UNIVERSITY OF SOUTHAMPTON

FACULTY OF ENGINEERING AND THE ENVIRONMENT

Civil, Maritime and Environmental Engineering and Science

Impact of tide gates on diadromous fish migration in the UK

by

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Thesis for the degree of Doctor of Philosophy

October 2014

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

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IMPACT OF TIDE GATES ON DIADROMOUS FISH MIGRATION IN THE UK

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Anthropogenic structures fragment river connectivity, impeding the migration of diadromous fish between essential habitats. Tide gates are used worldwide primarily for flood protection and land reclamation by closing under hydraulic pressure during the flood tide and opening when head differential is sufficient during the ebb. Although tide gates are known to decrease fish species richness, abundance, and movement, their impacts on the migration of ecologically and socioeconomically important diadromous fish in terms of passage efficiency and delay have not been reported elsewhere.

Acoustic and passive integrated transponder telemetry revealed that passage efficiencies of upstream migrating adult brown trout, *Salmo trutta* (92%), and downstream migrating juvenile sea trout smolts (96 - 100%) and adult European eel, *Anguilla anguilla* (98%), were high at top-hung tide gates in two small English streams. However, these fish experienced delay at the gates (adult brown trout, median = 6.0 h; sea trout smolts, mean = 6.5 and 23.7 h; eels, mean = 66.2 h) when compared to migration through unimpeded reaches. The percentage of time the gates were closed and mean angle of opening were positively related to delay in both species and life stages. Diel periodicity also influenced delay for smolts and eels, which were more active at night. For adult trout, water temperature was positively associated with delay. Upstream and downstream water temperature and salinity were influenced by the temporal operation of the gates.

Orifices installed in the gates did not mitigate delay for adult or juvenile trout. For adult eels, delay was decreased when an orifice was operational, although this coincided with more eels first approaching the gates when open, higher tides and greater saline intrusion upstream of the gates.

When gates were open, fish would not pass immediately through, indicating the potential influence of a behavioural avoidance component. To examine the effect of hydrodynamics created by top-hung tide gates with different aperture sizes, wild sea trout smolt behaviour was observed by video cameras in an experimental flume at night. Avoidance responses occurred within an average of 1.4 fish body lengths upstream of the gate. Fish were more likely to exhibit avoidance (switch in orientation from negative to positive rheotaxis, increased tail beat frequency and/or retreat upstream) in the vicinity of a model gate with a smaller angle of opening and passage aperture.

Overall, top-hung tide gates delayed the migration of diadromous fish, potentially increasing energy expenditure and predation risk. Delay was not decreased by orifices. Modifying or replacing top-hung tide gates with designs that allow them to open wider and for longer could reduce migratory delay and improve the environmental conditions that cause behavioural avoidance.

Keywords: tide gate, diadromous, telemetry, trout, eel, passage efficiency, delay

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Declaration of Authorship

I, Gillian Victoria Wright, declare that the thesis entitled ‘Impact of tide gates on diadromous fish migration in the UK’ 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;
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Wright, G.V., Wright, R.M., and Kemp, P.S., 2014. Impact of tide gates on the migration of juvenile sea trout, *Salmo trutta*. *Ecological Engineering* 71, 615-622.

Wright, G.V., Wright, R.M., and Kemp, P.S., *in press*. Impact of tide gates on the migration of adult European eels, *Anguilla anguilla*. *Estuaries and Coasts*.

Signed:..

Date:...

Acknowledgements

I am extremely grateful to everyone who has helped and supported me throughout the completion of this thesis. Thank you to my supervisor Dr Paul Kemp for all your support and constructive criticism over the years, I have learnt a lot. I also thank my supervisor at the Environment Agency, Dr Ros Wright, for all your help, especially in the field.

Thank you to Cefas, Martin Lucas, Aquatic Control Engineering and Luke Myers for lending equipment. I would also like to thank all those that have supported this research by assisting with access to study sites and fish, including Abbey Farm, Broadlands Lakes Coarse Fishery, Buxton Conservation, Hill Head Harbour Sailing Club, Holkham Estate and Fishing Syndicate, Park Gate Royal British Legion Angling Club, Titchfield Haven Nature Reserve, Wild Trout Trust, Lady Kay Buxton, Rosie Edgington, Sam Sykes, and Tom Harrison.

I am also grateful to Barry Bendall, Charles Crundwell, Perikles Karageorgopoulos, Cormac Meenehan, Peter Marchant, Peter Carter, Luke Mitchell, the EA Norfolk Fisheries Team, Hull International Fisheries Institute and Mark Watson for their help during the project.

To my field assistants and all of those who kindly volunteered their time to help in the field - Emma Dyson, Freddie Wells, Joana Nunes, Josh Nightingale, Lee Corsi, Nick Stokes and Toby Diggens - I am very grateful for your assistance and enthusiasm no matter the weather or how many times the nets were empty.

I would like to say a special thank you to Kay Buxton for all your help and support during my time in Norfolk, including the use of your caravan. I am not sure this project would have gotten off the ground without your kindness and assistance.

Thank you to everyone in Team Fish at the University of Southampton (in alphabetical order): Dr Adam Piper, Dr Andrew Vowles, Dr Iain Russon, James Kerr, Dr Laura Watkin, Lynda Newbold, Marnie Woods, Simon Karlsson, and Dr Tom Worthington for all your help and support. Thanks to James Ward who helped me collect data in the flume, and to Joanna Key for her assistance during this time. Also thank you to Dr Malcolm Hudson, Prof Robert Nicholls, Dr Patrick Osborne, and Dr Gustavo de Almeida.

Finally, a massive thank you to my parents, Ralph and Silvana Wright, and Ben Kerley, for all your help and support not only in the field and with proof reading, but throughout my PhD. I am certain I could not have done it without you. Also to everyone else who has assisted; Dr Caroline Wright, Roz Wright, Jenny Bird, Dr Sandra Vellucci, Dr Andrew Sullivan, Leslie Krohn, and Josie Hingley.

This project was funded by the University of Southampton, the Environment Agency and the Interreg IVB Living North Sea Project.

Glossary

Abstraction: removing water, either permanently or temporarily, from a water source e.g. river, stream, lake, groundwater

Accelerating velocity: an increase in water velocity over a specified distance

Acclimation: the process by which an organism adjusts to environmental changes

Anadromous: a lifecycle where fish spawn, hatch and rear in freshwater and mature in salt water (e.g. salmon, sea trout)

Anguilliform locomotion: a sinusoidal swimming motion in eel-like fish that uses the entire body length

Anthropogenic: relating to impacts originating from human activities

Amphidromous: a life history where fish migrate between fresh and salt water for reasons other than to spawn e.g. to feed

Attraction efficiency: the probability that fish will be attracted to the entrance of a route of passage

Barrage: an artificial barrier across a river or estuary used for flood protection, irrigation, navigation or hydropower

Benthic: the lowest portion of the water column; benthic organisms utilise habitat near, or within, the ocean or riverbed substrate

Bypass: an alternate route around an anthropogenic riverine structure for downstream moving fish

Carangiform locomotion: a swimming motion where fish use posterior muscular undulations

Catadromous: a lifecycle where fish, e.g. eels, spawn in salt water and mature in freshwater

Connectivity: the water-facilitated transfer of energy, materials and organisms across a hydrological environment

Counterbalanced gate: a tide gate modified with a weight above the hinge which decreases the restorative force of the gate and the head differential required to open it

Critical swim speed: the maximum swimming speed that can be maintained over a set time period, usually 20 seconds to 200 minutes

Culvert: a tunnel or pipe through an embankment such as a dike or levee through which water can pass

Damper: a modification that can be applied to a tide gate to increase the head differential required for it to close

Delay: the time taken to pass an aquatic structure after first approach

Detection range: the maximum distance from an acoustic receiver or PIT antenna that a tag can be detected

Detection efficiency: the proportion of tags within range of an acoustic receiver or PIT antenna that can be detected

Diadromous: a life history that involves migrating between marine and freshwater environments

Dike: an artificial embankment used to prevent flooding from the sea (also used to refer to a ditch or watercourse)

Discharge: the volume rate of water flow ($m^3 s^{-1}$)

Dissolved oxygen (DO): the amount of oxygen dissolved in water

Dual-frequency Identification Sonar (DIDSON): a sonar imaging system that creates digital pictures by transmitting sound pulses

Dummy tag: inactive tags with equivalent dimensions, weight and shape to an active transmitter tag

Entrainment: the passage of fish through a physical screen or intake at a hydropower or pumping facility

Epithelium: the thin external tissue layer of a fish’s body

Escapement: passage from fresh to marine waters for the purpose of reproduction

Exploitation: the removal of fish from a stock by fishing

Fecundity: the reproductive potential of an organism, measured by the number of gametes produced

Fishpass: a structure on or near an anthropogenic barrier (e.g. dam or weir) designed to facilitate fish passage upstream, often through a sequence of weirs, orifices or baffles conveying flow

Fishway: see fishpass

Fitness: the genetic contribution of an individual to the next generation’s gene pool relative to the average for the population

Floodgate: see tide gate

Flow: see discharge

Fork length: the length of a fish measured from the tip of the snout to where the central caudal fin rays end in fork tailed fish

Freshet: an increase of freshwater flowing through a river into the sea

Fyke net: a net consisting of a series of tapering chambers with narrowing entrances used to trap fish

Galvanotaxis: the influence of an electric current on the orientation and/or motion of an organism

Gamete: a mature haploid male or female reproductive germ cell

Glass eel: a translucent juvenile eel at the time it first enters brackish or fresh water

Habitat: the area that provides resources, e.g. food and space, for an organism or life stage to exist

Habitat connectivity: a measurement of the size and distribution of habitat patches, and the ease with which species can move between them

Habitat fragmentation: the anthropogenic or natural subdivision of habitat into smaller and/or more isolated patches

Hydraulic head: the force exerted by a column of liquid, expressed as its height above the point at which the pressure is measured

Hydraulics: the study of the conveyance of liquids through channels and pipes

Hydrodynamics: the study of fluid motion, specifically concerning the forces acting on, or exerted by, fluids

Impoundment: a body of water confined within an enclosed area

Iteroparous: a reproductive strategy characterised by multiple reproductive cycles over an organism’s lifetime

Kelt: a salmonid that has spawned, but before it returns to the sea

Keystone species: an organism that plays a crucial role in the functioning of an ecosystem

Levee: an embankment built to prevent river overflow

Managed area: and area enclosed by a dike or levee where water levels and discharge are managed by water control structures

Mark-recapture: a method whereby organisms are captured, marked, released and recaptured

Maximum burst speed: the maximum swimming speed of a fish which can be maintained for a maximum of 20 seconds

Migration: to move from one location to another, e.g. for the purposes of spawning or feeding

Mitigator fish passage device: a tide gate design that uses floats to close the remaining lower portion of a gate at a predetermined tide height

Multi sea winter fish: a salmonid that spends more than one winter at sea before returning to freshwater to spawn

Muted tide regulators: a tide gate design where closure is regulated by upstream water levels via the use of floats and pulleys

Neuromast: a sensory organ that typically forms part of a fish's lateral line system

Orifice fish pass: a hole installed in a tide gate for the purpose of fish passage

Parr: a juvenile salmonid life stage that inhabits freshwater

Passage efficiency: the number of fish that pass a structure as a proportion of those that approach

Poikilotherm: an organism whose internal temperature varies with the surrounding environment

Radial gate: a convex manually operated gate mounted on radial arms used in barriers such as dams and locks to control water level and discharge

Recruitment: the number of fish surviving to enter a fishery or reach a specific life stage

Restorative force: the force that helps a body return to its original position

Restricted area: see tidal restriction

Retarder: a modification that can be applied to a tide gate to increase the head differential required for it to close

Rheotaxis: the orientation of an organism in relation to water current

Salmonid: a fish belonging to the family *Salmonidae* e.g. Atlantic salmon, brown trout, coho salmon, chinook salmon

Sea trout: an anadromous form of brown trout, *Salmo trutta*

Self-regulating tide gate (SRT): a tide gate design consisting of a buoyant flap or rotary valve that closes when floats set at a predetermined height are submerged

Semelparous: a reproductive strategy where organisms die after reproducing only once

Side-hung gate: a tide gate hinged from the side

Silver eel: an adult eel that has undergone physiological changes around the time of sexual maturity during which time the spawning migration is undertaken

Sluice: a manually operated gate used to control water levels and flow

Smolt: an anadromous salmonid life stage where juveniles adapt for the marine environment by undergoing a series of physiological and behavioural changes, including migration downstream to sea

Smoltification: the process of physiological change that anadromous salmonids undergo in freshwater to prepare for entry into salt water

Spatial velocity gradient: the change in velocity over a fish's body length

Species abundance: the number of individuals within a species in a habitat

Species diversity: the measure of diversity within a community by combining species richness and evenness of species abundances

Species richness: the number of species in a habitat

Speed of migration: the duration of fish movement between two points divided by the distance

Stock: a unit of management comprising one or more populations of a single fish species, often originating from, or occurring in, a particular area

Stop-log: a log, plank or beam of wood, metal or concrete fitted into the opening of a water control structure to control water levels and discharge

Telemetry: the measurement and transmission of data at a remote source to a monitoring station

Temporal estuarine barrier: a man-made barrier created in an estuary that maintains fluvial connectivity when environmental or management conditions permit

Tidal restriction: the restricted access of tidal water to natural areas of inundation caused by dikes, levees, and water control structures

Tide gate: a water control structure that discharges river flow during the ebb tide and closes during the flood as a result of hydraulic head differential, primarily for flood protection and land reclamation

Tide limit: the limit of tidal influence at the mouth of a river

Top-hung gate: a tide gate design that is hinged from the top

Total length: the length of a fish measured from the tip of the snout to the furthest tip of the caudal fin

Turbidity: a measure of suspended particulate matter in the water

Turbulence: a flow regime characterised by chaotic changes in property

Velocity gradient: the difference in velocity over a specified distance

Water control structure (WCS): a structure in a dike or levee used to control water levels and discharge from an impounded water body upstream, such as a culvert, weir, or gated culvert

Water velocity: the speed of water flow over a set distance (m s^{-1})

Weir: a low-head dam constructed across a river to increase water levels upstream, or regulate flow

Abbreviations

ADV	Acoustic Doppler Velocimeter
ASV	Air Saturation Value
BACI	Before After Control Impact
DIDSON	Dual-frequency Identification Sonar
DO	Dissolved Oxygen
FL	Fork Length
GBP	GB Pound sterling
HDX	Half-Duplex
ICER	International Centre for Ecohydraulics Research
IR	Infra-Red
PIT	Passive Integrated Transponder
PL	PIT Loop
PPT	Parts Per Thousand
PSU	Practical Salinity Units
SRT	Self-Regulating Tide gate
SSSI	Site of Special Scientific Interest
TL	Total Length
WCS	Water Control Structure

Chapter 1

Introduction

The commercial capture fisheries sector contributes approximately US$274 billion to global gross domestic product (The World Bank *et al.*, 2010). Fish comprise 15.7% of the global human population's animal protein consumption (FAO, 2010), and in developing countries this contribution rises to 80% (Halls *et al.*, 1999). Further, links between red meat consumption and cancer could increase the demand for fish in developed countries (World Cancer Research Fund, 2007).

Recreational fisheries generate approximately US$190 billion worldwide (The World Bank *et al.*, 2010), whilst supporting billions of jobs (FAO, 2010). In Europe alone, approximately 25 million people angle, and in England and Wales more people take part in recreational fishing than any other sport (Environment Agency, 2003). Anglers contribute £3 billion to the English and Welsh economy each year (Environment Agency, 2003), and £113 million to the Scottish economy (Scottish Executive, 2004). Diadromous fish, contribute to these figures, with almost 250 species existing worldwide (McDowall, 1992).

Diadromous fish migrate between salt and freshwater, displaying one of three distinct life histories. Anadromous fish, such as sea trout, *Salmo trutta*, and Atlantic salmon, *Salmo salar*, mature in marine waters and migrate to freshwater to spawn, whilst catadromous fish, such as European eel, *Anguilla anguilla*, mature in freshwater and spawn at sea. Amphidromous individuals migrate between salt and freshwater for purposes other than spawning, such as feeding.

