratory silver eel behave at barriers, but also in predicting the scenarios under which catchment scale management could be effective.

Chapter 3 Research aims and thesis outline

There is need to mitigate for the negative impacts of anthropogenic river infrastructure which hinders migration, and may impose considerable injury and mortality, of the European eel. This catadromous species undertakes migration in two very different physiological states; as upstream migrating juveniles and downstream migrating adults, yet both lifestages are impacted by barriers and effective barrier mitigation strategies must be developed for each. Knowledge of the capabilities and behaviours of both these key migratory lifestages in relation to the dominant physical and hydrodynamic parameters experienced at riverine structures will ultimately aid the development of more effective barrier mitigation for this under-researched species.

The broad study aims of this thesis are to:

1) Assess the influence of physical and hydrodynamic parameters on eel movement and behaviour at riverine barriers and passage facilities

2) Aid the development of more effective upstream and downstream passage solutions for European eel

To meet these aims, an initial objective was formulated:

1) Review current literature to highlight research trends and biases, and to identify knowledge gaps that may present opportunity to improve eel passage

Through completion of the first objective, the following additional objectives were formulated to address current knowledge gaps and meet the broad study aims:

2) Quantify the passage efficiency of eel specific passes in relation to plunging and streaming attraction flow

3) Quantify the behavioural responses of upstream migrants to the hydrodynamic conditions associated with fish passage facilities

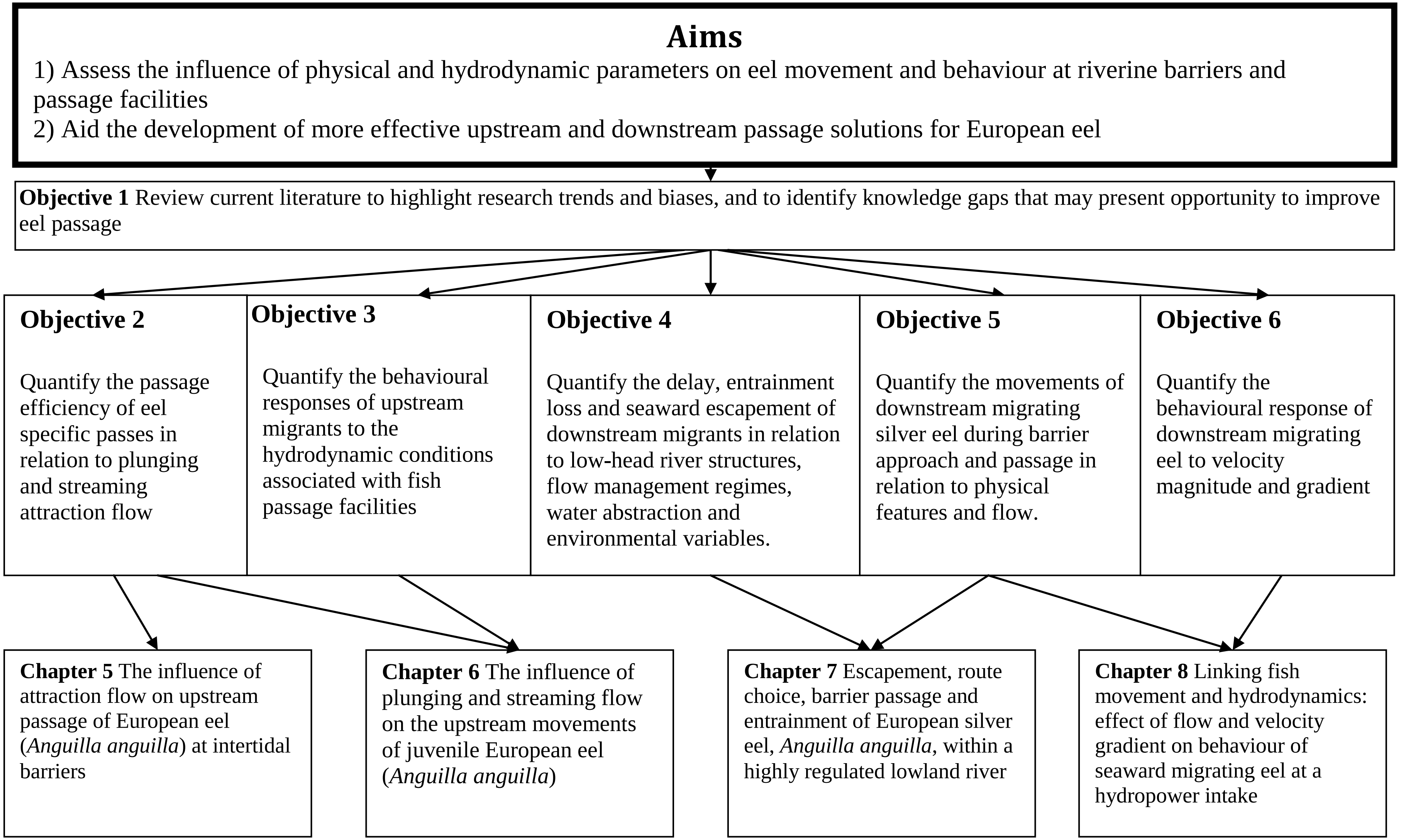
4) Quantify the delay, entrainment loss and seaward escapement of downstream migrants in relation to low-head river structures, flow management regimes, water abstraction and environmental variables.

5) Quantify the movements of downstream migrating silver eel during barrier approach and passage in relation to physical features and flow.

6) Quantify the behavioural response of downstream migrating eel to velocity magnitude and gradient

Chapter 5, the first research chapter of this thesis, addresses the second study objective by quantifying the change in catch efficiency of eel ladders operated on an intertidal barrier due to the addition of plunging and streaming attraction flow. A fully randomised field experiment was conducted to test the efficacy of this measure, which has been suggested to offer potential to improve upstream eel passage facilities. To meet objective 3, an open channel field flume facility was used to investigate the behavioural responses of upstream migrating eel to water velocity and turbulence created by plunging and streaming sources (chapter 6) (Fig. 3.1).

An assessment of barrier impacts on downstream eel migration was conducted within a heavily regulated sub-catchment to meet objective 4. The movements, behaviour and escapement rate of adult eel were investigated using telemetry as they moved through the impounded lower reaches of a river catchment (chapter 7). For objective 5, eel behaviour and route choice on the approach to an array of barriers within a forebay was quantified using sub-metre positioning telemetry and related to flow (chapter 8). Through identifying specific behaviours such as rejection and milling in relation to the water velocities and velocity gradients synonymous with water abstraction and hydropower intakes, this chapter also addresses objective 6 (Fig 3.1).



Aims

1) Assess the influence of physical and hydrodynamic parameters on eel movement and behaviour at riverine barriers and passage facilities

2) Aid the development of more effective upstream and downstream passage solutions for European eel

Objective 1 Review current literature to highlight research trends and biases, and to identify knowledge gaps that may present opportunity to improve eel passage

Objective 2

Quantify the passage efficiency of eel specific passes in relation to plunging and streaming attraction flow

Objective 3

Quantify the behavioural responses of upstream migrants to the hydrodynamic conditions associated with fish passage facilities

Objective 4

Quantify the delay, entrainment loss and seaward escapement of downstream migrants in relation to low-head river structures, flow management regimes, water abstraction and environmental variables.

Objective 5

Quantify the movements of downstream migrating silver eel during barrier approach and passage in relation to physical features and flow.

Objective 6

Quantify the behavioural response of downstream migrating eel to velocity magnitude and gradient

Chapter 5 The influence of attraction flow on upstream passage of European eel (*Anguilla anguilla*) at intertidal barriers

Chapter 6 The influence of plunging and streaming flow on the upstream movements of juvenile European eel (*Anguilla anguilla*)

Chapter 7 Escapement, route choice, barrier passage and entrainment of European silver eel, *Anguilla anguilla*, within a highly regulated lowland river

Chapter 8 Linking fish movement and hydrodynamics: effect of flow and velocity gradient on behaviour of seaward migrating eel at a hydropower intake

Figure 3.1 Schematic summary of thesis aims and data chapters undertaken to meet these

Chapter 4 General Methodology

This chapter provides a general overview of the approaches and methods applied during the research presented in chapters 5-8 of this thesis. A combination of field and flume-based approaches were used, dependent on the nature of each study question. The advantages, limitations and justifications for each method are presented, along with a general description of the equipment and facilities used.

4.1 Open channel field flume

Work conducted in open channel flumes has contributed greatly to advancements in our knowledge of fish movement and behaviour. Most notably, the performance and behavioural metrics gained through flume-based experiments has enhanced development of effective fishways (Williams *et al.*, 2012). In comparison to studying fish in their natural environment, flumes offer some key advantages. First, isolation of test variable(s) is possible to a greater extent than in field environments. Second, laboratory settings afford greater control for confounding environmental variables such as light, sound; thus increasing the replicability of findings. Third, the resolution at which it is possible to quantify fish movement through direct observation or filming is greater in flumes than is currently possible using field techniques.

Through recent developments in acoustic telemetry it is now possible to obtain continuous, near real-time, swim tracks of fish in their natural environment; however resolution is still only within 50 cm (Brown, 2005), in contrast to the sub-centimetre positioning afforded by flumes (Enders *et al.*, 2009a; Rice *et al.*, 2010). High resolution acoustic filming techniques (e.g. Dual-Frequency Identification Sonar, DIDSON) provide accurate real-time images of passing fish, however individuals may only be observed within a limited field of view, and it is not possible to determine if individuals entering the area of view are passing for the first time, or re-entering. The filming techniques currently possible only in flumes permit images of fish to be obtained at high resolution and spatial accuracy; and fish may be re-captured with relative ease if required, for example to inspect test subjects for damage, or to quantify delayed mortality. Furthermore, within the wider aim of this research to understand the behavioural responses of eel in relation to hydrodynamics, it is necessary to map hydrodynamic conditions at high resolution. The scale and infrastructure of the flume permit hydrodynamic conditions to be quantified with high accuracy and precision.

There are, however, some limitations associated with flume facilities which should be considered and minimised where possible. Laboratory-based studies may necessitate greater periods of movement and holding of study animals than field trials, often for unstated periods (e.g. Adam *et al.*, 1999; Russon *et al.*, 2010). The act of transportation, change of water chemistry, temperature and altered light regimes prior to experimentation will inevitably cause some level of stress in test subjects, with potential impacts on natural behaviour (Portz *et al.*, 2006). The reduced drive and motivation which may result from transport and holding are key considerations for behavioural studies on migratory fish (Lucas & Baras, 2001).

In recognition of these constraints, some researchers use large-scale, flow- through flumes linked to natural river systems. This removes the need for recirculation, retains ambient environmental cues (e.g. water chemistry and temperature), and permits naturally migrating fish to either be captured at associated facilities (e.g. Enders *et al.*, 2009a), or diverted into the facility (e.g. Kemp *et al.*, 2006), thereby minimising handling and holding time.

Mindful of these issues, a field flume was developed in which to study the behavioural responses of upstream migrating juvenile eel to a number of physical hydrodynamic test conditions (Chapter 5). A plexiglass flume (7m length x 0.6m width x 0.6m depth) was constructed adjacent to the river Stour at Flatford Lock, Suffolk, UK (51º57’32.57´´N, 1º01´13.76´´E), and oriented parallel to the channel. The flume was sited in close proximity (400m upstream) of the capture site for study fish; hence transport and holding time were minimal. A single flow-through system was used. River water was pumped to the flume from the main river channel (2 pumps with combined maximum capacity 0.048 $m^3 s^{-1}$) into a header tank (1.5 m^3) then passed through a honeycombed crosswall (to smooth flow) before flowing into the main flume channel, terminating in an adjustable overshot weir (to manage water level), and flowing back into the river via a footer tank (1.5 m^3) and set of gate valves (Fig. 4.1). The system avoided water recirculation, which may cause temperature increases through frictional forces (Kemp, 2010), and disruption of olfactory cues due to mechanical agitation within pumps. Use of natural river water was considered particularly important as olfactory cues are key drivers during upstream migration of juvenile eel (Sola, 1995; Briand *et al.*, 2002).

Figure 4.1 Field flume facility, river Stour, Suffolk, UK

4.2 Fish Telemetry and its effects

A multitude of capture and non-capture methods have been used to investigate the spatial behaviour of fish in natural environments (Lucas & Baras, 2000). Fish telemetry is one such widely used approach and broadly can be considered as the attachment of a device to a fish which relays biological information, typically via ultrasonic or radio waves, to a remote receiving system (Winter, 1996).

The development of telemetry technologies and techniques has been highlighted as a key component to advancing knowledge of fish life history traits, behaviour and movement (Lucas & Baras, 2000; Cooke, 2008). Telemetry allows individuals to be tracked over a wide range of spatial and temporal scales (Castro-Santos *et al.*, 2009; Cagnacci *et al.*, 2010), and is one of the most appropriate, and sometimes only, available method to study free ranging fish in natural environments which can be inherently taxing or inaccessible to human observation (Winter, 1996; Lucas & Baras, 2000; Cooke *et al.*, 2011). In addition to providing location data, an increasing range of sensors such as temperature, salinity, pressure and acceleration, are being incorporated within tags to simultaneously collect correlative environmental and physiological data (Cooke, 2008).

In common with any method that involves the capture and handling of test subjects, particularly one that necessitates operative procedures, there are inherent limitations and assumptions that must be recognised.

4.2.1 Tagging procedure and fish welfare

Stress, damage and infection can all induce atypical behaviour and limit physical capabilities, so efforts must be made to limit the influence of the capture and tagging procedure, or the tag itself, on the physical and behavioural condition of the fish. It is of limited use to collect data about individuals whose movement, behaviour and habitat use is atypical of their non-tagged counterparts (Rogers *et al.*, 2007). Aseptic techniques should be maintained at all times through the tagging procedure. Post-operative infection will increase mortality rates, but also induce less predictable effects such as lethargy (Rogers *et al.*, 2007). In this impeded state individuals will presumably become more susceptible to predation, fishing and mechanical damage.

4.2.2 Transmitter selection and attachment methods

A number of transmitter attachment methods have been used in telemetry studies of large yellow and silver phase eel, including external attachment (McGovern &

McCarthy, 1992) and internal methods: gastric (orally inserted) (Cottrill *et al.*, 2006); and peritoneal (surgically implanted into peritoneal cavity) (Brown *et al.*, 2009). In an experimental comparison of these three methods in silver phase American eel, post tagging retention rates of identical size tags over 12 weeks varied significantly between methods (Cottrill *et al.*, 2006). Only surgical implantation into the peritoneal cavity resulted in 100% retention, a result mirrored in similar studies (Winter *et al.*, 2005). Of the gastric implants, 72.7% were retained, though this method was discouraged as a long term option due to risks of regurgitation and rupture of the stomach wall. External attachment provided only 9.1% retention and is thus considered unsuitable for eel due to their thigmotactic behaviour (Haro & Castro-Santos, 2000; Cottrill *et al.*, 2006). Swimming performance did not differ between attachment method or sham (operated on, but no tag attachment) groups, suggesting presence of the tag did not hinder swimming, though performance was lower for all groups relative to control group which suggests that the attachment procedure, not the tag, impaired swimming (Cottrill *et al.*, 2006).

There is much variation in the post-tagging mortality rates reported for different methods. Cotrill *et al.* (2006) found 0% mortality after 12 weeks for eels subjected to external, gastric and interperitoneal tagging methods. However, up to 60 % mortality of yellow European eel in the 10 weeks after interperitoneal implantation has been reported (Baras & Jeandrain, 1998).

After consideration of these issues, it was deemed that interperitoneal implantation with suture closure offered the optimum combination of tag retention, survival and minimal behavioural/ performance impacts for silver phase eel, and was used during the telemetry studies described in chapters 7 and 8.

Transmitter weight relative to that of the fish is a principle consideration. It is generally accepted that transmitter weight should not exceed 2% of the fish body weight in air or 1.25% of the weight in water (Winter, 1983), to prevent negative effects on swimming capability. Technological advancement limits the minimum size of transmitter, and accordingly fish that can be studied by this method (Brown *et al.*, 1999). For eels, tag volume may be a more important consideration than weight due to the elongated body shape and relatively narrow peritoneal cavity, coupled with an anguilliform mode of swimming (Baras & Jeandrain, 1998; Jepsen *et al.*, 2005; Moser *et al.*, 2007). The transmitters used within this programme of research were therefore always <2% body weight, and of maximum diameter 9mm (model V92L 29 mm x 9 mm, 2.9 g in water, VEMCO, Nova Scotia, Canada), hence they exerted minimal pressure on sutures or the body cavity.

4.2.3 Assessment of post-operative impacts

The post-procedure retention of tagged fish is necessary to ensure as far as possible that health, survival and behaviour have not been impaired by tagging. There is no consensus on the recommended time period for recovery. If a post-procedure fish is released into a natural aquatic environment while still experiencing impaired swimming and sensory capabilities, it will be more susceptible to predation, as well as physical injury and mortality from natural and anthropogenic structures such as rapids, weirs, screens, turbines and pumps; particularly under high flows (Jepsen *et al.*, 2002). Conversely, holding groups of fish, especially wild fish, in confined unfamiliar environments for extended periods can be counterproductive, increasing stress and agonistic interactions (Otis & Weber, 1982; Jepsen *et al.*, 1998; Jepsen *et al.*, 2002). Eels were kept for 10-12 hours post-tagging which corresponded to a recovery period during which eel appeared to have regained typical movement and behaviour in previous tank observation studies (Michael Goddard, pers. comm.).

The capture, handling and transportation of study fish impose inherent stresses and disrupt normal behaviour (Portz et al., 2006). These were minimised by careful handling, maintenance of ambient temperatures and oxygen level, and through general good husbandry techniques. Due to the invasive nature of tag implantation, it is advocated that the impacts of this procedure, and the individual operator, on tag retention, recovery, wound healing and survival be determined (Ross & McCormick, 1981; Moore *et al.*, 1990; Moser *et al.*, 2007). A study was conducted in October 2009 with the aim to quantify such impacts on silver phase European eel implanted with dummy acoustic and PIT tags.

4.2.3.1 Methods

Silver eels were captured during downstream migration using fyke nets at Stratford St. Mary, on the river Stour, Suffolk, UK. Individuals (n = 45) were randomly selected, only being rejected if there were visible signs of damage. Selected individuals were approximately size matched (visually assessed), and separated into 3 groups, 15 individuals per group. Each group was transferred into separate perforated holding containers submerged at the edge of the main river channel. A separate treatment was applied to each group (control, sham and tagged).

1) Control – eels were bulk weighed in water to minimise handling stress then returned to an in-river holding container.

2) Sham – eels were transferred (by pouring) from the holding container (3 h post sorting) into an aerated holding tank (1.5m length x 1.5 m width x 1m height) filled with river water. Eels were individually transferred to an anaesthetic bath (Benzocaine 0.2 g L^{-1}), and only removed after complete loss of righting response (maximum duration 4.77 min). Individuals were then placed in a half-pipe cradle and the following morphometric measurements collected: total length; mass; left pectoral fin length; and left eye height and width. Eels were then returned to the in-river holding tank to recover.

3) Tagged - identical procedures as for sham group, with the addition of surgical tagging. Individuals were placed upside down in a half pipe cradle, morphometric measurements collected and an incision (1.5 cm) was made approximately 50 mm anterior to the ventral opening. Two tags: PIT tag (Texas Instruments, 3.65 mm diameter,32 mm length, 0.8 g mass in air); and dummy acoustic tag (model V92L 29 mm X 9 mm, 2.9 g in water, VEMCO, Nova Scotia, Canada), were inserted through the opening into the peritoneal cavity. The incision was closed with two equidistantly spaced dissolvable sutures (Vicryl Rapide^{R}; Ethicon Inc., Cornelia, GA, U.S.A.). Eels were then returned to the in-river holding container to recover. The duration of surgical procedures was always less than 3 mins.

All three groups were held for a total 12 weeks. Mortalities were checked for once per week and removed if present. At the end of the 12 week period, each group was anaesthetised (as previously described) and weighed (bulk for group 1, individually for Group 2 and 3). Each eel was then visually inspected for signs of external damage or disease. The tagged group were further assessed for tag retention, and healing level recorded on a subjective scale (1 to 3) whereby 1 indicated no healing; 2, partial healing; and 3, that the incision had fully healed. Additional observations were made regarding the presence of inflammation, necrosis, number of sutures retained, and if sutures were bisecting body tissue.

4.2.3.2 Findings and summary

One mortality occurred within the study, in the sham group (Table 4.1). The otherwise high survival within the sham and tagged groups, suggests that the handling, anaesthetic and operative procedures conducted had minimal impact on survival over the observation period. No tag loss occurred in the tagged group, and complete or partial healing of the implantation incision occurred in 93% of eels (Table 4.1) (Fig 4.2). Of the 15 tagged eels, 6 individuals (40%) retained one or more sutures; in 2 individuals, sutures had become embedded in the surrounding tissue, with evidence of necrosis for one individual. All 3 groups reduced in mass (36 to 58 g, mean reduction) over the 12 week holding period (Table 4.1).

Table 4.1 Results of an investigation to assess impacts of handling and surgical implant of acoustic tags in silver phase European eel, conducted October 2009

	Group		
	Control	**Sham**	**Tagged**
No. Mortalities	0	7 % (n=1)	0
% Acoustic tag retention	NA	NA	100
% PIT tag retention	NA	NA	100
% complete wound heal	NA	NA	60 (n=9)
% partial wound heal	NA	NA	33 (n=5)
% no wound heal	NA	NA	7 (n=1)
Pre trial mass (g)	872 (mean from bulk)	933 ± 165 (mean ± S.D)	843 ± 156 (mean ± S.D)
post trial mass (g)	814 (mean from bulk)	884 ± 132 (mean ± S.D)	807 ± 149 (mean ± S.D)

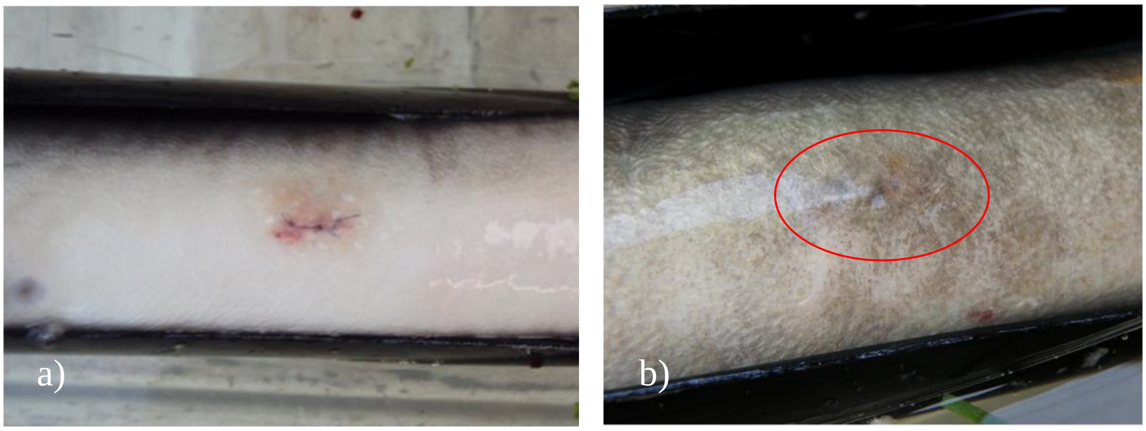


Figure 4.2 Ventral surface of silver phase European eel, a) immediately following tag implantation, b) 12 weeks after tag implantation, showing the wound fully healed.

The high survival and 100% tag retention observed, suggest that the handling, anaesthetic and operative methods used were appropriate and reliable. Individual variability in operator technique has been shown to account for variable and, in certain instances, inexplicably low tag detection within field studies, inferring low survival (Sam Johnson, pers. comm.). The same, single operator carried out all procedures within this trial, and all tag implantations described in chapters 7 and 8.

4.2.4 Optimisation and validation of telemetry systems

At fixed telemetry receiving stations it is important to understand the accuracy, precision, and range over which tags can be detected (Heupel *et al.*, 2006; Semmens, 2008). In chapter 7, fixed acoustic receivers (VEMCO, Nova Scotia, Canada) were employed at multiple locations within freshwater and saline habitats. This study required that receivers were configured to achieve spatially separated detection zones between receivers (typically located upstream and downstream of structures) to permit movement and structure passage of tagged fish to be determined from time stamped positive detection data. Prior to study commencement all receivers were activated and deployed in theoretically optimum field locations. Detection range tests were conducted at each receiver location which involved placing a test tag at known locations at increasing distances (typically 5 m intervals) from the fixed receiver up to a maximum of 200 m (which is beyond the maximum detection range for this telemetry system in shallow water environments). The number and time of tag transmissions (detected with mobile receiver VR100, VEMCO) were manually recorded at each test location. Detection data was then downloaded from each fixed receiver and the two data sets were compared to ascertain the precision and range at which fixed receivers were able to detect known tag transmissions. Finally, the range mapping for each receiver was checked for crossover between receiver detection zones (i.e. a tag transmission received at multiple receivers at the same time). If zones were found to overlap, receivers were repositioned and the process repeated. Range testing was repeated monthly as detection range may vary with water temperature, depth, velocity; and biotic factors (e.g. macrophyte and algal growth) (Heupel *et al.*, 2006; Heupel *et al.*, 2008; Semmens, 2008). The detection range of PIT antenna in chapters 7 and 8 was also determined monthly, though over smaller distances as typical maximum read range does not exceed 1 m. Test results are discussed in the appropriate sections of chapter 7 and 8.

To achieve fine-scale (< 1m) tag location using acoustic positioning telemetry systems (chapter 7), it is important to not only determine maximum boundaries of the detection area as previously described, but also to ascertain the accuracy and precision of geo-referenced tag detections. The accuracy of a tag position is particularly important when looking at near-continuous swim paths and behavioural responses in relation to a stimulus at a specific location (e.g. light, sound, water velocity). Acoustic positioning systems require multiple hydrophones, connected to a receiver unit, to be deployed at fixed geographically known locations, in an approximate square (for 2D positioning) or cuboid (for 3D positioning), typically around the perimeter of the study area (hydrophone array). The position of an individually coded tag transmission within the hydrophone array is determined through triangulation, using the difference in detection times at each hydrophone converted to differences in distance by applying speed of sound. To validate the positioning accuracy of the system and specific configuration described within chapter 8, a series of tests were conducted. In each test a transmitting tag was deployed at a known fixed location, as determined by digital GPS, then left to transmit (1 ping per second) for a 1 h period. The variation of recorded detection positions from the known location defined the positioning accuracy, similar to methods described by others (Brown *et al.*, 2009; Svendsen *et al.*, 2011). Fixed location tests were conducted throughout the study area (35 locations in year 1, and 20 locations in year 2) and within the top, middle and bottom of the water column at each location. Moving tag position tests were conducted by pulling a transmitting test tag between fixed hydrophones along a tensioned guide line (as described by Svendsen *et al.*, 2011). Test results are discussed in chapter 7.

4.2.5. Data processing and analysis

Time stamped detection data from single fixed location acoustic receivers were extracted using Vue v1.8.1 (VEMCO, Nova Scotia, Canada) and post-processed to exclude false detections (Chapter 7). Positive detection data were used to determine eel barrier approach and passage times, which were compared to corresponding environmental parameters and structure management regimes. Detections from sub-metre acoustic positioning telemetry (chapter 8) were manually marked and processed using MarkTag v5 and AcousticTag v5 (Hydroacoustic Technology Inc., Seattle, USA). Two- dimensional fish swim trajectories were exported to ArcGIS (ESRI, Redlands, USA) and overlain on corresponding flow velocity maps.

4.3 Fish capture methods

The capture methods used to obtain eels for study were selected so as to primarily target actively migrating fish, and secondly to minimise holding time within traps. By capturing eels as close as feasibly possible to each study site, it was possible to minimise the handling, holding and transportation time before use, thereby limiting the potential physical damage and stress which may have otherwise occurred through purchasing fish from commercial suppliers and transporting to site.

4.3.1 Upstream eel trap

Eel passes or ‘ladders’ are commonly installed at cross channel structures to facilitate upstream migration of eel. The addition of a catch pot at the upstream exit of the pass enables migrants to be captured. The trap used within chapters 4 and 5 consisted of a rectangular fibreglass trough (200mm width; 100mm depth; 4.6m length) with anti-predator cover, fitted to the sloping weir face at a 34° angle (Fig. 4.3). The trough was lined with longitudinal strips of net and bristle media to provide a climbing substrate to facilitate ascent.

Figure 4.3 Eel traps located at Judas Gap intertidal weir, river Stour, Suffolk, UK.

4.3.2 Eel rack to capture downstream migrants

Eel racks are designed to capture downstream migrating fish and typically installed on the downstream side of overshot or undershot weirs and sluices. A large proportion, or indeed all, of river flow is diverted to pass over a fixed panel of bars or mesh (rack). Eels are conveyed onto the rack with the main flow, and are captured as the water dissipates through the bars or mesh. The gradient of the rack is such that eels collect in a channel or catch box (Fig. 4.4 a,b).

Figure 4.4 a) Eel rack with water spilling from undershot sluice gates (right-hand side) onto mesh deck with catch boxes, Longham, river Stour, Dorset, UK, b) Eels captured on the rack during night-time operation (photo courtesy of Roger Castle).

4.3.3 Fyke nets

Fyke nets are comprised of reducing concentric chambers held open with hoops, which in effect form a net ‘funnel’ that is closed at one end. Narrow panels of netting (wings or leaders) extend from each side of the open end, with the intention to guide fish that encounter the leaders toward the entrance (Fig. 4.5a,b). The fyke nets used in chapter 6 were positioned at an approximate 45˚ angle across the river channel to intercept downstream migrating eel.

Figure 4.5 a) Setting fyke nets from a boat (photo courtesy of Rosie Hallam), b) Fyke net showing mesh panel (leader) which guides the fish into a reducing net funnel.

4.4 Quantifying hydrodynamics

4.4.1 Acoustic Doppler Velocimeter (ADV)

Acoustic Doppler Velocimeters (ADVs) have been widely adopted since the early 1990s to quantify hydrodynamic conditions (Cea *et al.*, 2007), principally within flumes (as in chapter 5) (Enders *et al.*, 2009a; Silva *et al.*, 2011), though also in field studies (as in chapter 4) (Dermisis & Papanicolaou, 2009; Enders *et al.*, 2009b), ADVs offer a number of advantages compared to traditional flow measuring devices (e.g. impeller and electromagnetic current meters): they are minimally intrusive; have greater accuracy; and have 3-dimensional velocity measurement capability (Muste *et al.*, 2010). An ADV enables measurement of instantaneous velocity components in 3 dimensions (x,y and z), within a small volume of water at discrete measurement points, using the Doppler effect. The apparatus transmits short pairs of sound pulses and measures the change of frequency of the sound returned to the device after being reflected off tiny particles suspended in the water. Conducting multiple measurements at a fixed position enables determination of the velocity fluctuation around a time-averaged mean.

A sampling rate of 50 Hz was used for all ADV (Nortek, Vectrino+) measurements. Tests were conducted to define a sampling period which adequately captured the fluctuation in velocity components at a single position. Sample periods of increasing duration (e.g. 5 s, 10 s, 20 s up to 350 s) were tested to define the duration at which the variation in velocity around the mean (S.D.) became constant (Silva *et al.* 2010).

Within this thesis, ADV measurements were used to: 1) quantify velocity magnitude at increasing distance from an input of attraction flow in the field (chapter 4); 2) quantify velocity magnitude at various heights in the water column, under manipulated flow conditions in a flume (chap 5); and 3) quantify turbulent kinetic energy at various heights in the water column, under manipulated flow conditions in a flume (chapter 5).

Only measurements that fell within the manufacturer's recommended boundaries for correlation values and signal to noise ratios, which are representative values for measurement accuracy, were retained. ADVs can produce inaccurate measurements when used in conditions where air bubbles are entrained within the water column, and in highly turbulent flow (MacVicar *et al.*, 2007). In chapter 5 these issues required that test measurements be taken at increasing distances from a turbulent flow source to devise a suitable sampling plan in which all measurements would full within recommended ranges.

All raw ADV data were processed using a maximum/minimum threshold filter that removes erroneous data points falling outside of a pre-defined range (Cea *et al.* 2007). The maximum and minimum threshold values were calculated as follows:

$$u_{min} = \bar{u} - \sqrt{21n(N)}\sigma_u$$

$$u_{max} = \bar{u} + \sqrt{21n(N)}\sigma_u$$

where $u_{min/max}$ are the minimum and maximum velocity thresholds in the x (streamwise) direction, $\bar{u}$ is mean streamwise velocity, σ_u is the standard deviation of u, and N is the total number of data, similar expressions are used for the y (lateral) and *z* (vertical) velocity components. Filtered data were used to calculate the required metrics (velocity vectors and turbulent kinetic energy) and were plotted using ArcGIS v10 (ESRI, Redlands, USA).

4.4.2 Acoustic Doppler Current Profiler (ADCP)

Acoustic Doppler Current Profilers (ADCPs) are designed to rapidly quantify water velocities and depth over large areas, i.e. within field environments, and are principally employed to quantify river flow. The instrument uses multiple transducers which transmit acoustic pulses of a set frequency into the water column along narrow beams. The acoustic signal is reflected back (backscattered) to the transducer from particulate matter within the water. Particles are assumed to be moving at the same speed as the water and the instrument uses Doppler shift principle to measure velocity at a set depth based on the frequency change between transmitted and backscattered acoustic signals. Based on the speed of sound, the ADCP uses the time difference taken for backscattered acoustic signals at different water depths to return to the transducer, to measure velocities through the water column. These measurements are segregated into depth cells/bins ('bins' hereafter), enabling velocity components to be calculated simultaneously at multiple depths. A vertical velocity profile at each lateral position is constructed from these multiple depth cells (collectively called an 'ensemble') (Gordon, 1996; Simpson, 2001).