Although diadromous fish constitute less than 1% of fish fauna globally, their contribution to socioeconomics is considerable (Limburg and Waldman, 2009). In England and Wales, diadromous salmonid (sea trout and Atlantic salmon) rod fisheries had an estimated commercial fishing rights market value of £128 million (Environment Agency, 2003). The estimated net economic value of recreational salmonid fisheries in England, Wales and Scotland was estimated to be £326.8 million in 1988 (Radford *et al.*, 1991), £350 million in Scotland alone in 1995 (Scottish Office, 1997) and £108 million in England and Wales in 1996 (IUCN, 2003). For European eel, the livelihoods of more than 25,000 people rely on this fisheries industry (Moriarty and Dekker, 1997). Juvenile European eels, contributed approximately £18 million to estuarine fisheries turnover in France in 1997 - 1998 (*c*. 75% of total estuarine fisheries turnover) (Ringuet *et al.*, 2002). The Northern Ireland eel fishery was valued at £4 million in 1995 (IUCN, 2003) and at £2 million in 2010 (Department of Culture, Arts and Leisure, 2012), whilst the export value of eels from England and Wales in 1998 was £2.6 million (Environment Agency, 2003). Fishing for eels also supports many local rural economies (Peirson *et al.*, 2001).

Diadromous fish are also of ecological importance, transferring energy between marine and freshwater environments (Hilderbrand *et al.*, 2004). Semelparous anadromous fish (i.e. those that die after spawning once, such as Atlantic salmon) are a keystone species that transport energy derived from marine productivity to freshwater and terrestrial ecosystems (Willson and Halupka, 1995). For example, more than 95% of biomass in Pacific salmonids is accumulated in the ocean (Groot and Margolis, 1991) and in streams utilised by spawning coho salmon, *Oncorhynchus kisutch*, juveniles have been observed to exhibit twice the growth rate of those without fish returning from the sea (Bilby *et al.*, 1996). Nutrients derived from salmonids and their decomposing carcasses can increase the productivity of riparian vegetation (Bilby *et al.*, 1996; Hilderbrand *et al.*, 1999), algae and invertebrates (Kline *et al*. 1990; Wipfli *et al*. 1998). Diadromous life stages inhabiting rivers also provide an enhanced source of nutrition for terrestrial species compared to alternative terrestrial mammalian prey (Darimont *et al.*, 2008), whilst seaward migrating life stages are a food source for commercially important marine species such as cod, *Gadus morhua* (Stevenson, 1899). Further, diadromous species are often regarded as bioindicators that reflect ecosystem health (e.g. salmonids, Burger *et al.*, 2013; eels, Feunteun, 2002).

Diadromous fish stocks are declining worldwide. Relative abundances of 11 out of 35 diadromous species that inhabit the North Atlantic basin have decreased by more than 90% of their historical levels, and 13 species by more than 98% (Limburg and Waldman, 2009). In North America, Pacific salmonids have undergone significant decline with coho and chinook salmon, *Oncorhynchus tshawytscha*, populations affected most severely (Noakes *et al.*, 2000). North American Atlantic salmon are also at historic lows with 11 populations classed as endangered under the Endangered Species Act (Kocik and Sheehan, 2006). Across Europe, Atlantic salmon and sea trout have undergone serious declines when compared to historic catches (Environment Agency, 2009; Harris and Milner, 2006), leading to Atlantic salmon being listed as a protected species under Annex II of the Habitats Directive (EC, 1992) and sea trout classed as threatened under the UK Biodiversity Action Plan (JNCC, 2010). Multi sea winter fish that spawn over a number of years and thus tend to be large and highly fecund are particularly depleted (Environment Agency, 2003). For European eel, recruitment has decreased by more than 90% since the early 1980s (Dekker, 2003; ICES, 2012) leaving this species designated as critically endangered (Freyhof and Kottelat, 2008) and populations below sustainable conservation limits (Bult and Dekker, 2007). Recruitment has also declined significantly for other eel species, including American, *Anguilla rostrata* (Haro *et al.*, 2000), Japanese, *Anguilla japonica* (Han *et al.*, 2008), longfin, *Anguilla dieffenbachia*, and shortfin, *Anguilla australis* (Jellyman *et al.*, 2002) eels. Distribution and abundance of anadromous lamprey species have also declined (Renaud, 1997; Close *et al.*, 2002), with river, *Lampetra fluviatilis*, and sea, *Petromyzon marinus*, lamprey considered endangered (Lelek, 1987; Renaud, 1997) and receiving protection under the Habitats Directive (EC, 1992).

Climate change (Friedland *et al.*, 2007), altered oceanic currents (Baltazar-Soares *et al.*, 2014), overfishing (Moriarty and Dekker, 1997), pollution (Limburg and Waldman, 2009; Robinet and Feunteun, 2002), siltation, decline in lower trophic levels, non-native diseases, parasites (Feunteun, 2002), alterations in flow regimes and abstraction pressures, channelisation, predation by and competition from protected (Environment Agency, 2008) or non-native species (Hedger *et al.*, 2010), and anthropogenic barriers (Boubée *et al.*, 2001; Travade and Larinier, 1992) have all been attributed to the declining trend in diadromous fish abundance. Of these influences, the deleterious effect of anthropogenic barriers on upstream and downstream migrating diadromous fish has been well demonstrated (e.g. Aarestrup and Koed, 2003; Acou *et al.*, 2008; Naughton *et al.*, 2005). Industrialisation drove the implementation of numerous anthropogenic infrastructure in rivers worldwide, such as dams and weirs, for flood defence, water abstraction (McCulley, 1996), flow gauging, hydropower, navigation, and agriculture (Haselbauer and Martinez, 2007). These structures alter flow and sediment transport downstream causing changes in biogeochemical cycles and riparian and aquatic habitats, modifying thermal regimes which affects organism bioenergetics (Poff and Hart, 2002) and decreases connectivity between essential maturation, spawning and feeding habitats for diadromous fish (Cote *et al.*, 2009). Fragmented habitat can result in reduced population fitness or even local extinction (Lucas and Baras, 2001; Moriarty and Dekker, 1997; Pringle *et al.*, 2000). Mitigation or removal of barriers can significantly increase fish abundance and productivity over a relatively short timescale by economically viable means (Roni *et al.*, 2002), showing the benefits of enhancing fish passage at obstructions.

Considerable attention has been paid to the impact and mitigation of large infrastructure such as dams on diadromous fish (e.g. Noonan *et al.*, 2012; Roscoe and Hinch, 2009), while smaller obstructions, thought to be two to four orders of magnitude more abundant, have received comparatively little consideration (Lucas and Baras, 2001). Such obstructions, which include weirs, culverts, and tide gates, may limit connectivity by only permitting access to sections of the watercourse under certain environmental conditions (O'Connor *et al.*, 2006), which can alter fish species assemblage (Gillette *et al.*, 2005 Tiemann *et al.*, 2004) and population sizes of salmonids (Meldgaard *et al.*, 2003). Even less consideration has been given to intermittent obstructions in estuaries.

Estuaries are one of the most anthropogenically altered ecosystems worldwide (Edgar *et al.*, 2000), with 21% of the global population inhabiting areas within 30 km of the coast (Gommes *et al.*, 1997). One of the most common estuarine modifications used to meet the population’s demands is the installation of levees, dikes, and associated water control structures (WCSs) (Kennish, 2002). Dikes and levees are raised embankments that can be constructed across or around tidally influenced channels. WCSs in the dike wall, such as culverts, connect upstream wetlands and rivers with the estuary downstream, whilst the addition of a tide gate at the estuarine end provides further control over the volume of water discharged from, and saline intrusion into, the impounded area upstream. Traditional top-hung tide gates (Fig. 1.1a) are flap valves that discharge water in only one direction, influencing connectivity by opening and closing every tidal cycle. During the ebb tide, sufficiently greater head differential upstream overcomes downstream water pressure and the restorative force of the gate (caused by gravity, gate weight, buoyancy and friction from the hinges), enabling the gate to open (Fig. 1.2). Fluvial connectivity ceases during the flood tide as the head differential between upstream and downstream reverses, causing the gate to close.

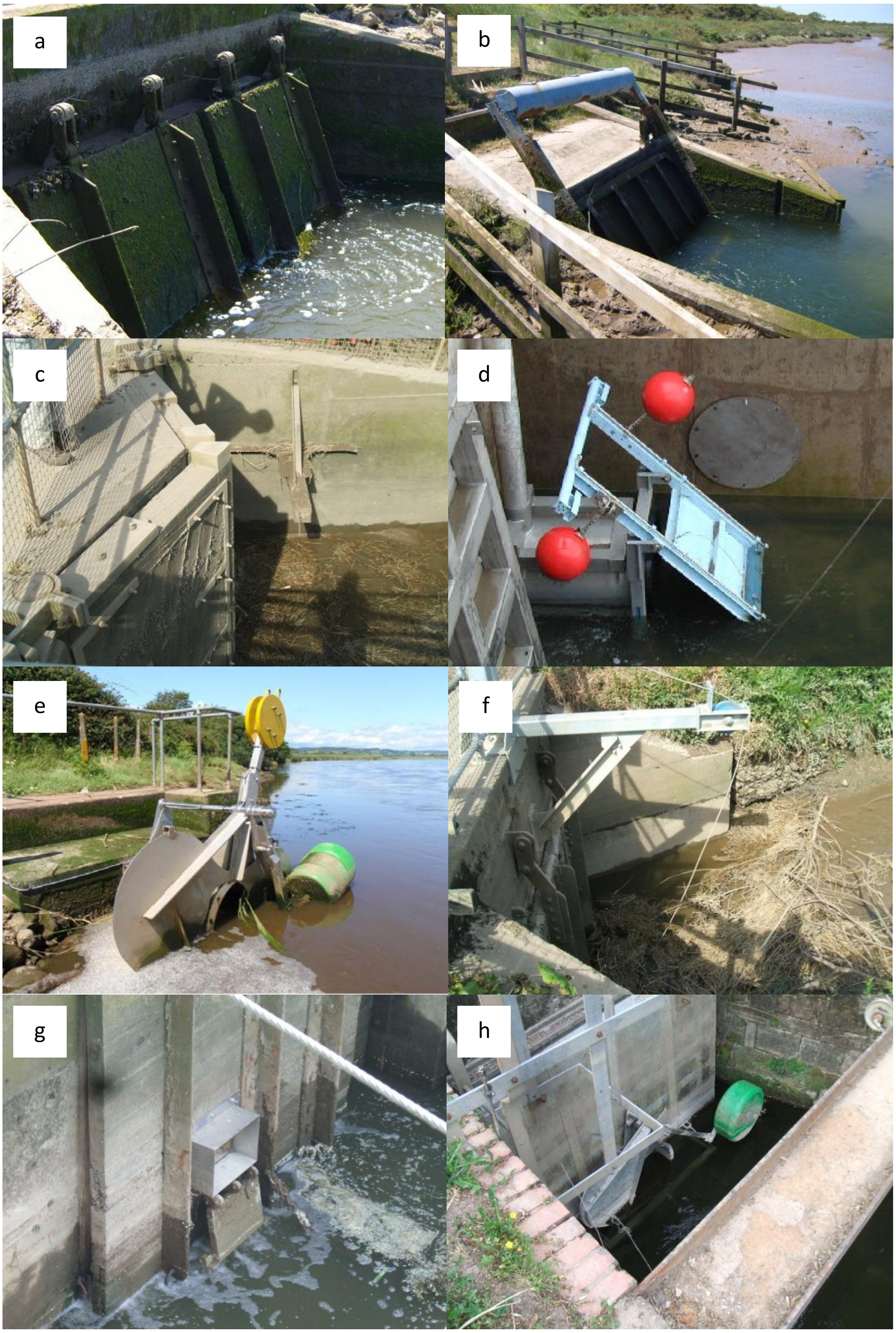


Fig. 1.1. Tide gate designs: (a) top-hung; (b) counterbalanced top-hung; (c) side-hung; (d) self-regulating (SRT) (photo courtesy of Charles Crundwell, Environment Agency); (e) rotary valve SRT (Environment Agency, 2011), and modifications: (f) retarder; (g) orifice; (h) rotary valve orifice.

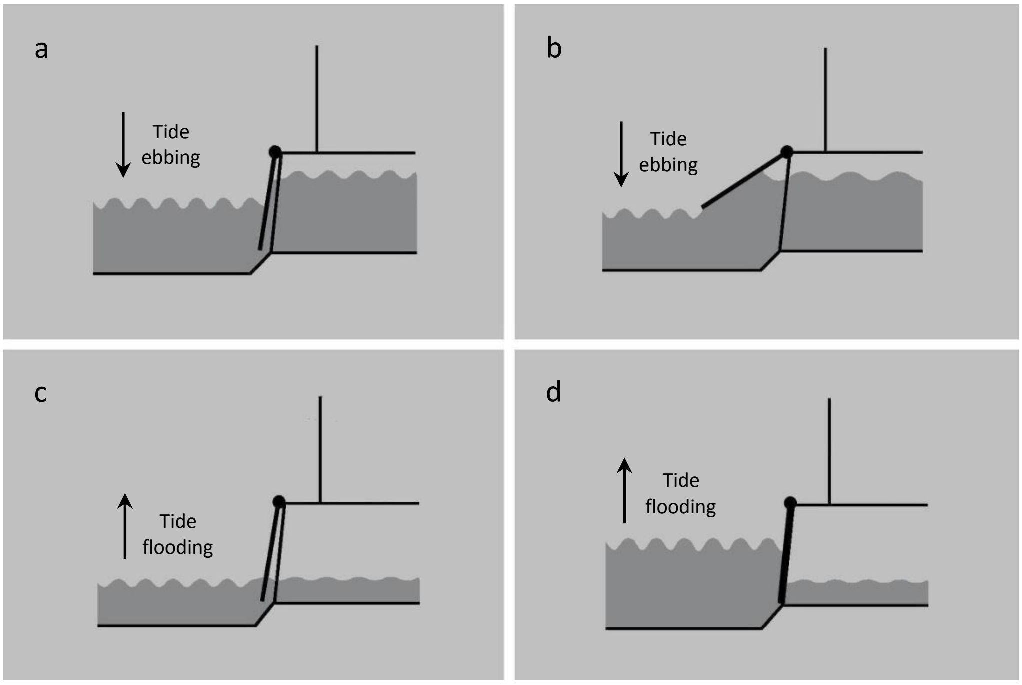


Fig. 1.2. Cross section of a tide gate and associated culvert from the side. (a) Tide level starts to decrease, upstream water level high, gate starts to open. (b) Tide level continues to decrease, gate opens further. (c) Tide level starts to increase, upstream water level decreases, tide gate starts to close. (d) Flood tide, gate closed (adapted from Giannico and Souder, 2005).

Since the eleventh and twelfth centuries, dikes and tide gates have been used in coastal areas in Europe to create land for urbanisation and agriculture (Daiber, 1986). The adoption of this practice in other continents such as Asia, Australasia and USA has made this form of land use the leading cause of wetland eradication worldwide (Middleton, 1999). Wetland draining has also been historically used for mosquito control for many centuries (Doody, 2001), and some areas, such as the south-eastern United States, still exercise this today despite mixed and sometimes counterproductive results (e.g. Portnoy, 1984). Tide gates constituted a third of all barriers in New South Wales, Australia (Gordos *et al.*, 2007), with no less than 1700 km of gated water courses and drainage systems in the Clarence River floodplain alone (Williams, 2000). Gated flood control schemes comprise 30% of the total land area of Bangladesh (Halls *et al.*, 2008), whilst across the UK there are thought to be thousands of tide gate installations (Solomon, 2010).

Although tide gates are one of most tidally restrictive WCSs (Ritter *et al.*, 2008) and abundantly used worldwide, their impact on fish has received little attention (Giannico and Souder, 2005). In the absence of this data, river managers must assess the need for mitigation from anecdote or broad-scale qualitative observations, which can lead to ineffective or unwarranted modification or removal. Obstruction removal has previously been proven successful for re-establishing and increasing fish population sizes (e.g. for dams: Bednarek, 2001; Meadows, 2001; Scully *et al.*, 1990). This method can be expensive and release vast amounts of accumulated sediment, negatively affecting salmonid eggs and fry, delaying colonisation and population increase (Pess *et al.*, 2008). Further, removal may not be an option for structures used for flood defence, water abstraction or for those with historical or community value (Garcia de Leaniz, 2008).

Where managers choose to apply modifications to mitigate perceived effects of tide gates on fish, a number of options exist. Fish ladders, lifts and bypasses can improve fish passage at riverine infrastructure (Katopodis and Williams, 2012; Larinier, 2002) but are often unsuitable for tide gates due to the cost of traversing high levees at numerous sites. Therefore, a number of unique options have been designed for tide gates that decrease the hydraulic head differential required for them to open, thus increasing the aperture and duration of connectivity through them e.g. by counterbalancing top-hung designs with a weight (Fig. 1.1b), or retrofitting with side-hung or lightweight gates. Side-hung doors (Fig. 1.1c) are mounted at an angle, allowing them to close under restorative force and operating under the same principle as top-hung designs. In the Coos Bay Estuary, USA, side-hung doors were reported to open by 45^o with only 1 inch of hydraulic head differential (Giannico and Souder, 2005). Lightweight top-hung gates, made from materials such as aluminium, fibreglass and plastics, also exert less restorative force thus opening wider for longer. Using a theoretical static hydraulic model that accounted for specific gate weight, submergence, and pressure head, Bates (1997) calculated the maximum opening of a 1.2m diameter cast iron top-hung gate at a head differential of one foot and no submergence to be 0.15 m compared to 0.75 m for a lightweight aluminium gate.

Whilst counterbalances, side-hung doors, and lightweight gates enhance fluvial connectivity during the ebb tide, all close at a similar stage of the flood tide. Self-regulating tide gates (SRTs) do not close under the pressure of hydraulic head, enabling them to remain open for a preset proportion of the flood tide. SRTs consist of a buoyant flap (Fig. 1.1d) or rotary valve (Fig. 1.1e) that closes when floats, mounted at a predetermined height, are submerged. Similar designs include mitigator fish passage devices, which use floats to close the remaining lower portion of the gate at a predetermined tide height, and muted tide regulators, where gate closure is regulated by upstream water levels (Giannico and Souder, 2005). Extending connectivity during the flood tide can also be achieved by appending existing gates with retarders (Fig. 1.1f) and dampers which increase the hydraulic head required for closure, or installing orifices. Orifices can remain open for the full duration of each tidal cycle, or they can incorporate a small-scale lightweight flap (Fig. 1.1g) or SRT (Fig. 1.1h), extending fluvial connectivity for a limited period post closure of the gate they are installed in. Further, manually pegging gates open can maintain connectivity throughout the tidal cycle. A number of other mitigation options exist, including rubber duckbills and reversed fishways (Giannico and Souder, 2005), although these designs are comparatively rare worldwide and in the UK. Manually operated over and undershot sluices, radial gates and weirs can also be used for tidal regulation.

Selection of appropriate tide gate mitigation to decrease their impacts on fish will depend on a number of factors. First, it is important to establish if gates are impacting fish, and if so to what extent. Second, the budget available will be highly influential, with managers potentially faced with choosing more cost effective measures (e.g. modifying gates with retarders, dampers or orifices) over retrofitting with expensive designs entailing high maintenance costs (e.g. SRTs and side-hung doors) (Giannico and Souder, 2005). Third, upstream land use will dictate the suitability of modifications that increase saline intrusion and water levels (e.g. orifices, retarders, and SRTs) and/or risk of failing to maintain integrity of the tidal barrier (e.g. by damage from debris for lightweight gates and some SRTs, or failure of floats for SRTs and flapped orifices, Giannico and Souder, 2005). Finally, the impact of mitigation on target and non-target fish species requires consideration. As for the impact of tide gates on fish, the effectiveness of mitigation has received little scientific attention and is therefore unknown.

In recognition of the decline of diadromous species and the impact of barriers on them, several items of legislation have been enforced. The EU Eel Regulations (1100/2007) have led to the development of Eel Management Plans that require all Member States to meet silver eel biomass escapement targets of 40% relative to that expected in the absence of anthropogenic impacts (EC, 2007). The EU Water Framework Directive (2000/60/EC) also requires all Member State surface waters to meet ‘good ecological status’ by 2015, which encompasses a requirement for fish fauna composition and abundance similar to that expected with minimal anthropogenic impact (EC, 2000). In the UK, the Salmon and Freshwater Fisheries Act 1975 states that fish movements must not be impeded by barriers, and particular emphasis on protecting salmonid stocks has been promoted through the Environment Agency’s Sea Trout and Salmon Strategy in 2008 which led to implementation of river and catchment-scale Salmon and Sea Trout Action Plans (Environment Agency, 2008). Legislation driving the protection of environmentally and socioeconomically important diadromous fish requires understanding of the impact of tidal outfall structures on fish passage.

Declines in environmentally, economically, and socially important diadromous fish combined with legislative requirements identifies the need for free fish passage past infrastructure in rivers and estuaries. Whilst a considerable body of knowledge continues to build for mitigation at large riverine structures (Noonan *et al.*, 2012), comparatively little is known about low-head, intermittent barriers. Even scarcer is knowledge of the impact of temporal intertidal barriers to migration, specifically tide gates which, although used worldwide, are considered one of the most tidally restrictive (Ritter *et al.*, 2008). Therefore, the aim of this project is to assess the impact of tide gates on diadromous fish passage. To fulfil this aim, an initial objective was to review existing literature to identify trends and biases in research aims, findings and methods on fish passage at tide gates and other temporal estuarine barriers (Chapter 2). From this, specific objectives were derived (Chapter 3) and fulfilled (Chapters 5 - 8) to achieve the aim of this research.

Chapter 2

Literature Review

2.1. Introduction

In rivers and estuaries, low-head and intermittently permeable infrastructure, such as weirs, culverts, and tide gates, are thought to be two to four orders of magnitude more abundant than larger structures such as dams (Lucas *et al*., 2009). Despite this, the impact of smaller, periodic obstructions to fish migration have received comparatively little attention (but see Aarestrup and Koed, 2003; Gauld *et al.*, 2013; Ovidio and Philippart, 2002 for some exceptions). In particular, the effect of tide gates and other temporal estuarine barriers, such as intertidal sluices, culverts, and weirs, on diadromous fish migration is infrequently considered. To establish the current extent of knowledge, a literature review was completed comprising two parts. First, a quantitative review was employed to identify trends and biases in tide gate and other temporal estuarine barrier research relating to fish. Specific objectives were to ascertain (1) the aims and findings of studies, and (2) how impacts on fish have been quantified in terms of the methods and experimental designs used. Second, a critical narrative review was completed to explore the wider body of fish passage research and identify existing knowledge, including key factors affecting migration and passage at structures, whilst identifying areas requiring further research. Both the quantitative and narrative constituents of this literature review led to the development of specific aims and objectives, which are outlined in Chapter 3.

2.2. A quantitative review of the impact of temporal estuarine barriers on fish

2.2.1. Introduction and methods

Peer-reviewed literature has undergone critical scientific appraisal and is widely accessible (Roscoe and Hinch, 2009), thus forming the basis of this quantitative review. To assess the extent of worldwide, peer-reviewed knowledge on the impact of tide gates on fish, a Boolean search of article titles, abstracts and key words was performed in Web of Knowledge (ISI Inc.) on 11th March 2012 and again on 13th July 2014 using the following search expressions:

(floodgate* or “tid* gate*” or “tid* flap*” or “flap valve*” or “radial gate*” or sluice* or “flood control” or “tid* control” or “water control” or "tid* rest*" or culvert*) and (fish* or salmon* or eel* or ichthyofauna or nekton)

and

(floodgate* or “tid* gate*” or “tid* flap*” or “tid* barr*” or “estuar* barr*”)

All records returned by Web of Knowledge were assessed. An additional search was performed in Google Scholar using the search expression ‘tide gate and fish’, whereby the first 40 pages of results were reviewed. Records with titles and abstracts referring to fish and at least one intertidal structure were retained for assessment of the full text. Articles that were not readily available in the public domain, and not published in English, were not considered any further. The search confirmed that relatively few studies had considered the impact of tide gates on fish. Therefore, article selection criteria were broadened to include studies that assessed the impact of other temporal estuarine barriers, such as sluices, weirs and un-gated culverts, on fish. Retained literature was further reviewed to identify publication year, country of execution, fish species, life stage, type of intertidal structure, design of tide gates (if present), study aim, research methodology and experimental design.

Tide gates in this thesis were defined as gated one-way flap valves that close under hydraulic pressure during the flood tide, and open when hydraulic head differential is sufficient during the ebb. Sluices and radial gates were defined as manually operated gates that do not shut under the pressure of water.

Study aims were categorised as:

- *Abundance* – quantification of fish upstream, downstream or both sides of the intertidal structure via presence/absence, species abundance, richness, diversity, or recruitment
- *Passage* – assessment of movement either upstream or downstream past the intertidal structure
- *Condition* – quantification of Fulton's K, heavy metal accumulation in tissues, or presence of disease or parasites
- *Habitat use* – assessment of temporal and/or spatial variation in areas inhabited
- *Diet* – evaluation of stomach contents and food webs
- *Socioeconomic* – identification of the impact of intertidal structures on fish catches with primary assessment of the effects on fishermen and the wider community

Experimental designs were grouped as:

- *Before/after* – assessment of fish before and after the modification or removal of an intertidal structure at a site
- *Control/impact* – comparison of fish monitored at a site with an intertidal structure (impact) and an unimpeded reference site (control)
- *Before after control impact (BACI)* – comparison of fish at two (or more) sites where each is monitored before and after changes made to one (or more) site(s)

- *Temporal* – temporal assessment of fish in relation to an intertidal structure at a single site
- *Spatial* – spatial assessment of fish in relation to an intertidal structure at a single site

Methodologies using *trapping* included the use of nets, traps and electric fishing.

Literature that had not undergone peer review was also attained from the internet by individually inputting: fish, ichthyofauna, nekton, salmon, trout or eel into the search engine Google, combined with one of the following terms: tide gate, floodgate, tidal flap, tidal barrier, tidal barrage or estuarine barrage. The first 10 pages of results for each search were reviewed and the full text of any relevant grey literature was assessed and subsequently discussed in Section 2.2.3.

2.2.2. Results

2.2.2.1. Tide gates

Twenty-two articles considered the impact of tide gates on fish. One additional article that was not found during the literature search but was cited by a number of authors was also included in the quantitative analysis (Rey *et al.*, 1990). Publication dates ranged from 1990 to 2014, with 35%, 22% and 48% being published each decade (1990 - 1999, 2000 - 2009, and 2010 - present, respectively) (Fig. 2.1). The majority of studies were concentrated in USA (48%), followed by Australia and New Zealand (35%), UK and Belgium (13%), and Brazil (4%) (Fig. 2.2).

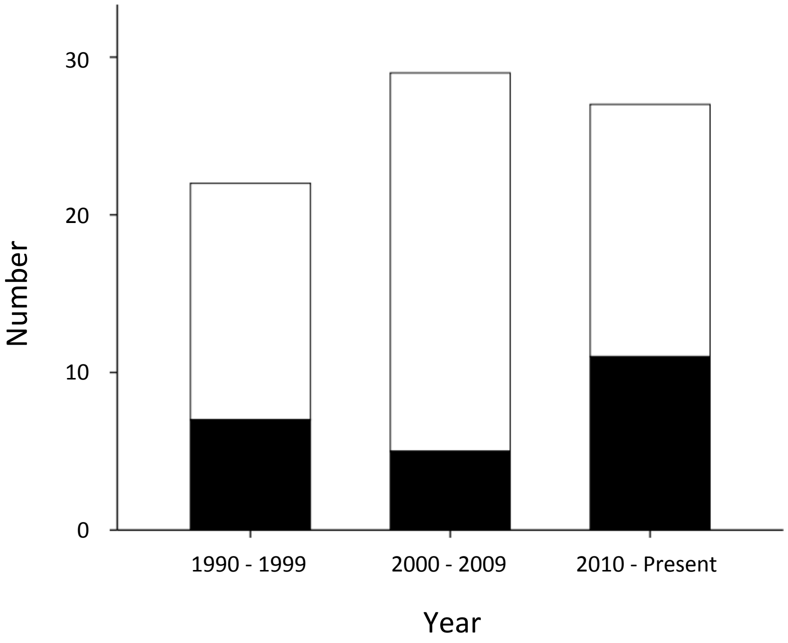


Fig. 2.1. Decade of publication for articles assessing the impact of tide gates (■) and other intertidal structures (□) on fish.

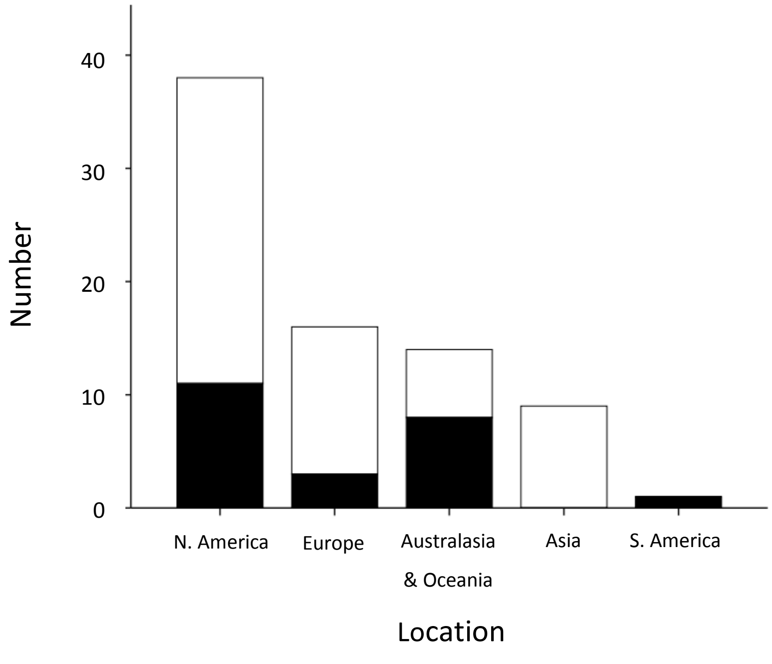


Fig. 2.2. Location of studies that assessed the impact of tide gates (■) and other intertidal structures (□) on fish.

Thirty-nine percent of the studies assessed failed to report tide gate design. Where design was reported (61%), all gates were top-hung. Most studies considered intertidal structures where tide gates were the only route of passage (91%), and 3 considered gate modifications, including orifices, slots, or replacement with lightweight gates. Before/after (38%) and control/impact (38%) experimental designs were most common (Fig. 2.3), with the prevalent aim of assessing the impact of gates on fish abundance (61%) (Fig. 2.4) for which trapping was always used (Fig. 2.5). Passage was the next most predominant aim (35%) (Fig. 2.4), where in trapping (50%), telemetry (25%) and Dual-frequency Identification Sonar (DIDSON) (25%) were used as assessment methods (Fig. 2.5).

Since 1990, there has been an increase in the proportion of studies aiming to assess passage rather than abundance (Fig. 2.6). Species and life stages considered for each study tended to be numerous and were dominated by estuarine inhabitants (65%), although some studies did concentrate on specific species, including European eel, *Anguilla anguilla,* (13%) and Pacific salmonids (9%) (Table 2.1).

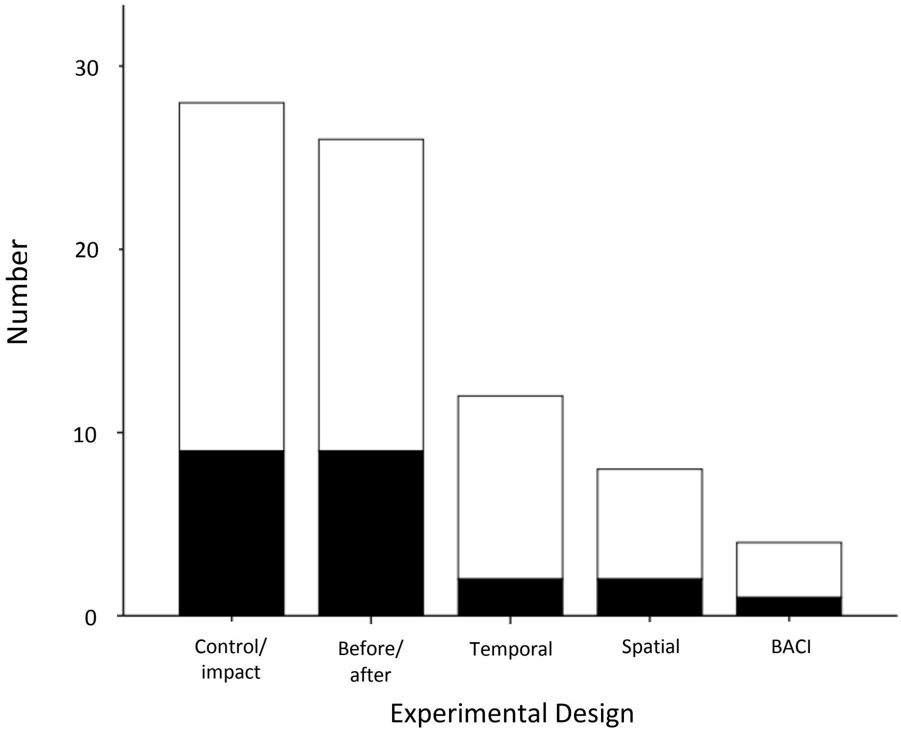


Fig. 2.3. Experimental design of studies assessing the impact of tide gates (■) and other intertidal structures (□) on fish.