The ADCP measures 3-dimensional velocity components by transmitting acoustic signals along four individually operating beams arranged in a Janus configuration at 20 - 30° from the vertical axis. Internal software transforms velocities relative to the x,y and z coordinates of the instrument itself using trigonometric calculations. If measurements are taken from a moving vessel, it is necessary to subtract the vessel velocity from the relative velocity in order to obtain the true water velocity. Vessel speed can be measured by either an onboard Global Positioning System (GPS), or by a function called 'bottom tracking' which uses the Doppler shift of acoustic signals reflected from the stream or lake bed.

The ADCP used within this thesis (M9, SonTek/YSI, San Diego, USA) employs 4 transducers to collect velocity measurements, operating at either 3 MHz or 1 MHz

(Fig. 4.6). A technology called SmartPulse^{HD} selects the optimum operating and processing configuration by adjusting components such as transducer frequency and bin size based on water depth, maximum velocity and turbulence. An internal compass records orientation, while an on-board GPS provides real-world positions for each sample point. Alternatively, bottom tracking data can provide the relative position of the vessel between known start and end points. Bed depth measurements are simultaneously recorded via a fifth vertical acoustic beam (0.5 MHz) enabling bathymetric datasets to be collected.

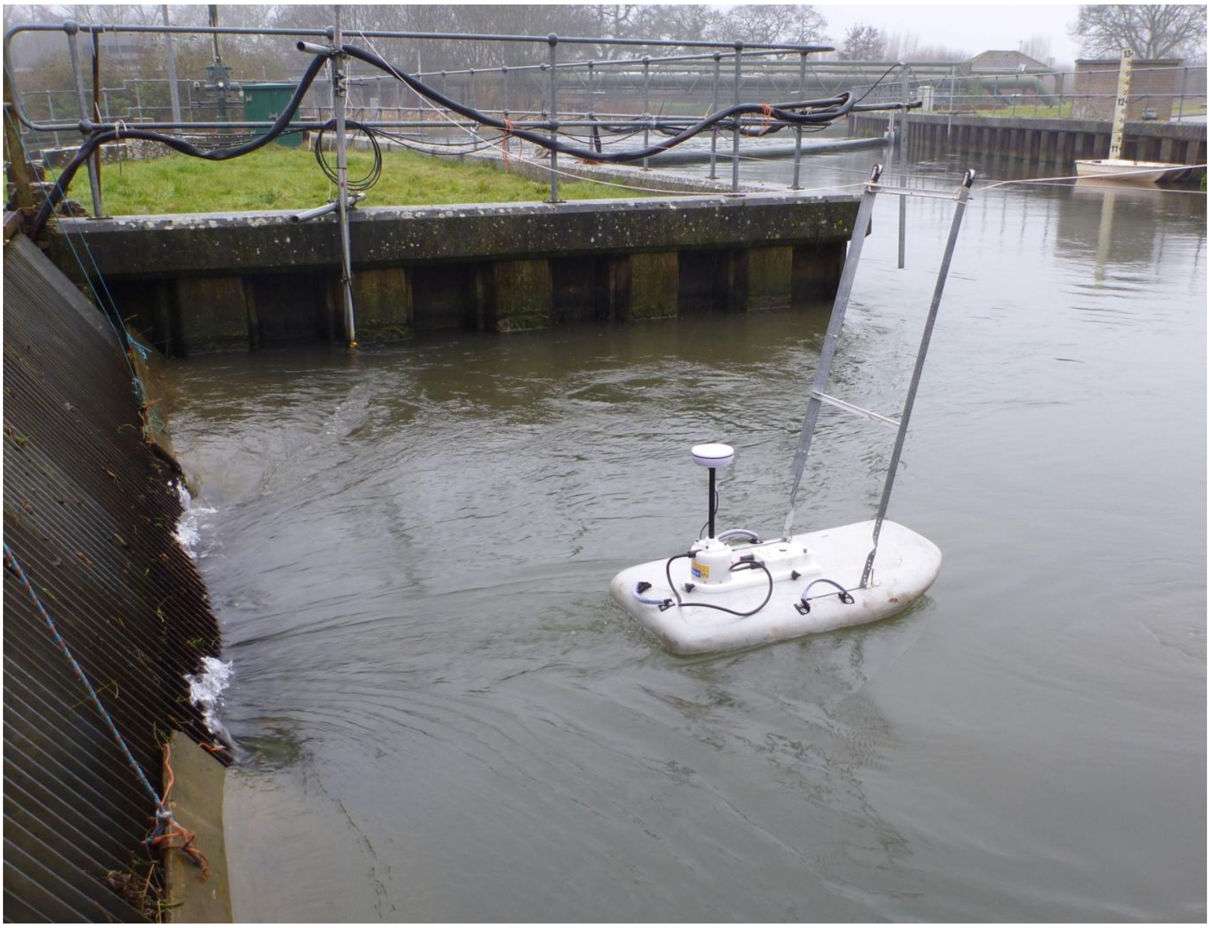


Figure 4.6 Raft-mounted Acoustic Doppler Current Profiler (M9 RiverSurveyor, SonTek) attached to transect guide line

Methods are increasingly being adapted to use ADCP’s for applications such as mapping velocity distribution (e.g. Sheilds *et al.*, 2003), estimation of turbulence quantities (e.g. Stacey *et al.*, 1999), and riverine transport and bed morphometry applications (e.g. suspended sediment concentration, bed survey and bedload transport) (Shields *et al.*, 2003; Wall *et al.*, 2006).

Quantifying hydrodynamic components such as three dimensional velocity and turbulent factors at biologically meaningful scales using ADCP devices is of great interest (Crowder & Diplas, 2002), though there are several limitations inherent with using current ADCPs for this application. First, the architecture of transducer beams (the separate beams required to measure velocities in the x, y and z planes) mean that velocity components at a given depth are measured in different locations, but are combined to describe a single central cell location on the assumption that water currents are homogenous across layers of constant depth (Gordon, 1996). Second, increasing sample cell size dependent on water depth i.e. sample cell height remains constant for all bins, though cell width increases with depth in the water column (Muste *et al.*, 2010). Third, measurements cannot be collected within the very top of the water column (approx. 0.15 m) because of the pause required between the transmission and echo reception of the sound pulse, or the bottom of the water column (approx. 0.25 m) due to stronger signal from bottom echo reflection obscuring echoes from cells above (Shields *et al.*, 2003). Studies have attempted to measure broad scale (> 20 m) circulation patterns and vorticity within rivers (Shields *et al.*, 2003; Shields & Rigby, 2005), and to quantify turbulent metrics such as turbulent kinetic energy using rigidly mounted ADCP conducting multiple measurements at fixed locations (Lu & Lueck, 1999); however due to the aforesaid limitations, it is at present not considered viable to quantify fine scale turbulence from ADCP moving transect data (Lu & Lueck, 1999; Muste *et al.*, 2010).

In laboratory-based tests, Nystrom *et al.* (2002) demonstrated that commercially available ADCPs measured mean water velocities to an accuracy within 1cm s^{-1} of an ADV, when stationary. Further laboratory studies were conducted by Nystrom *et al* (2007) to assess the accuracy of turbulence components derived from ADCP and ADV measurements. ADV's are considered to have greater accuracy under such controlled conditions, yet there was close agreement between the two types of instruments for quantifying Reynolds stress in the upper 75% of the measurement profile. Turbulent kinetic energy, however, was significantly overestimated by the ADCP; thought to be a consequence of instrument noise.

The confined and acoustically reflective test chambers used in laboratories limits the reliability of such validations for predicting how an ADCP will perform in field environments (Oberg and Mueller 2007). Field investigations conducted by Mueller (2002) indicated that ADCP, and simultaneous mechanical current meter measurements, of stream flow were within 5%, though there were insufficient data to robustly demonstrate biases. The stream flow measurement accuracy of commercially available ADCPs (not type used in this study) was validated at 22 field sites using reference measurements obtained from more conventional flow measuring techniques i.e. a mechanical current meter, stable-rating curves, salt dilution measurements and acoustic velocity meters (Oberg and Mueller 2007). The authors concluded that flow measurements collected using ADCPs were unbiased when compared to reference flow methods.

The particular operation and processing methods of different ADCPs may have a strong influence on the accuracy of each device. To the author’s knowledge, there is no comprehensive, independent, peer-reviewed comparison between the M9 ADCP used within this study and conventional flow-measurement devices; or indeed, other models of ADCP. The manufacturer reports that the M9 has an accuracy of ± 0.25% at measuring water velocity, relative to the ADCP position (SonTek, 2010). Additionally, there are a number of site-specific elements that can significantly affect the accuracy of measuring velocity components, and the geospatial referencing and orientation of measurements. These including GPS signal quality, stability of bottom sediments (if using bottom tracking to determine vessel speed), and compass interference from ferrite materials.

Within this thesis, ADCP measurements conducted along moving transects were employed to: 1) quantify mean channel flow (chap 6 & 7); 2) quantify depth average velocity magnitudes within a partially obstructed river channel under 3 manipulated flow conditions (chap 7); and 3) compile a bathymetric map of the study site (chap 7). Data quality was initially assessed visually (Fig. 4.7) and optimum transects selected within RiverSurveyor Live v3.01 (SonTek/YSI, San Diego, USA), using methods described in SonTek (2010). Several quality parameters were examined including: signal to noise ratio detected within acoustic beams; boat speed relative to water velocity (as boat speed should always be maintained below streamwise velocity for accurate measurement); and positioning metrics such as GPS quality, pitch and roll and compass readings. Selected transect data were exported to MATLAB (R2010a, Mathworks, Natick, USA) for further processing.

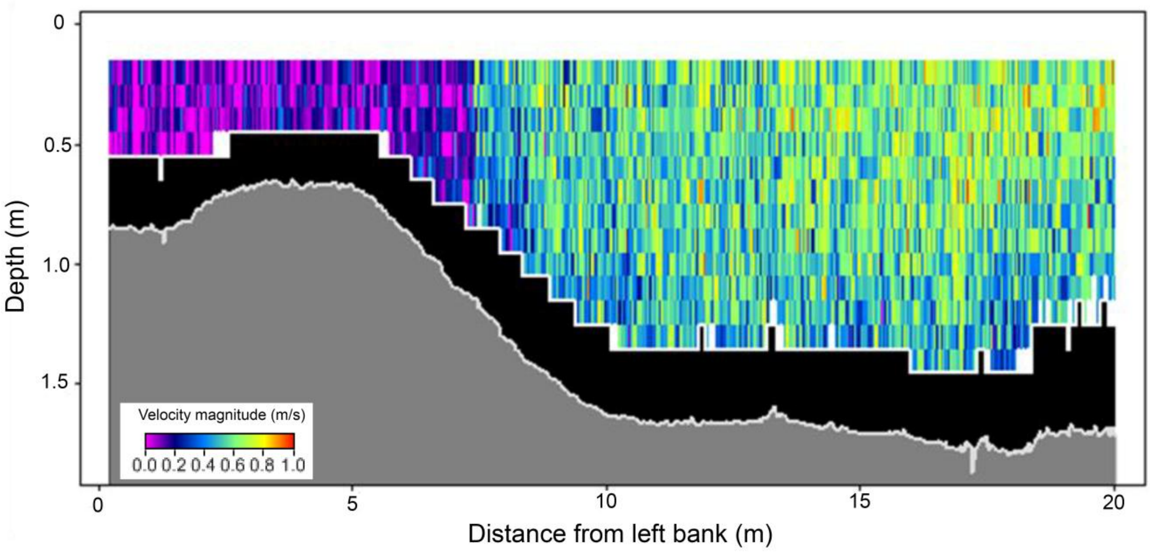


Figure 4.7 Example of a cross-river channel profile showing rectangular array of velocity magnitudes collected from a raft-mounted ADCP and displayed in RiverSurveyor Live.

Data are collected per time interval, regardless of distance travelled along the transect, hence the spacing of data points is not uniform. Therefore, to standardise horizontal spacing of measurements, reduce redundant overlap, and aid interpolation, assemblages were deleted where necessary to achieve minimum spacing (0.5 m). Near-bed measurements are often associated with ambiguity errors (Gordon, 1996), and the initial filtering based on predefined criteria in RiverSurveyor Live may not have removed all erroneous data values so further filtering was conducted to remove outliers at the bottom of each assemblage. Following the methods of Dinehart and Burau (2005), an additional filter was applied to remove any values of a component within the assemblage that differed from the mean value for that component within the whole assemblage by more than 2 standard deviations. Spurious values were replaced by an average of the adjacent values. All cells within an assemblage were then averaged to produce single depth-averaged velocity components.

Depth averaged data were imported to ArcGIS and plotted as velocity vectors overlain on a bathometric map of the site. Visual inspection of plots allowed any remaining erroneous data points to be easily detected and removed. For example, an internally uniform assemblage may vary substantially from adjacent assemblages. Where necessary, such assemblages were removed and replaced with averaged values from adjacent assemblages (Dinehart & Burau, 2005).

4.5 Using filming techniques to record fish behaviour

Previous flume research has quantified fish movement via a number of methods including: direct visual observation (Silva *et al.,* 2009); telemetry (Castro-Santos, 2005); recapture (Amaral *et al.*, 2003); and filming techniques (Haro *et al.*, 1998). Flume studies conducted within this thesis required fine-scale movements of juvenile eel to be quantified in response to created hydrodynamic test conditions. All trials were conducted at night in keeping with predominant activity time for this lifestage (Tesch, 2003; Laffaille *et al.*, 2007). Due to these restrictions, and the relatively small size of study fish, it was deemed most appropriate and least obtrusive to use filming techniques. Digital video cameras with infrared filming capabilities were configured to allow direct overhead and side-oriented filming to be conducted throughout the flume channel. This allowed lateral, transverse and vertical position of study fish to be recorded in a digital format. The flume was tented over with black plastic to maintain consistent light conditions between trials. An infrared LED array was employed to illuminate the filming area, emitting light of 850nm wavelength, which is outside the sensitivity of European eel (Archer *et al.*, 1995; Hope *et al.*, 1998).

4.5.1 Data processing and analysis

Video data were analysed within specialist software (LoggerPro v3.8.2, Vernier Software, Beaverton, USA). Eel head positions were manually marked to provide time-stamped swim paths enabling metrics such as time to passage, distance travelled and swim speed to be calculated. Eel positions were then overlain on corresponding hydrodynamic maps of test conditions within ArcGIS. Flow features such as water velocity and turbulent kinetic energy were extracted for each fish position and interrogated further.

4.6 Summary

The overall aim of this research, to quantify eel behaviour in relation to the physical and hydrodynamic features at cross-channel structures, water withdrawal intakes and fish passage facilities, presented inherent methodological challenges; in particular, the measurement of fine scale fish movements and hydrodynamic parameters in field environments. The methods outlined above were considered to be among the best approaches available at the outset of the research. Some of the methods and technologies used, for example sub-metre fish positioning telemetry and use of a ADCP for flow field mapping, are relatively new and novel so do not benefit from the development and historic precedence of many ‘tried and tested’ techniques. Nevertheless, it was considered that the benefits gained by applying these novel approaches outweighed their uncertainties and limitations.

Chapter 5 The influence of attraction flow on upstream passage of European eel (*Anguilla anguilla*) at intertidal barriers

5.1 Summary

River structures can delay or prevent upstream migration of the critically endangered European eel *Anguilla anguilla*. Eel ladders are frequently installed to mitigate for the impacts of barriers. There has been little quantitative testing to optimise attraction to pass facilities. The effect of plunging and streaming flow on pass efficiency was tested within field trials using four eel ladders at an intertidal weir with little seaward freshwater flow. Eel passage was 2 fold higher in the presence of plunging flow. Water temperature and height of tide were also significant factors influencing daily catch. A strong ‘edge effect’ influenced route choice, with greatest catches in traps positioned at the channel sides. Route choice was related to body size with largest size classes (>121 mm) mostly passing towards the centre of the channel. The findings show that simple manipulation of hydrodynamic conditions at the entrance to upstream eel passes can improve passage efficiency for both juvenile and adult lifestages.

5.2 Introduction

The European eel, *Anguilla anguilla* (Linnaeus, 1758) occurs in estuarine and inland waters throughout Europe, and is of high ecological and commercial importance (Starkie, 2003). Eels have declined markedly across their range, with estimated recruitment reduced in some catchments by as much as 90 - 95% since the early 1980s (Moriarty, 2000; Dekker, 2003). Exact causes remain unclear, although suggested threats include: the swim-bladder parasite *Anguillicola crassus* (Kirk, 2003; Palstra *et al.*, 2007); bioaccumulation of PCBs and heavy metals (Palstra *et al.*, 2006); climate change and long-term shifts in oceanic currents including North Atlantic Oscillation and the Gulf stream (Knights, 2003; Kettle *et al.*, 2008); and overfishing (Briand *et al.*, 2003; ICES, 2006). However, the impact of anthropogenic barriers to migration and subsequent reduction in availability of accessible habitat has been identified as a key factor contributing to population decline (Moriarty & Dekker, 1997; White & Knights, 1997; Feunteun, 2002).

Since 2006 the European eel has been designated as ‘critically endangered’ and the stock considered outside safe biological limits (ICES, 2006; Darwell *et al.*, 2009). In 2007 the European Union adopted Council Regulation 1100/2007/EC, requiring each member state to produce Eel Management Plans (EMP’s) outlining actions to achieve escapement to the sea of at least 40% of the silver eel biomass relative to the best estimate of escapement prior to anthropogenic impact. Many member state’s EMPs highlight mitigation for the effects of riverine barriers and improvements to upstream and downstream passage as key means of achieving escapement targets (e.g. U.K., Denmark, Greece). Furthermore, the EU Water Framework Directive (WFD) (2000) requires that water bodies meet good ecological status, of which unobstructed passage for fish is a key component (Moss, 2004).

From spawning grounds thought to be in the Sargasso sea, larval leptocephali are carried for between 10 months to over 2 years on oceanic currents to the European continental shelf (Schmidt, 1923; Bonhommeau *et al.*, 2009) where they metamorphose into transparent glass eels (70 - 80 mm body length). This lifestage moves up tidal estuaries and rivers using coastal currents and Selective Tidal Stream Transport (STST), rising in the water column to optimise transport on tidal ingress, then moving to areas of least velocity in benthic and littoral zones on tidal egress (McCleave & Wippelhauser, 1987; Briand *et al.*, 2005a), thus maximising distance travelled relative to energy used (McCleave, 1980; Wippelhauser & McCleave, 1988). Fully active migration occurs primarily during spring whereby the now pigmented elvers continue upstream in response to rheotactic and olfactory cues, predominantly at night (Tesch, 2003; Laffaille *et al.*, 2007; White & Knights, 1997). Riverine barriers can significantly restrict or completely prevent eel recruitment into freshwater systems (Moriarty & Dekker, 1997; Feunteun *et al.*, 1998; Knights & White, 1998).

This study considers the intertidal barriers commonly first encountered by eels at the interface between freshwater and marine environments. Tidal barriers for flood alleviation and freshwater retention for abstraction are present in many European catchments. Such structures can foreshorten estuaries, and stop or severely limit STST (Briand *et al.*, 2003; Bult & Dekker, 2007; Laffaille *et al.*, 2007), reduce the olfactory attraction of freshwater in the estuary hindering eel orientation (Crivelli *et al.*, 2008), and weaken water currents and alter orientation factors thought to provide key cues for navigation (Feunteun *et al.*, 2003). Restricted flow may be inadequate to stimulate the positive rheotactic behaviour exhibited by juvenile eels colonising rivers (Gascuel, 1986).

Intertidal or estuarine barriers are an important driver of density dependent mortality in juvenile lifestages (Jessop, 2000; Briand *et al.*, 2003;). The impact of fishing (Briand *et al.*, 2003; Beaulaton *et al.*, 2007), parasites and infectious diseases (Garcia de Leaniz, 2008), and predation (Menzies, 1936; Solomon & Beach, 2004) may increase when eels are delayed downstream of barriers, while elevated energetic costs cause fewer individuals to migrate upstream (Edeline *et al.*, 2006; Du Bureau du Colombier *et al.*, 2007), and high population densities due to accumulation downstream of barriers is also suggested to skew the sex ratio towards a male dominated state (Roncarati *et al.*, 1997; Tesch, 2003).

Effective tidal barrier mitigation has been achieved by allowing controlled saltwater ingress on flood tides (Bult & Dekker, 2007), facilitating continuation of STST during the glass eel stage and more gradual physiological adaptation to freshwater conditions (Porcher, 2002). However, saltwater incursion makes this approach undesirable to catchment managers in many systems. More commonly, eel passage at intertidal barriers is facilitated by the provision of eel ladders which are widespread across Europe and North America. In England and Wales alone, 265 passes have been installed at estuarine and riverine barriers (Andy Don, Environment Agency, pers. comm.). Typically, eel passes comprise of a sloping channel (5˚- 45˚), furnished with mesh or bristle substrate to facilitate climbing, and fed by water diverted from upstream, referred to as the conveyance flow (Knights & White, 1998; Porcher, 2002; Solomon & Beach 2004). Although recovery of upstream eel stocks has been widely reported after pass installation (Briand *et al.*, 2005b; Laffaille *et al.*, 2005), there appears little consensus as to optimum positioning of the pass entrance or “attraction conditions” that should be presented.

Attraction is a crucial component of fish pass effectiveness; a two step process consisting of guidance to the fishway and subsequent entrance (Castro-Santos *et al.*, 2009). Pass design frequently incorporates attraction flow to mimic energy of natural lotic systems, thereby denoting upstream directionality and emulating the hydrodynamic properties of larger quantities of water to outcompete background river flow (Clay, 1995; Nestler *et al.*, 2000). Positive rheotaxis and olfactory detection of salinity gradients and organic components in freshwater are thought to form principal cues for upstream navigation in juvenile eel (Tosi *et al.*, 1990; Briand *et al.*, 2002; Du Bureau du Colombier *et al.*, 2007). It is advocated that delivering a small plunging flow above the surface of the downstream entrance of passes may improve attractiveness and consequently efficiency (Clay, 1995; Porcher, 2002; Solomon & Beach, 2004). The provision of this supplementary flow is not routinely included in eel pass design and lacks quantitative field testing (Solomon & Beach 2004).

To investigate attraction and route selection of upstream migrating eels at a tidal barrier, this study aimed to assess the effect of: i) flow treatment (plunging versus streaming); and ii) trap position, on individual trap catch and size distribution of captured eels. The influence of environmental factors, temperature, tide cycle and flow, on trap catch and size distribution of eels were also assessed.

5.3 Materials and methods

5.3.1. Study site

The River Stour is a lowland river in East Anglia (UK), flowing approximately 98 km to the tidal limit at Manningtree (51°57'10.78"N, 1° 3'14.21"E) with a catchment area of 85.8 km^2. This highly regulated system has over 52 manmade within-channel structures, many of which are considered partial or complete barriers to eel migration by the Environment Agency.

Historic trapping data for the river Stour showed immigration of juvenile eel typically occurs from late March to August, similar to that reported for other UK catchments (Naismith & Knights, 1988; Matthews *et al.*, 2001). Immigrant eels are presented with two possible routes to enter the freshwater Stour catchment. They can pass through a tidal sluice gate at Cattawade North Channel (Fig. 5.1.), but abstraction and flood protection demands require this remains closed throughout much of the peak elver migration. Alternatively, eels can surmount Judas Gap, a 20.80 m wide concrete broad-crest weir, comprising of 4 identical bays with a spill height of 1.80 m above ordnance datum Newlyn (AODN). This structure spans the full width of the South Channel, below which is an intertidal pool with mean depth 3.8 ± 1.2m, varying with tide (Fig. 5.1). Over the last 3 years (2008 - 2010), this weir has on average remained dry for 73% of the key migration period.

A pool and weir fishpass located on the southern end of Judas Gap weir has failed to function effectively since its construction in 1972 due to disparity between its design spill height and maintained river levels. From 2002 -2009 an eel monitoring station (simple trough-type) (see Naismith & Knights, 1988) mounted within the existing fishpass has been operated by the Environment Agency, from March to September. Annual combined glass eel and elver catches ranged from 625 in 2005 to 33771 in 2007. This station was removed prior to the study, in preparation for future installation of a permanent eel pass.

5.3.2 Experimental design

During April to September 2010, 4 elver traps were deployed across the downstream face of Judas Gap intertidal weir, one against either wing wall (hereafter termed left and right bank traps) with the remaining two traps spaced equidistant in the centre of the weir (hereafter termed centre left and centre right traps). Traps consisted of a rectangular fibreglass trough (200 mm width; 100 mm depth; 4.6 m length) with anti-predator cover, fitted to the sloping weir face at a 34 degree angle. The upstream end of the trough projected 1m above the weir crest and terminated in a catch pot (40 x 40 x 60 cm). Climbing substrate was provided by longitudinal strips of netting (Knotless nylon 12 mm diamond mesh) and bristles (nylon 100 mm long, 18 mm spacing), each covering 50% of the channel base. The downstream trough entrance projected to bed level. The proportion of the downstream trough submerged varied (range 14 to 25%) with tidal fluctuation, but was identical for all traps. Submersible pumps situated upstream of the weir (Rule bilge pump 3.14 x 10^{-4} m^3 s^{-1}) diverted a continuous freshwater conveyance flow to the head of the pass and freshening flow to catch-pots (Fig.5.1).

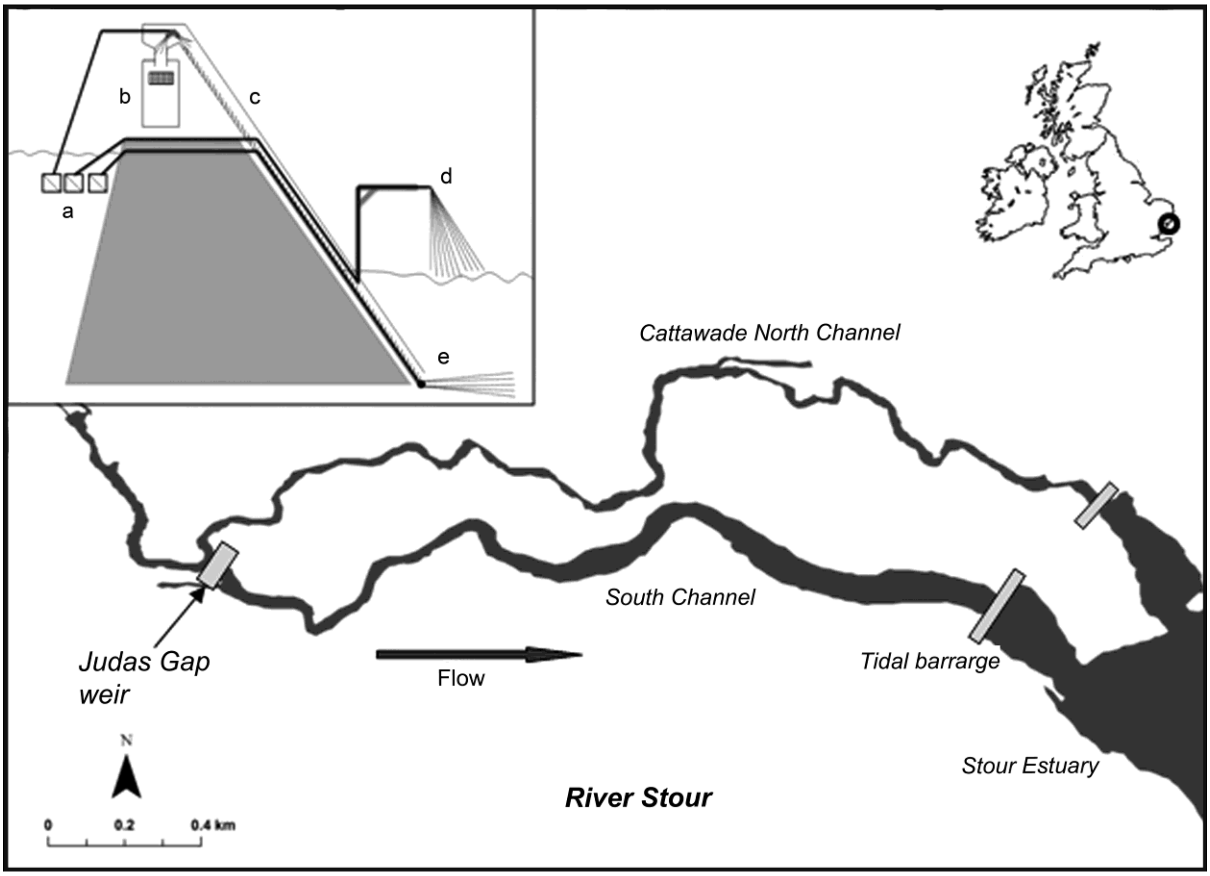


Figure 5.1 The lower river Stour with location of Judas Gap intertidal weir (study site) and tidal control structures on North and South Channels. Insert shows a schematic of the eel trap configuration used within the study (not to scale). Submersible pumps (a) supply conveyance flow to the catch pot (b) and bristle-lined climbing trough (c); and flow to experimental treatments, plunging (d) and streaming (e).

Two alternating treatments; streaming and plunging flow, were created at the base of each pass by means of an additional submersible pump (Rule bilge pump 5.25 x 10^{-4} m^3 s^{-1}). Plunging flow was created by positioning the outlet pipe 1.9 m directly above the downstream end of the trap, with a sprinkler head fitted to the pipe. Submerged streaming flow, was delivered via a spray bar positioned 90˚ across the downstream trough base, discharging through 10 equidistantly spaced downstream facing jets. Attraction flow was maintained constant at 4.97 x 10^{-4} m^3 $s^{-1}$for all traps in both flow treatments. To ensure flow was not reduced over time or between treatments due to algal growth, opaque black pipes were used throughout and flow treatment outlets were cleaned weekly. Maximum velocities created at trap entrances were less than the burst swimming capabilities (sustained swimming for 20 seconds) of eels 60mm TL, the smallest lifestage likely to be found this far upstream (capable of burst swimming at 0.41 ms^{-1} at >11.1°C) (Clough & Turnpenny, 2001). Daily dissolved oxygen concentration and water temperature in the intertidal pool ranged between 5.6 - 15.8 mg L^{-1} and 14.1 - 24.4˚C respectively throughout the study period.

5.3.3 Trapping protocol

Field trials were conducted over 78 days between 3 June and 19 August 2010. Each day, two traps were set as plunging and two as streaming flow treatments. To control for spatial variation in passage approach and possible interplay between adjacent traps, the treatments were rotated on a 6 day programme. This programme was repeated 13 times during the study, yielding 13 'trapping cycles' (Table 5.1).

Table 5.1 All possible configurations repeated on a 6 day programme of the two flow treatments (plunging and streaming) presented at 4 eel traps placed on Judas Gap, an intertidal weir on the river Stour UK.

	Trap position			
6-day cycle	**Right bank**	**Centre right**	**Centre left**	**Left bank**
Day 1	streaming	plunging	streaming	plunging
Day 2	plunging	streaming	plunging	streaming
Day 3	streaming	plunging	plunging	streaming
Day 4	plunging	streaming	streaming	plunging
Day 5	streaming	streaming	plunging	plunging
Day 6	plunging	plunging	streaming	streaming

Eel movement is predominantly nocturnal so traps were checked at 10am daily to collect captures from the previous trapping day and night and therefore avoid the stress associated with holding fish for extended periods at high densities. Eels from each trap were passed through a series of sieves with decreasing mesh sizes to sort into groups (0-80 mm; 81-90 mm; 91-100 mm; 101-120 mm; >121 mm), further hand sorted where necessary, and then counted. A subsample of up to 50 individuals from each category were measured (TL to nearest mm). Processed eels were released 500 m upstream of the weir in an area of low flow velocities to prevent fish being swept back downstream and thus reduce probability of recapture.

5.3.4 Environmental factors

River levels (± 0.01 mAODN) were recorded every 15 mins immediately upstream of Judas Gap by an ultrasonic level measuring device (Pulsar Blackbox, Pulsar Process Measurement, Malvern, UK). The freshwater spill level at Judas Gap was subtracted from recorded river levels to enable number of 15 min overspill periods/24hr trapping period to be calculated.

Prior to the start of the trials, velocity measurements were collected for each flow treatment using an instantaneous 3D Acoustic Doppler Velocimeter (ADV) (Vectrino$^+$, Nortek AS, Rud, Norway) which simultaneously measured instantaneous velocities and standard deviations in three-dimensions (x,y,z). The probe was orientated vertically down and mounted to a boom and offset support assembly, with heavy stationary base to ensure stability and reduce disturbance to the flow field. All 4 traps were simultaneously set to plunging flow treatment and mean downstream velocities were collected at 0.02m from water surface and 0.02m up from pool bed at: 0.05, 0.30, and 1m, then at 1m intervals for 5m downstream of each trap. The procedure was repeated separately for the streaming flow treatment and a control with only conveyance flow and no supplementary attraction flow. Mean downstream (x) velocities and standard deviations were calculated from a total of 3000 (50Hz for a period of 60 seconds) instantaneous measurements, recorded at each sampling point, taken at high tide with no freshwater spill over the weir.

Mean daily water temperatures (˚C) were calculated from hourly data recorded with fixed data-loggers (Tinytag Aquatic T-2100) located in the intertidal pool, 5m downstream of the trap entrances and 0.5m above the channel bed. Maximum tide heights for each trapping day (10am - 10am) were obtained from the UK Hydrographic Office.

5.3.5 Data analysis

Generalised linear models (GLM) with negative binomial error distributions and a logarithmic link function were used to investigate the effect of flow treatment, trap position, flow periods, water temperature, tide height, trap cycle and day within trap cycle on untransformed total daily catch data. First, a model with 1st order interaction terms was fitted. Flow treatment and trap position were specified as fixed factors, and mean daily water temperature, maximum daily tide height, trap cycle, day within trap cycle and number of flow periods (number of 15 min weir spill periods/24hr) as covariates. Stepwise deletions were performed using chi-square tests to identify non-significant terms and reach the model with lowest Akaike Information Criterion (AIC) value (Akaike, 1973). Second, a main effects model without the interaction terms was fitted. This was to assess solely main effects in the case where interactions were significant, but explained a relatively small amount of variance. The minimum adequate model (MAM) was arrived at as the most parsimonious model with lowest AIC value. Appropriateness of the negative binomial error structure was checked using plots of standardised residuals against square root of the fitted values.

GLMs with negative binomial error distributions were used to explore the effects of the fixed factors and covariates on daily mean eel lengths, which were calculated using overall median values for each length category. The MAM was reached using stepwise deletion as above. All analyses were carried out using R v2.11 (R development core team, 2011).

5.4 Results

5.4.1 Flow treatment

During the 78 day study period a total of 14 732 eels were captured, with 0 - 611 individuals captured per trap in a 24hr period (mean 47 ± 85 (S.D)). Flow treatment was an important explanatory variable in the minimum adequate model of daily trap catches (Table 5.2), with the number of eels captured in traps with plunging flow more than double that captured in the streaming treatment; 69% and 31% of total catch respectively.

Table 5.2 The deviance explained relative to null (%), degrees of freedom (df) and significance (p-value) of variables within the Minimum Adequate Model (MAM) fitted to daily trap catch data at 4 eel traps across Judas Gap, an intertidal weir on the river Stour, UK.

Model terms	Deviance explained relative to null (%)	df	p-value
flow treatment + trap position + trap cycle (temporal variation) + mean daily temperature + max. daily tide height + (mean daily temp. * max. daily tide height) + (mean daily temp. * trap cycle)	66.42 (Minimum Adequate Model)		
flow treatment	17.0	1 & 310	<0.05*
trap position	35.4	3 & 307	<0.01*
trap cycle (temporal variation)	9.98	1 & 306	<0.01*
max. daily tide height	1.12	1 & 304	<0.01*
mean daily temperature	0.18	1 & 305	0.244
mean daily temp. * trap cycle	1.69	1 & 302	<0.01*
mean daily temp. * max. daily tide height	1.05	1 & 303	<0.01*

The measured subsets of eels taken throughout the study ranged from 73 to 321mm (TL), with most (66%) in the length category 81-90mm. The smallest category (0-80mm) comprising 20% of the catch corresponded to the glass eel developmental stage, within which individuals began to pigment (pigmented glass eels) towards the last 5 weeks of the study. The fully pigmented elver stage comprised individuals ranging from 81-120mm (78%). Individuals ≥121mm (2%) were classified as yellow eel (adult) stage. Flow treatment was not a significant factor in the minimum adequate model describing length distribution of eels captured.

Mean velocities 20cm (10%) below the water surface for all 4 traps declined from 20.1 cm s^{-1} to 0.9 cm s^{-1}, and 8.7 cm s^{-1} to 0.9 cm s^{-1} from 5cm to 500cm downstream of the traps for the plunging and streaming flow treatments respectively. Mean velocities 20cm (10%) above bed level for all 4 traps declined from 5.4 cm s^{-1} to 0.9 cm s^{-1}, and 19.1 cm s^{-1} to 0.6 cm s^{-1} from 5cm to 500cm downstream of the traps for the plunging and streaming flow treatments respectively. The effect of plunging flow treatment on downstream velocity was detectable above background flow for 3m downstream of the traps at 20cm (10%) below water level, and at 1m downstream at 20cm (10%) above bed level. The effect of streaming flow was detectable for 1m downstream of the trap at 20cm below water level, and for 2m at 20cm above bed level (Fig. 5.2). A surface disturbance (ripple effect) created by the plunging flow was observed as far as 7.4m downstream of the trap entrances; no surface disturbance was observed in the streaming flow treatment.

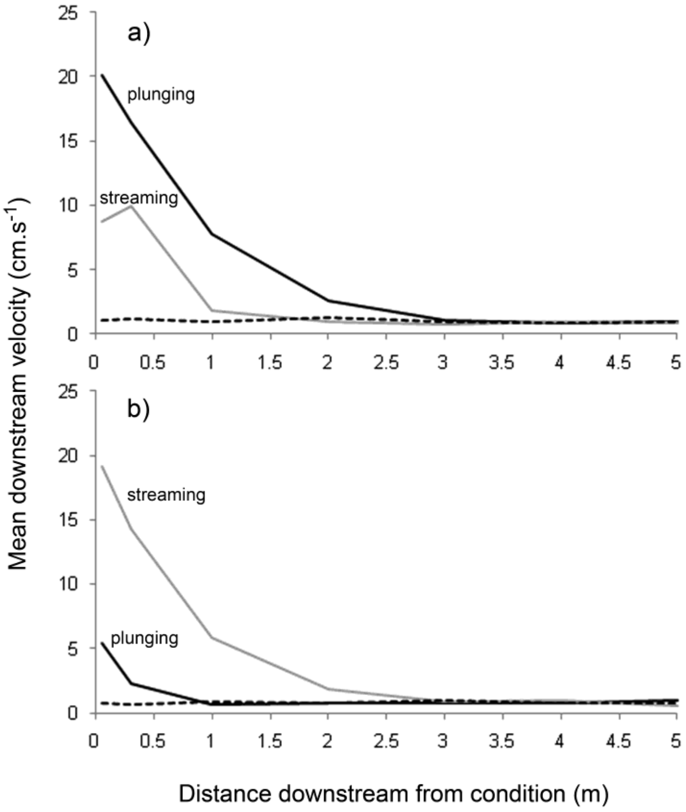


Figure 5.2 Mean velocity downstream of traps with plunging (-) and streaming (-) flow treatments and no treatment(--) for intertidal pool (n=3000x5), measured at water depths 20cm (10%) below surface level (a) and 20cm (10%) above bed level (b).

5.4.2 Route selection

The left bank and right bank traps together captured significantly more individuals (90%), than the two centre channel traps (10%) (F=79.96, P<0.001, 3d.f.). Trap position was the most important explanatory variable in the MAM of daily trap catches explaining 35.4% of residual deviance (p<0.01, 3, 307 d.f.) (Table 2). There was no difference in mean CPUE between the left bank and right bank traps, or between the two centre channel traps. The overall capture ratio of 2.2:1 for plunging to streaming flow treatment, was observed in both bank and centre trap pairs.

Trap position was the only significant predictor of weighted eel lengths in the minimum adequate model, explaining 56.8% of deviance. Glass eels and pigmented elvers smaller than 91mm dominated the catches of the bank-traps, where as yellow eels were mostly captured in the centre traps (Fig. 5.3).

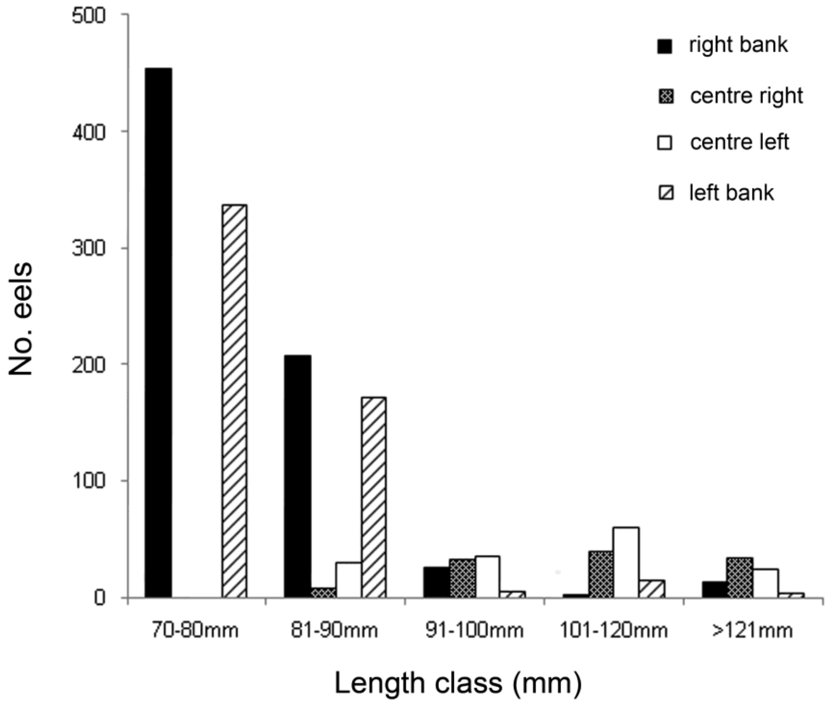


Figure 5.3 Number of eels captured in 4 traps (right bank, centre right, centre left and left bank) at Judas Gap weir, river Stour, through 13 trapping cycles (6-days each), Jun-Aug 2010.

5.4.3. Environmental factors

Temporal variation (trap cycle) explained 10% of variation in trap catch, but day within trap cycle was not significant. Total catch reached a peak within the ninth trapping cycle (21st to 26th July) (Fig. 4) coinciding with onset of water temperatures exceeding 20˚C. Temperatures ranged from 14.1 to 24.4˚C, generally rising through the study period, with overall mean 18.7 ± 4˚C (S.D). The South Channel Barrage limits tidal influx to prevent saline intrusion upstream of Judas Gap, but likely due to the short distance between the barrage and Judas Gap, the effect of tide cycle remained apparent in the trap catch data. Peak catches were found in the periods following highest tide heights; increased temperatures heightened the effect of tide.

There was a tri-modal pattern to catch peaks, with declines in catch during cycles 5, 10 and 12 (Fig. 5.4). Flow over Judas Gap was minimal with freshwater overtopping the weir on 7 out of 78 days and total spill duration only 1.6% of the study period. Freshwater spill over Judas Gap was not a significant predictor of trap catches. Environmental factors were not important influences on the length distribution of eels captured during the present study.

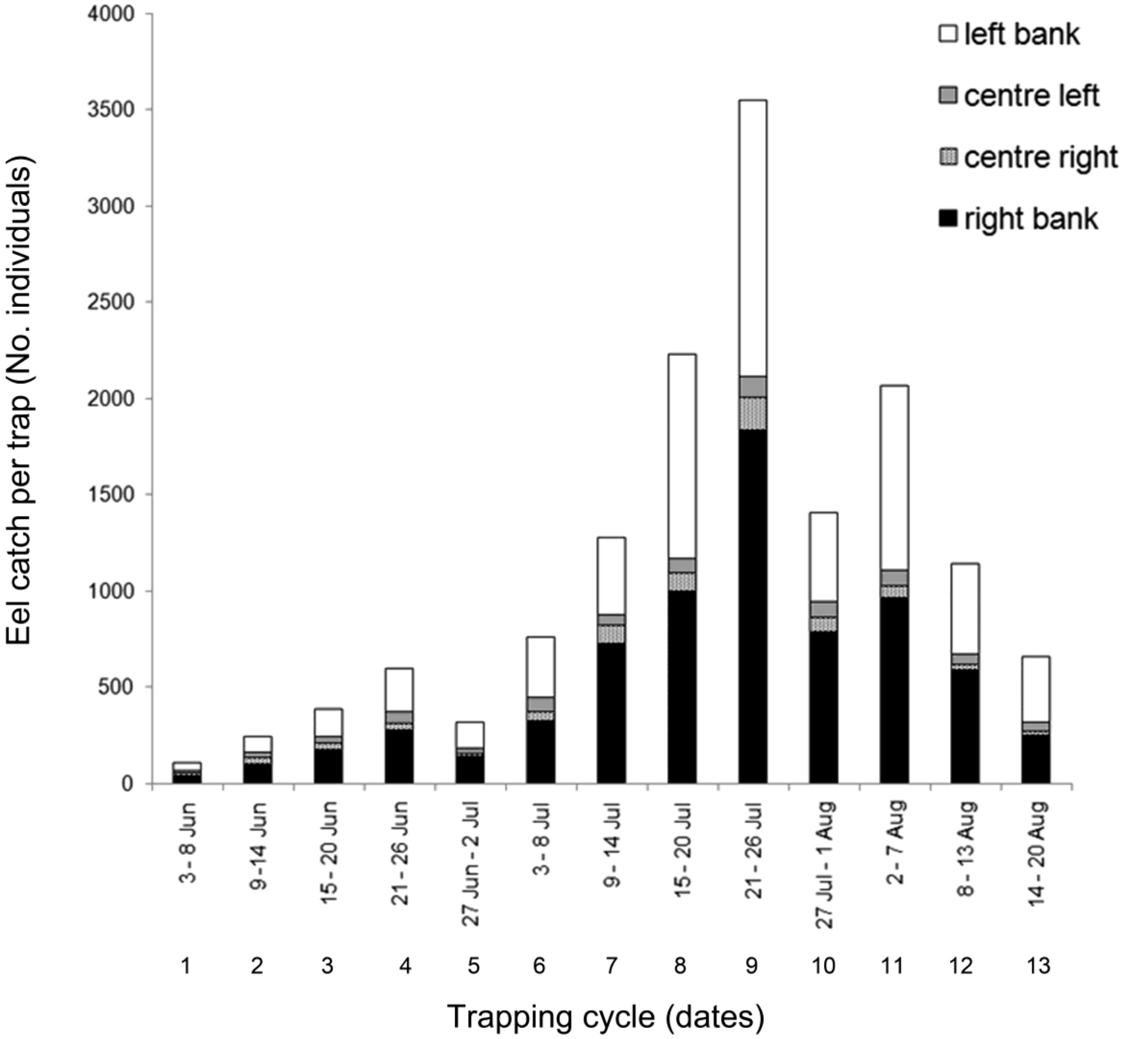


Figure 5.4 Total numbers of eel of 5 length classes captured in 4 traps (right bank, centre right, centre left and left bank) across Judas Gap weir, river Stour, June-Aug 2010.

5.5 Discussion

Eels attempting to pass upstream of Judas Gap weir from saltwater to freshwater habitat were able to do so using the passes installed. A plunging attraction flow resulted in capture of over twice as many eels compared with the streaming condition. The majority of eels were caught in the bankside traps, and these tended to be smaller than those captured at the centre of the weir. Catch was also improved when high tides correspond with high temperatures.

5.5.1 Flow treatment

The importance of providing an attraction flow has previously been recognised, and supplementation of conveyance flow with volumes ranging from 0.005 - 0.02 $m^3 s^{-1}$ have been adopted at a range of eel pass facilities (Solomon & Beach, 2004). Although jetting or plunging attraction flow has previously been advocated (Clay, 1995; Porcher, 2002; Solomon & Beach, 2007), this study provides the first experimental evidence that a simple modification, provision of a plunging flow, can considerably improve attraction efficiency.

The eels were clearly attracted to a single, or combination of, elements (e.g. hydrodynamic, chemical, acoustic or visual cues) created by the plunging flow. In terms of hydrodynamic attraction, the velocity increase created in both flow treatments was localised and depth dependent. It is known that upstream migrating eels exhibit strong rheotactic behaviour, with flow rate and orientation providing important migratory cues (Knights & White, 1998; Feunteun *et al.*, 2003). Juvenile eels have been recorded using all levels of the water column, though early stages are predominantly surface oriented during active swimming in the intertidal zone (Moriarty, 1978; Tesch, 2003). This may explain the higher catches in plunging flow where the area of influence on near-surface velocity was greatest.

High turbulence may have enhanced attraction (and hence capture) at the plunging flow treatment. Although poorly understood for eel, turbulence is considered an important attraction and navigation cue in the riverine migration of salmonids (Coutant, 2001; Katopodis & Williams, 2012). Design recommendations have suggested that the creation of turbulent conditions at the pass entrance may aid attraction of upstream migrating eels (Clay, 1995). Conversely, excessive turbulence may deter upstream migrants and thus restrict passage (Clay, 1995; McGrath, *et al.* 2003).

The two treatments inevitably produced different visual signatures. Plunging flow may have resulted in a stronger visual trace due to bubble entrainment and surface disturbance. However, the importance of visual signals as an eel attractant should perhaps not be overstated as juvenile and adult yellow eel are considered to have poor sight on which they rely little (Tesch, 2003), and upstream migration predominantly takes place when dark (McGrath *et al.*, 2003; Laffaille *et al.*, 2007).

The upstream eel passes such as those used in this study are ineffective at facilitating barrier passage for early phase glass eel, a life stage relying primarily on STST with limited swimming and climbing capabilities (Bult & Dekker, 2007). This, in combination with distance from the sea, explains the absence of this life phase within the trap catches. However, the wide range of sizes caught (73 to 321 mm) highlights the value of these passes in aiding passage for all but the smallest upstream migrants. The physical and hydrodynamic conditions measured in both test treatments were indeed within the burst swim capabilities specified for this range in body size (0.41 ms^{-1} – 1.25 ms^{-1} at >11.1°C, McCleave, 1980; Clough & Turnpenny, 2001; Clough *et al.*, 2002; Solomon & Beach, 2004).

5.5.2 Route selection

The high daily elver catches achieved at bank located traps infers a strong ‘edge effect’ in passage route selection at the barrier. This phenomenon is widely reported and underlies the current convention to position pass entrances along barrier wing walls (Porcher, 2002; Solomon & Beach, 2007). Strong size selectivity was also observed between bank oriented and centre channel traps. Bank oriented upstream migration of juveniles may in part reflect the use of structural features as orientation aids. Due to their relatively short lateral line, juveniles require close proximity to structures to detect them via changes in pressure waves and currents (Tesch, 2003). Although at the study site minimal velocity was created by natural river flow, tidal ingress and egress may have encouraged smaller eels to seek lower velocity refuge near the banks. Littoral zones provide both lower velocities in fluid to solid boundaries layers, shown to be selected by juvenile eel in high flows (Barbin & Krueger, 1994), and offer shelter from predation (Solomon & Beach, 2004). Larger eels, with their greater swimming capabilities and lower predation risk, are able to utilise habitat towards the centre of the channel, with potential advantages such as increased food availability, and reduced competition (Solomon & Beach, 2004). However, this may only be apparent in low flow systems as it has been observed that many fish including eels, shad and salmonid species preferentially select bank-oriented upstream migration routes; a behaviour that is more pronouced during high flow (Larinier, 2002c).

5.5.3. Environmental factors

A number of studies have attempted to model eel recruitment in relation to possible environmental correlates such as tide, moon phase, temperature and flow (Feunteun *et al.*, 2003; Laffaille *et al.*, 2007; Crivelli *et al.*, 2008; Acou *et al.*, 2009) with great variation between different systems. This study also found environmental factors influenced catch as peak catches occurred during the period immediately following high tides, particularly when temperatures were high.

There were few periods where freshwater spilled over the weir and no relationship was found between these and eel catches. It is noteworthy that a monitoring trap located in the redundant fish pass at the southernmost end of the barrier had been operated and checked daily for 2 months prior to commencement of the study, during which there was little freshwater spill and only 6 individuals caught. At the end of the 2 months, dispensation was granted to spill freshwater water for a 4 day period to alleviate low dissolved oxygen levels in the downstream intertidal pool. Oxygen levels rapidly increased during this spill period and 98 eels were captured. Although spill ceased immediately after the 4 days, it was apparently sufficient to induce the main upstream migration recorded. Other work has similarly demonstrated that high freshwater flow events stimulate newly arriving eels, or those settled in the estuary, to migrate upstream (Crivelli *et al.*, 2008; Acou *et al.*, 2009). The lack of relationship between freshwater flow events and catches observed in this study is likely due to the minimal and short duration of spill events.

5.5.4 Management recommendations

The restoration of fluvial connectivity inevitably requires the mitigation of anthropogenic intertidal barriers. Arguably the optimum solution from an ecological perspective is allowing tidal ingress into a catchment to its natural limit, thereby enabling all life stages of eel free passage. The benefits of complete barrier removal have been highlighted by several authors (e.g. Tomsic *et al.*, 2007; Garcia de Leaniz, 2008; Kemp & O'Hanley, 2010), yet with ever increasing pressures to abstract freshwater and manage flood risk it is unfeasible to think all intertidal barriers can be removed or permanently opened.

A number of studies indicate that fish passage at intertidal barriers may be improved through the allowance of partial tidal ingress (Legault, 1990; Mouton *et al.*, 2011), using novel technologies such as siphons to simulate tidal connectivity cycles, but with limited saline ingress (Bult & Dekker, 2007). However, such work also frequently highlights the reluctance of catchment managers and riparian communities to allow tidal ingress; hence the most feasible option in many systems is the provision of fish passage facilities.

Eel ladders are used widely across Europe and North America both on intertidal and non-tidal barriers, and as such optimising their efficacy should be of key importance at any installation. This study confirms the merit of providing additional plunging attraction flow at the entrance of eel ladders. The efficacy of this design feature is expected to be greatest in systems where there is little or no competing background river flow, such as the river Stour, although it is likely to enhance attraction at most upstream eel passes to some degree. Furthermore, this relatively simple feature could be retrospectively fitted to existing passes with little cost and minimal increase in the freshwater loss to sea at intertidal barriers. It is therefore advocated that plunging attraction flow become a standard design feature at upstream eel passage facilities.

The observed dichotomy in passage route among size classes suggests facilities should be provided at both the edges and centre of intertidal barriers to efficiently cater for all lifestages, though larger individuals may use bankside passes if no centre channel facilities exist. If resources limit facilities to a single pass per barrier, this should be positioned at a channel edge to facilitate maximum juvenile immigration. Facilities should, as a minimum, operate throughout the peak juvenile migration period, though preferably remain operational throughout the year to aid individuals making opportunistic or facultative movements (Porcher, 2002; Feunteun *et al.*, 2003; Solomon & Beach, 2004). Where freshwater flow is limited or other restrictions only permit limited operation of passage facilities, precedence may be given to periods around spring tides and at warmer water temperatures.

Further work is required to quantify the efficiency of attraction flow at cross-channel structures that continuously spill water, but still present a restriction or complete barrier to upstream eel migration. In particular, a better understanding of the required volume of plunging flow relative to background weir spill needed to optimise attraction efficiency would be beneficial. It is also necessary to establish if exclusive provision of bank-oriented passes limits the upstream movement of larger eels, as suggested by the size dichotomy observed in the current study.

Chapter 6 The influence of plunging and streaming flow on the upstream movements of juvenile European eel (*Anguilla anguilla*)

6.1 Summary

Fish pass facilities commonly employ elevated flow velocity and turbulence at the pass entrance to attract migrants. The introduction of plunging or streaming (jetting) flow has been advocated to improve the efficiency of passes designed for anguillid eels; however there is incomplete understanding of the swim capabilities and behaviour of eels within turbulent flow, and passage technologies for this species are generally limited. The effect of turbulence and water velocity on the attraction, behaviour and swim capabilities of upstream migrating juvenile European eel (*Anguilla anguilla*) was assessed within an external flume channel. Eels ascending the flume were presented with low and high levels of 1) plunging attraction flow delivered from above, and 2) streaming attraction flow delivered via submerged jets. An additional condition, 3) control, consisting of low turbulent flow was used to determine if eels rejected test treatments. Turbulent plunging flow resulted in a greater than two fold attraction compared to main channel flow. Streaming flow was also attractive but was 30% less effective than plunging flow. Eels increased swim height when passing a point of high turbulence and water velocity, and ascended the flume using paths of lower than average water velocity. Swim speed increased with water velocity, but was not affected by turbulence. There was also evidence that eels rejected areas of high turbulence and selected routes of lower turbulent kinetic energy. The findings suggest that turbulent plunging flow is an effective attractant for upstream migrating juvenile eel, but that high turbulence may impair swim capabilities.

6.2 Introduction

Fish passage facilities are widely employed to mitigate for the loss of fluvial connectivity caused by river infrastructure. Despite a considerable legacy of development, passage facilities frequently perform less efficiently than expected (Roscoe & Hinch, 2009; Bunt *et al.*, 2012). Likely causes for this include a lack of understanding of both the motivational cues and biological constraints of target species, which can lead to ineffective pass design (Bunt *et al.*, 2012; Kemp, 2012). Successful fish passage comprises several key components. Fish must first be attracted or guided towards a pass, and conditions must then encourage entrance and ascent through the facility. Each stage should impose minimal delay, stress, injury and energetic expenditure (Clay, 1995; Lucas & Baras, 2001; Castro-Santos *et al.*, 2009; Williams *et al.*, 2012).

Technical fish passage facilities designed for upstream migrants fundamentally work by the dissipation of energy generated by head through turbulence, with the aim to reduce flow velocities to within the swim capabilities of target species (Castro-Santos *et al.*, 2009). To achieve this, flow is commonly passed via a series of weirs, orifices, pools or baffles (Larinier, 2002a). Many existing passes have been designed to accommodate adult salmonids which are characterised by strong swim capabilities and high motivation (Clay, 1995; Katopodis, 2005). As a consequence, the flow velocities and highly turbulent conditions created may be energetically costly or physically impassable for species with different life history traits, modes of locomotion, and lower swimming capabilities (Lucas & Baras, 2001; Kemp, 2010). For example, the average velocity range of a typical pool and weir fishway is 2.5 – 3.0 m s^{-1} (Clay, 1995), which exceeds the burst swim capabilities for upstream migrating juvenile European eel (*Anguilla anguilla*) (ranging 0.46 – 1.5m s^{-1} for eel 70 mm-150 mm total length, respectively) (Sörensen, 1951; Clough & Turnpenny, 2001).

Turbulence is inherent in all aquatic environments and most simply defined as a flow pattern characterised by chaotic and stochastic changes in velocity. Turbulence is typically at elevated levels around water control structures and fish passes

(Dermisis & Papanicolaou, 2009), and has been linked to increased energetic cost during swimming for several fish species. Lupandin (2005) demonstrated that the swimming speeds of perch (*Perca fluviatilis*) were negatively correlated to turbulence intensity, inferring that increased energetic costs resulted from additional muscle activity for fin deployment necessary to hold position in turbulent environments. Similarly, Atlantic salmon smolts (*Salmo salar*) swum in turbulent flows incurred increased swimming costs compared to those in uniform flows (Enders *et al.*, 2003). Fish may preferentially select areas of low turbulent kinetic energy during upstream passage, as has been shown for Iberian Barbel (*Barbus bocagei*) (Silva *et al.*, 2011).

Conversely, fish may exploit turbulent elements to advance upstream under high flow velocities. Sockeye salmon (*Oncorhynchus nerka*) were suggested to take advantage of small reverse flow vortices (Hinch & Rand, 2000), and rainbow trout (*Oncorhynchus mykiss*) were able to reduce muscle activity, and thus energy expenditure, when utilising features of von Karman vortex streets to hold position in turbulent conditions created downstream of cylinder arrays (Liao *et al.*, 2003; Liao, 2004). As a relatively weak swimming species, European eel may select routes of low velocity and turbulence during upstream migration (Knights & White, 1998; Solomon & Beach, 2007), presumably to reduce energetic cost; yet, due to their limited ability to swim against laminar flow at even low water velocity (McCleave, 1980), it is postulated that they exploit flow heterogeneity to ascend barriers (Porcher, 2002). Eels have been observed attempting to move upstream through technical salmonid passes by utilising fluid-solid boundary layers and turbulent areas (Porcher, 2002). However, no study has quantified the effects of turbulence on the swim capabilities and behaviour of upstream migrating eel.

Turbulent flow may also be employed to attract fish. The volume of water passing via a passage facility typically constitutes only 5-10 % of total river flow, so to provide a sufficient stimulus to attract migrant fish, it is important that the hydrodynamic characteristics at the pass entrance emulate that of a much larger volume of water (Coutant, 2001). Passes designed to facilitate upstream salmonid passage commonly enhance attraction by introducing turbulence near the entrance using flow delivered from above the water surface (plunging), or via submerged jets (Clay, 1995; Larinier, 2002c). The addition of turbulent plunging or submerged flow has similarly been advocated to improve attraction at eel specific passes (Solomon & Beach, 2004). This feature has been adopted at many such facilities (e.g. Whitfield & Kolenosky, 1978), but its influence on attraction has only recently been quantified in the field (Piper *et al.*, 2012). Furthermore, the mechanisms underlying the behaviour and movement of individuals in response to hydrodynamic factors remain unclear; poor understanding of the conditions required to achieve efficient attraction is cited as a principle constraint within current fish pass design (Castro-Santos *et al.*, 2009; Bunt *et al.*, 2012).

Unhindered migration of fish is a key component of watershed management for meeting ‘good ecological status’ under the EU Water Framework Directive (2000) (Moss, 2004; Roscoe & Hinch, 2009). Barriers to migration have been implicated in the decline of the critically endangered European eel (Legault & Porcher, 1990; Moriarty & Dekker, 1997; Feunteun, 2002), hence there is a need to develop effective passage solutions to restore fluvial connectivity for this species. A clear understanding of the swim capabilities and behavioural responses of target species in relation to the hydrodynamics inherent at river structures, including fish passes, is fundamental for the development of effective passage facilities (Castro-Santos *et al.*, 2009; Kemp *et al.*, 2012; Williams *et al.*, 2012). Previous studies have quantified swimming capability metrics for juvenile eel under relatively uniform flow (Sörensen, 1951; Clough & Turnpenny, 2001), and in relation to heterogeneous flow over natural pebble/cobble substrate (Barbin & Krueger, 1994). There remains a need, however, to quantify the effect of hydrodynamic conditions synonymous with structural barriers and passage facilities on the upstream movements and behaviour of juvenile eel. This study aimed to assess the influence of water velocity and turbulence on the movements and swimming capabilities of juvenile European eel as they ascended an experimental flume. It was predicted that eels would: 1) on a coarse scale, be attracted to areas of high turbulence 2) on a fine scale, adjust swim path to exploit low turbulence and velocity routes to ascend the flume, and 3) would move closer to structures as average velocity and turbulence increases to exploit low velocity fluid-solid boundary layers.

6.3 Methods

6.3.1 Experimental flume configuration

Experiments were conducted in an outdoor plexiglass flume (7m length x 0.6m width x 0.6m depth) situated on the river bank, parallel to main channel, of the river Stour at Flatford Lock, Suffolk, UK (51º57´32.57´´N, 1º01´13.76´´E). A Perspex panel (1.5 m length) was used to longitudinally divide the flume at the upstream end, creating 2 equal channels (test channels hereafter), each 29.5 cm wide (Fig. 6.1). Two impeller pumps were used to convey water from the main river channel into a header tank, and provided a constant flow of 0.048 $m^3 s^{-1}$ during all experiments. A honeycomb baffle panel was installed at the outlet of the header tank to smooth the flow as it entered the flume channel. Water depth in the flume was maintained at 30 cm during all experiments by adjustment to the height of an overshot tilting weir at the downstream end.

To test the effect of velocity and turbulence on the movement, attraction and passage of juvenile European eel as they ascended the flume, three flow treatments were created (plunging, streaming and control). Plunging and streaming treatments were designed to create distinctly different hydrodynamic conditions downstream, which persisted below the test channels to varying degrees (Fig. 6.2). Plunging flow was formed by delivering water vertically to the surface through a spray nozzle (2.5 cm diameter) positioned 50 cm above the in the centre of the test channel. Streaming flow was created using a submerged rigid pipe (2.5 cm diameter) located on the base of the flume from which water was discharged via 14 equidistant downstream facing jets which spanned the width of the test channel. Two additional submersible pumps conveyed water from the main river channel to the plunging and streaming treatments under low (2.4 x 10^{-3} $m^3 s^{-1}$), and high (5 x 10^{-3} $m^3 s^{-1}$) flow levels. The control condition consisted of background flow only.

Eel movement was monitored and recorded using five low-lux cameras (Samsung, SDN-550 High Resolution) connected to a viewing monitor and digital recording system. Three cameras were positioned directly above the flume at a distance of 1 m above the water surface to capture longitudinal and transverse fish movements. Due to disturbance to the water surface created by plunging flow, it was only possible to view fish from above in a restricted area (observation zone) which extended from 80 cm downstream of the termination of the crosswall, to 20 cm upstream of the crosswall (1 m longitudinal distance) (Fig 6.1). Additional side-viewing cameras monitored eel movement through the 2 test channels. The filming area was lit using an LED Infrared array emitting light of 850nm wavelength, which is outside the sensitivity of European eel (kmax = 482 nm (Archer *et al.*, 1995; Hope *et al.*, 1998). The white base of the flume was marked with a 10 cm x 10 cm black line grid, to aid accurate determination of eel positions relative to measured hydrodynamic environments (see below).