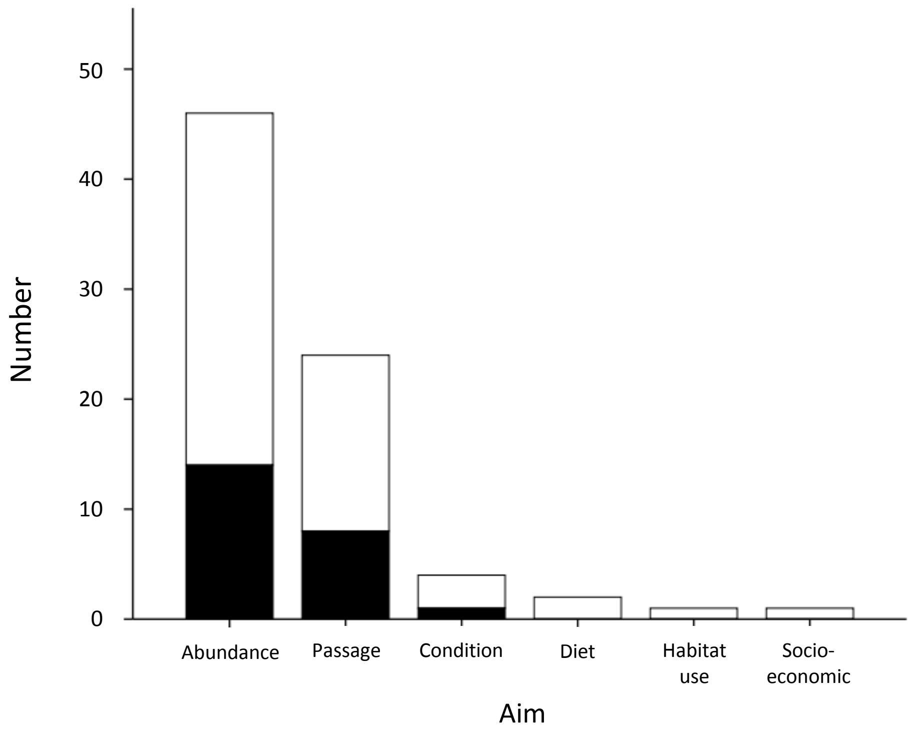


Fig. 2.4. Aim of studies assessing the impact of tide gates (■) and other intertidal structures (□) on fish.

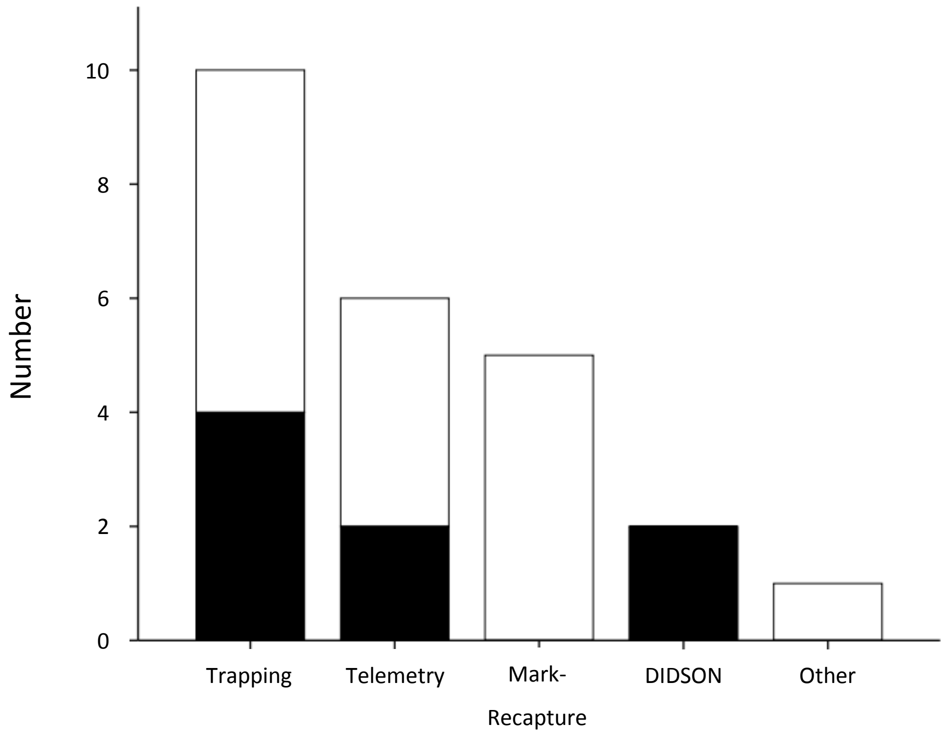


Fig. 2.5. Methods utilised by studies aiming to assess fish passage at tide gates (■) and other intertidal structures (□).

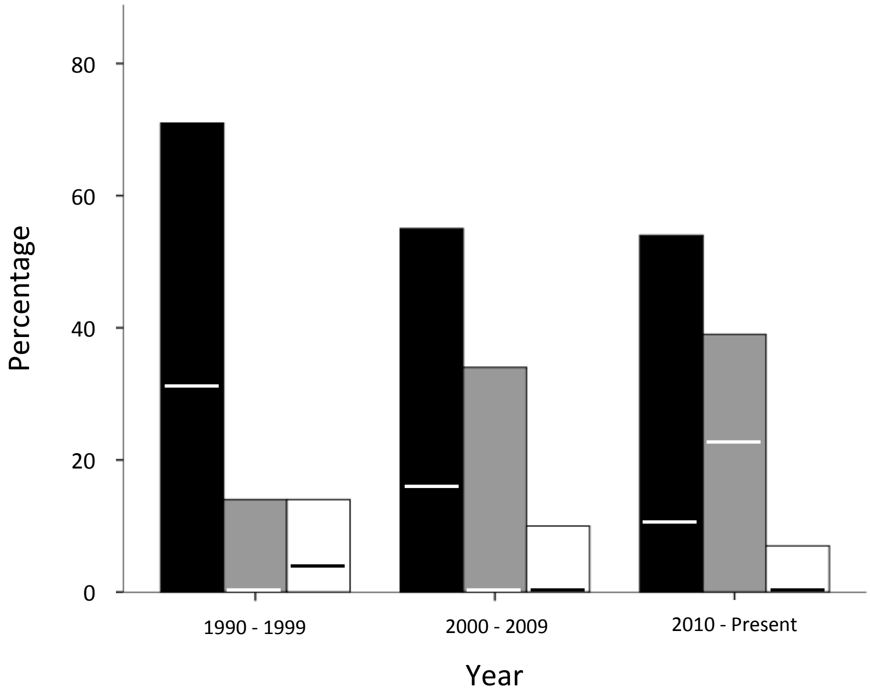


Fig. 2.6. Percentage of studies that aimed to assess fish abundance (■), passage (■) or physiology, condition, habitat use and socioeconomics (□) at tide gates (lower portion of bars) and other intermittent intertidal structures (upper portion of bars) each decade.

Table 2.1. Species, life stage (juvenile, adult or both) and direction of movement (upstream, downstream, both, or not applicable [NA]) considered by studies on the impact of tide gates and other intertidal structures on fish.

Species	Total (%)	Structure	*n*	Life stage	Direction
Numerous	65	Tide gates	15	Both	Both
		Other	36	Both	Both
European eel (*Anguilla anguilla*)	9	Tide gates	3	Both	Both
		Other	4	Both	Both
Salmonids	9	Tide gates	2	Both	Both
		Other	5	Both	Both
Fundulus sp.	6	Tide gates	1	Adult	NA
		Other	4	Both	NA
Striped bass (*Morone saxatilis*)	1	Tide gates	1	Adult	NA
Galaxiid sp.	1	Tide gates	1	Juvenile	Both
River Lamprey (*Lampetra fluviatilis*)	1	Other	1	Adult	Upstream
Flounder (*Platichthys flesus*)	3	Other	1	Unspecified	NA
Smelt (*Osmerus eperlanus*)	1	Other	1	Adult	Both
Carp sp.	1	Other	1	Both	Both
Non-salmonid sp.	1	Other	1	Both	Upstream

2.2.2.2. Other temporal estuarine barriers

An additional fifty-five articles fulfilled the broadened selection criteria concerning the impact of temporal estuarine barriers other than tide gates on fish. Although tide gates were the most frequently reported intertidal structure, they formed only 29% of articles (Fig. 2.7). Manually operated undershot sluices (28%) and un-gated culverts (24%) were the most commonly considered structures after tide gates. North American articles were most numerous (49%) (Fig. 2.2), and dominated by those from the USA (96%). As for tide gates, the majority of studies concentred on numerous estuarine species (Table 2.1) and aimed to assess fish abundance (58%) (Fig. 2.4), via trapping (96%), followed by passage (29%), by using trapping (38%), mark-recapture (31%), and telemetry (25%) (Fig. 2.5).

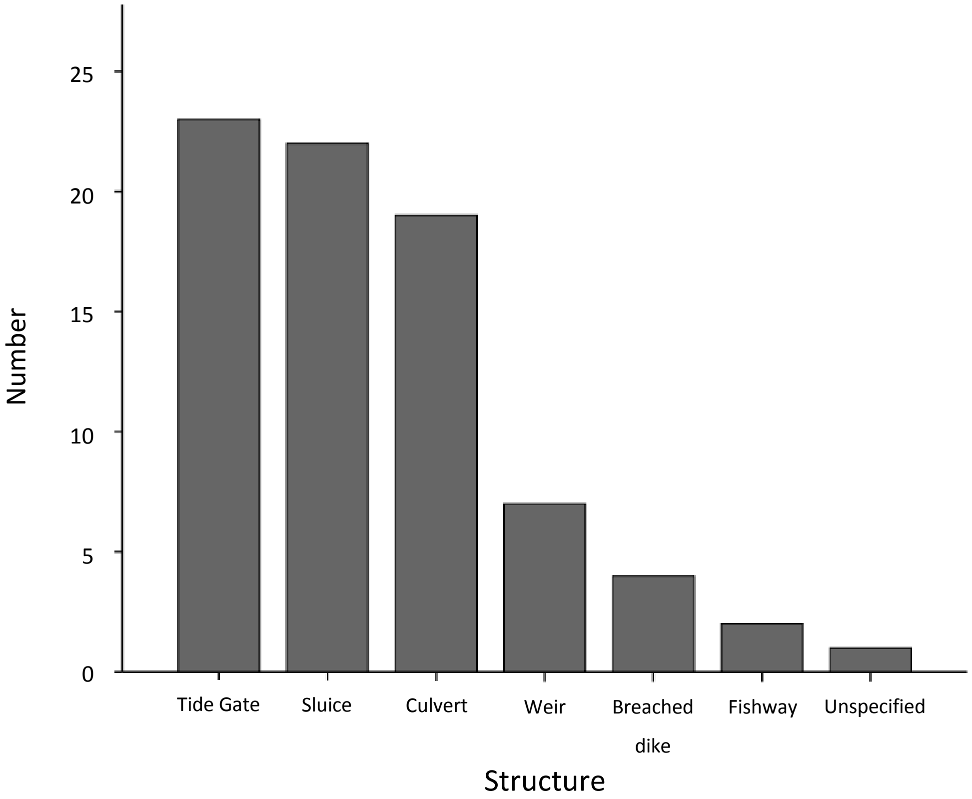


Fig. 2.7. Type of temporal estuarine barrier considered by studies assessing their impact on fish.

2.2.3. Discussion

Peer-reviewed literature is widely accessible, providing a critically evaluated resource from which knowledge can be attained and expanded (Roscoe and Hinch, 2009). Quantitative examination of literature regarding the impact of tide gates and other temporal estuarine barriers on fish revealed the limitations of this resource when articles contain inconsistent and/or ambiguous terminology. Authors used a variety of terms to describe tide gates, including floodgates (e.g. Pollard and Hannan, 1994), flapgates (Rulifson and Wall, 2006), salinity control-gates (Vincik, 2013), tidal barriers (e.g. Mouton *et al.*, 2011), and culverts (Rey *et al.*, 1990). Other articles concerning tide gates neglected to identify the types of structure under examination in the title and abstract, referring only to water control structures (WCSs) (e.g. Kimball *et al.*, 2010; Rozas and Minello, 1998), impounded (McGovern and Wenner, 1990), tidally restricted (Dibble and Meyerson, 2012), or managed areas (e.g. Rogers *et al.*, 1992b). Where tide gates were described, more than a third of authors failed to report basic details relating to their design, such as gate size, top-hung or side-hung, or average opening durations or apertures. Logical and informative terminology, as well as reporting basic physical characteristics of the structures assessed, is essential for ensuring that research is accessible whilst providing wider application of findings beyond the site of study alone.

Temporal estuarine barriers decrease fish species abundance, richness and diversity when compared to tidally inundated reference channels (e.g. Pollard and Hannan, 1994; Ritter *et al.*, 2008; Rozas and Minello, 1998, for tide gates; Raposa and Roman, 2003, for culverts; Rogers *et al.*, 1992a, for slotted and fixed-crest weirs). Similarly, mitigation by opening or removing tide gates (e.g. Roegner *et al.*, 2010; Russell *et al.*, 2011; Taylor *et al.*, 1998) or enlarging un-gated culverts (Rochlin *et al.*, 2012) can improve fish abundance. Few articles reported no benefit from reinstating tidal influence in restricted marshes (but see Raposa and Roman, 2001; Buchsbaum *et al.*, 2006, for restriction by undersized culverts). Other negative effects of intermittent tidal barriers included increased disease prevalence and decreased fish condition. For example, one third of euryhaline flounder, *Platichthys flesus*, in sluiced drainage channels of the IJsselmeer Lake near the Dutch Wadden Sea possessed skin ulcers compared to < 2% in the open sea and freshwater areas upstream (Vethaak *et al.*, 2011). Further, parasitic infection and lipid reserves of common mummichog, *Fundulus heteroclitus*, were lower in tidally restored New England marshes, USA, which included one site with a self-regulating tide gate (SRT), when compared to channels with restricted culvert size (Dibble and Meyerson, 2012).

The number studies on tide gates have increased over the past 25 years, with almost half conducted within the last 4 years. During this time, the predominant research aim has changed from assessing the impact of temporal estuarine barriers on fish abundance to identifying their effects on passage. Recent legalisation (e.g. EU Water Framework Directive and Eel Management Plans), species designations (e.g. EU Habitats Directive and USA Endangered Species Act) and advances in fish passage research identifying the potential negative impacts of low-head, intermittent barriers to fish migration (Aarestrup and Koed, 2003; Ovidio and Philippart, 2002) highlight an increasing requirement for this research.