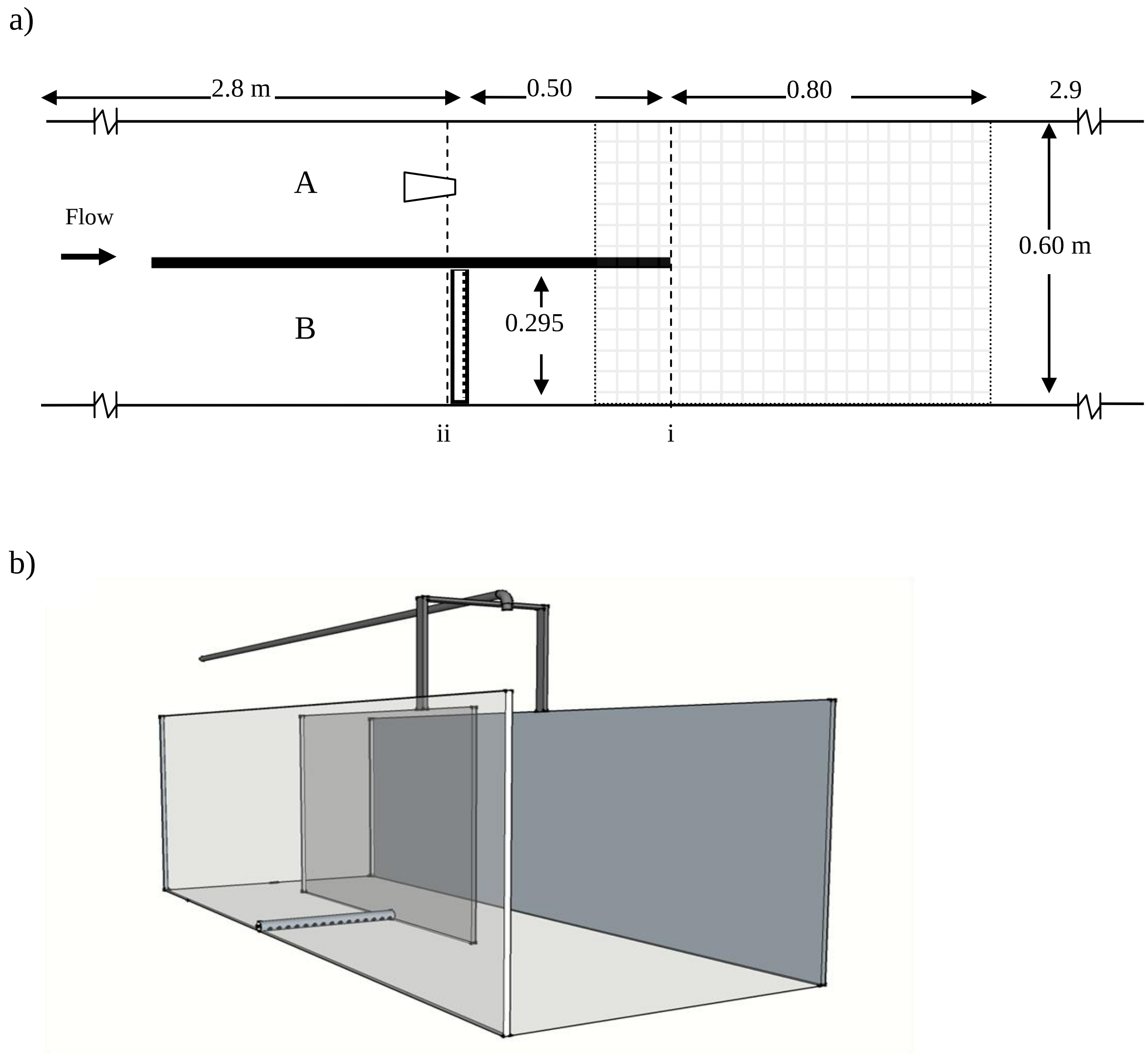


Figure 6.1 a) Plan view of field flume showing test channels with overhead plunging flow (channel A) and submerged streaming jets (B), observation zone (gridded area) and approach (i) and passage (ii) lines; b) Three-dimensional view of field flume with perspex crosswall forming two test channels of equal width, showing submerged jets used to deliver streaming flow and overhead inlet used to deliver plunging flow.

6.3.2 Fish capture and maintenance

Actively upstream migrating juvenile eels were captured using a ladder-pass and trap (see Knights & White, 1998 for description) located at a broad crested weir approximately 400 m downstream of the flume facility. The trap was run overnight and emptied daily (approx. 10 am). Captured eels of a similar size (81- 90 mm TL, mean 84 mm) were transported to the flume facility in a 0.5 m^3 tank filled with ambient river water and maintained in an adjacent holding tank (1.5 m^3) supplied with flow through river water (1 m^3 hr^{-1}). Eels were held for between 10 and 15 hours prior to the start of trials.

6.3.3 Experimental protocol

Trials were conducted during June and July 2011. All trials were undertaken at night (21:00 to 03:00), corresponding to the peak natural migration period (Desrochers & Fleury, 1999). Mean water temperature in the flume ranged from 17.9 to 20.1°C. To control for variation in natural light, and thus visual cues within and between nights, a blackout hide was erected over the facility.

At the start of each night's experimental period, eels were transferred to individual assay tubes (60 mm diameter, 20 mm length) with mesh over each end and held within a floating micromesh cage (5 x 10^{-5} m^3) within the header tank. Test subjects were allowed to acclimate in background flow conditions for a minimum of 1 h before the start of trials.

Before commencement of each trial, a single eel was poured from its assay tube into a micromesh release cage at the downstream end of the flume. Eels were able to exit the cage volitionally through a pipe (50 mm diameter) opening at bed level in the channel centre, at a location 3.2 m downstream of the entrances to the test channels, and the trial was deemed to have started when the eel left the cage (as observed from live video images). Trials ended either when the eel passed the condition i.e. crossed the 'passage line' (Fig.6.1), or after a maximum of 15 minutes. On completion of each trial, eels were recaptured and removed from the flume. Each eel was used only once during the study.

A total of 180 trials were conducted. Each trial presented a pairwise choice between 2 of the test treatments (plunging, streaming and control), under 2 flow levels (low, and high), yielding 6 test configurations with 30 replicates of each (Table 1). Treatments and flow levels were alternated throughout the experiments to minimise temporal and lateral bias.

Table 6.1 Summary of flume trials conducted to test the effect of plunging and streaming attraction flow under two flow levels (low and high) on juvenile eel movement and behaviour, June – July 2011.

Treatment	**Flow level of plunging/streaming flow**	**No. replicates**
Plunging flow *vs* streaming flow	Low	30
Plunging flow *vs* streaming flow	High	30
Plunging flow *vs* control	Low	30
Plunging flow *vs* control	High	30
Streaming flow *vs* control	Low	30
Streaming flow *vs* control	High	30

6.3.4 Hydrodynamic mapping

Velocity measurements were collected using an instantaneous 3D Acoustic Doppler Velocimeter (ADV) (Vectrino$^+$, Nortek AS, Rud, Norway) oriented vertically down. Measurements were taken at 5 cm longitudinal and lateral intervals from 10 cm downstream of the plunging and streaming delivery points, to 1.4 m downstream of test channels. Additional measurements were taken within 3 cm of the main channel and test channel walls, at 5 cm longitudinal spacing. Measurements were taken at a water depth of 25cm, representing the bottom 17% of the water column as pilot studies indicated that eel movement was predominantly benthic orientated within the observation zone. Preliminary tests were used to determine the minimum sampling period required at each point for accurate determination of mean velocity (*V*) and turbulent kinetic energy (TKE). TKE is a measure of the kinetic energy of velocity fluctuations, i.e. greater fluctuation from the mean velocity represents greater TKE, and has been linked previously to fish behaviour (e.g. preference for areas of low

TKE, Silva *et al.* 2010). Velocity measurement was conducted at 50 Hz, for a set sample volume of 0.31 cm^3 and for a period of 60 seconds, yielding a total of 3000 instantaneous measurements at each sampling point.

The ADV simultaneously measured instantaneous velocities and standard deviations in three-dimensions (*x*,*y*, *z*) at each sample point, enabling calculation of mean velocity and turbulent kinetic energy profiles for the flume area downstream of the attraction flow inputs. The mean velocity vector was calculated for each sampling location by incorporating the three planes of water velocity using the equation:

$$V = \sqrt{(\bar{u}^2 + \bar{v}^2 + \bar{w}^2)}$$

where $\bar{u}, \bar{v}$ and $\bar{w}$ are mean longitudinal, lateral and vertical components (m s^{-1}). Vector data were then processed using a macro within Microsoft Office Excel, with a velocity correlation filter employed to remove spurious data and outliers (Cea *et al.*, 2007). TKE (J m^{-3}) was calculated as:

$$TKE = 0.5\rho(\sigma_u^2 + \sigma_v^2 + \sigma_w^2)$$

where ρ is water density (1000 kg m^{-3}) and σ_u , σ_v and σ_w are standard deviations of the longitudinal, lateral and vertical velocities.

After filtering, ADV data were imported into ArcGIS v10 (ESRI, Redlands, USA) for production of *V* and TKE plots. Values were interpolated across a plan of the measurement area to create raster V and TKE datasets for each treatment configuration using the ‘splines with barrier’ function.

6.3.5 Quantifying fish movements and behaviours

After leaving the release cage eels could either move upstream towards the test channels, or downstream. Video footage of eels that entered the observation zone was processed using LoggerPro v3.8.2 (Vernier Software, Beaverton, USA). The ‘approach’ and ‘passage’ treatments and times for each eel were determined. An eel was considered to have approached a treatment when its head crossed the approach line of the test channel (i, Fig. 6.1), and to have passed the treatment when its head crossed the passage line (ii, Fig. 6.1). Passage time denotes the time elapsed between start of the trial and passage. The swimming heights of eels at both the approach and passage lines were recorded as head height in the water column (height above channel floor, cm). Eels that did not pass either treatment by the end of the 15 min trial (n = 13), even if they had entered the observation area, were excluded from the dataset.

Swim paths were manually tracked by marking eel head positions on a frame-by-frame basis. The *xy* coordinates of tracks were exported to ArcGIS v10 and used to determine the following:

Proximity to structures - A buffer was drawn 5 cm inside all flume walls within the observation zone and the proportion of each swim path falling within the buffer calculated.

Hydrodynamics encountered – Eel swim paths were overlain on the appropriate V and TKE plots and the cell values underlying each head position were extracted. To test whether eels were selecting routes of significantly higher or lower V and TKE than that expected for random ascent through treatments, swim paths were compared to an equal number of random swim paths generated using the Correlated Random Walk (CRW) facility in Hawth's tools v3.24 (Beyer, 2009). The CRWs were generated using step length and turn angle distributions with mean and standard deviation values calculated from the actual swim paths, and were informed by a counter-streamwise compass persistence to ensure that all 'random fish' ascended the flume. Due to software limitations in boundary constriction, only within-flume CRW paths were retained for analysis. The CRWs were overlain on V and TKE plots in ArcGIS and cell values extracted as for the eel swim paths.

Swim speed - The distance travelled between successive video frames (frame distance) was calculated for each individual using the change in *xy* coordinates of the head position generated during manual tracking. Mean ground speed for each frame was calculated using frame distances and time between frames (0.08 s). Mean ground speed per frame was adjusted to swim speed per frame by the addition of water velocity at the appropriate location.

6.3.6 Statistical analysis

Chi-squared tests were used to test for treatment preference during approach and passage.

Continuous datasets were assessed for normality before analyses through examination of departure from normal quantile - quantile plots and Shapiro-Wilk test.

Generalised linear models (GLM) with quasipoisson error distributions were used to test the effect of fixed factors: treatment (plunging, streaming or control); trial type (e.g. stream v control), and flow condition (low or high), along with all first order interaction terms on swim height at approach and swim height at passage. Non-significant terms were deleted stepwise to reach the minimum adequate model. Model fit was assessed using plots of standardised residuals against square root of the fitted values.

Passage time (s) were log-transformed to obtain normality and a two-way ANOVA with post-hoc Tukey’s HSD test was used to test for differences in passage time between eels that passed under the 3 treatments, and under low and high flows.

A two-way ANOVA with post-hoc Tukey’s HSD test was used to test for differences in mean swim speed of eels that passed under the 3 treatments, and under low and high flows.

Linear regression was used to investigate the relationship between mean velocity and TKE and the mean swim speed of eels (adjusted for water velocity), using pooled data from all trials and flows.

To compare the V and TKE encountered by eels to the random paths generated by CRW, average V and TKE values along each path were calculated. Mann-Whitney tests were used to compare mean values for eels to random paths within the same treatment and flow level.

All statistical analyses were carried out in R v2.14 (R development core team, 2011).

6.4 Results

6.4.1 Hydrodynamic conditions

The addition of plunging and streaming flow created elevated velocities and TKE in the vicinity of the outlets which persisted downstream beyond the end of the test channels. This persistence was more apparent under high flow (Figs. 6.2 and 6.3). The highest velocities within the observation zone were within the streaming treatment test channel under high flow (0.34 m s^{-1}), and the highest TKE within the plunging treatment under high flow (31.65 J m^{-3}). The control treatment channel was characterised by comparatively uniform flow with velocity range (0.04 to 0.11 m s^{-1}) and TKE (0.24 to 4.56 J m^{-3}) (Table 6.2).

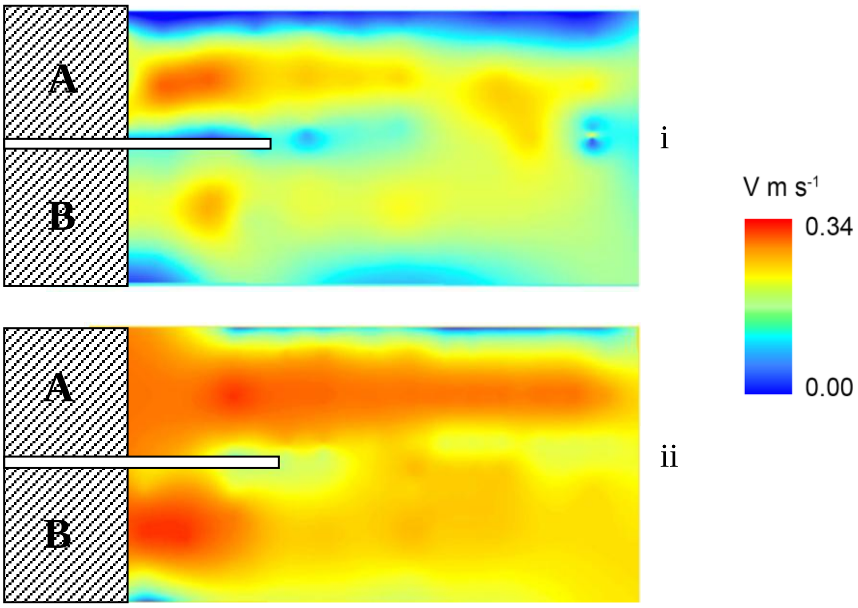


Figure 6.2 Plan view velocity (m s^{-1}) plot at 83% water depth in an experimental field flume under low (i) and high (ii) flow conditions. Channel A - streaming treatment; Channel B - plunging treatment.

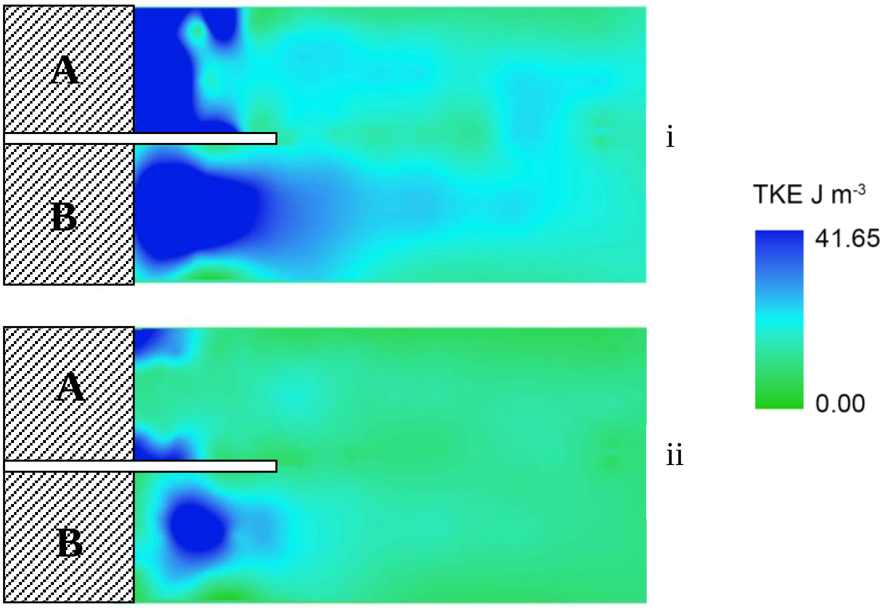


Figure 6.3 Plan view turbulent kinetic energy (J m^{-3}) plot at 83% water depth in an experimental field flume under low (i) and high (ii) flow conditions. Channel A - streaming treatment; Channel B - plunging treatment.

Table 6.2. Mean velocity and turbulent kinetic energy for the observation zone extending 30 to 130 cm downstream from plunging and streaming flow points, and each longitudinal half corresponding to individual test treatments (plunging, streaming and control).

Flow Level	Trial	Location	Mean V ($m s^{-1}$)	Range V ($m s^{-1}$)	Mean TKE ($J m^{-3}$)	Range TKE ($J m^{-3}$)
Low	**Plunging v streaming**	Whole observation zone	0.14	0.03 – 0.18	4.78	0.35 – 14.6
		Plunging route	0.12	0.03 – 0.15	5.23	0.64 – 14.6
		Streaming route	0.15	0.06 – 0.18	4.33	0.35 – 7.37
	Plunging v control	Whole observation area	0.10	0.04 – 0.15	4.29	0.32 – 16.1
		Plunging route	0.11	0.05 – 0.15	6.67	0.40 – 16.1
		Control route	0.09	0.04 – 0.11	1.91	0.32 – 4.56
	Streaming v control	Whole observation area	0.11	0.03 – 0.19	3.28	0.45 – 8.59
		Streaming route	0.14	0.06 – 0.19	4.69	0.53 – 8.59
		Control route	0.09	0.03 – 0.12	1.88	0.45 – 4.25
High	**Plunging v streaming**	Whole observation zone	0.17	0.04 – 0.34	9.25	0.83 – 31.65
		Plunging route	0.14	0.04 – 0.19	11.93	0.97 – 31.65
		Streaming route	0.19	0.05 – 0.34	6.56	0.83 – 14.3
	Plunging v control	Whole observation area	0.12	0.01 – 0.23	5.80	0.36 – 29.42
		Plunging route	0.14	0.02 – 0.23	10.42	0.97 – 29.42
		Control route	0.08	0.01 – 0.10	1.18	0.36 – 4.25
	Streaming v control	Whole observation area	0.14	0.02 – 0.34	3.91	0.24 – 16.7
		Streaming route	0.20	0.05 – 0.34	6.62	0.43 – 16.7
		Control route	0.08	0.02 – 0.10	1.19	0.24 – 4.20

6.4.2 Approach and passage route

Eels showed greater than two fold attraction towards the plunging and streaming treatments, compared to the low turbulence (control) condition, under both low and high flows (Fig. 6.4). When eels were presented with a pairwise choice between plunging and streaming treatments, more approached plunging, under both low ($X^2 = 3.85$, $p = 0.05$, 1 d.f.), and high ($X^2 = 12.4$, $p < 0.01$, 1 d.f.) flows.

Under low flow, more eels passed via the plunging (n = 39), and streaming (n = 35) treatment channels relative to control (n = 11) ($X^2 = 16.18$, $p<0.01$, 2 d.f.) (Fig. 6.4). There was no difference in the total number of eels passing via each treatment under high flow ($X^2 = 2.42$, $p = 0.23$, 2 d.f.). While there was a similarly high attraction to plunging under both flow levels, under high flow many fish were observed moving back downstream and subsequently selected and passed via the alternate channel.

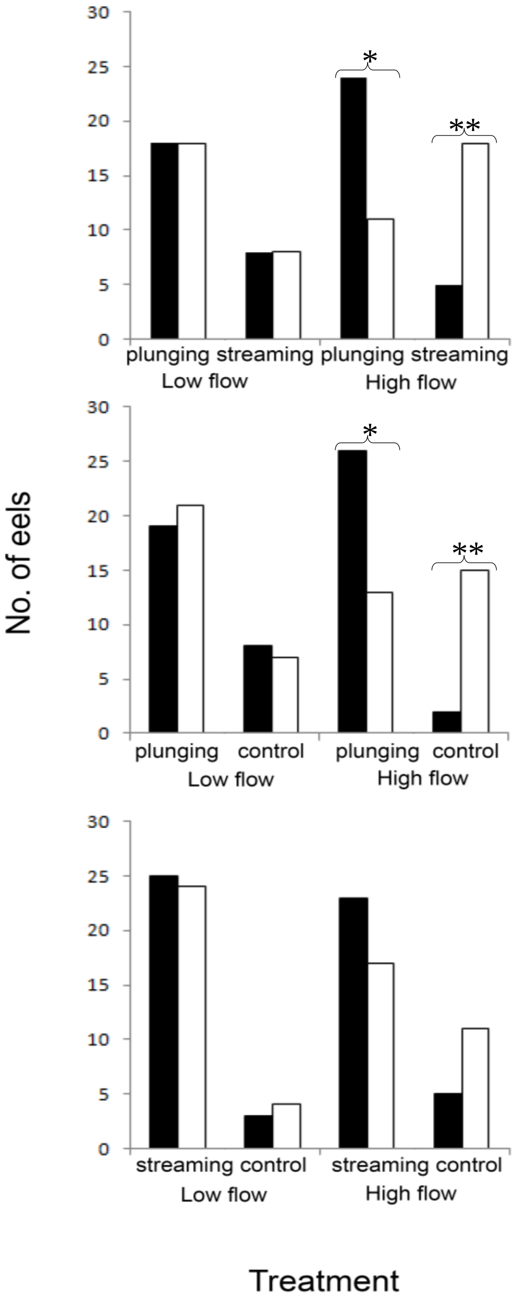


Figure 6.4 Selection of treatments by eel during approach (solid bars) and passage (clear bars) within paired tests (n = 30) under low and high flow conditions. (*) and (**) denote observed values significantly different from expected at 0.05 level, and 0.01 level respectively (chi-squared test).

6.4.3 Swim height above channel floor

Swim heights at approach and passage did not vary between trials under the same treatment, independent of pairing, so data were pooled.

Eel movements were predominantly benthic oriented for all treatments at low flow. Swim height at approach did not vary between treatments or between low and high flow levels (Fig. 6.5). There were two significant predictors of swim height at the passage point: treatment (28.9% residual deviance, $p < 0.01$, 2,162 d.f.), and the interaction between treatment and flow level (7.18% residual deviance, $p < 0.01$, 2,160 d.f.). In plunging treatment under high flow, approximately 70% of eels displayed a propensity to rise in the water column either before, or on reaching, the passage line (Fig. 6.5). Eels were frequently observed near the water surface, swimming with an exaggerated anguilliform undulation and often with their heads breaking the water surface. This behaviour was not observed for eels under the streaming treatment, as these fish tended to rise only to the mid water column.

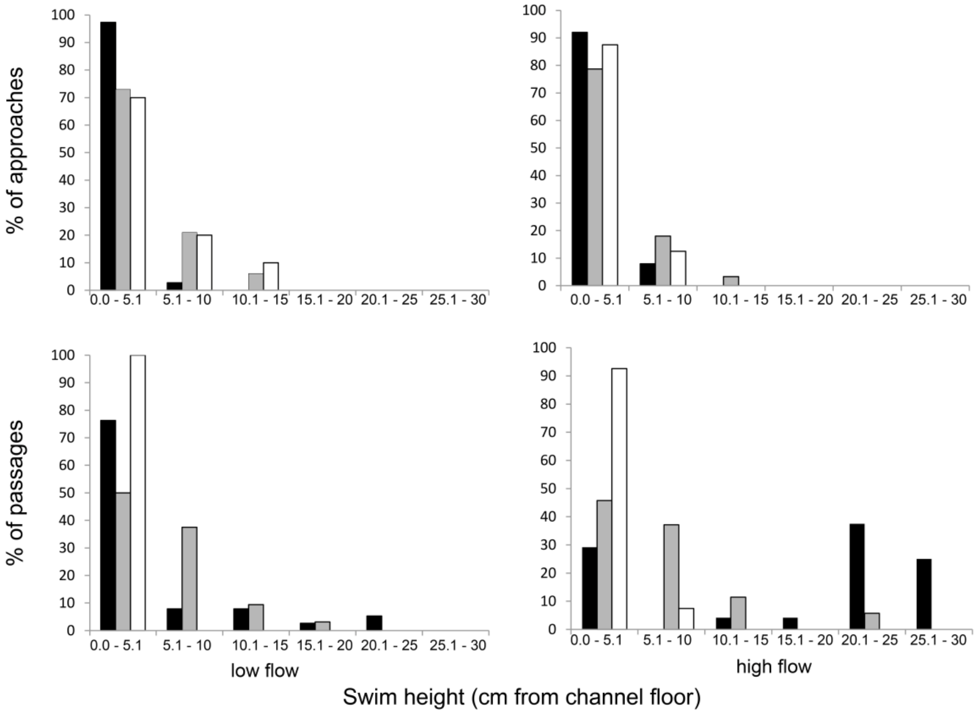


Figure 6.5 Swim height of juvenile eel above the channel floor (cm) at approach and passage when ascending test treatments: plunging flow (black bars); streaming flow (grey bars), and control condition (clear bars), under low and high flow conditions within an experimental flume.

Eels were more frequently associated with the flume walls when flow was high, with on average more than half of the swim paths (mean 53 ± 24 %, ± S.D.) within 5 cm. When flow was low, eels were in close proximity to the flume walls for on average 22 ± 14 % (± S.D.) of their path through the observation zone.

6.4.4 Time to passage

Eels that selected and passed the plunging treatment took less time (48.2 ± 42.5 s, S.D.) than those that passed the control (76.7 ± 69.6 s, S.D.) (F = 6.19, $p<0.01$, 2 and 76 d.f.). Mean passage time under streaming did not differ from plunging or control treatments (52.9 ± 31.8 s) ($p = 0.21$ and $p = 0.29$, respectively). For both plunging and streaming treatments, fish passed more quickly under high, compared to low flow (F = 10.20, $p<0.01$, and 156 d.f.). Passage times for the control treatment were similar for low and high flow (mean 80.83 ± 77.3 s within low, and 74.3 ± 65.3 s within high).

6.4.5.Swimming speed

The mean swimming speed of eels that passed via the streaming and plunging treatments was significantly higher than those passing via control (F= 3.6, $p<0.05$, 2 and 164 d,f), and eels swam faster when the flow was high (F= 7.8, $p<0.01$, 1 and 164 d.f.). Swim speed was positively correlated with mean water velocity encountered along the swim path ($b=3.20$, $r^2 = 0.53$, $p<0.01$) (Fig 6.6), but there was no relationship with mean TKE ($b=0.09$, $r^2 = 0.02$, $p=0.08$).

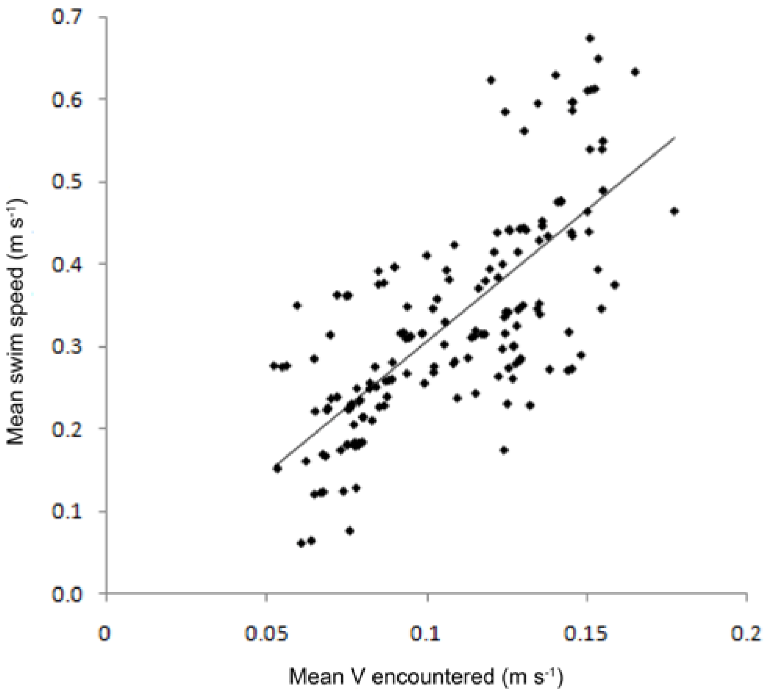


Figure 6.6 Mean swim speed of individual eels in relation to the mean velocity (V) encountered along their swim path during ascent of an experimental flume.

6.4.6 V and TKE encountered

When flow was high, eels selected routes of lower velocity than random paths under both plunging and streaming treatments, but only under the plunging treatment when flow was low. Swim paths under the control did not vary from random paths for velocity or TKE. When flow was high, eels selected routes of lower TKE than random under the plunging treatment.

Table 6.3. Mean velocity (V) and turbulent kinetic energy (TKE) encountered by eels that passed 3 test treatments plunging, streaming and control (clear bars), under low and high flow conditions, compared to random swim paths.

Treatment passed	**Flow**	**Sample size**	**Mean V (m s^{-1})**		**Mann-Whitney U Test**	**Mean TKE (J m^{3})**		**Mann-Whitney U Test**
			Eels	Random		Eels	Random	
Plunging	low	39	0.08	0.10	P = 0.11	3.91	4.54	P = 0.13
Streaming	low	32	0.09	0.14	P = 0.02 *	3.99	4.29	P = 0.43
Control	low	11	0.08	0.09	P = 0.18	0.90	1.65	P = 0.21
Plunging	high	24	0.10	0.13	P <0.01 *	7.60	10.47	P <0.01 *
Streaming	high	35	0.15	0.19	P = 0.01 *	4.83	5.85	P = 0.09
Control	high	26	0.09	0.07	P = 0.19	1.04	1.31	P = 0.15

6.5 Discussion

Fish passes are commonly provided in an attempt to mitigate for the negative impacts of anthropogenic barriers on migratory fish such as the European eel. Attraction is an important component of the overall effectiveness of upstream fish passes and is considered a principle limitation to the efficacy of current fish pass design (Larinier, 2002b; Castro *et al.*, 2009). Turbulence is suggested to be important for attracting migrants to fish pass entrances (Clay, 1995; Larinier, 2002c), though may have both positive and negative effects on fish swim capabilities (Lupandin 2005), energy expenditure (Enders *et al.*, 2003), and ability to ascend fish passed against high velocities (Clay, 1995). This study addressed the effect of turbulent plunging and streaming flow on the attraction and movements of upstream migrating juvenile eel.

Relatively few studies have investigated the effect of magnitude and characteristics of turbulent flow on attraction and passage efficiency at fish passes (Bunt *et al.*, 2012). This study demonstrated that turbulent flow, delivered via an overhead plunging source or from submerged jets along the channel bottom, increased attraction efficiency and reduced the time taken for eels to ascend the flume. The increased velocity and TKE created downstream of treatments may have provided the stimuli needed to induce eel ascent of the test channel, with attraction being improved under both treatments. This finding highlights the potential of provision of plunging or jetting turbulent flow to attract juvenile eels to fish passes, as is already commonly adopted for salmonids (Clay, 1995; Larinier, 2002c). However, the higher attraction than passage rates observed under high plunging flows suggests that swim performance was challenged during this condition.

Eels are predominantly benthic-oriented. This allows relatively weak swimming species to exploit the low velocities at the substrate-water interface, thereby minimising energetic cost during upstream movements (Barbin & Krueger, 1994). In this study eels moved primarily within the lowest 5cm of the water column when approaching all treatments, as is commonly observed in laboratory studies under uniform flow (Clough *et al.*, 2002). However, a significant departure from this behaviour was observed when eels encountered plunging and streaming high flow treatments, where more than half of individuals entered the mid or surface water column at the point of passage; this was rarely observed under the control condition. Unfortunately it was not possible to measure water velocities corresponding with the positions where individuals rose in the water column, so interpretation of the hydrodynamic parameters potentially causing this behaviour is limited. In a natural environment eels may encounter plunging or jetting flows at water discharge pipes, weirs, culverts and undershot sluice gates. Findings suggest that such turbulent flow may elicit a departure from benthic oriented swimming in upstream migrants, which may incur energetic cost and increase susceptibility to avian predation (Menzies, 1936; Matthews *et al.*, 2001).

Eels showed a greater propensity to ascend the flume close to the channel walls under high flow, and frequently made contact with structures. Exploitation of lower velocity at the fluid-structure boundary has previously been reported for juvenile American eel (Barbin & Krueger, 1994), and may represent an energy saving strategy employed by shallow bodied organisms in lotic systems (Vogel, 1994). This finding supports field observations of juvenile eel orienting towards river banks and structural features, such as wing walls at weirs and dams when migrating upstream (Knights & White, 1998; Tesch, 2003; Piper *et al.*, 2012), and emphasises the need to locate passage facilities at channel edges to optimise guidance of juvenile eels to the entrance (Porcher, 2002; Solomon & Beach, 2007).

Eels increase swim speed linearly as water velocity increases (Barbin & Krueger, 1994, for juvenile American eel; McCleave, 1980, for European eel), presumably as a strategy to pass through energetic environments as rapidly as possible (Hinch & Rand, 2000; Peake, 2004; Standen *et al.*, 2004). Alternatively, this may reflect increased motivation due to rheotactic cues (Bolliet & Labonne, 2008; Bureau du Colombier *et al.*, 2009). At higher swim speeds fish are better able to stabilise in turbulent flow due to both the increased momentum and energy of the fish, and reduction in perceived eddy size (Adrian *et al.*, 2000; Webb & Cotel, 2010). Thus, fish may increase swim speed to enhance stability in turbulent flows. Eels in the current study increased swim speed as a response to increased water velocity, but not TKE. However, the TKE levels measured within the observation zone were relatively low compared to similar studies (e.g. Silva *et al.*, 2011; Odeh *et al.*, 2002).

Examination of detailed swim paths through the observation area indicated that route choice was based on water velocity, and in the case of plunging flow, TKE. On a coarse scale, eels were attracted to ascend treatments of higher velocity and TKE; yet on a fine scale eels selected routes which minimised the magnitude of these components exposed to. The fitness and survival of fish undertaking long distance migrations may depend on minimising exposure to energetically expensive environments (Leonard & McCormick, 1999; Edeline, 2007). In the current study, individuals selected routes of lower velocity and TKE than would be expected by random upstream movement, presumably to maximise distanced travelled per unit of energy expended (Hinch & Rand, 1998). There was no evidence to support the suggestion that eels exploit features of turbulent flow to help ascend against high water velocity. However, it is acknowledged that the maximum velocities created were below burst swim capabilities for the size of eel studied (Sörensen, 1951; Clough & Turnpenny, 2001).