Species abundance and physiology are useful metrics for assessing environmental health in the close vicinity of intertidal structures (Dahlberg and Odum, 1970; Dauer, 1993). Whilst the majority of studies aimed to assess these factors, comparatively few considered the impact of infrastructure on fish passage. In those that did, the number of fish passing through restricted channels was lower when compared to unrestricted ones (e.g. Doehring *et al.*, 2011, for tide gates; Halls *et al.*, 2008, for sluices) or pre mitigation (e.g. Rulifson and Wall, 2006, for replacement with a lightweight gate; Mouton *et al.*, 2011, for permanently opening gates). Many of these studies utilised opportunistic trapping methods (e.g. Rulifson and Wall, 2006, for tide gates; Schultz *et al.*, 2007, for stop-log structures; Henning *et al.*, 2006, for an unspecified WCS design), resulting in samples dominated by estuarine and marine inhabitants. For example, Boys *et al.* (2012) concluded that tide gate remediation, in the form of installing smaller gates in larger ones or extending opening periods by winching, increased passage of predominately estuarine-marine dependent species in New South Wales creeks, Australia. However, decreased passage by resident fish may have resulted from negligible drive to pass the structure if conditions were sufficient on the side of occupancy (Calles and Greenberg, 2005; Schmutz *et al.*, 1998) and/or the environment on the other side was inferior (Ovidio *et al.*, 2007). For example, Boys *et al.* (2012) found that gate remediation increased upstream colonisation by the opportunist crustacean *Acetes sibogae australis*. Increased prey density could heighten the motivation of fish to pass structures, without indicating the impact of the structure on fish passage itself. In addition to altered food webs (Wozniak *et al.*, 2006), which may also result from decreased organic matter decomposition rates and bioavailable nutrient concentrations (Dick and Osunkoya, 2000), other factors caused by gates may influence desire to pass. Restricted tidal flushing can decrease the dissolved oxygen (DO) concentration of water (Rulifson and Wall, 2006), particularly during high temperatures (Portnoy, 1991; Winn and Knott, 1992), and increase sediment acidity (Anisfeld and Benoit, 1997; Portnoy and Giblin, 1997) and metal concentrations which can accumulate in the tissues of some flora and fauna (Hall and Pulliam, 1995).

Environmental impacts of barriers will affect local inhabitants differently than for transient diadromous species. Studies that have concentrated on diadromous species have utilised methods such as DIDSON to count the number of juvenile galaxiids passing gated and un-gated channels (Doehring *et al.*, 2011). Assessment of passage by the use of methods like DIDSON and traps precludes authors from fully quantifying the impact of the structure on the population by neglecting to identify (1) attraction efficiency, (2) passage efficiency, and (3) delay (Kemp and O'Hanley, 2010).

Attraction efficiency is the probability of a fish being attracted to the entrance of a route of passage at a structure e.g. a fishway (Kemp and O'Hanley, 2010). Passage efficiency is defined as the number of fish that successfully pass a structure as a proportion of those that attempted to pass (Haro *et al.*, 2004). Separation of these metrics allows researchers to identify the aspects of infrastructure and fishway design causing bottlenecks in fish passage. For example Aarestrup *et al.* (2003) found that > 90% of Passive Integrated Transponder (PIT) tagged adult sea trout were attracted to a nature-like bypass channel in the Tirsbæk brook, Denmark, yet only approximately half successfully ascended. These findings enabled the authors to focus on studying conditions inside the fishway, leading to the conclusion that length and low discharge were likely culpable. According to Lucas and Baras (2001) structures should permit safe and prompt entry for 90 - 100% of adult migratory fish.

The duration or speed of passage, hereon referred to as delay, is also an important factor in infrastructure passability (Castro-Santos and Haro, 2003). Adult salmonids often cease feeding at the onset of migration (Jonsson *et al.*, 1997) and expend up to 70 - 80% of their energy reserves during river ascent and spawning (Brett, 1986; Jonsson *et al.*, 1991b). Similarly, migratory adult European eels stop feeding (Olivereau and Olivereau, 1997) as the alimentary tract degenerates during the silvering process (Pankhurst and Sorensen, 1984). Accordingly, many diadromous fish have finite energy reserves to partition between gonad development and migration (Van den Thillart and Dufour, 2009), which for eels travelling to spawning grounds in the Sargasso Sea can be 5000 - 6000 km (Tesch, 2003). Therefore, delay, particularly when characterised by multiple passage attempts (Jansen *et al.*, 2007; Jepsen *et al.*, 1998), and searching and milling behaviour (Croze *et al.*, 2008; Gowans *et al.*, 1999, for salmonids; Behrmann-Godel and Eckmann, 2003; Brown *et al.*, 2009a; Haro and Castro-Santos, 2000; Travade *et al.*, 2010, for eels) increases energy expenditure during this critical period. Greater depletion of energy reserves can increase susceptibility to disease (Schreck *et al.*, 2006), probability of spawning in suboptimal habitats (Caudill *et al.*, 2007; Naughton *et al.*, 2005), and pre and post spawning mortality (Budy *et al.*, 2002; Geist *et* *al.*, 2003; Gerlier and Roche, 1998), whilst decreasing ability to successfully evade predators (Ryan *et al*., 2003), ova viability (de Gaudemar and Beall, 1998), and reproductive success (Geen, 1975). Delay can also cause fish congregation near obstructions, enhancing the transfer of parasites and disease (Garcia de Leaniz, 2008), and increasing predation risk (Schilt, 2007). For example, over 90% of trout smolts were consumed by female pikeperch, *Stizostedion lucioperca*, who altered their spatial distribution in a Danish reservoir during the smolt run to target individuals delayed prior to passing a sluice (Jepsen *et al.*, 2000). Finally, delay may cause mismatch with marine productivity (Chittenden *et al.*, 2010) or with the window of physiological preparedness of fish to traverse between salt and freshwater (McCormick *et al.*, 1998; Solomon and Sambrook, 2004).

Unlike trapping and DIDSON, mark-recapture methodologies enable researchers to establish passage efficiency and in some cases coarse-resolution delay. However, this methodology has only been used to describe reduced passage at intertidal sluices (Halls *et al.*, 1998) and undersized culverts (Eberhardt *et al.*, 2011). Telemetry allows the movements of individual fish to be spatially and temporally tracked (Cagnacci *et al.*, 2010; Castro-Santos *et al.*, 2009), permitting quantification of attraction and passage efficiencies, and delay. Only 6 studies used telemetry to assess the impact of intermittent tidal barriers on fish passage. These studies suggest that temporal barriers could be significantly impacting migratory fish. For example, 49% of radio tagged adult sea trout released below a barrage in the Wadden Sea, The Netherlands, migrated upstream through sluices (Bij de Vaate *et al.*, 2003). During the same study, sea trout released along the south-west coast of The Netherlands passed upstream via sluices in another barrage (14%) or a man-made canal (20%). For radio tagged adult European eels that migrated to sea along the same length of Dutch coast, only 6% exited via the sluices (Breukelaar *et al.*, 2009). In the Sacramento Delta, USA, an average of 49% of acoustic tagged adult Chinook salmon, *Oncorhynchus tshawytscha*, released 2.4 km downstream of an intertidal structure subsequently passed into the river via tide gates when other routes were blocked (Vincik, 2013). Moreover, only 18% of acoustic and radio tagged adult river lamprey, *Lampetra fluviatilis*, released downstream of a tidal barrage passed via sluices into the River Derwent, UK (Lucas *et al.*, 2009). Unfortunately, these studies did not differentiate between attraction and passage efficiency, preventing identification of the impact of the tidal structures themselves on passage. Conversely, Piper *et al.* (2013) reported high attraction and passage efficiencies (100%) for acoustic tagged downstream migrating adult European eels at a complex of intertidal structures, which included tide gates, in the River Stour, UK. Primarily aiming to identify route choice and barrier impacts over a catchment-wide scale, this study did not report delay at the intertidal barriers, or isolate the impact of tide gates from other passage routes. Only one study fully quantified the impact of an intermittent tidal barrier on fish passage. Seventy-three percent and 42% of adult Atlantic salmon and sea trout were attracted to and passed, respectively, an intertidal barrage on the River Tawe, UK (Russell *et al.*, 1998). Delays of hours and days are reported for some individuals. At the same location, attraction and passage efficiencies of smolts were 100% and 78%, respectively (reported in a supplementary analysis by Moore *et al.*, 1996) taking an average of 54.8 and 42.9 h to pass each year (Russell *et al.*, 1998). Only one piece of grey literature attempted to identify the impact of tide gates on fish passage efficiency and delay (Bass, 2010). In Coos Bay, Oregon, USA, Bass (2010) found that more PIT tagged coho salmon, *Oncorhynchus kisutch*, smolts passed downstream through an un-gated creek (92%) when compared to two channels containing top-hung (50%) or side-hung (36%) gates. Median duration of downstream movement past the gates was faster (top-hung = 0.0013 days [1.9 min]; side-hung = 0.0002 days [0.3 min]) than through a section of similar length in the un-gated channel (1.23 days). However, this study used PIT loops that floated at the water's surface, preventing coverage of the entire water column and likely influencing the accuracy of passage efficiency and duration reported. For example, PIT loops located downstream of the top-hung gate in Palouse Creek covered a depth of 0.89 m from the water's surface, while the water depth ranged from 2.0 - 5.5 m.

Equally, few studies used mark-recapture or telemetry to quantify the effects of riverine infrastructure that may create similar conditions to open tide gates, e.g. culverts and sluices, on diadromous fish. Where such riverine research does exist, reduced passage (Calles *et al.*, 2010; Croze, 2008; Travade *et al.*, 2010) and delay have been reported (Aarestrup *et al.*, 1999; Jepsen *et al.*, 2000). This reinforces the need to quantify the impact of tide gates on diadromous fish passage.

2.3. Fish passage research - a wider context

2.3.1. Introduction

To supplement the findings of the targeted quantitative review on the impact of tide gates and other temporal estuarine barriers on fish, a narrative literature review was conducted. The aim of this analysis was to understand the influence of confounding variables on diadromous fish migration and passage at obstructions, identifying any gaps in knowledge. The findings will aid the development of specific objectives required to assess the impact of tide gates on diadromous fish (Chapter 3).

2.3.2. Flow

Adult diadromous spawning migrations are positively correlated with river flow (Jonsson *et al.*, 2007; Jonsson and Jonsson, 2002; Svendsen *et al.*, 2004, for salmonids; Davidsen *et al.*, 2011; Vøllestad *et al.*, 1986, for eels) particularly in small rivers (Solomon *et al.*, 1999). Freshets, even those occurring during suboptimal flows, may trigger river entry in salmonids (Arnekleiv and Kraabol, 1996; Huntsman, 1948; Tetzlaff *et al.*, 2005). Increased water levels, velocities, turbidity and turbulence associated with high flows (Banks, 1969; Jonsson, 1991) impair the success of piscivorous predators (Allouche and Gaudin, 2001; Blair, 1992; Utne-Palm, 2002) and increase the probability of evading predators (McMichael *et al.*, 2005). Elevated flow also decreases encounters with natural obstructions whilst facilitating ascent of larger fish (Jonsson *et al.*, 1991a). For downstream migrants, increased flow may reduce transit time through the river (Aarestrup *et al.*, 2002; Vøllestad *et al.*, 1986) decreasing the period of exposure to predators and patches with high predator densities (Melnychuk *et al.*, 2007), although this is not reported in all river systems (Aarestrup *et al.*, 2002; Boubée and Williams, 2006).

During low flows, migration may be delayed (e.g. salmonids: Erkinaro *et al.*, 1999) or terminated (Solomon and Sambrook, 2004), and structures are more likely to impede migration (Winstone *et al.*, 1985). Flow is thought to be less influential for adult salmonids entering larger rivers (Karppinen *et al.*, 2004; Rustadbakken *et al.*, 2004), where spawning ground location, distance of migration and temperature become more important (Hinch *et al.*, 2006).

Flow is also critical in the porosity of anthropogenic infrastructure to fish. To successfully facilitate fish passage, structures that manipulate natural flows must provide adequate depth, velocity, and attractance to a suitable route (Bunt, 2001; Castro-Santos *et al.*, 2009). Swimming capabilities of fish determine the maximum water velocities and distances over which swimming can be maintained through passage routes, particularly for those migrating upstream. Initial investigations considered the association between swimming speed and endurance, resulting in the identification of three types; burst, prolonged, and sustained swimming (Beamish, 1978; Webb, 1975). To traverse short high flow velocity obstacles, ambush prey, or evade predation, burst swimming is used (Domenici and Blake, 1997; Nelson *et al.*, 2002). Burst swimming is anaerobic, utilising white muscle fibres with low vascularisation and few mitochondria to create a single unsustainable effort that lasts less than 20 seconds (Beamish 1978). Prolonged and sustained speeds are aerobic, utilising highly vascularised red muscle fibres which enable continuous swimming for 20 seconds - 200 minutes or more than 200 minutes, respectively (Hammer, 1995).

In swim chambers, burst swimming performance of adult European eel of ≥450 mm total length (TL) was 1.0 - 1.5 m s^{-1} (Clough *et al.*, 2002). Burst swimming speeds are much higher for adult brown trout, *Salmo trutta* (1.89 - 4.18 m s^{-1}) and Atlantic salmon, *Salmo salar* (3.87 - 8.08 m s^{-1}) (Bell, 1986). Swim chambers and respirometers force individuals to swim in a confined space against unnatural rectilinear flows (Brett, 1964; Van den Thillart *et al.*, 2007) which can underestimate swimming performance that may otherwise be attainable volitionally (Haro *et al.*, 2004; Peake, 2004). For example, maximum critical swim speed of smallmouth bass, *Micropterus dolomieu*, in an open channel flume was 22% higher than for those swimming in a respirometer (Peake, 2004) which prevented efficient swimming behaviours (Peake and Farrell, 2004; Tudorache *et al.*, 2007). Uniform flow characteristics typical of swim chambers may also produce unrealistic results, whereby the introduction of turbulence to create hydraulic heterogeneity more similar to natural conditions expected in rivers showed a 1.9 to 4.2 fold increase in overall swimming costs in juvenile Atlantic salmon, (Enders *et al.*, 2003). Therefore, recent research in an open channel flume challenges the burst speed of adult eels reported previously, demonstrating volitional swimming against 1.75 m s^{-1} (Russon and Kemp, 2011b). For juvenile European eel (TL = 60 - 300 mm) burst speeds of 0.41 to 1.50 m s^{-1} have been reported (Clough *et al.*, 2004; Clough and Turnpenny, 2001).

As tide gates begin to open during the onset of the ebb tide, river flow channelled through the gate and culvert may cause water velocities to exceed the swimming abilities of upstream migrating fish. Although flow through gates decreases with diminishing head differential as impounded water is discharged seaward, heavy top-hung gates can cause small gate apertures and high velocities at low water that could physically block the movements of fish or influence hydrodynamic conditions that may induce passage avoidance behaviour (see Section 2.3.8.1). Modifications to top-hung gates, such as counterbalances, retarders, and orifices, or replacement with SRTs or side-hung gates, could minimise these effects. For example, a top-hung gate replaced with side-hung gates in the Coos Bay Estuary, USA, opened to a 45^{o} angle with a hydraulic head differential of just one inch (Giannico and Souder, 2005).

Flow is also instrumental in attracting fish to suitable routes of passage (Bunt, 2001). Insufficient flow exuding from fish passes, such as nature-like passes, can cause low passage efficiencies (Larinier, 2002; Moser *et al.*, 2000). For fish migrating downstream, the predominant direction of discharge may enable fish to locate suitable routes (Jansen *et al.*, 2007). While tide gates typically offer the only route of passage into and out of a river system, meaning that being attracted to them is of less concern, modifications such as orifices may not discharge high enough flows to attract fish when gates are open. This would confine the ability of orifices to assist fish passage only when tide gates are closed, but to date the effectiveness of such modifications has not been reported.

2.3.3. Temperature

Decreasing temperatures are related to increases in adult salmonid (Jonsson *et al.*, 2007; Svendsen *et al.*, 2004) and eel (Boubée *et al.*, 2001; Haraldstad *et al.*, 1985; Vøllestad *et al.*, 1986) migration typically from late summer to winter. Juvenile migration is related to increasing temperatures (White and Knights, 1997b, for glass eels; Jonsson and Ruudhansen, 1985, for salmonid smolts). Water temperature is negatively correlated with flow (Sinokrot and Gulliver, 2000), often making its effects on migratory fish difficult to dissociate from flow. Vøllestad *et al.* (1986) highlighted the importance of temperature rather than flow for promoting physiological changes that prepare adult eels for migration and triggering migratory events. The inability of fish to directly sense freshwater flow volume, and differences in discharge during dry weather periods between four rivers in South West England, led Solomon and Sambrook (2004) to conclude that delayed entry of radio tagged adult Atlantic salmon was a result of high temperatures. Changes in temperature regimes throughout historical data sets are linked with altered timings of spawning runs. For example, adult pink salmon, *Oncorhynchus gorbuscha*, in Auke Creek, Alaska, USA, migrated earlier each year as annual temperatures increased (Taylor, 2008). Adult American shad, *Alosa sapidissima*, and sockeye salmon, *Oncorhynchus nerka*, ascended the Columbia River, USA, ~38 and ~6 days earlier than they did in 1938 and 1949, respectively, when spring temperatures were lower (Quinn and Adams, 1996). Over a period of 41 years, upstream migration of Pacific lamprey, *Lampetra tridentata*, in the Columbia River occurred earlier during warm years with low discharge (Keefer *et al*., 2009).

Fish are poikilothermic, with body temperatures varying within 1 - 2°C of the ambient water temperature (Hoar and Randall, 1971). Metabolic rate and cardiac performance increases with temperature until a thermal optimum is reached (Beamish, 1981; Farrell, 2007), influencing swimming performance. For example, a temperature increase of 10°C can double tail beat frequency (Videler and Wardle, 1991) and passage at obstacles can be inhibited during colder temperatures (*c.* 6°C, Rustadbakken *et al.*, 2004; 5.5°C, Smith *et al.*, 1994). Above the thermal optimum, temperatures increase the energetic costs of swimming (Enders *et al.*, 2005; Glebe and Leggett, 1981). Adult salmonids have been found to cease migration at temperatures above 20.0°C (Alabaster *et al.*, 1991), with an estimated upper lethal limit of 27.8°C (Garside, 1973). High water temperatures can increase the presence of, and susceptibility of fish to, parasites, pathogens and/or diseases (Dietrich *et al.*, 2014; Rees *et al.*, 2014). Increased metabolic demands may divert energy away from the development of gonads, reducing egg viability (Berman and Quinn, 1991; Kinnison *et al.*, 2001; Rand and Hinch, 1998). For silver European eels, migration occurs between 4^{o}C (Vøllestad *et al.*, 1986) and 23^{o}C (Acou *et al.*, 2008), with the range varying with country (e.g. Cullen and McCarthy, 2003; Hvidsten, 1985; Lobon-Cervia and Carrascal, 1992).

Anthropogenic structures alter the natural thermodynamics of water courses (Gregory *et al.*, 2002). Impoundment increases water temperature (Quinn and Adams, 1996; Rulifson and Wall, 2006) suggesting that tide gates may exacerbate the negative effects of high temperatures when compared to river mouths without tidal restriction. Armour (1991) found that an unimpeded river channel was 1.0^{o}C - 3.1^{o}C colder than two other channels that had tidal outfall structures in the same area between March and September 1990. Sheer differences in temperature may also be expected either side of an estuarine barrier which prevents natural mixing of water at the estuarine/riverine interface (Smith and Hawkins, 1995). For example, the maximum difference in daily average water temperature between upstream and downstream of a top-hung tide gate in Coos Bay, Oregon, USA, was approximately 1.5^{o}C (Bass, 2010). In Tillamook Bay, Oregon, USA, a temperature difference of 2^{o}C - 5^{o}C was recorded between locations upstream and downstream from a tide gate (design unspecified) (Giannico and Sounder, 2005). Migratory fish show a preference for progressive alterations in temperature (Berggren and Filardo, 1993; Jonsson, 1991). Where avoidance of steep temperature gradients is not exhibited, fish may experience thermal shock or even death (Boyd and Tucker, 1998). By replacing the existing tide gate in Tillamook Bay, Oregon, USA, with a new one (design unspecified) that improved connectivity, the difference in temperature on either side of the gates was reduced to 1^{o}C (Giannico and Souder, 2005).

2.3.4. Dissolved oxygen

The solubility of oxygen in water decreases at higher temperatures (Ozaki *et al.*, 2003; Sinokrot and Gulliver, 2000) and entrainment decreases at low flows (Tetzlaff *et al.*, 2008), which can influence fish migration and passage at structures. The European

Community Directive specifies a median of 9 mg l^{-1} oxygen equivalent to 90% of ASV (Air Saturation Value) at 15^{o}C and a lowest permitted level of 7 mg l^{-1} (70% ASV) DO in freshwater and 40% in estuaries for salmonids (Priede *et al.*, 1988). Below this recommended level migration may be impeded. For example, Atlantic salmon exhibited passage avoidance when oxygen levels in the Ribble estuary, UK, fell below 5.5 mg l^{-1} (Priede *et al.*, 1988). Migration has been reported at lower DO levels however, with adult Atlantic salmon successfully migrating through the Thames estuary, UK, when median DO concentration across 10 km was 3.8 mg l^{-1} (Alabaster and Gough, 1986).

Aerobic swimming performance can also be limited by DO availability. For example, the sustained swimming speed of Atlantic salmon was enhanced from 50 cm s^{-1} to 80 cm s^{-1} when DO was increased from 4 mg l^{-1} to 5 mg l^{-1} at 15^{o}C (Beamish, 1978). In extreme cases, moderately hypoxic conditions can exacerbate blood lactate to lethal levels (Farrell, 2007) which accumulate during continuous or repeated bursts of anaerobic activity. Such conditions occur when fish make recurrent attempts to pass a structure, leading to metabolic acidosis or even delayed mortality (Wood *et al.*, 1983). Further, this effect may be exacerbated at structures where delayed fish are congregating during low water levels and high temperatures (Hinch and Bratty, 2000). Impoundment by anthropogenic structures can decrease DO (Portnoy, 1991; Rulifson and Wall, 2006; Tonnes, 2007), particularly where pyrite soils exist (Sammut *et al.*, 1996). This may cause fish to avoid hypoxic waters when gates open and fluvial connectivity is re-established (Richardson *et al.*, 2001).

2.3.5. Salinity

Prior to spawning migrations, diadromous fish undergo a series of physiological changes to prepare for the transition between salt and freshwater, such as alterations in plasma ion concentrations (e.g. Cl^- and Na^+) and augmented gill Na^+K^+ATPase activity (Strand *et al*., 2011), thyroid hormones (Iwata, 1995), growth hormone, cortisol and insulin-like growth factor I (Hoar, 1988; Sakamoto *et al*., 1995). During migration, fish actively seek gradual changes in salinity as they continue to physiologically adapt (Prunet and Boeuf, 1985). Tide gates inhibit natural mixing, which may induce avoidance behaviour or prevent successful acclimation. In Coos Bay, Oregon, USA, salinity downstream of tide gates was up to 17 PPT greater than upstream (Scalisi, 2001). If acclimation is not gradual, osmotic shock may occur, increasing susceptibility of fish to disease (Vethaak *et al.*, 2011), decreasing swimming performance (Brauner *et al.*, 1994; Brauner *et al.*, 1992), ability to evade predators (Handeland *et al.*, 1996) and overall survival (Otto, 1971; Virtanen *et al.*, 1991). Conversely, a period of acclimation is not apparent in all studies, species and life stages (e.g. salmonid smolts, Moore *et al.*, 1998b; adult salmonids, Solomon and Sambrook, 2004; adult eel: Chan *et al.*, 1967; Maetz and Skadhauge, 1968; Rankin, 2008).

2.3.6. Tides

Estuarine barriers modify tidal cues used by some species to orientate. For example, acoustic tagged adult Atlantic salmon and sea trout showed a loss of orientation which was characterised by an average delay of 60 hours after passing upstream over the Tawe Barrage, UK, where tidal cues used to facilitate migration were generally absent (Russell *et al.*, 1998). Obstructions in estuaries can also alter the natural tidal limit. Prior to construction of a dike, Bult and Dekker (2007) recognised that tides would have extended 100 km further upstream in Lake Ijsselmeer, The Netherlands. Modified tidal limits affect diadromous fish that utilise selective tidal stream transport to minimise the energetic costs of migrating upstream (e.g. salmonids: Alabaster *et al.*, 1991; Potter, 1988; Priede *et al.*, 1988; glass eels: White and Knights, 1997a). Where WCSs possess traditional top-hung tide gates that are sensitive to small rises in head differential on the downstream side, the pathway of upstream migrants is likely to be blocked by closed gates which may lead to falling back with the ebb tide (Priede *et al.*, 1988). Installing orifices or retarders, or refitting gates with side-hung doors or SRTs that close later in the flood tide could mitigate this impact. Nekton in the Breton Sound estuary, Louisiana, USA, passed through permanently open vertical slots next to tide gates during flood tides (Kimball *et al.*, 2010). Passage was monitored by DIDSON alone, preventing quantification of passage efficiency and delay, as well as species identification. Opening gates in a tidal barrier in the Yser River, Belgium, during the flood tide increased the passage of glass eels by a multiple of 237 (Mouton *et al.*, 2011).

The effectiveness of similar gate modifications still remains to be fully quantified for larger fish.

2.3.7. Diel periodicity

Activity in juvenile salmonids is often observed to be greater at night (Moore *et al.*, 1998a; Moore *et al.*, 1998b), although migration is also recognised during daylight hours as the migratory season progresses (Thorpe and Morgan, 1978). Adult salmonids have also been reported to be active during the day, particularly during high flows (Jonsson, 1991) or in environments with high predator densities and hydraulic complexity, such as dam fishways (Keefer *et al*., 2013b). Conversely, lamprey in less hydraulically complex habitats have been observed to be active throughout the majority of the diel cycle, changing to nocturnal movement at dams and fishways (Keefer *et al*., 2013b). For eels, migration occurs predominately at night (Tesch, 2003), often during dark moon phases (Bruijs and Durif, 2009; Haraldstad *et al.*, 1985). Therefore, when high tides occur at night, the temporal closure of gates may delay fish approaching during this time until subsequent nights, or force migration during the day when gates open, thus increasing the risk of predation by visual predators in locations with low turbidity and/or water levels (reviewed in Thorstad *et al.*, 2012).

2.3.8. Hydrodynamics

2.3.8.1. Velocity gradients

Neuromasts in the mechanoseosory lateral line detect changes in the fluid environment surrounding fish (Montgomery *et al.*, 1997), assisting with predator avoidance (Hoekstra and Janssen, 1985), preservation of school integrity (Partridge and Pitcher, 1980), detection of prey (Hoekstra and Janssen, 1985), physical bodies (von Campenhausen *et al.*, 1981), and changes in velocity (Bleckmann, 1994).

While high water velocities may attract fish to bypasses (Bruijs and Durif, 2009; Kemp *et al.*, 2005a), entrances that constrict flow induce velocity gradients which may elicit avoidance responses in fish. For example, wild Pacific salmonid smolts diverted at the McNary Dam, USA, into an open channel flume typically rejected passage through a constricted route when compared to an unconstricted channel (Kemp *et al.*, 2005a). Route rejection in this study was often characterised by switches in orientation from negative to positive rheotaxis, enabling controlled downstream progression and rapid upstream escape if conditions become potentially hazardous. Atlantic salmon smolts have also been observed to pass a modified weir with a uniform increase in flow velocity (1 m s^{-1} m^{-1}) more freely than a sharp-crested weir generating a greater velocity gradient (2 m s^{-1} m^{-1}) (Haro *et al.*, 1998). Similarly, reluctance of fish to enter passes at riverine obstructions in the field may be a result of velocity gradients (Johnson and Moursund, 2000; Piper *et al.*, *in prep*). However, migrating fish process and respond to numerous environmental stimuli and many of the aforementioned studies neglected to separate the influence of hydraulic and visual cues (Haro *et al.*, 1998). For example, Pacific salmonid smolts avoided continuous overhead cover in an open channel flume regardless of discharge (Kemp *et al.*, 2005b) while radio tagged sea trout smolts avoided covered routes at power plants in the Emån River, Sweden (Greenberg *et al.*, 2012). Recent research in an experimental flume identified that rapidly accelerating velocities induced avoidance responses in downstream moving hatchery-reared brown trout in the absence of visual cues (Vowles and Kemp, 2012). The addition of light caused responses at lower spatial velocity gradient thresholds and further upstream (Vowles and Kemp, 2012), characterising the complexity of successful fish passage at man-made structures.

Eels have also been observed to avoid passage through routes likely to create accelerating velocity gradients (Calles *et al.*, 2010; Jansen *et al.*, 2007), exhibiting recurrent and milling behaviours (Brown *et al.*, 2009a; Gosset *et al.*, 2005). Conversely, avoidance of an accelerating velocity gradient created by an orifice weir was not evident in adult European eels moving downstream in an experimental flume (Russon and Kemp, 2011a). Tide gates and associated culverts would likely induce similar hydrodynamic conditions, but to date this remains unquantified.

2.3.8.2. Turbulence

Turbulent flow is characterised by the highly irregular small-scale motion of fluid particles in trajectories other than that of the overall direction of flow (Vogel, 1994). Such conditions typically occur around fish passes that dissipate energy created by head differential (Castro-Santos *et al.*, 2009) and thus may also be expected at recently opened tide gates. Turbulence can attract fish to suitable passage routes (e.g. adult eels: Coutant and Whitney, 2000; Russon *et al.*, 2010, salmonids: Coutant, 2001) and decrease energetic costs. For example, rainbow trout, *Oncorhynchus mykiss*, have been observed to use turbulent flows in the form of a von Kármán vortex street to minimise the costs of maintaining position in flows (Liao, 2004; Liao *et al.*, 2003). Elsewhere, swimming in turbulent flows has shown increased energetic costs (Enders *et al.*, 2005; Lupandin, 2005) and reduced stability (Tritico and Cotel, 2010). Tide gate modifications that allow gates to open earlier during the ebb tide, such as refitting with lightweight gates, may decrease turbulence and influence the passage of fish (Giannico and Souder, 2005), but again this remains unquantified.

2.3.9. Species and life stage

Historically, fish passage research has focused on the upstream migration of commercially and socially important salmonids (Castro-Santos and Haro, 2006; Larinier and Travade, 2002; Roscoe and Hinch, 2009). However, intraspecific variation in size, morphology, sensory capacities, and orientation between life stages and species indicate that advances in facilitating adult salmonid passage upstream may not always benefit other fish (Castro-Santos *et al.*, 2009).

The ability of fish to negotiate passage routes at structures varies with species (Knaepkens *et al.*, 2006), morphology (Webb, 2004) and length (Lupandin, 2005). Carangiform swimmers, such as salmonids, use posterior muscular undulations (Vogel 1994) enabling rapid propulsion (Sfakiotakis *et al.*, 1999). Species utilising anguilliform locomotion, such as eel and lamprey, exhibit broad undulations along the entire body length which results in a more efficient mode of swimming (van Ginneken and Maes, 2005) that is comparatively less powerful than carangiform locomotion (Dauble *et al.*, 2006), also inhibiting the capability to leap (Vogel, 1994). For example, burst swimming speeds of adult sea trout and Atlantic salmon are 1.89 - 4.18 m s^{-1} and 3.87 - 8.08 m s^{-1}, respectively (Bell, 1986), whereas adult European eels and river lamprey have been observed swimming volitionally against maximum water velocities of 1.75 m s^{-1} (Russon and Kemp, 2011b) and 1.66 m s^{-1} (Kemp *et al.*, 2011), respectively, in an open channel flume. For juvenile eels (60 - 300 mm) migrating upstream, burst speeds are substantially less, ranging from 0.41 to 1.50 m s^{-1} (Clough *et al.*, 2004; Clough and Turnpenny, 2001). As a result, routes that athletic salmonids can successfully pass may not facilitate multi-species passage, even under low velocities (Porcher, 2002). Upstream migrating juvenile eels often utilise fluid boundary layers near constructions to assist passage (Barbin and Krueger, 1994), while their ability to climb saturated surfaces (Legault, 1988; Linton *et al.*, 2007) highlights a requirement for multi-species passage research and how it may be successfully incorporated at different types of infrastructure. Mouton *et al.* (2011) found that vertically opening gates during the flood tide at a tidal barrier improved the passage of glass eels from an average of 3 to 632 individuals per tidal cycle in the Yser River, Belgium. Orifice modifications to tide gates might provide similar advantages, but such methods of mitigation have received no quantification for salmonids whose passage may depend on different criteria.