Attraction is an important component of the overall effectiveness of upstream fish passes (Larinier, 2002a), and it is suggested that turbulence, even at low intensity, may provide a behavioural cue that enhances fish detection of flow direction (Coutant, 2001). This work indicated that plunging and streaming flow provides effective attraction for juvenile eel, with plunging eliciting the greatest response. However, eels were also deterred by the highest levels of turbulence, which may indicate a trade-off for fish pass design between providing sufficient attraction, without exceeding the swim capabilities of target fish (Laine *et al.*, 1998; Bunt *et al.*, 1999; Aarestrup *et al.*, 2003; Pratt *et al.*, 2009). Further to providing effective attraction, it is important that hydrodynamic conditions within the passage facility allow rapid ascent without imposing high energetic costs. Findings from this study suggested that air-entrained turbulent flow may have a negative impact on the passage of juvenile European eel. Eel passes are widely employed to mitigate the impacts of fluvial barriers on upstream migration. This study highlights the potential of adapting hydrodynamic conditions to improve the attraction and passage efficiency of both eel-specific and multi-species pass facilities. Enhancing freshwater recruitment and habitat accessibility is key to meeting legislative targets and reversing the decline in eel stocks.

Chapter 7 Escapement, route choice, barrier passage and entrainment of downstream migrating European eel, *Anguilla anguilla*, within a highly regulated lowland river

7.1 Summary

Fluvial disconnectivity can have important impacts on fish populations, including hindering movement between habitats required for different ontogenic stages. Recruitment of the European eel (*Anguilla anguilla*) has reduced by over 90% since the early 1980's, in part due to the effect of riverine barriers on its catadromous migration. There is a legislative requirement to restore free passage, increase habitat availability, and limit anthropogenic losses at intakes to aid eel recovery and good ecological status; necessitating an improved understanding of underlying processes. Escapement, route choice, delay at structures, and entrainment at water abstraction points of downstream migrating silver eels were examined using acoustic and Passive Integrated Transponder (PIT) telemetry in the heavily regulated lower river Stour, UK. Downstream migrating adult eel (n = 69) were trapped approximately 10 km upstream of the tidal limit, surgically implanted with an acoustic transducer and PIT transponder, and released between October and December in 2009 and 2010. Movements of tagged individuals were monitored by a linear array of 19 fixed acoustic receivers extending from the release site, through the last 9.2 km of the freshwater catchment. Three groups of water control structures, two water abstraction intakes and several possible routes of migration are present in the reach. Seventy six and 65% of tagged eels escaped from the study reach in 2009 and 2010, respectively. Entrainment at a single intake was the principal cause of loss and positively related to rapid increases in abstraction whilst eels were in the vicinity of the intake. Route choice into the estuary was dependent on discharge over a large intertidal weir; opening regimes of a tidal gate at the termination of the alternative channel; and abstraction rate at a nearby water intake. Long delays (up to 68.5 days) and recurrent behaviour were associated with several structures in the study reach; high variability between individuals reflected the management of spill at weirs. Potential scenarios for minimising entrainment and delay through integrated management of water level control structures and abstraction rates are discussed

7.2 Introduction

Fluvial ecosystems have been impacted globally by the construction of in-channel structures such as weirs and dams for water regulation and flood defence; abstraction for consumptive water; hydropower generation, and navigation (Jungwirth, 1998; Nilsson *et al.*, 2005). The consequences, including disrupted flow regimes, changes to water chemistry, and altered geomorphology are widely documented (Ward & Stanford, 1995; Poff *et al.*, 1997; Opperman *et al.*, 2010). The impact of in-channel structures on fish communities can be considerable. Obstructions hinder movement between the habitats required for different ontogenic stages (Werner & Gilliam, 1984; Northcote, 1998; Lucas & Baras, 2001), which has been directly linked to loss of populations and occasionally entire species of fish (Nilsson *et al.*, 2005). Furthermore, while the impact of certain structures such as dams are well studied, the implications of smaller features such as weirs, ramps, culverts and road bridges on fish populations are rarely considered by catchment managers, although they are likely to be 2-4 orders of magnitude more numerous than large structures (Lucas *et al.*, 2009).

The focus of research into barrier impacts on fish migration has historically been biased towards restoring connectivity between growing and spawning habitats for anadromous salmonids, influenced by economic and social drivers (Clay, 1995; Roscoe & Hinch, 2009). The perceived high abundance of the European eel (*Anguilla anguilla*) prior to the early 1980’s, coupled with highly variable life-history traits and habitat use (Daverat *et al.*, 2006), has meant the impact of barriers on the species is poorly understood and has, until recently, received little attention. Recruitment in some parts of Europe has reduced by 90% since the early 1980's (Moriarty, 2000; Dekker, 2003; ICES 2011a), and the stock is now considered outside safe biological limits (ICES 2011b). Exact causes of the decline remain unclear; however, riverine barriers to both inward migrating juvenile lifestages and seaward migrating sexually mature (silver) eels are considered a key factor (Feunteun, 2002; Bruijs & Durif, 2009).

In-channel structures, hydropower facilities and water abstraction intakes for irrigation, domestic, and industrial supply can delay downstream movement of silver eels resulting in cessation of migration (Behrmann-Godel & Eckmann, 2003; Durif *et al.*, 2005; Durif & Elie, 2009); damage (Bruijs & Durif, 2009); and direct mortality (Calles *et al.*, 2010). Eels are particularly vulnerable at intake screens, pumps and turbines due to their elongated morphology and poor burst swimming capabilities. Typical hydropower mortality has been estimated at between 15 and 38% per turbine encountered (Hadderingh & Bakker, 1998; ICES 2007; Winter *et al.*, 2007), though may be as high 100% in some cases (Carr & Whoriskey, 2008). Delay of fish at barriers also exacerbates pressures such as predation and disease (Lucas & Baras, 2001; Garcia De Leaniz, 2008). There are potential population level consequences if silver eel escapement is impaired and less breeding stock reach the spawning grounds; however, long-term viability of escaped spawners is also important. Energy reserves (vital for successful oocyte production and an oceanic migration of 5000 to 6000 km) may be depleted due to milling and searching whilst delayed at barriers (Haro & Castro-Santos, 2000; Behrmann-Godel & Eckmann, 2003; Brown *et al.*, 2009; Travade *et al.*, 2010).

Silver eel migration typically occurs over short periods or 'runs' induced by environmental cues including increased river discharge, a fall in water temperature and lunar phase (Haro, 2003; Tesch, 2003). Barrier mitigation primarily focusing on hydropower sites, e.g. opening of spill gates during these key periods, can effectively increase escapement. In New Zealand, the release of spill for 2.5 hours enabled 70% of longfin eels (*A. dieffenbachii*) released upstream of a hydropower facility to pass without damage (Watene & Boubee, 2005). The same principal may be applied for systems without hydropower but with major water regulation structures. There is strong evidence that eels make route selection choices based on those localities with highest flow (Breteler *et al.*, 2007; Jansen *et al.*, 2007). The operation of sluices can influence route choice and the rate of eel migration in some systems (e.g. Breukelaar *et al.*, 2009); although few studies have investigated this.

To reverse the decline in European eel populations, the European Union has adopted the Eel Recovery Plan (2007) (Council Regulation No 1100/2007/EC). This requires all Member States to produce Eel Management Plans (EMPs) detailing actions to meet the target to permit with high probability the escapement to 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. Methods for achieving this target may include stocking of juveniles (which may only be achieved by translocation of wild stocks, thus potentially impacting source populations), reducing fishing mortality, increasing habitat availability, and reducing entrainment in turbines and pumping stations. Mitigation for the effects of riverine barriers and improvements to upstream and downstream passage has been highlighted as a key means of achieving escapement targets across Europe (e.g. U.K., Denmark, Greece EMPs). Furthermore, under the EU Water Framework Directive (WFD) (2000/60/EC) member states are obliged to ensure fish passage at all artificial structures (Kemp *et al.*, 2008b).

The initial phase of EMP development required determination of current catchment escapement. Beyond this, it is critical to identify key locations of silver eel loss and delay during the freshwater migration (Breukelaar *et al.*, 2009). To formulate effective mitigation measures there is a need to understand the physical and environmental conditions that influence route choice, successful barrier passage, and delay of silver eel (Breukelaar *et al.*, 2009). Current knowledge gaps concerning the type of structures, management regimes, and environmental conditions that prevent or delay eel passage, hinder attempts to conduct meaningful barrier impact assessment and prioritisation for mitigation (Acou *et al.*, 2008; Defra, 2010a). In particular, the individual and cumulative effect of low-head, and often only temporally restrictive structures, on eel migration is poorly understood. Detailed studies of eel escapement, route choice and barrier delay within a catchment are invaluable to help managers and policy makers develop cohesive solutions for specific systems. More importantly, many of the principals from such studies will be directly transferable between catchments and countries.

The aim of this study was to assess the impact of low-head structural barriers, flow regime management, and environmental variables on seaward migration of adult silver phase eels. To achieve this, six key objectives were addressed. Acoustic and PIT telemetry were used to quantify 1) escapement, which in the context of this study refers to escapement from the study reach to sea, 2) escapement duration, 3) barrier delay, 4) migration velocity, 5) entrainment loss, and 6) route choice of eels as they migrated through a highly regulated section of the river Stour, UK. The information gained will provide valuable guidance for optimising escapement of adult eels in line with EU requirements.

7.3 Methods

7.3.1 Study area

The river Stour is a lowland river in Southeast England flowing eastwards for approximately 98km from its source north of Haverhill to its tidal limit at Manningtree (51°57'10.78"N, 1° 3'14.21"E) where it enters the estuary and ultimately the North Sea. Land-use within the 85.8 km^2 catchment is predominantly agricultural, although the wider region is one of the most densely populated areas of the UK placing great demands on freshwater systems. Downstream migrating silver eels have several options of route to sea and may encounter up to 52 cross-channel structures before reaching the tidal limit.

The lower Stour is typically 10 to 15 m wide and has a 10 year mean daily flow of 2.91×10^5 m^3 day^{-1}. The present study was conducted in the lower 9.2 km of the freshwater river which encompasses 12 cross-channel structures for water level management and navigation; two water abstraction intakes, and several points where the main channel bifurcates. Moving downstream from Stratford St Mary the river passes Stratford intake (Fig. 7.1) where water is abstracted to augment potable water storage at Abberton reservoir (2.54×10^4 m^3 day^{-1}, 10 year mean). The 6.12 m wide intake oriented perpendicular to flow is fitted with a vertical bar trashrack (14 cm spacing), with further debris screening provided by a travelling band screen (8 mm mesh opening) set back (4 m) from the river. The main river channel flows relatively unobstructed to Dedham mill, only diverting down, a small side channel, Stratford Brook (A, Fig.7. 1). At Dedham the main channel divides briefly into: 1) a mill channel intersected by 6 undershot penstock sluice gates (B, Fig. 7.1) , and 2) a channel forming a navigation lock with manual side hung lock gates that operate under low flows, and an automatic level controlled overshot radial gate to control high flows (C, Fig.7. 1). The channels rejoin immediately downstream. A similar configuration exists at the next downstream structure, Flatford Mill, with a navigation lock within the right-hand channel (D, Fig. 7.1) and 6 undershot sluice gates on the left (E, Fig. 7.1). Additionally, fish may migrate down the old mill channel over a stopper-board weir adjacent to the sluices (F, Fig.7.1).

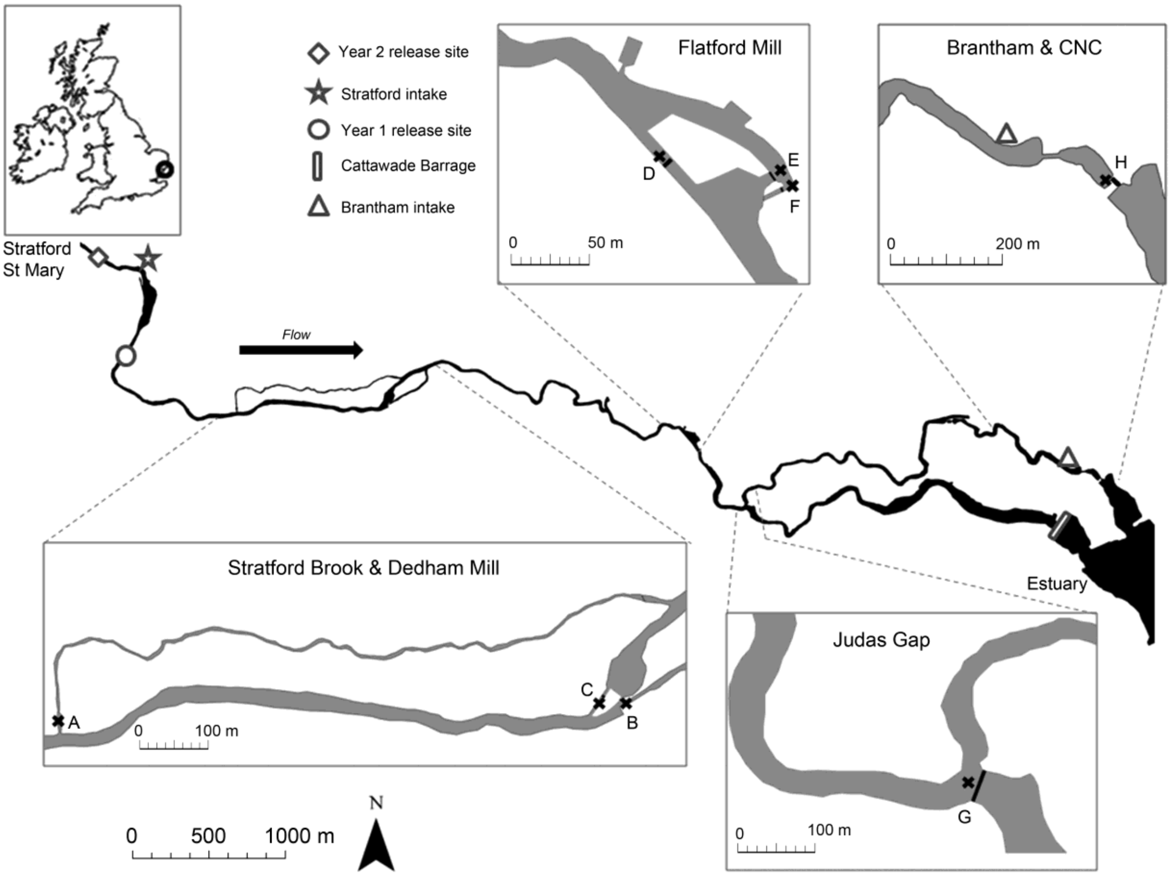


Figure 7.1 Lower Stour catchment indicating river structures at A - Stratford brook, B - Dedham Sluice, C - Dedham Lock, D - Flatford Lock, E - Flatford Sluice, F - Flatford mill channel, G - Judas Gap intertidal weir, H - Cattawade North Channel (CNC) intertidal sluice

Downstream from Flatford (0.68 km) the main channel is intersected by Judas Gap (G, Fig. 7.1), a broad crest weir (20.8m wide, 1.8m AODN height) (for description see Piper *et al.*, 2012). Principally constructed for water level management, this intertidal weir contains a pool and weir fishway at its southern end that has failed to function effectively since its construction in 1972 due to disparity between its design spill height and maintained river levels. An additional structure, Cattawade Barrage (Fig. 7.1), located at the end of the intertidal South Channel (SC) controls the height of tidal ingress to provide flood protection through a combination of undershot lifting gates and top-hung tidal flaps (50 m total width). This structure operates to maintain tide cycles up to Judas Gap weir, while preventing saline water inundating the freshwater catchment.

Directly upstream of Judas Gap the river bifurcates, flowing down a historic navigation channel which terminates at the Cattawade North Channel (CNC) sluice. This second intertidal barrier comprises an overshot sluice gate on the freshwater side and top-hung tidal flap on the estuary side (Fig. 7.1). Brantham intake, 185m upstream of the sluice, abstracts at a maximum pumping rate of 5.5 x 10^4 m^3 day^{-1}, dependent on requirements. Screening facilities are similar to those at Stratford intake, although after the trashrack, water is drawn approximately 0.5 km through an enclosed pipe (107 cm diameter) before reaching the travelling band screen and pumps.

No commercial fishing for eels is licensed within the freshwater catchment, although low level fishing (<10 fyke nets) is conducted within the estuary.

7.3.2 Fish capture and telemetry

Actively migrating silver eels were captured in small batches (6 to 11 individuals) from October to November in 2009 (year 1) and from October to December in 2010 (year 2) using fyke nets set nightly upstream of the study area and checked each morning. Captured individuals were visually assessed for signs of external damage or disease and only selected for tagging if undamaged (approximate 2% rejection rate in both years). Eels selected for tagging were transferred to in-river perforated holding barrels and held for a maximum of 2 h, before being anaesthetised (Benzocaine 0.2 g L^{-1}), weighed (wet mass , WM, g), and measured (total body length, mm). The length of the left pectoral fin (FL, mm) from insertion to the tip, and maximum vertical and horizontal left eye diameter (mm) were also measured. Degree of sexual maturation or "silvering" was quantified prior to tagging using two metrics: the Ocular Index (OI), according to Pankhurst (1982), and Fin Index (FI), according to Durif *et al.* (2009). All eels captured within the study exceeded 450 mm and were thus considered female (Tesch, 2003). European eel with OI ≥ 6.5, and FI ≥ 4.3 (females only), are considered to be at the migratory silver stage (Durif *et al.*, 2009; Pankhurst, 1982). Only eels fulfilling these criteria were selected for tagging (87% and 92% in year 1 and 2 respectively).

Selected individuals ranged in size from 581 - 921 mm TL, 434 - 1398 g WM in Year 1, and 569 - 853 mm TL, 357 - 1211 g WM in Year 2. Mean OI was 8.3 (range 7.1 - 11.9) and 9.4 (range 8.5 - 14.6) in year 1 and 2, respectively. Mean FI was 4.8 (range 4.4 - 5.5) and 5.1 (range 4.3 - 6.0) in year 1 and 2 respectively. An acoustic tag (model V92L, tag interval 15 - 25 s, 29 mm x 9 mm, 2.9 g in water or V72L, tag interval 15 - 25 s, 20 x 7 mm, 0.75 g in water VEMCO, Nova Scotia, Canada; dependent on eel size) and Passive Integrated Transponder (PIT) tag (23 x 4 mm, 0.6 g, Wyre Micro Design, Poulton-Le-Fylde, Lancashire) were surgically implanted into the peritoneal cavity of each eel following methods similar to Baras and Jeandrain (1998), and the incision closed with two separate dissolvable sutures (Vicryl Rapide^{R}; Ethicon Inc., Cornelia, GA, U.S.A.).

After tagging, eels were transferred into a perforated holding barrel for 10 - 12 h to allow post-operative recovery and acclimation before release. No eels died or showed signs of sustained damage during recovery. Tagged eels were released at Stratford St Mary (Fig. 7.1) (12th October to 22nd November) in year 1, and 1.3 km further upstream in year 2 (5th October to 19th December) to include the Stratford St Mary abstraction point (Fig. 7.1). Releases took place in darkness (2000 - 2100 h) from a holding barrel tethered in the channel centre to eliminate bias in route choice. The lid was removed allowing individuals to leave volitionally.

Movements of tagged individuals were monitored through the study reach from October to March in both years using a linear array of 19 fixed acoustic receivers (VEMCO, model VR2W) extending from 0.6 km upstream of the Stratford St Mary release site, to a point 1.6 km into the estuary. Receivers were placed immediately up and downstream of each structure and at mid points between barrier locations. Weekly tag detection and range testing was conducted throughout the study period, and demonstrated consistency in both range and precision of detection. In addition, manual tracking (VEMCO, VR100) using canoe and bank walking was conducted to locate individuals “lost” between fixed receivers. Detection loss may occur for a number of reasons including large amounts of background noise, shielding of a receiver e.g. by macrophytes and debris, or if a tagged fish passes a receiver detection zone quicker than the delay time between tag transmissions. PIT telemetry with loop antennae (half duplex, Wyre Micro Design) was used to confirm passage at the entrance of Brantham intake (Fig. 7.1), and within the mill channel at Flatford (F, Fig.7.1).

7.3.3 Hydrometry, barrier operation and environmental variables

The operation of sluices and intakes varied during the study period in response to abstraction requirements and water level management. Barrier position setting, river level, and water temperature were recorded at 15 minute intervals throughout the study period. Data were obtained from operational records and the Environment Agency's fixed monitoring sites at Stratford St Mary, Dedham, Flatford, Judas Gap and Cattawade North and South Channels using an ultrasonic level measuring device (Pulsar Blackbox, Pulsar Process Measurements, Malvern, UK). Total river flow (River Q) ($m^3 s^{-1}$) was calculated immediately upstream of Dedham, Flatford and Judas Gap structures using 15 minute gauging data recorded at Langham flow gauging station, 1.2 km upstream of the study site upper limit, and adjusted for additional inputs and abstractions throughout the study reach accordingly. At the Judas Gap bifurcation, the proportion of flow passing down either channel was attained by calculating Q over Judas Gap weir (Judas Q) using the flow equation for a British standard rectangular broad-crested weir (BS3680; ISO 3846:1989):

$$Q = \left(\frac{2}{3}\right)^{3/2} g^{1/2} b C {h_1}^{3/2}$$

where g is the acceleration due to gravity, b is the width of the weir perpendicular to the direction of flow, C is the gauged head discharge coefficient and h_1 is the upstream gauged head relative to the crest elevation. The discharge coefficient C was obtained from ISO data for rectangular broad-crested weirs (BSI 1990). Where data were below recommended limits (h_1 values <0.07 in this study), a conservative value of C = 0.8 was used (3% of dataset). Judas Q was deducted from river Q to provide a Q value for CNC.

Judas Gap was not constructed to conform to BSI standards, so to assess the accuracy of calculated Q, empirical point sampling was conducted under a range of flow conditions using an Acoustic Current Doppler Profiler (ADCP) (M9, SonTek/YSI, San Diego, USA). The ADCP was mounted on a raft (Hydroboard) and manually pulled across the channel in a series of moving transects perpendicular to flow immediately upstream of Judas Gap, and 100m downstream in CNC. Mean river Q was calculated from 4 repeated transects conducted at each sampling location on each occasion (8 non-consecutive sampling days). Calculated and empirical flow values were similar. Water abstraction rates (m^3 day^{-1}) were obtained at 15 minute resolution for Brantham and Stratford St Mary intakes from Essex and Suffolk Water company.

Mean daily water temperatures (˚C) were calculated from hourly data recorded using fixed data-loggers (Tinytag Aquatic T-2100, Gemini Data Loggers, Chichester, UK) located upstream of each set of structures. Mean water temperature ranged from 3.2 to 16.4 ˚C and from 3.5 to 13.6 ˚C over the two study periods (Oct – Mar, both years). Maximum tide heights and lunar phase for each day were obtained from the UK Hydrographic Office. River flow measured immediately upstream of the study site (Langham flow gauging station, Environment Agency) ranged from 0.5 to 25.7 m^3 sec^{-1} over both study periods , with mean daily flow of 5.2 ± 5.0 m^3 s^{-1} (S.D.) and. 3.5 ± 3.9 m^3 s^{-1} (S.D.), in year 1 and 2 respectively.

7.3.4 Fish movement, behaviour and data analysis

Detection data were downloaded monthly from receiver stations then combined and filtered to provide chronological records for each fish as they migrated downstream. The data were used to address the six objectives of the study:

Escapement was deemed to have occurred when an individual was first detected at the receiver immediately downstream of either of the intertidal barriers (Judas Gap or Cattawade sluice).

Escapement duration was calculated as time (h) between release and escapement.

Barrier delay was defined as the duration (mins) between first detection of an individual at the receiver immediately upstream of a structure, and the last detection on the same receiver prior to confirmed barrier passage (*passage event*). A *passage event* was confirmed by detection on the receiver immediately downstream of the structure. At both abstraction points, delay for each individual was defined as the duration (mins) from first to last detection at the receiver positioned immediately within the intake entrance.

On occasion, individuals passed a receiver without being detected. Detection on subsequent downstream receivers enabled interpolation to determine route choice, but interpolated data were excluded from delay time and passage event analyses.

Mean migration velocity (MMV) (m s^{-1}) was calculated for individuals that passed through both a) an unobstructed reach (immediately downstream of Dedham to immediately upstream of Flatford, 2.26 km) and b) an obstructed reach (immediately upstream of Dedham to immediately downstream of Flatford, 2.66 km). The calculation used time taken (between detections) to travel the distance between receivers, assuming shortest possible swim path. MMVs within each year were compared using related samples Wilcoxon signed ranks tests.

Entrainment loss was deemed to have occurred when an individual was detected at the acoustic receiver located within a water abstraction intake, with no subsequent detection at the receiver immediately outside the intake entrance, or those further upstream or downstream (monitored for 3 months beyond study termination). At Brantham, this was corroborated by detection at a PIT antenna set 1 m into the intake. It was not feasible to install PIT telemetry at Stratford due to the steel construction of the intake which made the detection range unreliable. To assess detection efficiency within Stratford intake, a beacon tag transmitting approximately every 120 s was secured within the intake sump and was consistently detected throughout the study.

Eels that selected the CNC either travelled into Brantham intake and became entrained, or moved downstream and out to the estuary via the CNC sluice gate.

Generalised linear models (GLM) with binomial error distributions and a logarithmic link function were used to investigate the effect of a number of factors on entrainment (a binary response of either entrained or not entrained i.e. passed out of CNC sluice), for both years combined. Variables within the maximum model were: River Q; mean temperature; position of CNC sluice gate (% open), and abstraction rate at Brantham intake (all at the time of entrainment or gate passage); total time fish spent in the immediate vicinity of intake and sluice gate, and relative difference between mean abstraction rate for 0.5 h leading up to, and including, entrainment or passage vs the mean abstraction rate for the 1 h prior to this. These time periods were decided on using data mining techniques. A model with 1st order interaction terms was fitted and stepwise deletions were performed using chi-square tests to identify non-significant terms. The minimum adequate model (MAM) was arrived at as the most parsimonious model with lowest AIC value (Akaike, 1973). Suitability of the binomial error structure was evaluated using plots of standardised residuals against square root of the fitted values.

Route choice – was defined using receivers positioned strategically at locations where routes diverged. The '*time of route choice*' was defined as the last detection by a receiver upstream of the divergence.

Where quoted, percentage values refer to the proportion of eels approaching each bifurcation, rather than as a proportion of total eels within the study.

Eels approaching both the Dedham and Flatford structures could pass downstream via either of two principal routes: 1) the sluice or 2) lock/radial gate. Eels moving towards Dedham could alternatively pass down Stratford Brook, but as the entrance to this channel is 830 m upstream of the lock and sluice complex these eels were excluded from route choice analyses for Dedham. At Flatford the mill channel also presented an additional route option, but this was excluded from analyses due to the small number of eels (4) that passed this route. Eels approaching Judas Gap could either continue downstream within the CNC or pass over Judas Gap weir into the South Channel. Generalised linear models (GLM) with binomial error distributions and a logarithmic link function were used to investigate route choice for the 3 locations: Dedham, Flatford (both binary response, sluice or lock), and Judas Gap (binary response, Judas or CNC). In all cases, a model with 1st order interaction terms was initially fitted, and then stepwise deletions were performed to obtain the MAM using previously described methods. For route choice at Dedham and Flatford, independent variables included in the maximal models were: River Q, upstream water level, radial gate position (% open), sluice gate position (% open), water temperature, and lunar phase (all at time of passage), study year, and duration of delay (time of arrival to time of passage, mins). For Judas Gap, variables in the maximal model were: River Q; Judas Q; position of CNC gate (% open); rate of abstraction at Brantham intake; temperature; lunar phase, and year.

All statistical analyses were carried out in R v2.14 (R development core team, 2011).

7.4 Results

7.4.1 Escapement

Downstream eel migration predominantly took place from the start of November to the end of Jan with 96% of escapement occurring within this period. Overall escapement from the study reach was 76% in year 1 (n = 29), and 65% in year 2 (n = 40).

7.4.2 Escapement Duration

Escapement duration was highly variable between individuals within both years. In year 1 the time taken to reach the estuary ranged from 188 h (8 days), to 2722 hours (113 days), with median escapement duration of 700 h (29 days). In year 2, escapement duration (for eels released 1.3 km further upstream than in year 1), ranged from 122 h (5 days) to 2402 h (100 days), with a median duration of 915 h (38 days).

7.4.3 Barrier Delay

Some eels were delayed upstream of structures or in the vicinity of intakes for substantial periods before continuation of downstream migration. Longest delays were associated with two structures in year 1: Dedham, where 15 % of fish (n = 28) experienced delay in excess of 350 h; and Brantham intake, with median delay of 147.8 h. In year 2, Stratford Intake and Flatford Lock were associated with longest delays. At Stratford Intake 45% (n=18) (year 2 only) of eels experienced delay, with 28% delayed longer than 50 h, with a maximum of 947 h. At Flatford, 25 % of fish (n = 36) took longer than 15 h to pass the structure. There was high variability between individuals and between years.

Substantial delays were observed at both water abstraction intakes for some fish. At Stratford St. Mary individuals spent between 4 minutes and 947 h within the intake sump. Of the eels that moved through the CNC (n=15 year 1, n=14 year 2), all were detected within the entrance, or immediately upstream of Brantham intake, and spent between 8 min and 787 h, and 5 min and 192 h in the area, during year 1 and 2 respectively. Abstraction pumps were in operation at Brantham intake for 93% and 87% of the year 1 and 2 study periods. Abstraction pumps were in operation at Stratford St Mary intake for 89% of the year 2 study period.

7.4.4 Mean Migration Velocity

Eels travelled more rapidly through an unobstructed (MMV ranged 0.16 to 2.55, median= 1.89 m s^{-1}, in year 1; and ranged 0.01 to 5.76, median = 1.97 m s^{-1}, in year 2) than through an obstructed (2 structures) (MMV ranged 0.006 to 2.54, median = 1.04 in year 1; and ranged 0.003 to 5.26, median = 1.50 in year 2) reach during both year 1 (W = 16, p = 0.02, 13 d.f.) and year 2 (W = 66, p = 0.02, 23 d.f.).

7.4.5 Entrainment Loss

Stratford St Mary abstraction point was only included in the study reach in year 2, during which no eels were entrained at this intake.

There were two main outcomes for eels that reached the lower section of the CNC. First, to enter Brantham intake, or second, to pass into the estuary via Cattawade intertidal sluice. Entrainment loss of 12% (n = 3) and 26% (n = 9) in year 1 and 2 respectively occurred at Brantham intake. Two significant predictors of entrainment loss were identified: difference in mean abstraction rate between passage event and delay (44.6% of residual deviance, p = 0.02, 28 d.f.), and gate position at Cattawade sluice (% open) (12.9% of residual deviance, p = 0.03, 27 d.f.). Entrainment loss principally occurred when abstraction levels increased abruptly (i.e. pumps were turned on), combined with reduced opening of Cattawade sluice gate.

7.4.6. Route Choice

Two principal downstream route options were available at each of the 3 main structure locations (Dedham, Flatford and Judas Gap) (Fig. 7.1). Although Flatford and Dedham comprise similar structure types, route choice differed between the two locations. Eels that did not move downstream via Stratford Brook subsequently approached the main Dedham structures, at which point 71% (36 of 51 fish) passed downstream via the undershot sluices, and the remainder passed via the lock route (containing overshot radial gate). In contrast, at Flatford, 74% of individuals (45 of 61 fish) passed via the Lock route (overshot radial gate), and 20% (12 of 61 fish) via the undershot sluices, the remainder passing via the mill channel (Fig.7.2).

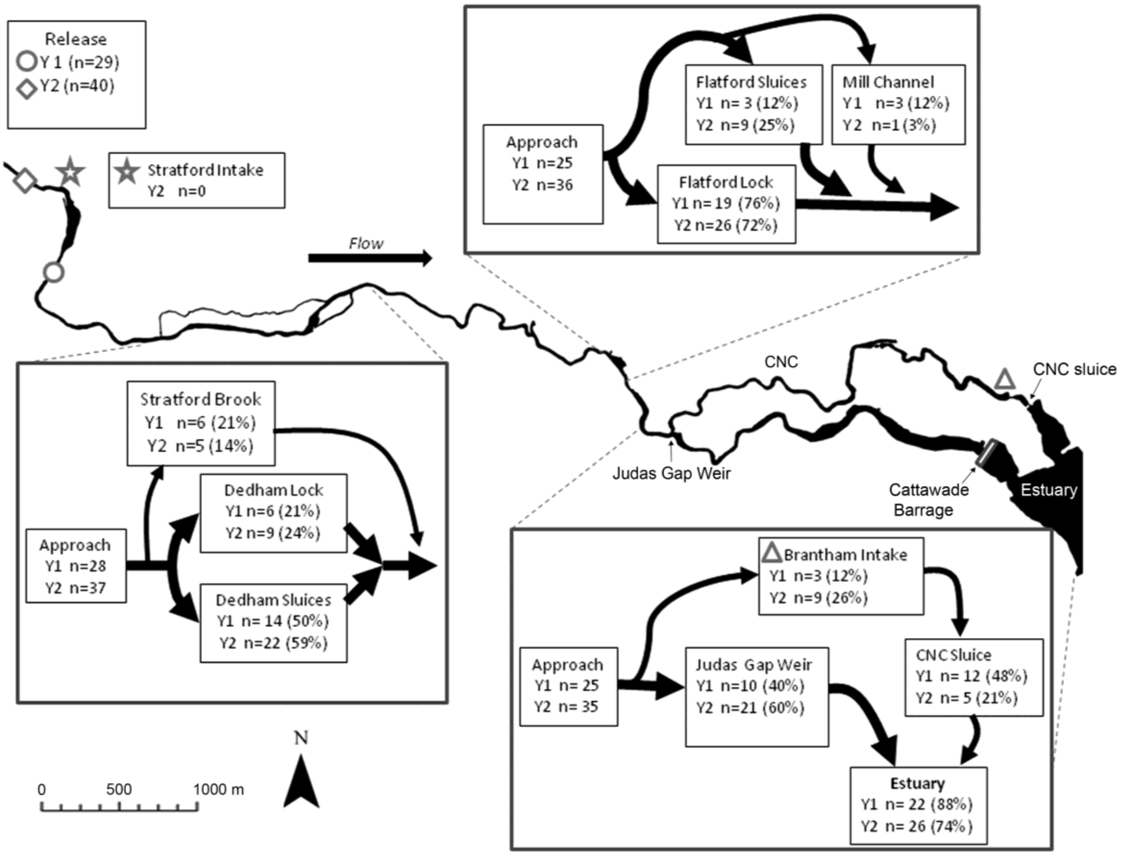


Figure 7.2 Route choice of combined acoustic and PIT-tagged silver eels at structures and entrainment at water abstraction intakes during seaward migration through lower Stour catchment to the estuary in year 1, 2009 (n = 29) and year 2, 2010 (n = 40). Percentages denote proportion of eels that approached the structure.

The MAM describing route choice at Dedham for both years identified the position of the radial gate and an interaction between gate position and upstream water level as significant predictors. Increased passage via the lock channel was strongly associated with greater opening of the radial gate (31% of residual deviance, $p < 0.001$, 42 d.f.), and a combination of high water level upstream and gate opening (18%, $p < 0.001$, 40 d.f.). The MAM describing route choice at Flatford for both years identified sluice gate position, radial gate position and delay time as significant predictors. Sluice gate and radial gate positions explained 20.5% and 29% of deviance, respectively ($p < 0.01$, 45 d.f.; $p < 0.01$, 44 d.f.), delay time explained 15.1% of deviance ($p = 0.03$, 43 d.f.). Obviously, eels were unable to pass via the sluice when it was in the full closed position, and passed via the lock at these times. Opening of the sluice increased probability of fish passing via this route. Extended delay upstream of the structures resulted in more fish passing downstream via the sluice when open.

Of the eels that approached Judas Gap, 40% passed over this broadcrest weir in year 1 and 60% in year 2 (Fig.7.2). Flow over this structure was the only significant predictor of route choice, explaining 64% of residual deviance ($p < 0.01$, 55 d.f.). Selection of Judas Gap occurred during periods of highest flow, and no eels passed via this route until spill level exceeded 0.18 m.

7.5 Discussion

This study highlights the negative impacts of low-head river infrastructure on the migration and escapement of adult European eel to an estuary in the UK. Structures, such as sluices, locks, water intakes, and weirs, are abundant across European catchments, but seldom considered as impediments to fish migration (Lucas *et al.*, 2009). Migration speed was lower in obstructed reaches; long delays were apparent at some barriers; and escapement of eels from the freshwater catchment was impacted, principally through entrainment loss. The management regimes applied, that included control of spill, sluice gate positions, and abstraction rates, strongly influenced probability of entrainment at intakes and the route choice of eels.

Eels, and indeed all riverine fish, may encounter a range of engineered features which can delay movement (e.g. at impoundments such as weirs), and result in impingement and entrainment (e.g. at hydropower and water abstraction intakes, and pumping stations). Eels are particularly vulnerable at intake screens due to their narrow, elongated body morphology and relatively poor swimming capabilities (Boubee & Williams, 2006; Calles *et al.*, 2010; Russon *et al.*, 2010). In heavily impacted rivers, the cumulative effect of multiple structures may reduce overall escapement to low levels. For example, previous studies on the rivers Meuse and Rhine, estimated silver eel escapement at 15% (Verbiest *et al.*, 2012), and 15 − 32% (Breteler *et al.*, 2007; Breukelaar *et al.*, 2009), respectively, which in both cases was influenced by entrainment at hydropower facilities. The current study focused on the most downstream 10% (9.5 km) of the freshwater river. Nevertheless, more than one-quarter of emigrating eels were prevented from escaping; and with additional water abstraction points present upstream of the study reach, values for the total catchment are likely to be higher.

Estimates of potential escapement of silver eel from a catchment in the presence and absence of anthropogenic pressures, are required to determine compliance, or lack of, with EU eel management targets. Due to a lack of quantitative data describing current escapement for many European catchments, several countries have adopted modelling approaches to estimate eel densities and escapement under scenarios with and without human induced stress (e.g. the Probability Model; Scenario-based Management of Eel Populations, SMEP) (Aprahamian and Knights, unpubl. data; Aprahamian *et al.*, 2007). Impacts of fishing and the operation of hydropower plants and pumping stations are however currently underrepresented in many models due to insufficient empirical data (Aprahamian *et al.*, 2007; ICES, 2011a).

Interestingly, all entrainment loss occurred at only one of two water intakes. Although delay was associated with both intakes, behaviour differed notably between sites. Eels made excursions into both, but returned to the main river at Stratford St Mary, while 12 individuals did not reappear at Brantham. This may have been due to the relative positions of the travelling band screens. At Stratford St Mary, eels encountered the screen 4 m behind the trashrack. In contrast at Brantham, a 0.5 km pipe exists between the intake and the screen, so eels that navigated the length of this pipe may have been more susceptible to disorientation, damage, disease and predation (ICES, 2011a). Abstraction rate also differed between the two intakes with the mean at Brantham being 1.4 times greater than at Stratford St Mary. Entrainment was associated with rapid increases in abstraction rate, although eels likely entered the intake volitionally as maximum velocities at the trashracks were always below burst swimming speed capabilities of large adult eels (≥450 mm TL) (1.30 – 1.75 m s^{-1}) (Solomon & Beach, 2004; Russon & Kemp, 2011b). When closure of the intertidal sluice coincided with low flows, abstraction volumes represented a significant proportion of, or at times, the entire river flow in the vicinity of Brantham intake, which may provide an explanation, at least in part, for these findings.

This study demonstrated that river infrastructure can delay seaward migration and reduce overall migration velocity in impounded reaches. Further, individual barrier delay was calculated from the point of first detection above a barrier; hence this may be considered to represent a minimum delay as individuals may have been deterred from entering the area upstream of barriers at a range that exceeded this detection range. Delay at critical structures in the river Stour was influenced by flow management and atypical operation. For example, malfunction of the radial weir within Dedham lock caused it to remain closed for the majority of the autumn migration in year 1, during which the sluices in the adjacent channel were also shut. Eels approaching these structures either settled for extended periods immediately upstream or showed milling behaviour, consistent with other studies (Haro & Castro-Santos, 2000; Brown *et al.*, 2009; Travade *et al.*, 2010).

The structures at Flatford were similarly associated with long delays. In year 2 a large piece of woody debris became lodged upstream of the undershot sluices and although the gates remained partially open for much of the time, eels were delayed for long periods and few ultimately passed. Silver eels have been observed to exhibit predominantly benthic-oriented movement at barriers during their migration downstream, and prefer undershot routes at structures (Behrmann-Godel & Eckmann, 2003; Gosset *et al.*, 2005; Russon & Kemp, 2011a; Russon & Kemp, 2011b). Although undershot passage was possible for eels at Flatford despite the debris, likely hydrodynamic conditions such as abrupt velocity gradients near the constricted openings may have induced avoidance behaviour (Coutant & Whitney, 2000).

The relationship between eel migration velocity and delay on energetic expense, depletion of fat reserves, general health, and subsequent migration and reproductive success is unclear. Degeneration of the alimentary tract during silvering (Pankhurst & Sorensen, 1984) causes eels to stop feeding, which continues to the end of their lifecycle (Ginneken, 2006; Dufour & van den Thillart, 2009), unless migration is prevented (Durif *et al.*, 2009). Oceanic migration and gonad production therefore relies on energy provided by body fat reserves (van den Thillart & Dufour, 2009). There is concern that insufficient adults may be reaching the spawning grounds, some 5,000-6,000 km from western Europe, which at the rate of 0.5 body lengths per second obtained in long distance swim trials, would necessitate up to 6 months of constant swimming, (without adjustment for the use of oceanic currents) (Van den Thillart *et al.*, 2004; Van Ginneken & Maes, 2005). Delay at barriers is undoubtedly associated with energy expenditure which may be high, particularly as eels do not remain sedentary (Castro-Santos, 2000; Behrmann-Godel & Eckmann, 2003; Brown *et al.*, 2009; Haro &; Travade *et al.*, 2010). The implication of such energetic costs for overall success of the spawning migration remains an important, and as yet, largely unaddressed subject.

7.5.1 Management Implications

Mitigation for fish damage and loss at abstraction and hydropower intakes is increasingly important as the global demands placed on water resources for consumption and power generation grow (Nilsson *et al.*, 2005). The protection of eels at these structures, increasingly important to meet legislative targets (e.g. WFD, EU Eel Regulations), is commonly provided by screens. Physical exclusion screens are primarily used to protect fish at intakes and can be highly effective (Environment Agency, 2011). Installing a physical fish exclusion screen (<18 mm spacing, Calles & Bergdahl, 2009) across the entrance of Brantham intake could provide an appropriate mitigation measure to reduce entrainment of silver eels in the river Stour; however, costs of screen installation, maintenance and cleaning can be substantial. Where a screened intake is flush with the river bank, natural sweeping river flows may be sufficient to guide eels to safe passage (Environment Agency, 2011). However, at locations such as Brantham, main river flow may be insufficient to do this; hence additional physical or behavioural methods may be required to guide fish to safe passage routes. Angled louvers, light and/or sound deterrents have shown guidance potential, although the development of such technology for eel is still in its infancy (Sand *et al.*, 2000; Patrick *et al.*, 2001; Amaral *et al.*, 2003).

There is need to develop safe and efficient downstream passage solutions to convey adult eel passed deleterious routes and barriers to migration. Though effective solutions are considered lacking (Bruijs and Durif, 2009; Calles *et al*. 2010), benthic-oriented bypass routes perhaps have the greatest potential (Adam *et al.*, 1999; Gosset *et al.* , 2005). Findings suggest that in many regulated systems, adapting management regimes may offer a cost effective alternative to installing fish passage facilities.

Distinct peaks in eel migration are typically observed. Strategic non-pumping during these short periods can be highly effective at improving escapement (Haro *et al.*, 2003). Findings also highlighted the importance of organising maintenance programmes to ensure that structures remain operable and passage routes free from blockages during this time. Abstraction rate was found to be a key determinant of entrainment loss in the current study; hence cessation of abstraction during migration periods, combined with opening of intertidal sluices is likely to reduce eel loss. Complete cessation of pumping for long periods may not be economically viable; however findings suggested that a slow start up of pumps and provision of alternate route of passage is likely to reduce entrainment loss at intakes where eel entrance is volitional.

It is important to highlight that only large female silver eels were tagged due to their dominance within the emigrating stock for this catchment; evident in both fyke net catches and previous monitoring (Environment Agency, unpubl.). The low eel density within this catchment is believed to be the cause of the population bias towards large females at the silver eel lifestage (Defra, 2010b). Nevertheless, many systems comprise a significant proportion of small males; therefore further work should determine if findings are comparable for this component of the population.

Telemetry enables quantification of entrainment loss from catchments, but also highlights the locations of key entrainment points and barriers associated with long delays during downstream migration. In light of findings that anthropogenic catchment management is an important factor in delay and entrainment losses, there exists an opportunity to work with catchment managers in many heavily regulated rivers to manipulate current regimes and optimise escapement of silver eels to the estuary.

Chapter 8 Linking fish movement and hydrodynamics: effect of flow and velocity gradient on behaviour of seaward migrating eel at a hydropower intake

8.1 Summary

Anthropogenic structures such as weirs, dams and hydropower facilities fragment river networks and restrict the movement of migratory fish. Hydrodynamic cues are a key influence on fish behaviour and navigation. Poor understanding of behavioural responses of adult migrating eel to hydrodynamic components synonymous with river infrastructure limits the development of effective barrier mitigation measures. This study aimed to assess the effects of structure type, flow and water velocity on the behaviour and downstream passage of European eel (*Anguilla anguilla*). Individuals were tracked using acoustic telemetry as they moved through a forebay upstream of an array of 5 structures, which included a redundant hydropower facility. Tracking was carried out over two study years (n = 25, year 1 and n = 60, year 2). In year 1 route choice through the forebay was influenced by bulk flow, though eels rejected at a floating debris boom that spans the channel. In year 2, eel were exposed to three hydrodynamic treatments within the hydropower intake channel: 1) open 2) constricted and 3) cylinder, designed to produce unrestricted intake flow, high and low accelerating water velocities, respectively. Movement paths were interrogated in relation to mapped water velocities. Distance travelled and passage times were greatest when flow was constricted. Eels elicited abrupt rejection and recurrent behaviour, independent of physical contact with structures, on encountering the highest water velocities and velocity gradients. Milling behaviour in front of the trashrack was more common in lower water velocities. Eels also showed a propensity to remain in close proximity (< 2 m) to structures, irrespective of flow. The findings have implications for guiding eel to passage facilities at barriers through the manipulation of flow fields.

8.2 Introduction

Freshwaters are among the most heavily impacted ecosystems worldwide (IUCN 2008). Anthropogenic structures such as weirs, dams and hydropower facilities increasingly impound and fragment river networks (Poff *et al.*, 1997; Malmqvist & Rundle, 2002), and have a major impact on the movement of aquatic biota (Kemp, 2012). For fish, physical barriers obstruct dispersal and migration between habitats required for different ontogenic stages (Werner & Gilliam, 1984; Northcote, 1998; Lucas & Baras, 2001). Additionally, hydropower and pumping facilities cause direct injury and mortality for those that pass through, due to blade strike, cavitation and grinding (Turnpenny *et al.*, 2000; Schilt, 2007; Larinier, 2008).

Fish passes and screens are widely employed to mitigate for the negative impacts of barriers, pumps and hydropower facilities on fish communities. The effectiveness of such measures is highly variable between species, lifestages and location. Fish passes often perform poorly (Aarestrup *et al.*, 2009; Caudill & Peery, 2009), particularly for non-salmonids (Bunt, 2001; Bunt *et al.*, 2001; Cooke *et al.*, 2005; Roscoe & Hinch, 2009); and screens can cause impingement, damage, and mortality; particularly impacting weak swimmers, juvenile lifestages and species with elongated body morphology e.g. eels (EPRI, 2005; Calles *et al.*, 2010; Environment Agency, 2011). Fish guidance technologies offer potential to improve mitigation measures, that is, deter fish from harmful features and guide them to more benign routes such as fish passes.

Guidance systems for downstream migrating fish may use physical methods (e.g. screens), or induce a behavioural response (usually avoidance) to stimuli such as sound (Popper & Carlson, 1998), infrasound (Sand *et al.*, 2001), light (Patrick *et al.*, 2001); or use combined physical and behavioural methods e.g. angled bar racks and louvers (Amaral *et al.*, 2003; Russon *et al.*, 2010). Hydrodynamic features such as velocity gradients, jets and turbulence have shown potential for guidance in some species (Coutant, 2001; Darland *et al.*, 2001; Perry *et al.*, 2005), though have have seldom been used to divert eels. The advancement of effective guidance relies on understanding the movement and behaviour patterns of the target species and lifestage in relation to environmental cues (Goodwin *et al.*, 2007; Schilt, 2007; Nestler *et al.*, 2008a).

Fish extract information about their spatial location from multiple stimuli (Pitcher, 1993). The discriminability of a specific stimulus and the subsequent response elicited is dependent on both its absolute and relative magnitude to other cues; but may also differ between species (Schilt, 2007), ontogenic stages (Lucas & Baras, 2001); and with motivation (Colgan, 1993), behavioural bias (Kemp *et al.*, 2012), prior experience, learning and habituation (Odling - Smee & Braithwaite, 2003). In the complex and hydraulically noisy environments encountered by fish at river infrastructure, hydrodynamic parameters are likely to constitute dominant cues that inform fine scale navigation and route selection (Goodwin *et al.*, 2007). Recent work has highlighted the importance of salient hydrodynamic features to fish behaviour, including accelerating flow (Haro *et al.*, 1998; Kemp *et al.*, 2005); velocity gradients (Enders *et al.*, 2009a; Vowles & Kemp, 2012), and turbulence (Liao, 2007; Tritico, 2009). This increased knowledge has been used with some success for improving fish passage (Williams *et al.*, 2012).

The European eel has declined severely, with 90 - 95% reduction in recruitment since the 1980s (ICES, 2011). Anthropogenic structures may limit or prevent juvenile immigration and adult seaward spawner escapement, and are considered the principle cause of reduced populations of diadromous species in some catchments (Larinier, 1998). Migrants experience long delays (Acou *et al.*, 2008) or cease to move (Durif *et al.*, 2005), with both high and low-head structures restricting free passage (Acou *et al.*, 2008; Piper *et al.*, in review). Eels experience high rates of injury and mortality at pumps and hydropower turbines, up to 100% at some facilities (Carr & Whoriskey, 2008), though more typically from 15 to 38 % per turbine encountered (Hadderingh & Bakker, 1998; Winter *et al.*, 2007). Attempts to improve downstream eel passage via surface (e.g. bypasses, ice chutes and surface collectors), and undershot routes (sluices, siphon, pipe passes), have shown variable success (Haro & Castro-Santos, 2000; Brown *et al.*, 2003; Legault *et al.*, 2003; Gosset *et al.*, 2005; Travade *et al.*, 2010).

Advances in telemetry enable animals to be tracked at high temporal and spatial resolution (Castro-Santos *et al.*, 2009; Cagnacci *et al.*, 2010; Lanzone *et al.* 2012), but field studies that examine eel movement and behaviour in relation to hydrodynamics are lacking. Eel behaviours are typically described from a coarse-scale perspective, considering variables such as mean channel flow or turbine and pumping rate (Brown *et al.*, 2003; Gosset *et al.*, 2005; Spierts & Kemper, 2008). This limits the transferability of results and insight into how fish respond to particular flow characteristics (Roscoe & Hinch, 2009).

Downstream eel migration has historically been considered semi-passive, part swimming and part transported by currents (Porcher, 2002; Tesch, 2003), with a tendency to follow bulk flow (Jansen *et al.*, 2007; Breukelaar *et al.*, 2009). However, eels demonstrate a wide range of behaviours on the approach to structures, ranging from direct collision and impingement, to multiple approaches, rejection, and extensive milling /search behaviour at a range of heights in the water column (Haro & Castro-Santos, 2000; Behrmann-Godel & Eckmann, 2003; Brown *et al.*, 2003; Travade *et al.*, 2006; Spierts & Kemper, 2008, Russon *et al.*, 2010). It is postulated that eels may be reluctant to enter routes with rapid accelerating velocities (Jansen *et al.*, 2007; Calles *et al.*, 2010) typical of fish pass, sluice and bypass entrances, as has been shown experimentally for juvenile salmonids (Kemp *et al.*, 2008a), though this has not been quantified. Understanding eel behaviour in response to the hydrodynamic environment will aid development of much needed, effective guidance and fishways for this species (Calles *et al.*, 2010; Russon *et al.*, 2010).

The study had two principal aims. First, to determine route selection and passage time of seaward migrating eel through a forebay and downstream via 5 possible in-channel structures. Second, to quantify eel behaviour in response to accelerating flow within an intake channel. Flow within the intake channel was manipulated to create 3 treatments: 1) unrestricted flow (open), 2) constricted flow (constricted), and constricted flow with cylinder array (cylinder). Eel movements and behaviours were quantified using the following parameters: 1) time to pass 2) residence time within key zones (e.g. intake channel); 3) swim track metrics (length and tortuosity); 4) average swim speed and depth, and 5) behavioural response in the intake channel (rejection and milling). The following hypotheses were tested: i) eels select downstream passage routes coinciding with highest flow; ii) eels follow structures i.e. predominantly display thigmotactic behaviour, and iii) eels reject abrupt velocity gradients.

8.3 Materials and Methods

8.3.1 Study site

The river Stour, Dorset, UK, flows 96 km from its source at Stourhead to Christchurch where it drains into the English Channel (50°43'28.26"N, 1°44'16.57"W). It has a mean flow of 13.9 $m^3 s^{-1}$ (10 yr mean) and is influenced by multiple water control structures and abstraction points along its length. Longham water treatment works (50˚46'31.98"N, 1˚54'41.08"W), 19 km upstream of the estuary, is a complex of structures which incorporates (from west to east): a broad crested crump weir (15.2 m width, S1, Fig. 8.1); a pool and weir fish pass (1.84m width, S2, Fig 8.1); a second broad crested crump weir (14.8 m width, S3, Fig. 8.1); an overshot radial weir (7.5 m width, S4, Fig. 8.1); with a set of 6 undershot sluice gates on the downstream side of an intake channel (7.6 m width) and sump structure constructed in the early 1920’s to house 2 turbines. This hydropower facility became redundant (hereafter RHP) in the early 1970’s and the turbines removed. Nevertheless, for the purpose of this study, the RHP was considered to represent a typical small hydropower intake (RHP intake, Fig. 8.1), furnished with a vertical bar trashrack which extended the full depth of the water column (7.6 m width, 55˚angle, 58 mm bar spacing). A rack trap located on the downstream side of the RHP facility has been commercially operated to capture silver eel from 1992 to 2010, and was used to catch fish for this study. A rubber floating debris boom spans the channel approximately 35 m upstream of the RHP intake (extends to depth 0.45 m below the surface) and diverts floating material downstream via the radial weir. The forebay upstream of the RHP intake ranges from 15 to 35 m width, and is bounded by steel revetments. Today, the complex is principally managed to maintain water levels for abstraction, with a withdrawal point approximately 30 m upstream of the forebay.

The forebay was considered as 3 zones (A, B and C, Fig. 8.1). Zone A extended from the head of the forebay to the debris boom, encompassing structures S1 – S 4. Zone B extended from the debris boom, downstream to a theoretical boundary across the opening of the RHP intake channel. Zone C encompassed the RHP intake channel only.

8.3.2 Bathymetry

Bathymetry was mapped 3rd November 2009 at water level 10.46 ± 0.03 mAODN using a raft-mounted Acoustic Doppler Current Profiler (ADCP) (RiverSurveyor ADP M9, SonTek, San Diego, USA) to measure distance to channel bed using a vertical acoustic beam (0.5 MHz). The ADCP was pulled from one bank to the other along a zig-zag path, oriented perpendicular to flow and moved in a downstream direction, to sample the entire forebay (see Dinehart & Burau, 2005 for detailed description). The raft position was continuously recorded by an on-board GPS. A distance of approximately 3m was maintained between each channel crossing.

Site bathymetry ranged from 0.4 to 3.78 m water depth (Fig. 8.1). The basin is deeper at the upstream end of the forebay due to abstraction practices, and quickly shallows in the downstream direction to a relatively constant depth of 1.3 to 1.6 m throughout zone A. Zone B is slightly shallower (1 to 1.4 m depth), with the exception of the north-east corner which is at 0.4 m depth due to sediment deposition. The intake channel directly upstream of the trashrack (zone C) has a concrete base at constant 1.5 m depth. Stationary depth measurements (see Mueller & Wagner, 2009) conducted in both study years showed bed material to be non-mobile.

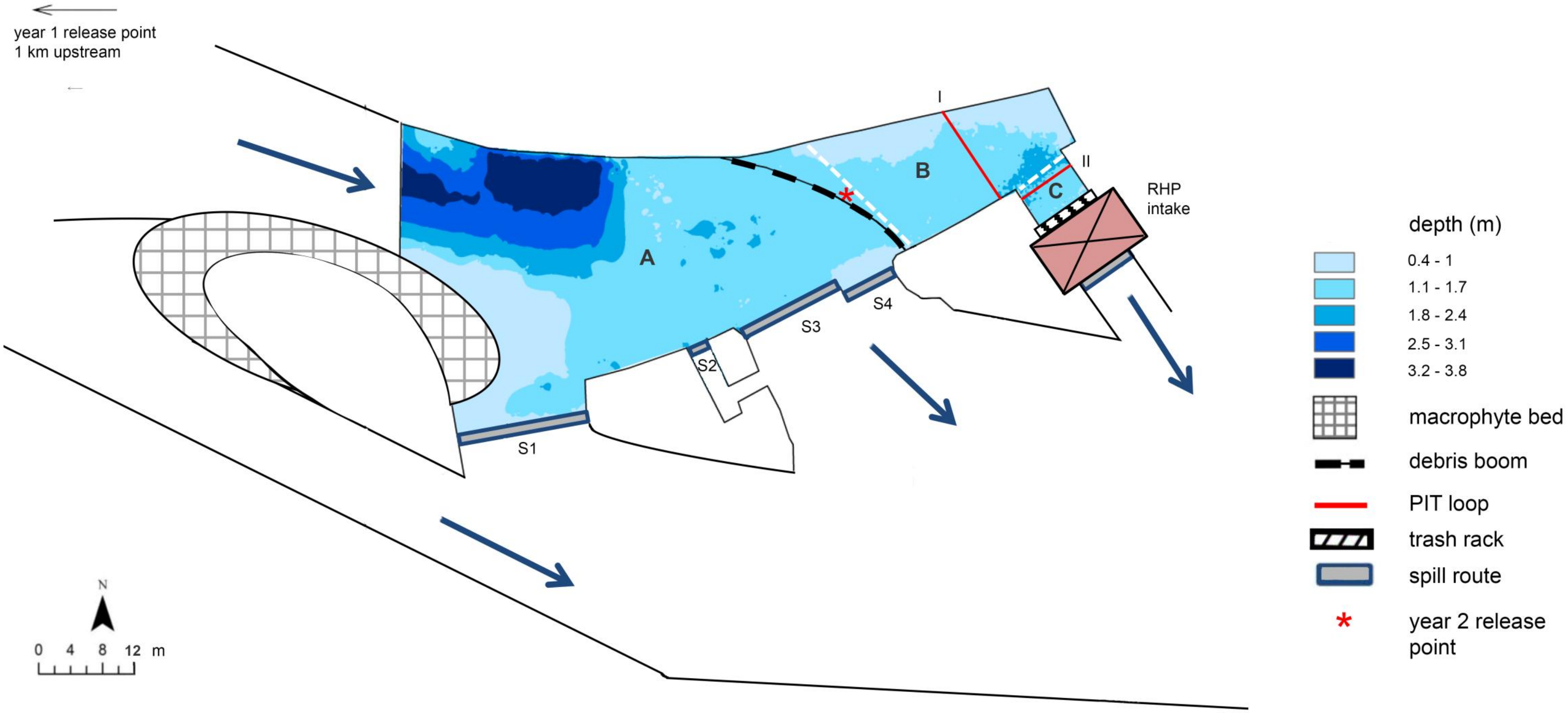


Figure 8.1 Forebay bathymetry and location of structures (S1, broadcrest weir; S2, pool and weir fish pass; S3, broadcrest weir; S4, radial weir, and RHP intake - redundant hydropower intake) at Longham water works, River Stour, Dorset, UK. For purposes of the study, the forebay was considered as 3 separate zones (A, B & C).

8.3.3 Experimental Design

Year 1

Downstream migrating eels were tracked through the forebay (Zones A, B and C) during November 2010 using acoustic telemetry. All adjustable water control structures were set to typical conditions: RHP sluice gates 50% open and radial gate dropped to 0.6 m below mean crest height of the two fixed crump weirs. An automatic flood control gate is operated upstream of the forebay to divert excess flow (in high flow conditions) down an alternate channel. Flow into the forebay was 12.88 ± 0.9 $m^3 s^{-1}$ and water depth of approximately 1.54 ± 0.06 m within zone B throughout the study period.

Year 2

Eel movements were tracked using acoustic and PIT telemetry within zones B and C, under 3 hydrodynamic treatments created within the RHP intake channel.
First, flow passed through the trashrack over the full width of the intake channel (open hereafter). Second, to test if eels rejected areas of rapid velocity acceleration, the trashrack was constricted by 66 % with an opening in the centre channel at full water depth (constricted hereafter). Third, to test the influence of more heterogeneous flow patterns within the constricted channel, and the interaction of eels with physical structures, an array of vertical cylinders (2.53 m width x 2 m height; 110 mm dia., 110 mm spacing) was positioned perpendicular to the flow in the channel centre, 2.5 m upstream of the trashrack (cylinder hereafter). The trashrack was constricted by 66% and the cylinder array spanned the width of the centre channel opening.

The 3 test treatments (open, constricted and cylinder) were alternated every other night to reduce temporal bias (12 trials over 24 nights), and provide 4 replicates per treatment. On alternate nights, eels were captured for the following night's trial (under unmanipulated flow conditions). Five eels were released and tracked through the site per test night (a total of 20 eels per condition). Undershot sluice gates were manipulated to pass approximately equal flow under all 3 treatments (6.43 ± 0.9 m^3

s^{-1}). Natural fluctuations in water level were controlled during the experimental period by adjustment to the overshot radial weir (S4, Fig.8.1).

8.3.4 Hydrodynamic mapping

Hydrodynamic conditions within the site were mapped using an Acoustic Doppler Current Profiler (ADCP) (M9, SonTek/YSI, San Diego, USA), which enables accurate three dimensional velocity profiles to be constructed rapidly over large areas (Shields & Rigby, 2005). All mapping was conducted using transect surveys in which the ADCP raft was pulled slowly bank to bank (with a raft speed below water velocity) along a tensioned guide wire stretched across the channel, approximately perpendicular to flow. Instantaneous velocity measurements in the *x*,*y* and *z* planes were collected at 3 MHz within cells of 0.1 m height throughout the water column, to build up a vertical velocity profile (ensemble) at each lateral position. Due to limitations of the acoustic technique, the ADCP is unable to measure velocity in the top 0.15 m, or in the bottom 0.25 m of the water column. Ensembles were recorded at approximately 0.05 m lateral intervals along each transect (dependent on craft speed). In both years transects were conducted each study night prior to fish release. To determine total flow flowing into the forebay and via each principle downstream route in year 1, transects were conducted across the inlet channel of the forebay, 4 m downstream of the rubber debris boom (4 replicates, 5 min duration), and 2m upstream of structures S1 – S4 (2 replicates, 10-15 min duration). Year 2 transects were conducted 1m downstream of the debris boom; then at 3m intervals downstream throughout Zone B, and at 1 m intervals throughout zone C. Two replicates were taken for each transect position per night.

Water level (± 1 cm) and temperature (± 0.1˚C) were recorded every 30 minutes throughout the study period by a fixed logger located in Zone B (Hobo U20, Onset, Cape Cod, USA). Weir geometry and spill levels were surveyed using a laser level staff with differential GPS (± 1 cm) (Leica 1230 base and rover, Leica Geosystems, Heerbrugg, Switzerland).

8.3.5 Telemetry configuration and validation

Acoustic telemetry (Hydroacoustic Technology Inc., Seattle, USA) was employed to track 2-dimensional movements (x and y) of eels within the study site. Eight hydrophones (300 kHz) were positioned around the perimeter of zones A, B and C in year 1 and Zones B and C in year 2, and configured to optimise coverage of the detection area (Ehrenberg & Steig, 2003). A receiver (HTI, Model 290) logged all tag detections. Due to the shallow nature of the site, it was not possible to accurately determine position in the z dimension (depth), so PIT telemetry was employed to provide swim depth indication at 2 locations. Two flat bed pass-over antennas (14 m length, 0.5 m width and 7.5 m length, 0.5 m width) were positioned to cover the full channel width in zone B and C, respectively (Fig. 8.1, I and II), and connected to a receiver and logger (Model LF-HDX-RFID Oregon, Portland, USA).

Acoustic tags used within the study were HTI model 795G (11mm diameter, 25mm length, 4.5 g mass in air, 300kHs, 0.7 − 1.3 s transmission rate), and Passive Integrated Transponder (PIT) tags (Texas Instruments, HDX, 3.65 mm diameter,32 mm length, 0.8 g mass in air). Detection range-testing was conducted throughout the site to determine optimal positioning of hydrophones, and ensure consistent tag detection. Known tag locations (GPS positioned) demonstrated a minimum accuracy and precision of < 1m in year 1 and < 0.5 m in year 2, which is comparable to other studies (Brown *et al.*, 2003; Svendsen *et al.*, 2011). Similarly, a PIT tag was towed over each antenna at a range of depths and speeds; consistent detection (100 %) was demonstrated for depths < 0.2 m across both antennas. Both telemetry systems logged continually throughout the study and for 1 month after the last tag detection in both years.

8.3.6 Fish capture and tagging procedure

On five consecutive nights (November 2009, year 1), and 12 alternate (non-trial) nights (November 2010, year 2), actively migrating silver eels were captured in the rack trap onsite. All captured eels were visually assessed for signs of external damage or disease and only deemed “fit” if not damaged (approximate 6% rejection rate in both years). Fish were transferred to in-river perforated holding barrels and held for a maximum of 8 h before being individually anesthetised (Benzocaine 0.2 g l^{-1}), weighed (wet weight ,W, g), and measured (total length, mm). The length of the left pectoral fin (mm) from insertion to the tip, and maximum vertical and horizontal left eye diameter (mm) were recorded. Degree of sexual maturation or "silvering" was quantified prior to tagging using two metrics; the Ocular index (OI), according to Pankhurst (1982), and Fin Index (FI), according to Durif *et al.* (2009). European eel with OI ≥ 6.5, and FI ≥ 4.3 (females only), are considered to be at the migratory silver stage (Pankhurst, 1982; Durif *et al.*, 2009). The first 5 eels >450 mm total length (TL) and fulfilling these criteria, thus considered female (Tesch, 2003), were selected for tagging each night (Table 8.1).

Table 8.1 Morphometric summary of downstream migrating European eel tagged during two study years (2009 and 2010)

Study year	No. eels tagged	Total length (mm)	Mass (g)	Mean Ocular Index	Mean Fin Index
Year 1	25	635 – 827	596 – 1049	8.8 (range 6.2-12.3)	4.5 (range 4.4 to 5.0)
Year 2	60	639 – 921	566 – 1207	9.1 (range 7.5-13.5)	4.9 (range 4.3 to 5.8).

An acoustic and PIT tag were surgically implanted into the peritoneal cavity of each selected eel following methods similar to Baras and Jeandrain (1998). No individual surgical procedure exceeded 3 minutes.