Salmonid species are typically surface oriented, swimming in the upper part of the water column (e.g. Arnekleiv *et al.*, 2007). In acknowledgement of this behaviour, bypass entrances designed for salmonids have often been elevated in the water column (Larinier and Marmulla, 2004), neglecting to account for swimming depths of non-salmonids, which may vary with species, life stage and season (Coutant and Whitney, 2000). For example, juvenile Pacific lamprey were more likely to become entrained at hydropower turbines than salmonid smolts as a result of swimming low in the water column while moving downstream (Moursund, 2001). Passage success of benthic oriented adult river lamprey, *Lampetra fluviatilis*, and European eel was also decreased by a 0.2 m high overshot weir when compared to an undershot structure in an experimental flume (Russon and Kemp, 2011b). Although vertical searching behaviour has been observed at some locations, (Durif *et al.*, 2003; Gosset *et al.*, 2005; Watene and Boubée, 2005) benthic exploration elicited in the forebay of a hydroelectric facility by adult American eel, *Anguilla rostrata*, tracked with 3D acoustic telemetry indicated that submerged bypass entrances may be more effective for passage in this species (Brown *et al.*, 2009a). Exposure of different areas of the water column by traditional top-hung tide gate designs (lower water column) and mitigation options (e.g. entire water column for side-hung gates and SRTs; mid water column for orifices) present a number of potential options that may facilitate multi-species passage. However, assessment is required.

Downstream juvenile salmonid migration has generally received less consideration than upstream movements of their adult counterparts (Larinier and Travade, 2002). Previously, downstream migration was thought to be passive (Thorpe *et al.*, 1981). This theory has since been dispelled (Peake and McKinley, 1998), emphasising the importance of a behavioural component to downstream migration of smolts, including the impact of velocity gradients (Haro *et al.*, 1998; Kemp *et al.*, 2005a) and overhead cover (Kemp *et al.*, 2005b) that may be found at tide gates and associated culverts. The complexity required for successful bypass design has often been ignored, causing low success rates (Williams *et al.*, 2012). Research is increasingly looking to the application of bypasses for passing multiple species. While downstream migrating Atlantic salmon passed a modified weir with less velocity acceleration in higher numbers and faster than a sharp-crested weir, no difference was found for American shad that also exhibit carangiform locomotion (Haro *et al.*, 1998). Similarly, downstream moving brown trout have been observed to avoid accelerating velocities created by a submerged orifice weir in an open channel flume, however, European eel only responded if physical contact was made with the structure (Russon and Kemp, 2011a). Conversely, eels monitored via 3D telemetry in the River Stour, UK, were repelled by routes where flow rapidly accelerated (Piper *et al*., *in prep*), uncovering an area requiring further research.

Although turbulence may increase the energetic costs of salmonid motility (Enders *et al.*, 2005) and affect stability (Tritico and Cotel, 2010), its impact on fish with fewer (e.g. eel) or no paired fins (e.g. lamprey) may further inhibit passage (Kemp *et al.*, 2011; Liao, 2007). However, lamprey have the ability to attach to the surfaces of structures via an oral disc which could enable short periods of burst swimming through turbulent and high velocity routes (Keefer *et al.*, 2011; Quintella *et al.*, 2004), unlike eels. This highlights a need for independent research on different species, even those with similar body morphologies.

The ability of fish to acclimate to changes in salinity may also contribute to the impact of estuarine structures on successful fish passage. Avoidance and disorientation has been reported in some salmonids traversing barrages (Russell *et al.*, 1998), whereas similar effects have not been reported for eels (Chan *et al.*, 1967; Maetz and Skadhauge, 1968; Rankin, 2008), although research into post transition impacts is limited.

2.4. Conclusions

Diadromous fish are environmentally, economically and socially important, yet such species are undergoing serious declines in abundance worldwide (Limburg and Waldman, 2009). One of the contributing factors to this decline is anthropogenic infrastructure in rivers and estuaries (e.g. Roscoe and Hinch, 2009). Removing and mitigating the effects of obstructions to fish passage can improve fish abundances via economically viable means and under short timescales (Roni *et al.*, 2002).

Salmonids (Burger *et al.*, 2013) and eels (Feunteun, 2002) are regarded as bioindicators that reflect ecosystem health. Anadromous brown trout are classed as threatened under the UK Biodiversity Action Plan (JNCC, 2010), and have unique importance for angling, returning earlier in the year at lower flows than Atlantic salmon and to a number of rivers where Atlantic salmon are not found (Environment Agency, 2008). Eels have undergone significant declines in recent years (Vogel, 2010) and there is a legislative requirement to meet silver eel biomass escapement targets under the EU Eel Regulations (1100/2007) (EC, 2007). As a result, there is a need for research into multi-species passage provision at riverine and estuarine structures (Kemp and O'Hanley, 2010).

This Literature Review found that the impact of tide gates and their modifications on fish passage has received little scientific consideration and to date the decision to apply mitigation measures at such structures has largely been the result of hypothetical construct. This is reflected in the Environment Agency’s riverine and estuarine infrastructure database, which attempts to identify barriers and features in England and Wales, such as weirs, waterfalls, locks, dams, mills and barrages, yet neglects to incorporate tidal outfall structures and culverts (Environment Agency, 2010).

Where studies do consider the impact of tide gates on fish passage, the aims, experimental designs and methodologies employed do not quantify fish passage efficiency; the proportion of fish that approach a structure compared to the proportion that pass (escapement/entry) and the time it takes fish to pass (delay). Telemetry studies allow the determination of fish passage efficiency where most other methods fail.

A number of biotic factors influence fish passage efficiency, such as swimming ability (including species, morphology, life stage, condition) and behaviour. Abiotic factors also influence fish passage efficiency, such as flow, temperature, DO, salinity, tides, diel periodicity and hydrodynamics. Both biotic and abiotic factors should be considered when assessing fish passage efficiency at structures, including the determination of time based covariates rather than generalised mean averages (Roscoe and Hinch, 2009). The estuarine environment and temporal operation of tide gates present a unique set of potential influences on fish passage efficiency and delay. Further, tide gates may exacerbate the aforementioned variables, which may differ between gate designs and modifications.

This chapter identifies a requirement to assess the impact of tide gates on diadromous fish migration. Chapter 3 outlines how this thesis fulfils this aim based on the knowledge and gaps revealed by this literature review.

Chapter 3

Aims and Objectives

Despite declines in economically, ecologically and socially important diadromous fish (Limburg and Waldman, 2011) the impacts of low-head and temporal obstructions on fish passage between essential habitats have received little attention. Where research does exist, there has been an emphasis on riverine impediments (Aarestrup and Koed, 2003; Gauld *et al*., 2013; Ovidio *et al*., 2007). Consequently, the following research aim was established:

To assess the impact of tide gates and other temporal estuarine barriers on diadromous fish migration.

To satisfy this aim, a preliminary objective was defined:

1. To review existing literature to identify trends and biases in research aims, findings and methods on fish passage at tide gates and other temporal estuarine barriers

Fulfilment of Objective 1 (Chapter 2) revealed that relevant literature was dominated by assessment of estuarine dwelling species abundance, richness and diversity at intertidal culverts and sluices. Less consideration was given to the impact of more restrictive structures such as tide gates (Ritter *et al*., 2008). Where fish movement past estuarine infrastructure was assessed, studies neglected to identify passage efficiency and delay. These metrics are important for quantifying the impact of obstructions on fish and identifying where mitigation is required (Castro-Santos and Haro, 2003; Kemp and O'Hanley, 2010). Analysis of the wider body of fish passage literature highlighted the importance of confounding environmental variables when assessing the impacts of infrastructure, as well as a need for multi-species passage. Accordingly, four objectives were identified:

2. To quantify the passage efficiency and delay of juvenile and adult diadromous brown trout and adult European eel at top-hung tide gates using telemetry techniques

3. To assess the link between confounding environmental variables and the passage efficiency and delay of juvenile and adult diadromous brown trout and adult European eel at tide gates

4. To quantify how mitigation methods influence passage efficiency and delay for juvenile and adult diadromous brown trout and adult European eel using telemetry techniques

5. To assess the influence of top-hung tide gates and mitigation measures on the behaviour of brown trout smolts in relation to hydraulics under controlled conditions

To meet these objectives, four studies were completed (Chapters 5 - 8) (Fig. 3.1).

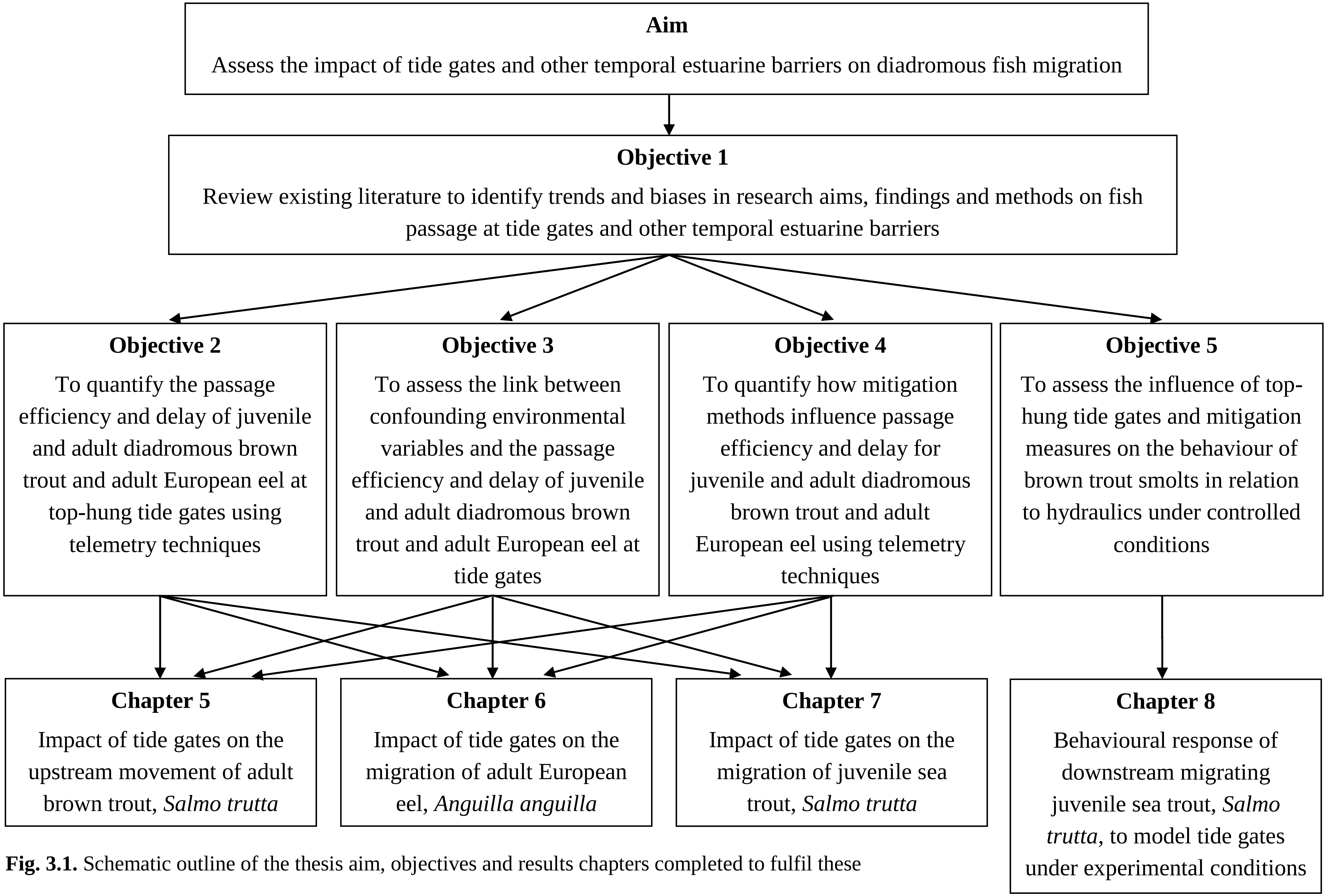


Fig. 3.1. Schematic outline of the thesis aim, objectives and results chapters completed to fulfil these

Chapter 4

General Methodology

This chapter presents an overview and justification of the equipment, methods and approaches used to achieve the research aims and objectives outlined in Chapter 3. A more detailed and site specific methodology can be found in Section 2 of each results chapter (Chapters 5 to 8).

4.1. Telemetry

Telemetry allows the movements of individual fish to be spatially and temporally tracked in the wild (Cagnacci *et al.*, 2010; Castro-Santos *et al.*, 2009), permitting quantification of attraction and passage efficiencies, and delay at structures. Two types of telemetry were used in this thesis: Passive Integrated Transponder (PIT) and acoustic telemetry.

4.1.1. Passive Integrated Transponder (PIT) telemetry

Half-Duplex (HDX) PIT tags contain a ferrite cored copper wire coil and integrated circuit encased in a bio-stable glass capsule. The presence of PIT tagged fish can be detected by HDX antennas, also known as PIT Loops (PLs) (Fig. 4.1). Constructed from coils of insulated stranded copper wire, PLs radiate an alternating magnetic field created by the alternating voltage from an interrogator or ‘reader’ powered by a battery. When a PIT tagged fish passes through the magnetic field created by a PL, the tag becomes energised and transmits a unique signal via its own alternating magnetic field back to the interrogator via the PL in the form of an alternating voltage. The height and width of a PL is limited to approximately 1.8 m and 10.0 m, respectively, which made this method suitable for tracking fish in the River Stiffkey (Chapters 5 and 6), but not the River Meon (Chapter 7). Recent studies have shown the potential for using HDX PIT telemetry to successfully track fish movement in brackish tidal channels (Meynecke *et al.*, 2008). Use of these systems in estuaries is otherwise infrequently reported. Increased levels of salinity/conductivity, turbidity, and depth attenuate the electromagnetic field of PLs, which can reduce tag detection range and efficiency. In this thesis, new technology that enabled PLs to periodically automatically retune maximised the potential for using this method in a brackish environment near moving metal tide gates that might also attenuate the electromagnetic field. The tag detection range and efficiency of PLs used in this thesis were therefore tested under a range of environmental conditions (Chapter 5, Section 5.3.2; Fig. 4.2).

Fig. 4.1. HDX PIT loops (PLs) located immediately downstream of Tide Gates 1 (left) and 2 (right) in the River Stiffkey, UK.

Fig. 4.2. Manual testing of a PIT loop (PL) located 65 m upstream from Tide Gate 1 in the in the River Stiffkey, UK.

Due to the absence of an integrated battery, HDX PIT tags are small (e.g. length = 23.0 mm, width = 3.0 mm, weight = 0.3 g) when compared to other telemetry tags. The small nature of the tags means less invasive implantation techniques and better healing and survival rates (see Section 4.1.3). PIT tags are also relatively cheap at just a few pounds (GBP), allowing for large samples of fish to be tagged compared to active transmitters.

4.1.2. Acoustic telemetry

Acoustic telemetry uses ultrasonic sound frequencies between 20 - 500 kHz to transmit short pings underwater from a tag to a receiver (Vemco, 2012). Coded tags transmit a unique number of pings in series, conveying a unique digital identification. As coded tags transmit at the same frequency (69 Hz for Vemco acoustic tags used in this thesis), pings occur at randomised intervals, e.g. between 30 to 90 seconds, to maximise the probability of large samples of fish being detected during passage past a single receiver (Vemco, 2012). Acoustic telemetry is particularly advantageous when tracking fish in rivers or estuaries that are too wide or deep to construct PIT loops, and/or require unimpeded access for boats, such as the River Meon (Chapter 7). The range and efficiency of tag detections by acoustic receivers can vary as environmental conditions change (Heupel *et al.*, 2006), therefore manual testing was performed over the study period (see Chapter 7, Section 7.3.2).

4.1.3. Tag selection and tagging procedures

Tagging can influence fish behaviour, growth and survival (e.g. Brown *et al.*, 2006; Lucas, 1989; Moore *et al.*, 1990). Therefore, appropriate selection of tag type, size, and implantation methods was crucial to minimise effects on fish welfare that could make data unrepresentative of the wider population of untagged fish. Fish can be tagged with acoustic and PIT tags externally, gastrically or intraperitoneally.

Externally attached tags have previously been used to successfully track adult Atlantic salmon, *Salmo salar*, during their spawning migration (Aarestrup *et al.*, 2000). For sea trout, *Salmo trutta*, tagged using the same technique, high mortality and large open wounds occurred in many survivors as a result of behavioural differences; trout were more likely to hide in densely vegetated areas (Jepsen *et al.*, 2002). External tags could also be unsuitable for eels, as they tend to hide in weedy or silty benthic areas and in between rocks (Tesch, 1974). External tags also decrease hydrodynamism of fish, elevating the energetic costs of swimming (Tesch, 1974), causing shedding rates to be as high as 100% (e.g. in the two-spined blackfish, *Gadopsis bispinosus*, which has an elongated, eel like body morphology, Broadhurst *et al.*, 2009).