After tagging, eels were transported to the release location in a tank ($0.5m^3$) of oxygenated ambient river water, then transferred into a holding barrel (positioned 1 km upstream of the forebay in year 1, and directly upstream of the debris boom in year 2) and held for 10-12 hours to allow post-operative recovery and acclimation before release. No eels died during these procedures. The holding barrel was tethered in the centre of the channel to reduce bias in route choice. The barrel lid was removed on each study night at 20:00 h (in darkness), allowing individuals to leave volitionally. A total of 25 and 60 individuals were tagged and released in year 1 and 2 respectively.

8.3.7 Data acquisition and processing

8.3.7.1 Hydrodynamic data

ADCP transect data were visually inspected using RiverSurveyor Live v3.01 (Sontek/YSI Inc, SanDiego, USA) Several quality parameters were examined including: signal to noise ratio detected within acoustic beams and boat speed relative to water velocity, to aid selection of the optimum transect from pairs of measurements for each location and night (for detailed methods see Sontek (2010)). Total channel flow was calculated within the software from selected transects using methods described in Sontek (2010). Selected transect data were exported to MATLAB (R2010a, Mathworks, Natick, USA) for further processing.

Data were collected at regular time intervals, regardless of distance travelled along the transect, hence the spacing of data points was not uniform. Therefore, to standardise horizontal spacing of measurements, reduce redundant overlap, and aid interpolation, ensembles were deleted where necessary to achieve minimum spacing (0.5 m). Following the methods of Dinehart and Burau (2005), further filtering was conducted to remove outliers at the bottom of each ensemble, which originated from ambiguity errors in near-bed measurements (Gordon, 1996), and to remove any values of a component within the ensemble that differed from the mean value for that component within the whole ensemble by more than 2 standard deviations.

The mean velocity vector (*V*) was calculated for each cell within a velocity ensemble as:

$$\boldsymbol{V} = \sqrt{\bar{\boldsymbol{u}}^2 + \bar{\boldsymbol{v}}^2 + \bar{\boldsymbol{w}}^2}$$

where $\bar{\boldsymbol{u}}$, $\bar{\boldsymbol{v}}$ and $\bar{\boldsymbol{w}}$ are the mean longitudinal, lateral and vertical velocity components (m s^{-1}) respectively. Depth-averaged velocity vectors were then calculated for each x,y measurement position and exported for further processing. The accuracy of geospatial referencing of measurement points may be inconsistent due a number of factors, including GPS accuracy. To account for this, recorded transect paths were cross-referenced against the known track locations and adjusted where necessary. Raster datasets of velocity vectors throughout zones B and C were interpolated within a map of the site boundaries (ArcMap v10, ESRI, Redlands, USA).

8.3.7.2 Fish movements

Acoustic tag detections were manually marked to remove background noise, then processed and corrected for speed of sound using MarkTag v5 and AcousticTag v5 (Hydroacoustic Technology Inc., Seattle, USA). For accuracy and precision, only detections within the hydrophone array were used (Ehrenberg & Steig, 2003). Time-stamped UTM designated detections (eel tracks) were then imported into ArcMap. To ensure comparability between fish, and to account for initial dispersal, orientation and poor detections in the vicinity of the boom, all tracks were deemed to start when fish passed a hypothetical cross-channel line immediately downstream of the boom (i.e. entrance to zone B). Passage was deemed to have occurred at the last detection point before an individual passed downstream of one of the 5 structures (S1 – S4, or RHP intake, Fig. 8.1). Residence time was calculated as time of 1st detection to last detection before ‘passage’. To determine the propensity of eel to follow routes associated with structural boundaries, an edge buffer was drawn 2 m within the site boundary and the proportion of track length falling within this buffer determined using ArcMap. Track length (m), and average swim speed (track duration divided by track length, not accounting for current speed), were calculated in Geospatial Modelling Environment v 6.0 (GME) (Beyer, 2012). Fractal dimension, as an indicator of track tortuosity, i.e. degree of deviation from a straight path, was calculated using Fractal v 5.20 (Nams, 2010).

The following behaviours in zone C were quantified for each fish:

Rejection – when downstream moving individuals abruptly switched (turn angle > 90 ˚) from negative rheotaxis to positive rheotaxis and moved upstream for a distance of greater than 2 m (i.e. > 2 body lengths) (Fig 8.2 a).

Milling – repeated lateral movements of > 2 m length and encompassing more than 2 turns, in a direction approximately perpendicular to principle streamwise flow (Fig. 8.2 b).

Swim depth – PIT detection records were examined for detections at the times when eels passed within 50cm of the antenna locations to ascertain positive or negative detection status. Positive detection on the appropriate PIT antenna provided a surrogate measure of near-bed movement.

In year 1 eel passage routes were interrogated relative to proportion of total flow ($m^3 s^{-1}$) spilling at each weir. Year 2 tracks were individually overlain on interpolated velocity vector raster maps of zones B & C for the appropriate study night. Velocity magnitude values were extracted along the track using line-raster intersect tool in GME. The velocity gradient experienced by each fish prior to rejection was calculated using the extracted water velocities at zone C rejection points, and at a distance of 2 body lengths prior to each rejection.

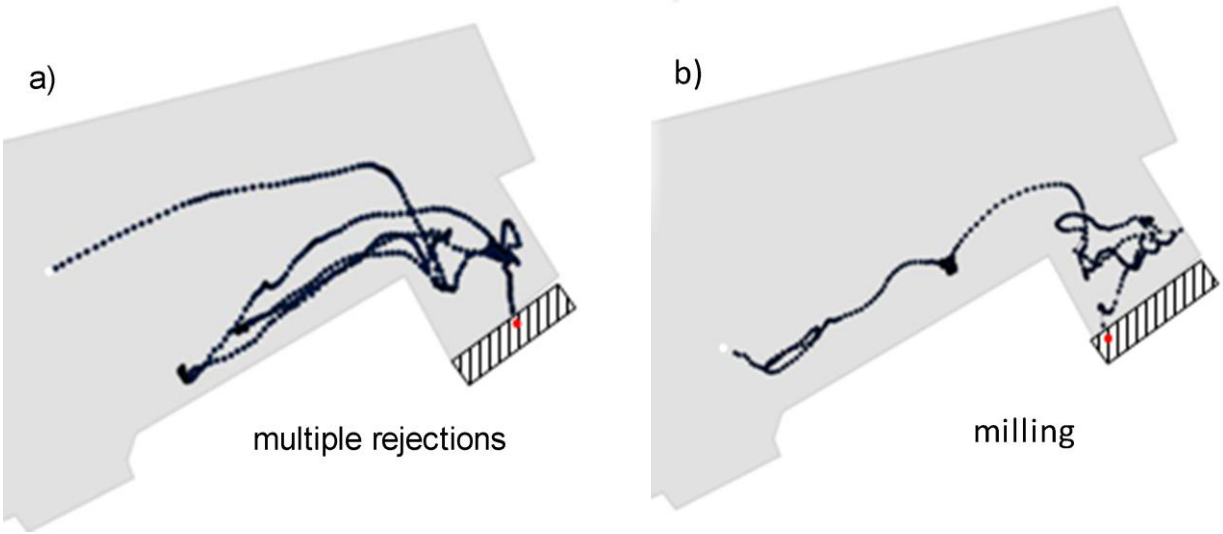


Figure 8.2 Swim tracks of downstream migrating adult eel showing a) multiple rejection and b) milling behaviours approaching a redundant hydropower intake trashrack (hatched area). White and red circles denote swim track start and end locations, respectively.

8.3.7.3 Statistical analysis

Dependent variables were assessed for normality using the Shapiro Wilk test. Where necessary, data were transformed (log10 or square root) to obtain normality prior to analysis. Differences between treatments (open, constricted, cylinder) were tested using ANOVA with Tukey's HSD post hoc test. To test if treatment was a significant predictor of the propensity for rejection and milling behaviours, the occurrence of each behaviour in zone C (binary response) was modelled as a function of treatment using a generalised linear models with binomial error distributions. All statistical analyses were carried out in R v2.14 (R development core team, 2011).

8.4 Results

8.4.1 Year 1

Of the 25 fish released over 5 nights, 76% passed the structures, with individuals using each of the 5 possible downstream routes (Fig. 8.3). Twelve percent of fish were never detected, and a further 12% were only briefly detected in the forebay entrance, but returned upstream and did not re-enter. Only 16% of individuals showed direct paths to the point of passage, while 36% explored and initially rejected the structures. Track lengths ranged from 48.85 m to 312 m. Fish took between 1.4 to 53 h to enter the forebay after release, and spent between 3 min and 9 h 37 min before passing the structures. Passage only occurred during the hours of darkness. Though, 67% of river flow passed through the RHP intake, only 20% of fish passed this structure (Fig. 8.3). Distinctive rejection behaviour was exhibited by 5 individuals immediately upstream of the debris boom. Only 4 individuals passed downstream of the boom, of which 3 showed rejection behaviour between 0.9 m to 2.8 m upstream of RHP trash rack, corresponding with a high velocity area (0.48 to 0.55 m s^{-1}); though all 4 ultimately passed through the RHP intake.

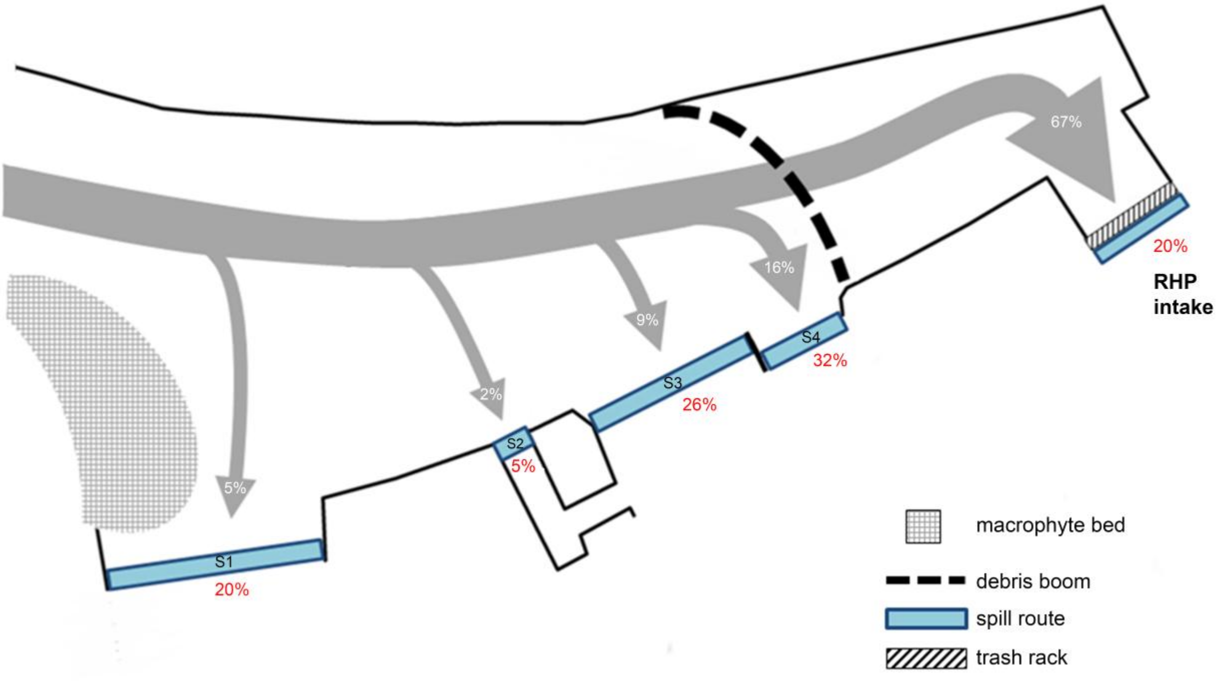


Figure 8.3 Route selection of silver eel (n = 19) (%) that passed structures at Longham Water Works, river Stour, UK, during 5 nights in October 2010 via spill routes S1 (broadcrest weir), S2 (pool and weir fish pass), S3 (broadcrest weir), S4 (drop weir) and the redundant hydropower intake (RHP intake). Arrows indicate water spill routes, with percentages (in arrow heads) of total mean channel flow.

8.4.2 Year 2

8.4.2.1 Hydrodynamics

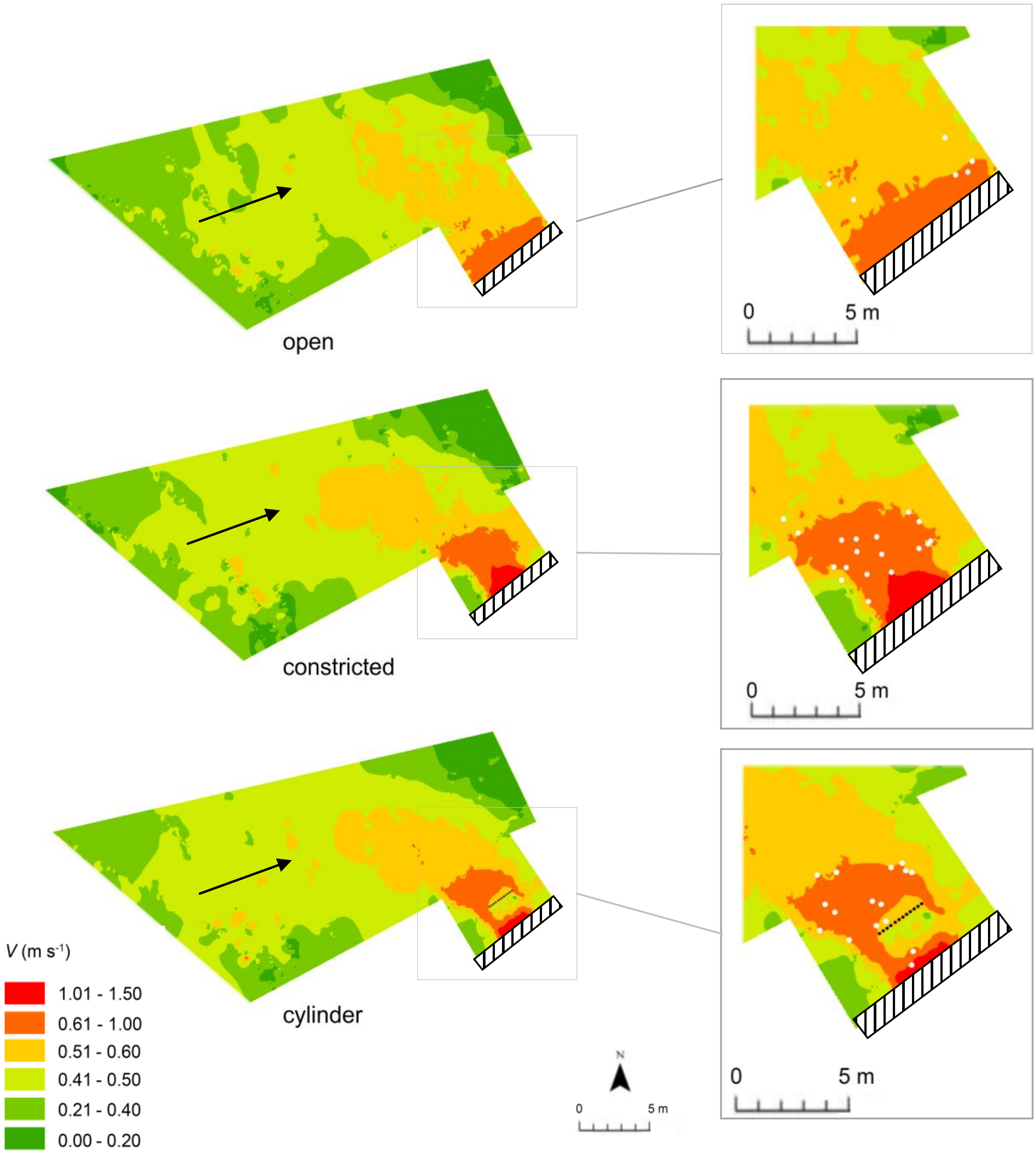


Figure 8.4 Velocity (*V*) profiles under 3 flow treatments (open, constricted, cylinder) in the forebay of a redundant hydropower intake. White circles depict first rejection points of silver eel within the intake channel. Black circles denote the cylinder array; hatched area denotes location of the trashrack, and black arrows indicate direction of flow.

Velocities within zone C ranged from 0.15 – 0.71, 0.13 – 1.49, and 0.11 – 1.36 for the open, constricted and cylinder treatments respectively. Assuming a linear gradient, the mid-channel streamwise velocity acceleration from the upstream perimeter of zone C to 1 m upstream of the trashrack (6 m) was 0.09, 0.21 and 0.11 m s^{-2} for open, constricted and cylinder treatments respectively (Fig. 8.4).

8.4.2.2 Fish Movements and behaviours

Of the 60 individuals released under the 3 treatments, 7 swam upstream of the boom shortly after release and did not re-enter the study area; these were omitted from further analyses. The number of eels that left the site did not differ between treatments. All 53 remaining eels passed through the RHP intake. Passage time though the study area (zones B and C) was highly variable between individuals, ranged from 2.6 to 98 mins, and did not vary significantly between treatments ($F_{2,50} = 0.5$, $p = 0.6$). The time spent in the intake channel (zone C) was different between treatments ($F_{2,50} = 4.6$, $p = 0.02$), with individuals spending longer in open compared to constricted condition. In all 3 conditions, eels predominantly remained in close proximity (< 2 m) to the structural perimeter of the site (Table 8.2).

The distance travelled prior to passage ranged between 39 m and 481 m, across all conditions. Track length differed between conditions ($F_{2,51} = 5.85$, $p < 0.01$), and was greater for the constricted compared to cylinder treatment; open treatment did not differ from either (Table 8.2). Track length within zone C only, was greater for open, compared to the other two treatments ($F_{2,49} = 7.05$, $p<0.01$), with no difference between constricted and cylinder treatments. Track tortuosity differed between all treatments, with the most and least tortuous paths in the open and cylinder treatments, respectively ($F_{2,47} = 16.25$, $p < 0.01$). Mean swim speed was lowest in the constricted treatment (Table 8.2).

Table 8.2 Residence times and track metrics for silver eel (n=53) passing through a forebay (zone B) and redundant hydropower intake channel (zone C) on the river Stour, UK, under 3 experimental flow treatments: open (full width intake opening); constricted (34 % centre opening) and cylinder (34% centre opening with upstream cylinder array). Data were back-transformed where necessary.

	Open	**Constricted**	**Cylinder**
	Mean (± S.D.)	Mean (± S.D.)	Mean (± S.D.)
Time to passage (sec)	807 ± 677	1193 ± 1406	808 ± 606
Residence time in Zone C (sec)	239 ± 165	158 ± 132	199 ± 124
Residence time within 2m of site boundary (%)	86.3 ± 11.1	79.5 ± 13.9	69.1 ± 20.9
Track length (zones B and C) (m)	108.7 ± 52.0	140.6 ± 55.3	83. 6 ± 45.9
Track length (zone C) (m)	42.9 ± 16.5	30.7 ± 10.7	24.4 ± 14.2
Tortuosity (Fractal dimension)	1.14 ± 0.5	1.11 ± 1.03	1.08 ± 0.02
Mean swim speed (m s^{-1})	0.19 ± 0.10	0.20 ± 0.08	0.14 ± 0.06

8.4.2.3 Behavioural responses at RHP intake

There was a bias in the position relative to the channel on entering zone C, under all treatments as the majority of eels approached either along the right-hand bank (39%), or in centre channel (38%).

Rejection

The majority of eels (75%) displayed rejection behaviour prior to passage, with a maximum of 3 rejections per individual. Treatment was a good predictor of the occurrence of rejection behaviour in Zone C (26% deviance, $p < 0.01$, 56 d.f.) with 90 and 85% of fish showing rejection in the constricted and cylinder treatments respectively, but only 30% of fish in the open treatment. Mean individuals rejection rate was highest under the constricted treatment (1.6 per individual), followed by cylinder (1.3) and open (0.7). Under the constricted treatment, the eels re-entered zone B on average twice as frequently compared with cylinder and open treatments (mean 1.8, 0.68 and 0.64 re-entries for constricted, cylinder, and open, respectively).

Eels first rejected further upstream from the trashrack under the constricted (mean 4.08 ± 1.42 m, S.D., n = 18), and cylinder (mean 3.71 ± 1.47 m, S.D., n = 16) treatments, compared to open treatment (mean 2.16 ± 0.88 S.D., n = 6) (F= 4.37, p = 0.02, 2 and 37 d.f.). Individuals that rejected multiple times (n=19) did so at increasing proximity to the trashrack in 74% of cases. There was no indication that eels were impinged on the trashrack (i.e. were not stationary at the structure for > 5 s), under any treatment.

Milling

Treatment was a good predictor of the occurrence of milling behaviour in Zone C (27% deviance, $p < 0.01$, 50 d.f.). Milling was more prevalent in the open (93% of individuals) compared to cylinder (32%) and constricted (25%) treatments. Location of milling varied between treatments. Milling predominantly occurred within a zone less than 2.5 m upstream of the trashrack under the open treatment, but at distances greater than 2 m from the trashrack under the constricted and cylinder treatments.

Swim depth

Of the downstream tracks that intersected with PIT antenna locations (I and II, Fig. 1), 81% were detected and therefore deemed benthic-orientated. In comparison, tracks in the upstream direction were less frequently detected (49%), inferring that eels swam upstream more than 20 cm above the channel bed.

8.4.2.4 Eel movement in relation to hydrodynamics

The water velocity at which individuals rejected (first rejections only) differed significantly between treatments ($F_{2,37} = 7.64$, $p< 0.01$). The mean rejection velocity was lower in the open, than in constricted or cylinder treatments, and the highest water velocity at which eel rejected under any treatment was 0.98 m s^{-1}, in constricted condition. The spatial velocity gradient that eels experienced over the 2 body lengths prior to rejection did not vary between conditions (Fig. 8.5).

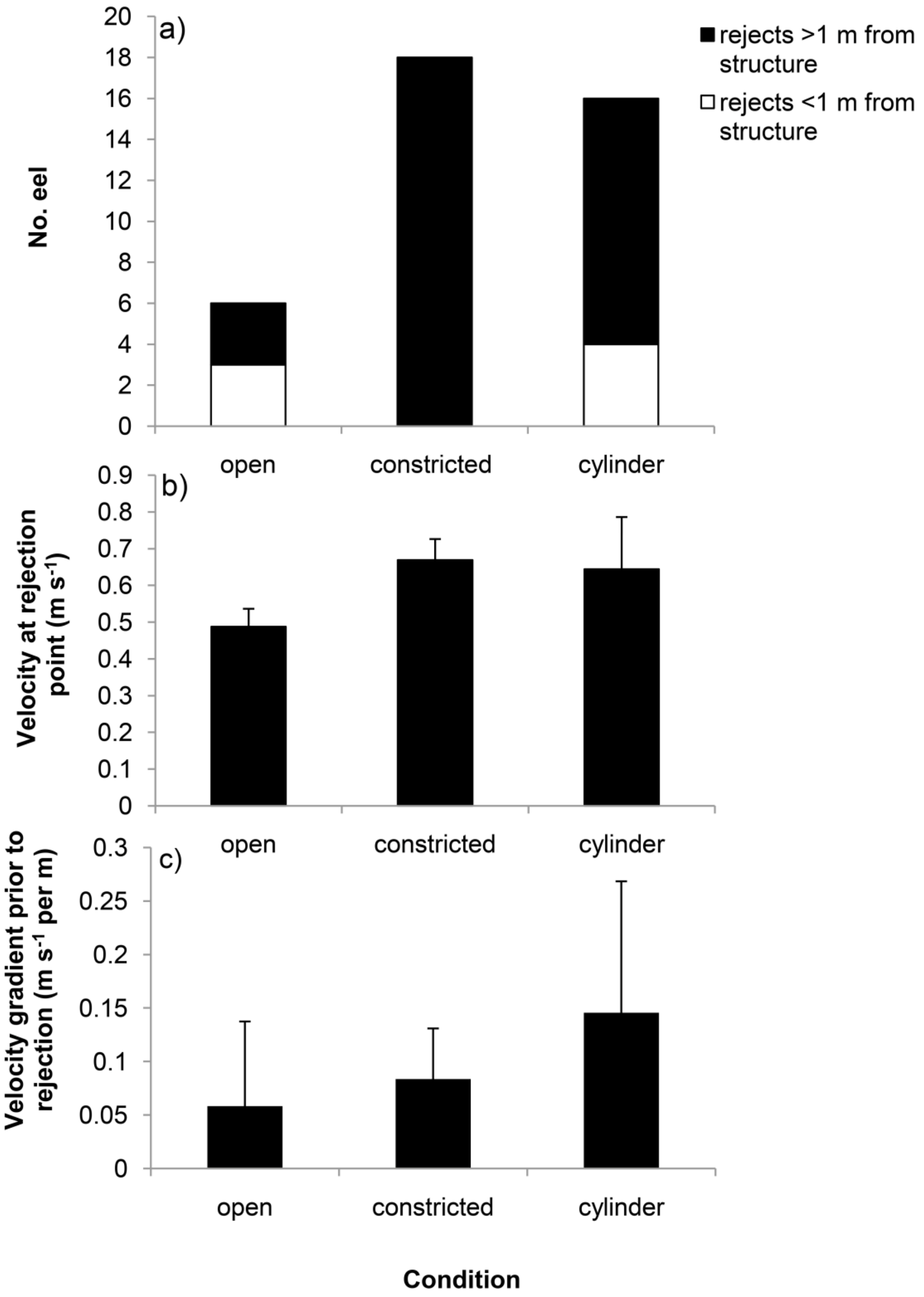


Figure 8.5 Rejection behaviour of eels in the intake channel of a redundant hydropower facility on the river Stour, UK, under 3 flow conditions: open, constricted and cylinder; a) number of that eels that rejected, b) mean velocity vector at point of first rejection, and c) mean velocity gradient experienced by eel over 2 body lengths prior to rejection. Error bars depict + 1 S.D. * indicates significant difference between means at 0.05 level, based on Tukey's HSD post-hoc tests.

8.5 Discussion

This study highlighted key behavioural responses of eels to the physical and hydrodynamic conditions encountered at structures. Findings may aid the development of guidance and passage solutions for seaward migrating eel at riverine barriers. To the author’s knowledge, this is the first field study to examine adult eel behaviour in relation to mapped flow fields at a fine scale (< 1m). Eels displayed abrupt rejection and recurrent behaviour on encountering the elevated water velocities and velocity gradients within a constricted intake channel, independent of structural contact. Rejections were also associated with physical contact at the cylinder array or trashrack, as often reported (Amaral *et al.*, 2003; Russon *et al.*, 2010; Keeken *et al.*, 2011), although these were less common (18 %). In lower velocities, milling behaviour close to the trashrack was more common. The findings have important implications for progressing guidance and passage technologies to ameliorate for the negative impacts of riverine infrastructure of downstream migrating eel.

Eels were predicted to select downstream passage routes coinciding with highest flow, as has been documented in previous studies (Jansen *et al.*, 2007; Breukelaar *et al.*, 2009). This was not the case in the current study, where the principal flow route through the RHP intake passed 67% of flow, but only 20% of eels. While most individuals initially approached this route, the debris boom unexpectedly influenced route choice. The majority of eels either rejected directly upstream (< 2.5 m) of the floating boom, or traced along its upstream edge before selecting an alternate route (Fig 8.6). Eel movements are considered predominantly benthic–orientated (Brown *et al.*, 2003; Travade *et al.*, 2006), as supported by findings of this study, but the floating debris boom projected only 40 cm down from the water surface, and so was unlikely to present a physical obstruction. One possible explanation for this behaviour is that eels were deterred by the hydrodynamic conditions created around the boom, which were characterised by chaotic, turbulent upwelling. Though the principle route of flow may have provided an initial cue for route selection, the hydrodynamic conditions at the boom potentially had a stronger influence on eel behaviour in the immediate vicinity. Surface guidance devices have been used to guide juvenile salmonids during downstream migration (Hanson, 1999; Scruton *et al.*, 2008) and findings suggest that surface-oriented structures may also have application for guiding downstream migrating eels in shallow water sites.

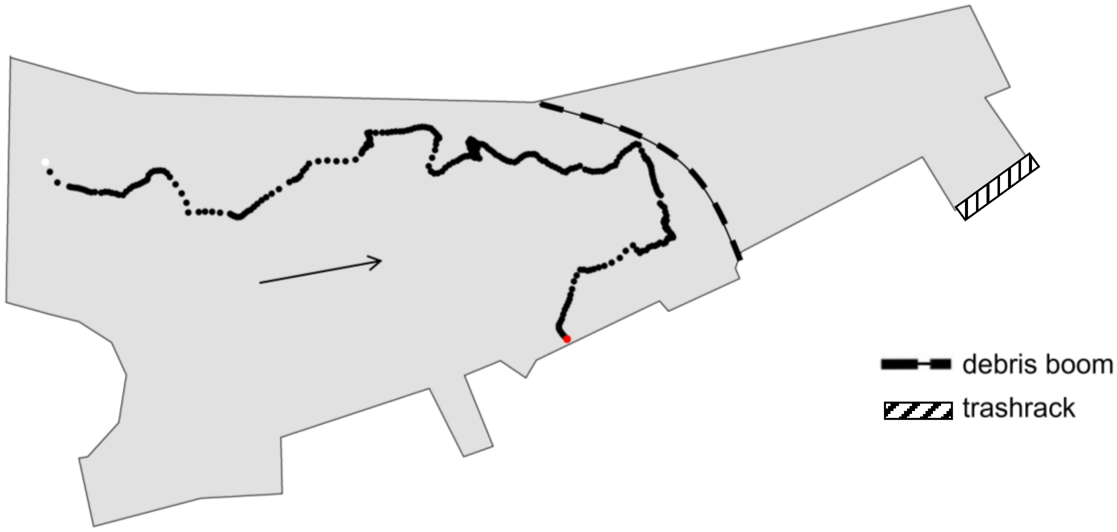


Figure 8.6 Swim track of a downstream migrating adult eel that rejected immediately upstream of a floating debris boom that spans the width of the forebay upstream of a redundant hydropower intake at Longham, Dorset, UK. White and red circles denote the start and end of the track, respectively.

Based on the highly thigmotactic behaviour reported for eel (Tesch, 2003; Russon *et al.*, 2010), it was predicted that the movements of downstream migrants would be structure-oriented. This was apparent as eels predominantly moved through the forebay using routes within 2 m of channel edges. Even when individuals approached the intake in the channel centre, they were observed to move towards the channel sides immediately after rejection. This behaviour may represent a strategy to seek refuge after this startle/escape response, i.e. physical cover or lower velocities within boundary layers at channel edges (Gosset *et al.*, 2005). Similar physical interaction with structures was observed within the cylinder treatment. Eels rejecting near the constricted trash rack, would commonly encounter the cylinder array on upstream rejection and were retained in the area, physically interacting with the cylinders and tracing along the downstream edges of the array. This retention resulted in eels travelling shorter distances prior to passage, compared to individuals experiencing the same constricted channel in the absence of cylinders. These findings reinforce the importance of thigmotactic cues within guidance and passage technologies for eel. Louvers, angled bar racks and benthic guide walls have shown potential to divert eels from deleterious routes such as hydropower and pumping intakes (Amaral *et al.*, 2003; Hassinger, R. & Hübner, D. 2009; Russon *et al.*, 2010), however, their guidance efficiency in field environments is largely unquantified.

Eels displayed clear behavioural differences in response to flow manipulation. Individuals more frequently rejected the conditions created by flow constriction, characterised by more rapid velocity acceleration and higher velocity magnitudes, than unconstricted flow. At low velocities, rejection occurred less frequently, and in 50% of cases only after physical contact with structures. Similar post-contact rejection has been reported in both laboratory and field studies (Adam *et al.*, 1999; Amaral *et al.*, 2003; Russon *et al.*, 2010; Keeken *et al.*, 2011), and although pre-contact rejection has been documented in the field (Holzner, 2000; Keeken *et al.*, 2011), it has not been previously linked to hydrodynamics.

It is suggested that for a hydrodynamic stimulus to elicit rejection behaviour in fish it must be discriminable from internal and external noise, and of a relative magnitude sufficient to induce a flight response (Kemp *et al.*, 2012). Rejection behaviour occurred at a range of water velocities, indicating no apparent velocity threshold. The spatial velocity gradient that a fish experiences over its body length may represent a more important stimulus to rejection than absolute water velocity, as has been demonstrated for juvenile salmonids (Enders *et al.*, 2009a; Russon & Kemp, 2011b). In the present study, the spatial velocity gradient (over two body lengths) at which eels rejected did not vary between treatments, suggesting that this behaviour was similarly elicited on detection of a threshold value; however, inference is constrained by the limited sample size and high variation between individuals. The avoidance of abrupt near field hydrodynamic transitions may represent a strategy to reduce exposure to harmful elements that could cause damage or disorientation (Haro *et al.* 1998; Coutant, 2001; Enders *et al.*, 2009a). For this reason, it is widely suggested that bypass intake velocities accelerate smoothly towards the opening to avoid fish rejecting at the entrance (Clay 1995; O'Keefe & Turnpenny 2005; Larinier & Travade, 2002). These findings further highlight the need to create a smooth acceleration in flow at the entrance to downstream passage facilities for eels, as recommended for salmonids (Environment Agency, 2011; Clay 1995).

Conversely, findings also suggest the potential for manipulating hydrodynamic conditions to guide eels away from deleterious intakes and towards safe passage routes. This may offer an alternative to, or be used in combination with, physical exclusion screens which are both costly and may cause damage and mortality through impingement (Calles *et al.*, 2010). There was also evidence of habituation over time, which must be taken into consideration for behavioural guidance technologies. Individuals that rejected multiple times predominantly did so at decreasing distance to the trashrack, until eventually passing after a maximum of 3 rejections. Eels that initially rejected at water jets and air bubbles in flume studies have similarly been shown to habituate after repeat exposure (Adam and Schwevers, 1997). To provide effective barrier mitigation, guidance devices must divert fish towards an alternate route e.g. fish pass, so they pass quickly, rather than remaining in the vicinity of the deterrent and becoming habituated.

When encountering lower water velocities and less abrupt spatial velocity gradients, milling, rather than rejection, was more frequently observed. Milling and search behaviour has been previously reported when eels encounter screens and trashracks at hydropower facilities (Brown *et al.*, 2003; Keeken *et al.*, 2011). As demonstrated in this study, a tendency to reject and mill resulted in greater distance travelled prior to passage causing migratory delay. Although the differences in distance travelled between treatments were only in the order of 10’s of metres, the cumulative effect of multiple structures within a system may impose significant energetic costs, with potential impacts for successful migration and spawning of adult eels (Larinier, 2001, Acou *et al.*, 2008).

The presence of the cylinder array resulted in less distance covered and shorter overall passage time for migrants. Velocities and spatial velocity gradients were lower in cylinder than constricted treatment, but not lower than the open treatment, which suggests other characteristics of the flow field may have influenced eel behaviour in the presence of the cylinder array. As previously mentioned, the cylinders themselves may have had a containment effect because individuals physically interacted with them, however, hydrodynamic heterogeneity downstream of the array may also have been important. Vortex trails, associated with turbulent flow, were observed in the wake of the cylinder array, extending 1.5 to 1.8 m downstream. Speculator findings may suggest that hydrodynamic parameters such as turbulence are important in eel behaviour, and flume work has suggested adult eels seek areas of elevated turbulence intensity during downstream migration (Russon *et al.*, 2010); though further work is required to elucidate this.

ADCPs offer the potential to rapidly quantify turbulence over a large spatial range. However, there are a number of inherent limitations including the architecture of the instruments beams, inherent noise in measurement techniques, and the special and temporal resolution of measurements. Accordingly, current commercially available ADCPs used to conduct measurements from a moving vessel are considered to have limited capabilities at accurately resolving the smallest scale turbulent characteristics present in rivers (Nystrom *et al.*, 2007 ; Muste *et al.*, 2010). Nevertheless ADCP derived water velocity and depth data has great potential for informing and validating 3-dimensional fluid dynamic models that are able to characterise complex flow fields including turbulence metrics. This approach was used, along with known fish hydrodynamic preferences, to predict optimal fishway entrance positioning for upstream migrating salmonids at the Stornoforrs hydropower facility in Sweden. Predicted locations were successfully verified by sonar and radio telemetry fish movement studies at the same site (Andersson *et al.*,2012 ;Lindberg *et al.*, 2012). Combining empirical ADCP data with hydrodynamic modelling techniques and fine-scale fish movement data, offers great potential to further our limited understanding of eel behaviour in relation to specific hydrodynamic parameters. This knowledge will contribute to the development of more successful barrier mitigation measures.

Chapter 9 General Discussion

The research presented in this thesis was conducted to address two primary aims. These were to assess the influence of physical and hydrodynamic parameters on the movement and behaviour of European eel at riverine barriers and passage facilities; and to aid the development of more effective upstream and downstream passage solutions for this species. Several biases and key knowledge gaps became clear through the literature review. Historic fish passage research has focussed on anadromous salmonids, with comparatively little attention given to catadromous and potadromous species. For the European eel there exists sparse and often contradictory information as to which physical and hydrodynamic conditions pose restrictions to the migration of both the juvenile and adult lifestages, and which parameters optimise attraction and passage. A lack of such knowledge has been highlighted as a principal restraint to the development of effective barrier mitigation methods (Castro-Santos *et al.*, 2009; Kemp & O'Hanley, 2010; Noonan *et al.*, 2011).

9.1 Upstream migrating lifestages: key findings and management recommendations

Several novel methods have been developed to increase the passage of glass eel, pigmented glass eel, and elver at intertidal and riverine barriers, including the allowance of tidal ingress by manipulation of tide gates (Mouton *et al.*, 2011) or siphons (Bult & Dekker, 2007); provision of small delay-closing tide flaps within larger tidal gates, so-called ‘pet flaps’ (Solomon, 2010), and Hidrostal ‘fish friendly’pumps (Patrick & McKinley, 1987). Nevertheless, barrier mitigation for upstream migrating juvenile eel is still predominantly attempted using eel-specific passes; the basic design of which has differed little since their conception (Solomon & Beach, 2004). Due to their simplicity and relatively low cost in comparison to technical fish pass facilities, 1000’s of these devices have been installed by organisations and private individuals across Europe, South America and Australasia (Larinier, 2001). Improving the efficiency of these facilities therefore offers great potential to increase freshwater recruitment.

The influence of plunging or streaming attraction flow on pass efficiency at eel-specific facilities was tested in a field experiment conducted at an intertidal barrier. This structure spills little flow during the peak upstream migration period and forms the principal constraint to eel recruitment into the freshwater study catchment. Passes with plunging attraction flow passed more than twice as many eels as those with submerged streaming flow, suggesting a strong attraction provided by the former. By locating experimental passes at both the centre and edges of the weir, a strong 'edge bias' was also identified.

A key recommendation arising from this work is that plunging attraction flow at pass entrances has the potential to greatly improve passage efficiency and therefore should be incorporated as a standard design feature for eel specific passes. This feature could be easily retrofitted to existing facilities, and due to the low quantities of water required, is feasible in situations where high abstraction demands severely limit the quantity of water available to operate passage facilities (as was the case at the study site). It is acknowledged that larger volumes of water, though delivered at similarly pressure, may be required to provide attraction where there is a greater influence of competing hydrodynamic cues.

To develop transferable fish passage design criteria it is important to quantify the swim capabilities and behavioural responses of target species to well defined hydrodynamic stimuli at biologically meaningful scales (Castro-Santos *et al.*, 2009; Kemp *et al.*, 2012; Williams *et al.*, 2012). Therefore, to understand the mechanisms underlying eel attraction and possible constraints, experiments were conducted in a purpose built field flume to quantify the influence of turbulent flow and velocity on the attraction, passage, swim capabilities and behavioural response of eel. The same plunging and streaming attraction flows previously tested in the field were replicated, and also tested at approximately twice the flow rate to determine the effect of magnitude of hydrodynamic components on attraction and behaviour. Plunging and streaming attraction flows were also compared with relatively uniform low velocity and turbulence background flow, to test the hypothesis that juvenile eel select routes of relatively benign flow conditions during river assent (Tesch, 2003; Knights & White, 1998).

Eels were more attracted to plunging and streaming than background flow alone at both low and high flow levels. Observation of swim paths at a fine scale demonstrated that routes of highest velocity and turbulence induced greatest attraction; however, within these general routes, eels selected swim paths so as to encounter lower than average velocity and turbulence kinetic energy. Individuals were shown to increase their swim speed at higher velocities, which may reflect a strategy to pass through energetically expensive environments as fast as possible (Hinch & Rand, 2000; Peake, 2004; Standen *et al.*, 2004). Overall these findings suggest a potential trade-off between creating the optimum conditions for attraction, and those required to facilitate rapid ascent through passage facilities with minimum energy expenditure. This is a widely recognised and important consideration in the development of effective fish pass design (Laine *et al.*, 1998; Bunt et al. 1999; Aarestrup *et al.*, 2003; Pratt *et al.*, 2009). As fish attempt to ascend or exit upstream passage facilities they may ‘fall back’ downstream of the barrier, either due to the unappealing or impassable hydrodynamic conditions encountered, or physical exhaustion (McLaughlin *et al.*, 2012). Some eels were observed to initially chose to approach, but then reject areas of higher turbulence. This infers that although turbulent flow should be provided in the vicinity of a pass entrance to facilitate attraction, turbulence within the pass should be minimised to avoid prohibitively high energy demands on the fish. This may be achieved through measures such as reducing the pass gradient, minimising air entrainment, and by providing appropriately-sized low turbulence resting areas (Clay, 1995; FAO/DVWK, 2002).

The field and flume approaches adopted within these studies both highlighted that upstream migrating juvenile eel have a strong tendency to orient to structures. The ‘edge tendency’ of eels has been previously postulated and anecdotally reported, but until this work, not fully quantified. Due to this perceived edge preference, the current convention is to position eel passes tight against channel banks or against the abutments of a structure. The optimum positioning of pass facilities for smaller size classes (73 – 90 mm) are at the channel edge, however edge bias is strongly influenced by eel size. Larger yellow eel (> 121 mm) passed almost exclusively in the channel centre, which concurs with the propensity of these size classes to occupy deeper centre channel routes, a behaviour thought to be related to habitat and food availability (Tesch, 2003). In light of this, multiple pass provision should be made at both the edge and channel centre of a barrier to accommodate distinctly different eel size classes, although obvious exceptions to this would apply where centre channel velocities exceed swim capabilities of even larger eels, likely resulting in their movement to lower edge velocities.

There is a current convention to position the entrance of eel passes away from the main flow spilling at barriers and technical fish passes, and in areas of low velocity and turbulence, so-called "quiet water" (Knights & White, 1998). In high flow situations, where the main channel or barrier flow exceeds the maximum swimming capabilities of migrating eels, this is indeed likely to represent the optimum location due to both the strong edge tendency and velocity refuge-seeking behaviour of upstream migrating eels. However, as found in this study, eels are attracted towards elevated levels of turbulence and velocity, so in many small and heavily abstracted rivers the hydrodynamics created downstream of water control structures such as flow gauging weirs, or at the entrances of technical fish passes, may provide a strong cue that attracts eels away from the channel edges (Fig 9.1). Therefore it is recommended when locating eel passes, that both the main channel velocities and dominant flow patterns at structures for the peak migration period be considered. For many low flow rivers this may constitute locating pass entrance alongside existing fish passes or in the centre of the channel to optimise on the strong attraction and rheotactic cues provided at such locations. Ongoing studies into upstream eel migration past small flow gauging weirs on the river Stiffkey, UK, have indicated that peaks in juvenile eel ascent past structures correspond to discrete periods of increased flow during summer low flow periods (Piper & Wright, 2010).

Figure 9.1 Eel attempting to ascend at the channel centre of a flat V triangular profile flow gauging weir, under summer low flow conditions.

It may also be viable to create routes of reduced velocity and turbulence to allow eel assent through existing technical fish passes, for example, through the addition of bristle media (Porcher, 2002). This feature was incorporated within a vertical slot pass and shown to improve upstream passage for river Lamprey (*Lampetra fluviatilis*) (Laine *et al.*, 1998), a species which employs a similarly weak anguilliform mode of swimming. There is a legislative emphasis within Europe on providing multispecies passage at all barriers perceived to restrict free migration, the scale and cost implications of this means that several species specific solutions at a structure may not be viable and it is therefore advantageous to pass all species through one.

Nature-like fishways, which are designed to emulate the hydromorphology of a natural stream, are considered to represent one of the most effective methods to achieve both up- and downstream passage of a wide range of species and lifestages

(Santos *et al.*, 2005; Calles & Greenberg, 2007). The relatively low gradient and hydraulic heterogeneity integral to this design results in fish being able to negotiate the pass channel using routes appropriate to their swimming capabilities and behavioural preferences. The optimum configuration should provide high flow routes for strong swimming highly motivated species such as salmonids, and routes of low velocity and turbulence with regular resting pools for weak swimming species and juvenile lifestages (FAO/DVWK, 2002). The passage efficiency (once fish have entered the pass) has been demonstrated to be higher in nature-like than achieved by more technical designs (e.g. pool and weir) (Bunt *et al.*, 2012), although there are some key limitations to this design. Inherent architectural restrictions mean that it may not be possible to locate the downstream entrance directly below a barrier, this in combination with the relatively low flow conveyed down the pass have been attributed to low attraction rates (Moser *et al.*, 2000; Sprankle, 2005). Also, the relatively low effective operating gradient (typically ≤ 5%) means more land is required than technical pass designs, and they are therefore not considered a viable passage solution at high head barriers. Findings of this programme of research may aid the development of such passes by providing insight into the swim capabilities and behaviours of juvenile eel under turbulent conditions.

There is much advantage in using a combined field and flume based approach for conducting fish passage research. There is a need to quantify the efficiency of laboratory derived components for pass design at realistic scales in natural environments (Lobón-Cerviá *et al.*, 2003; Calles & Greenberg, 2007). The field study allowed testing of proposed hydrodynamic attraction at full scale and to quantify the effects on naturally migrating fish, without pre-handling. By simultaneously recording key environmental variables, it was possible to determine that although water height and tides affected the magnitude of daily migration, the attraction effect persisted regardless. However, the precision and accuracy at which both hydrodynamic features and fish behaviour can be quantified in field environments may restrict determination of fundamental behaviours that lead to transferable design criteria. Flume experiments offered the opportunity to quantify movement in relation to particular components with the flow field at a scale unattainable in the field for such small fish (< 90 mm). Furthermore the flume facility enabled control over many confounding variables experienced within field studies, while still permitting volitional compensatory behaviour in relation to accurately quantified hydrodynamics. The latter is an important prerequisite for determining realistic swim capabilities to inform pass design and adapt existing structures (Rice *et al.*, 2010). This has been highlighted where fish allowed to respond naturally to more realistic flow conditions in large open channel flumes, have either over or under performed counterparts tested in the uniform flow and the restricted space of swim chambers (Enders *et al.*, 2003; Peake, 2004; Tudorache *et al.*, 2007; Russon & Kemp, 2011a).

9.2 Downstream migrating lifestage: key findings and management recommendations

It is widely recognised that high head barriers such as dams can restrict or prevent the seaward migration of silver eel (Acou *et al.*, 2008), and that the injury and mortality resulting from impingement at screens and entrainment at hydropower and pumping facilities can be significant (Winter *et al.*, 2007; Kunst *et al.*, 2008; Calles *et al.*, 2010). European countries have a statutory requirement to comply with the freshwater escapement targets of adult spawner stock set out in the European eel regulations; hence responsible bodies urgently require guidance on assessment criteria to decide which barriers are likely to be impacting eel populations, and how to provide effective mitigation. Previous work has highlighted the potential of altered flow management regimes, power generation and water abstraction schedules during peak migration periods to reduce deleterious impacts and improve passage (e.g. Bruijs *et al.*, 2003; Haro *et al.*, 2003). This approach relies on understanding how eel respond to different structure types, and the key cues created by often complex interactions of management regimes. Field research highlighted the substantial influence that management regimes of low head structures and comparatively minor water abstraction points may have on migratory delay, entrainment loss and overall probability of seaward escapement of eels. This study demonstrated that the quantity of water spilling over the principle intertidal barrier affected eel propensity to pass. At low flow, when spill depth over the weir crest was below 0.18 m, eel diverted down an alternate channel thereby increasing their risk of entrainment at a water abstraction intake which was the principle constraint on eels escaping to sea (12 – 26 % entrainment rate).

Previous studies have highlighted high intake velocity as a critical component to entrainment of seaward migrating eel (Bruijs & Durif, 2009). The current research suggests that substantial entrainment loss may also occur when intake velocities are below eels burst swim capabilities, but abstraction levels increase abruptly and are exacerbated by reduced flow and escapement opportunity via alternate routes. Several key management recommendations were borne from this study. It is recommended that water abstraction is either ceased during peak migration periods, or that, similar to the ramping-rate restrictions placed on hydropower operations (Moog, 2006), pumping regimes are altered to insure a gradual increase in abstraction over several hours to avoid the attraction created from rapid pump start-up (e.g. pumps switching from off to full abstraction rate) (Wanningen, 2011). It is also important to ensure flow is maintained to alternative benign passage routes. The need to regularly maintain structures was also made apparent in the study as debris blocking undershot passage routes and mechanical faults reduced structure openings and increased delays. Physical exclusion screens or behavioural deterrent devices such as strobe lights (Brown, 2000; Keeken *et al.*, 2011) or sound (Sand *et al.*, 2000), may also offer potential to reduce entrainment at water abstraction intakes, though effective behavioural guidance is not yet well developed for eel. While these findings highlight opportunities to improve escapement in the study catchment, it also provides broader transferable guidance applicable to highly regulated rivers of similar hydromorphological characteristics.

Physical exclusion screens are commonly used to prevent entrainment of fish at water abstraction and hydropower intakes, and can be highly effective (Turnpenny & O’Keefe, 2005). However, there may also be considerable disadvantages to screening methods including installation and maintenance costs, reduced pumping and power generation efficiencies, and damage and mortality caused to fish due to impingement (EPRI, 2005). The elongated body morphology, weak swim capabilities and thigmotactic behaviour of eels make them particularly vulnerable to impingement (Boubee & Williams, 2006; Calles *et al.*, 2010; Russon *et al.*, 2010).

For screens to effectively exclude adult eels from deleterious areas and not cause injury and mortality, it is recommended that cross-channel screens should be positioned at a steep angle (ideally $\leq$ 20 degrees to the channel axis), and that sweeping flows (parallel to screen) are lower than through flow velocities (Turnpenny & O'Keefe, 2005). Screen approach velocities (perpendicular to the screen face) are recommended to be maintained between 0.4 and 0.5 m s^{-1} (for eels >30cm total length) (Environment Agency, 2011b). These recommendations are based on laboratory swim trials, however, findings demonstrated that eels both chose to enter an intake volitionally at velocities below their burst-swimming capabilities, and that individuals were able to reject and swim against intake velocities greater than 1 m s^{-1}. These findings suggest that behaviour may be more important than swim capabilities in predicting adult eel impingement and entrainment at intakes; although it is acknowledged that there will be an intake velocity threshold at which the escape capabilities of individuals are exceeded and non-volitional impingement and entertainment results. This, and other work (Russon & Kemp, 2011), suggests that this maximum threshold is higher than previously thought (>0.98 – 1.75 m s^{-1}).

Irrespective of velocity, screens should have narrow mesh size/bar spacing (9 mm, for eel length 300) to overcome the tendency of eel to force through spaces smaller than body diameter (Russon *et al.*, 2010; Environment Agency, 2011b). Such criteria are perceived as unfeasible by many pumping station and hydropower facility owners (Kunst *et al.*, 2008), hence there is considerable interest in developing alternative methods which fulfil legislative requirements to protect fish, while not impacting operating efficiency of a facility (Bruijs *et al.*, 2003; Moria, 2008).

Developing effective guidance technologies is dependent on understanding how fish respond to specific and well defined cues (Anderson, 1988; Schilt, 2007; Williams *et al.*, 2012). Acoustic telemetry employed to relate the movements of downstream migrating adult eel to manipulated flow fields in the vicinity of a hydropower intake, at sub-metre accuracy, enabled distinctive behavioural responses to specific flow features to be identified. A link between accelerating flow and upstream rejection behaviour in adult eel was identified for the first time. Eels may reject safe passage routes such as undershot sluice gates and bypasses if water velocities at the entrance accelerate too rapidly (> 0.05 cm s^{-1} per cm of body length). Eel rejection at structures which constrict flow has previously been observed (Brown *et al.*, 2009) and postulated to be a response to hydrodynamic conditions (Jansen *et al.*, 2007; Calles *et al.*, 2010), though not directly linked.

Rejection from benign routes may increase the risk of entering alternative deleterious routes (Brown *et al.*, 2009), and incur increased energetic cost (Larinier, 2001; Acou *et al.*, 2008). A key recommendation arising from findings is that velocity should increase gradually towards constricted openings such as bypass entrances (Travade & Larinier, 1992; Clay, 1995). At bypass entrances, this gradual acceleration in flow may be achieved by a tapered entrance, forming a bell-mouth shape (Fig. 9.1a) (Turnpenny & O’Keefe, 2005). Alternatively, a flow control device similar to the cylinder array used within this study may be installed upstream of a bypass entrance. As evidenced within this thesis, eels predominantly move within the lower section of the water column, hence any bypass facility should have an opening which extends to the channel bed. However, to also accommodate midwater and surface dwelling fish and facilitate multi-species passage, an opening which extends the full height of the water column is desirable (Turnpenny & O’Keefe, 2005). This may be achieved by a vertical slot opening, or where this would pass an unacceptably high proportion of flow, the entrance may be gradually sloped from the bottom to a shallower bypass channel (Fig. 9.1b) (Bruijs & Durif, 2009; Environment Agency, 2011b).

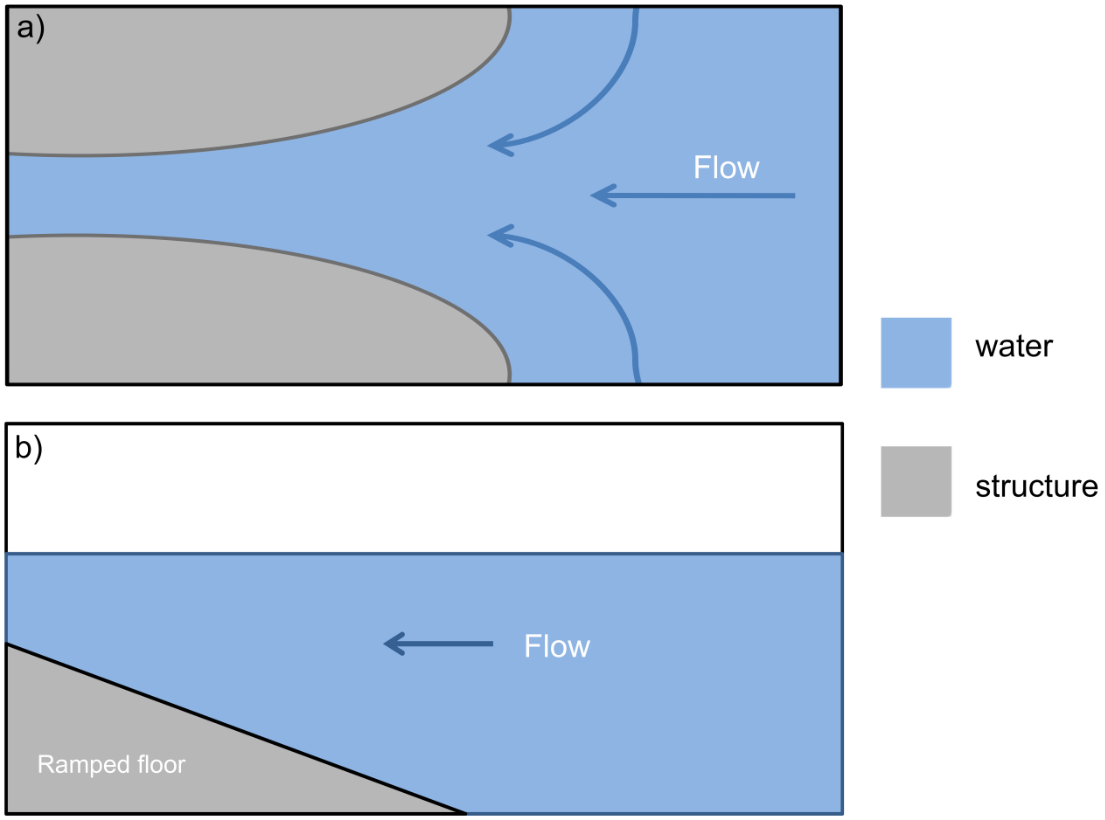


Figure 9.2a) Plan view of bell-mouthed entrance to downstream fish bypass facility, b) cross-section view of bypass entrance with sloping floor to guide benthic orientated species to surface opening (adapted from Environment Agency, 2011b).

Further, findings inferred that the observed rejection behaviour was principally elicited by the spatial velocity gradient the fish experienced on approach, rather than a critical velocity threshold. Despite the highest occurrence of rejection at highest water velocities, this behaviour was also observed at lower velocity magnitudes, but similar gradients. Rejection is unlikely to prevent impingement or entrainment at intakes as eels appeared to quickly acclimate to conditions after initial rejection, and finally passed through the trashrack. However, it does indicate the potential to deter eels from deleterious routes through manipulating flow fields. Similar mechanisms have been postulated for downstream migrating salmon responding to increasing velocity and hydraulic strain (termed free-shear flow gradients) (Goodwin *et al.*, 2006). It is proposed that a smolt will respond to a “just noticeable difference” in the intensity of a hydrodynamic stimulus above that of the background levels it is acclimated to, which elicits the reaction to move towards an area of lower velocity magnitude, or switch from negative to positive rheotaxis and swim against the principle flow (Goodwin *et al.*, 2006). Increasing acclimation is proposed to occur with exposure, until a threshold point is reached after which no reaction is elicited and a fish will pass through the previously rejected gradient (Goodwin *et al.*, 2006; Nestler *et al.*, 2008a). However, Kemp *et al.* (2012) propose that in addition to the ability of a fish to detect a stimulus above external and internal noise, the response elicited is largely dependent on individual bias. Clearly much further work is required before fish may be effectively and predictably guided. It must also be recognised that fish guidance is ineffective without the provision of alternative benign passage routes (Turnpenny *et al.*, 1998). Fish are otherwise likely to mill, increasing both the area covered, with inherent energetic cost, and the probability of passing through deleterious routes (Svendsen *et al.*, 2011).

Milling behaviour at the intake channels and particularly parallel to and often in contact with the trashrack was commonly observed in the study, particularly at low intake velocities. There are currently several technologies under development which aim to exploit both the milling and rejection behaviours of eels at trashracks to guide them to safe passage routes. One novel bypass facility called the Bottom Gallery® (Floecksmühle Ingenieursbüro, Aachen, Germany) has a benthic oriented entrance which faces the trashrack, with the aim to intercept rejecting eels as they move back upstream along the channel bottom. Another design employs a 40 cm diameter zig-zag pipe located on the bottom of the channel directly upstream of and perpendicular to a trashrack, with the intention that milling or recurrent eels will search along the pipe structure and enter it via one of several entrance holes. This pipe subsequently circumnavigates a hydropower or pumping facility and exits downstream (Hassinger & Hübner, 2009). While these technologies have both shown potential in laboratory tests, they are yet to undergo quantitative evaluation in the field. An alternative approach is to locate bypass entrances at regular interval along the face of a trashrack or screen, with the intention that eels will search along the structure then move into the bypass and be transported downstream (Calles & Bergendahl, 2010). The research presented in this thesis will aid the on-going development of such technologies by contributing to the mechanistic understanding of eel behaviour at structures, and informing how hydrodynamics may be used to guide eel away from deleterious routes and to safe passage facilities.

9.3 Recommendations for further research

During this programme of research a number of knowledge gaps were identified where further study would be beneficial to increase understanding of how eels behave at anthropogenic barriers, and what hydrodynamics are required for successful passage facilities. Furthermore, there are limitations to the applicability of certain findings, which must be acknowledged and may potentially inform future research directions.

It is important to conduct field studies to validate the impact of attraction flow at full-scale passage facilities in a natural environment. Due to limited tracking methods available for juvenile fish, it was only feasible to quantify the relative efficiency of plunging and streaming attraction in the field. Whilst this provides useful data for attraction at passage facilities (Bunt, 2001), it is acknowledged that findings tend to be less transferable than identifying true pass efficiency, which involves knowing 1) the potential total number migrating fish, attempt to pass; 2) the number of fish attracted to a facility, and 3) the number which successfully ascend. Further to this, to quantitatively evaluate components which affect fish attraction and passage requires fine-scale information on the movement and behaviour of individual fish (Bunt *et al.*, 2012).

Due to the apparent attraction provided by the simple addition of plunging flow in both field and flume studies, future research may quantify this effect over a greater range of attraction and background flow conditions. The field study undoubtedly represented an optimum scenario for a minimal amount of flow to be detected by eels due to its relative magnitude compared to that of the weir, and it is recognised that this relationship may not persist in locations of greater weir spill.

It is important to highlight that both telemetry studies only used large female silver eels, due to both their dominance within catches and the restrictions of transmitter size. It was apparent from fish catches over the two year study on the Suffolk Stour, and previous routine monitoring on the same river in previous years (Environment Agency, unpubl.), that tagged individuals represented a typical size of migrant for this river. The low eel density within this catchment is believed to be the cause of the population bias towards large females at the silver eel lifestage (Defra, 2010b). Many systems, including the Dorset Stour, comprise a significant proportion of small males which are likely to have been excluded by the capture method used (Environment Agency, unpubl.), therefore further work should attempt to determine comparable findings for this component of the population. Recent developments in transmitter design now make this viable.

ADCPs offer great potential within ecohydraulic research to quantify hydrodynamic features at biologically meaningful scales in the field. ADCP's are theoretically capable of rapidly obtaining accurate high resolution 3D velocity data over large areas. However, these devices have principally been designed to collect data for mean channel flow calculation, therefore there is at present a lack of established data collection methods and analytical tools to fully exploit these capabilities for mapping complex flow fields with high accuracy and precision (Muste *et al.*, 2010). In particular, there is currently limited scope for using data collected by moving raft and boat-mounted ADCP's for quantifying turbulence metrics in field environments. This is principally due to innate limitations of the device architecture and insufficient methods to screen variation from background noise (Lu & Lueck, 1999; Muste *et al.*, 2010). Further work is required to develop specific methods to provide these capabilities.

In view of these limitations, a combined modelling approach validated with ADCP data may offer the greatest potential to quantify additional hydrodynamic parameters which may be important in fish behaviour, such as turbulent components (Coutant, 2001; Odeh et al., 2002; Webb & Cotel, 2010). Computational Fluid Dynamic (CFD) modelling offers such an opportunity. While the fluid dynamic relationships of these models are well established, this technique can be inaccurate without empirical data to fine tune model iterations. It is proposed that a future development of the research presented should be to model key hydrodynamic parameters within the site using CFD techniques, and ground-truthed with the existing ADCP velocity data. This will enable the fish swim paths to be interrogated in relation to a wider range of hydrodynamic variables.

Technological advances in telemetry systems are continuously increasing our capabilities to study the behaviour of fish in their natural environment. A limitation of the sub-metre positioning acoustic telemetry method applied was an inability to measure the swim depth at which fish either rejected or passed the intake. This necessitated that depth-averaged velocities be used, and reduced the resolution at which fish tracks could be related to water velocity. The development of a sub-metre accuracy pressure tag for determining fish depth in shallow water sites would provide new insights. High resolution acoustic filming methods (e.g. DIDSON) can be used in shallow water depths and have been successfully applied to determine fish depth in the water column when approaching intakes (Keeken *et al.*, 2011) . However, this technology only operates within a limited viewing window so a combination of acoustic positioning telemetry and high resolution acoustic filming techniques may offer opportunity for studying fish behaviour at fine scale in shallow water environments.

While this thesis has considered the principal upstream migration of juveniles and the downstream migration of adults, it is acknowledged that a proportion of the population within any system may exhibit facultative catadromous life-history traits. Individuals may settle and spend some or all of their juvenile and adult growing life phases in estuarine environments, or make regular movements between fresh and saline habitats (Tzeng *et al.*, 2000; Daverat *et al.*, 2006; Tabouret *et al.*, 2010). The degree to which this occurs, and the causes of this behavioural plasticity, are poorly understood (Feunteun *et al.*, 2003), but it emphasises that eels may require passage at structures on multiple occasions throughout their continental life-phase, and at a range of sizes, which should be taken into account when designing fish passage facilities.

9.4 Research impact and closing remarks

As a consequence of the current and historic demands placed on freshwater systems, they are now among the most heavily impacted ecosystems in the world (Poff *et al.*, 1997; Nilsson *et al.*, 2005). Fish are an ecologically, socially and commercially important component of those ecosystems, and remedial measures are required to reduce anthropogenic impacts on them (Northcote, 1998: Marmulla, 2001). This thesis aims to improve fluvial connectivity for the European eel, primarily through the contribution of knowledge pertaining to how eels behave in response to the hydrodynamics encountered at structures, including fish passes.

Policy makers recognise the urgent need to reverse the decline of eel and have brought legislation into force to provide protection. It is widely recognised that our current state of knowledge and lack of appropriate mitigation measures are hindering capabilities to meet these obligations (EPRI, 2001; Bruijs & Durif, 2009; Calles *et al.*, 2010). Statutory bodies are therefore seeking guidance from the scientific community on how to improve mitigation measures for the European and other declining anguillid eel species.

This research is timely as recent legislation within England and Wales requires that no new infrastructure be constructed without provision for eel; no existing infrastructure be modified without the need for eel passage to be included, and that appropriate physical exclusion or behavioural screening be provided at all potentially harmful water abstraction or flow points (> 20 cumecs) by 2015 (The Eels (England and Wales) Regulations 2009 Statutory Instrument). There are significant cost implications of this legislation for both statutory organisations and private structure owners, yet current guidance outlining the most appropriate methods to adopt is largely lacking.

A research paper describing the work presented in chapter 7 outlining impacts of low head barriers and flow management regimes is currently under review for publication, with the aim to disseminate these findings to catchment managers and the wider scientific community. As a direct result of the evidence provided from this study, Essex and Suffolk Water Company are examining ways in which they can adapt their pumping regimes and provide effective screening or behavioural deterrence at the water intake that caused entrainment loss in the river Stour.

The work presented in chapter 5, highlighting the potential to improve the efficacy of eel passes through the addition of attraction flow was published as: Piper, AT, Wright, RM & Kemp, PS (2012). The influence of attraction flow on upstream passage of European eel (*Anguilla anguilla*) at intertidal barriers. *Ecological Engineering,* **44:** 329-336. As an outcome of this work, eel passes within the study region, and nationally, are now being modified to incorporate plunging attraction flow.

Though the requirements for eel passage are quite specific to its unusual behaviour, physiology, and life history traits, the development of multi-species passage facilities designed to accommodate the swim capabilities of eel will also benefit other weak-swimming species and lifestages that are currently not afforded the same legislative protection.

Riverine structures are acknowledged to be one of several potential causes of the dramatic decline of the European eel, and other anguillids. Concurrent research is underway to determine the impacts of pollutants, pathogens, and large scale changes in oceanic productivity and currents. Furthermore, there remains a considerable harvest of juvenile and adult lifestages, and a strong social and commercial impetus to protect this resource. As a panmictic species, sustainable management of the European eel will likely only come through strategies implemented at both local and global scales.

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