During gastric implantation, tags are inserted into the fishes' stomach via the oesophagus. Gastric implantation has been successfully used in some studies on juvenile salmonids (Hall *et al.*, 2009), although expulsion rates can be high (Stasko and Rommel, 1974) and often greater than for external or intraperitoneal implantation (Adams *et al.*, 1998b). Gastric implantation can also decrease feeding (Baras and Jeandrain, 1998) and growth rates (Martinelli *et al.*, 1998).

For intraperitoneal implantation, tags are surgically implanted into the peritoneal cavity of the fish. The procedure requires longer fish handling times than gastric implantations (Hall *et al.*, 2009), which can increase the risk of physiological disruptions (Jepsen *et* *al.*, 2001) and bacterial infection (Roberts *et al.*, 1973). Freshwater stage juvenile Chinook salmon, *Oncorhynchus tshawytscha,* (fork length [FL] = 160 mm) that were surgically implanted with transmitters (weighing 2.2 - 10.7% of fish body mass) showed 76 - 100% survival compared to 98 - 100% survival from gastrically implanted tags (Adams *et al.*, 1998b; Brown *et al.*, 2006; Martinelli *et al.*, 1998). Conversely, the survival of first-ocean-year hatchery-reared juvenile Chinook salmon, gastrically implanted with acoustic tags was significantly lower than those implanted intraperitoneally (Hall *et al.*, 2009). Fish that underwent a sham gastric tagging procedure (i.e. the same gastric tagging procedure but without the implantation of a tag) demonstrated the same survival rates as intraperitoneal tagged and sham tagged fish. Decreased growth and swimming performance has also been reported for gastrically tagged species (Adams *et al.*, 1998a; 1998b), but not for surgical implantation (Brown *et al.*, 2006), which decreases the potentially negative long-term effects of tagging on fish when performed properly (e.g. Brown *et al.*, 2009b; Jepsen *et al.*, 2002). Further, no significant differences were observed in the behaviour of Atlantic salmon smolts (Connors *et al.*, 2002) or rainbow trout, *Oncorhynchus mykiss,* (Swanberg and Geist, 1997) that were intraperitoneally implanted with radio tags. Therefore, intraperitoneal implantation was used when tagging fish for this thesis.

Tag weight and dimensions relative to the size and morphology of the fish may influence stress, feeding, growth, buoyancy, swimming performance, predator avoidance, tag expulsion and survival (Jepsen *et al.*, 2002). Therefore, it was important to assess whether PIT and acoustic telemetry were suitable for tracking the species and life stages (juvenile and adult trout, and adult European eels, *Anguilla anguilla*) studied in this thesis.

It was previously proposed that tag weight should not exceed 2% of fish body mass (e.g. Lefrancois *et al.*, 2001; McCleave and Stred, 1975; Ross and McCormick, 1981; Winter, 1983), although this guideline has recently been challenged by a number of studies. For example, Hall *et al.* (2009) found that juvenile Chinook salmon could successfully survive implantation with acoustic transmitters up to 5.8% of the fish's body mass. Tags up to 6.7% body weight of juvenile Chinook salmon did not affect swimming performance or predation susceptibility up to 21 days post tagging (Anglea *et al.*, 2004). Brown *et al.* (1999) observed that tags of 6% to 12% body weight did not significantly impact swimming performance of Atlantic salmon smolts, while tags comprising up to 14.5% of body weight did not influence the swimming ability of juvenile Atlantic salmon (Moore *et al.*, 1990) or juvenile Coho salmon (Moser *et al.*, 1990). Transmitter expulsion occurred in eels when tags were 2.5% to 3.0% of body weight (Baras and Jeandrain, 1998). Further, Pacific lamprey, *Lampetra tridentata*, exhibited decreased swimming performance immediately after being tagged with transmitters up to 2.5% of their body mass compared to controls, although this difference disappeared 24 hours post surgery (Close *et al.*, 2003).

Tag dimensions have also been reported to influence fish behaviour. Decreased swimming performance was observed in juvenile Atlantic salmon (total length [TL] = 200 mm) implanted with wide (length = 19 mm, diameter = 10 mm, 4.9% of body weight in air) compared to narrow tags (length = 33 mm, diameter = 8 mm, 6% of body weight in air) (McCleave and Stred, 1975). The body cavity of anguilliform fish is relatively narrow compared to salmonids, meaning tag sizes used in eels may be limited by size and shape rather than weight (Moser *et al.*, 2007). Therefore, PIT tags, which are narrower than other types of telemetry tag, were used for tagging and tracking fish in this thesis where river characteristics permitted the use of PIT telemetry (Chapters 5 and 6). Where acoustic telemetry was required to study sea trout smolt migration in the River Meon (Chapter 7), tag size and mass were kept to a minimum, and as close to or under 2% of body mass.

Duration of air exposure and physical contact is positively related to stress and adverse behavioural alterations in some species (e.g. rainbow trout, Ferguson and Tufts, 1992) and therefore was minimised during the tagging process (Cooke and Suski, 2005). All instruments, tags and gloves were sterile where possible to avoid bacterial contamination of the wound and any other adverse effects (Mulcahy, 2003). Alcohol was used to disinfect any tags and tools that could not be sterilised. Because fish epithelium is covered with a protective mucous barrier containing compounds such as lysozymes and proteolytic enzymes which prevent bacterial colonization and penetration into the wound (Alexander and Ingram, 1992), fish were not swabbed with antiseptic prior to incision.

An incision was made in front of the pelvic girdle on the fish’s ventral surface large enough to fit the smallest dimension of the transmitter (Wagner *et al.*, 2011). Incisions made along the linea alba, the ventral midline formed by collagenous connective tissue, may decrease the amount of tissue damage from an incision (Murray, 2002), decrease blood loss (Nygaard and Squatrito, 1996), and heal quicker when compared to muscle (Anderson and Roberts, 1975). However, previous research has observed there to be no difference in inflammation, behaviour (rainbow trout: Wagner and Stevens, 2000), or tag loss (Chinook salmon: Panther *et al.*, 2010) between the two incision locations. In this thesis, incisions were made adjacent to the ventral midline where dense fibrous tissue is absent to reduce operation times and prevent contact with benthic substrates which could impede healing or cause damage (Wagner *et al.*, 2011).

Incisions for implanting PIT tags into eel and trout in this thesis were small (approximately 3 mm) and thus not sutured. Suturing can prolong surgery time, decrease the rate at which a wound heals, and cause mortality (Baras and Jeandrain, 1998). Where larger incisions were required in this thesis to implant acoustic tags in sea trout smolts, absorbable braided sutures were used. Decreased transmitter loss and enhanced healing was observed in brown trout, *Salmo trutta*, where incisions were closed with absorbable braided sutures compared to non-absorbable monofilament sutures (Jepsen *et al.*, 2008). Suture type, i.e. monofilament or braided, may have more impact on wound inflammation, ulceration, and tag and suture retention than absorbable or non-absorbable properties (Deters *et al.*, 2010). Although Deters *et al.* (2010) used sutures with different needle types, other studies have identified similar reactions. For example, 80% of tagged bluefin tuna, *Thunnus thynnus*, shed absorbable monofilament sutures within 2 to 3 weeks of tagging compared to absorbable braided sutures which were lost faster (Block *et al.*, 1998). However, braided sutures were shed in 25% of the sample before the wound had started to heal. Other studies found that suture type did not influence wound healing and inflammation (largemouth bass, *Micropterus salmoides*, Cooke *et al.*, 2003), swimming behaviour (rainbow trout Wagner and Stevens, 2000), or fish survival (Cooke *et al.*, 2003). Another advantage of braided sutures (e.g. Vicryl) is reduced surgery durations due to faster knot tying, and increased knot security and thus tag retention (Wagner and Stevens, 2000).

Simple, interrupted sutures were used in this thesis as they minimise tissue inflammation (Wagner and Stevens, 2000, for rainbow trout), suture failure, tag loss (Hall *et al.*, 2009; Lacroix *et al.*, 2004) and the duration of surgery when compared to vertical mattress patterns. Steel staples may represent an alternative method for closing wounds, with decreased epidermal infection, abdominal bloating, tag loss (Swanberg *et al.*, 1999), and increased survival (Sanderson and Hubert, 2007) observed compared to braided sutures. Stapling has also been observed to increase transmitter loss in rockfishes (Starr *et al.*, 2000) and has not been trialled on fish smaller than 150 mm (the size of a small sea trout smolt), precluding its use in this thesis. Similarly, sealing incisions with adhesives can shorten surgery times, but can also increase tag expulsion (Petering and Johnson, 1991).

Post surgery, fish studied in this thesis were held in aerated tanks to recover. Holding densities were minimal to maintain high dissolved oxygen (DO) and minimal ammonia levels (Oldenburg *et al.*, 2011). To avoid thermal shock which could have altered fish physiology and or behaviour, water was regularly replenished to maintain ambient river temperature (Jepsen *et al.*, 2002; Portz *et al.*, 2006). Although holding fish for extended periods could prevent suture and tag loss in some species (Broadhurst *et al.*, 2009), stress could counteract these advantages (Schreck, 2000). For example, brown trout held in recovery tanks for 5 minutes after surgery showed less disturbance in behaviour than those that were not tagged but held for longer (Baras *et al.*, 1998). Therefore, fish in this thesis (Chapters 6 and 7) were released in vegetated areas of the river (to provide cover) near to the site of capture as soon as the effects of anaesthesia had worn off (up to a maximum of 1 hour), with the exception of adult trout, which were released downstream of the tide gate in the River Stiffkey (Chapter 5).

To assess the impact of tagging procedures on survival and tag retention, a separate sample of fish were caught and tagged during each telemetry study and held in the river in perforated containers receiving in-stream flow for 7 to 14 days. The results of survival and tag retention are reported in Sections 5.3.2, 6.3.2, and 7.3.2.

4.2. Video in the field

Video cameras require clear, calm waters and high light levels to observe fish, often precluding their use in the field. Chapters 5 and 6 assessed the passage of adult brown trout and European eel through an orifice modification in a tide gate. Two infrared (IR) submersible cameras (Sony, Model: IR 37CSHR-IR 25m) were fixed to a tide gate and perpendicular to the flow, successfully capturing the entire area of entry/exit through the orifice. By positioning the cameras, which had integrated IR LEDs for recording images at low light levels, either side of the orifice, the field of vision was extended across the entire opening even at night. Footage was captured on a digital video recorder powered by a 110ah 12v battery. Downloaded footage was used to complement data obtained from PIT telemetry, which identified the periods when tagged fish had moved through the tide gate but was unable to distinguish if fish had passed through the orifice modification itself.

4.3. Open channel flume

Telemetry has been successfully used to quantify the broad-scale movements of fish in their natural environment in a number of studies (e.g. Winter *et al.*, 2006). Such data is useful for assessing attraction, passage efficiency, delay, and linking movements to separately measured environmental variables, but precludes assessment of fine-scale behavioural mechanisms. Recent developments in acoustic telemetry have enabled fish movements to be tracked to an accuracy of ~1m (Brown *et al.*, 2009a). Acoustic imaging systems (e.g. Dual-frequency Identification Sonar, DIDSON) can also be used in combination with telemetry to observe behaviour at a higher resolution in turbid systems. However, these methods do not provide the fine-scale resolution (< 1cm) that can be attained in flumes (Rice *et al.*, 2010). Flumes also enable a high degree of control over confounding factors and isolation of the test variables when compared to studies in rivers and estuaries, enhancing knowledge of fish swimming performance and behaviour, improving the effectiveness of passage facilities (Williams *et al.*, 2012). Therefore, flume-based research has been undertaken in this thesis (Chapter 8) to assess the impact of a model tide gate (Fig. 4.3) on the behaviour of downstream moving juvenile sea trout to complement studies that tracked downstream migrants in the field (Chapters 6 and 7).

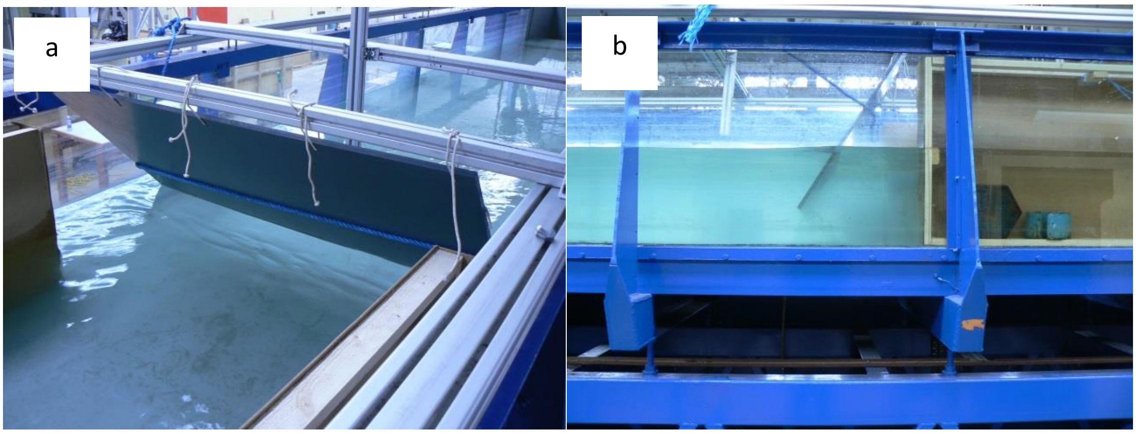


Fig. 4.3. A model tide gate in the re-circulatory flume at the International Centre for Ecohydraulics Research experimental facility, University of Southampton, UK, viewed from (a) upstream and (b) the side.

4.3.1. Experimental facility

The experiment described in Chapter 8 was carried out in an indoor re-circulatory flume (length = 24.4 m, width = 1.4 m, maximum depth = 0.6 m) at the International Centre for Ecohydraulics Research (ICER) facility, University of Southampton, UK. Three centrifugal pumps, each with a capacity of 0.09, 0.15 and 0.23 $m^3 s^{-1}$, could be used selectively to circulate water through the flume, with a maximum flow capacity of 0.47 $m^3 s^{-1}$. The flow through each pump could be further manipulated by regulating individual valves. An adjustable height weir at the downstream end was used to control water depth. To minimise the influence of the surrounding environment on fish behaviour, black plastic sheeting was fixed around the flume and its glass walls. Sheeting was also placed around an infra-red camera used to view activity through the glass wall of the flume. The flume base was constructed of grey painted steel, thus enabling fish to be clearly viewed by infra-red cameras mounted above the flume.

4.3.2. Video analysis

Overhead and side mounted IR cameras provided a non-intrusive method for observing fish behaviour in the flume. Experiments were conducted at night when sea trout smolts are reported to be most active (Moore *et al.*, 1998a). Infra-red (850 nm) illumination panels enabled cameras to capture fish behaviour during the hours of darkness.

The head and tail coordinates of fish in the flume at the time of their first reaction (e.g. orientation switch, increased tail beat frequency, or holding, see Chapter 8 for more details) were pinpointed from video stills using LoggerPro Version 3.8.2 (Verinier Software, Beaverton, OR, USA). Coordinates were then imported into ArcGIS 10.1 (ESRI, Redlands, CA, USA) velocity plots (see Section 4.3.3) to obtain fine-scale velocity measurements.

4.3.3. Quantifying hydrodynamics

To quantify the hydrodynamic conditions in the flume, an Acoustic Doppler Velocimeter (ADV) was used. Compared to traditional apparatus used to measure flows, such as electromagnetic or impeller velocity meters, ADVs provide greater accuracy and three-dimensional velocity measurements (Muste *et al.,* 2010). A number of studies have used ADVs to quantify hydrodynamics under flume conditions to assess the relationship with fish behaviour (e.g. Enders *et al.,* 2009).

The ADV sampled three-dimensional water velocities at points along the length, width and depth of the observation area in the flume (see Chapter 8). Using the Doppler effect, ADVs emit short pairs of acoustic pulses which bounce off suspended particles in the water. A sensor detects changes in frequency of the returning acoustic pulses, which are proportional to the speed of the particles in the water, which is used to establish water velocity. The relative quality of acoustic signals received by the ADV (signal to noise ratios) and velocity dispersion (measured as correlation values) were within the manufacturer's suggested range (20 - 25 and > 70%, respectively). To remove erroneous data points, raw data were processed in Microsoft Excel using a maximum/minimum threshold filter that replaces outliers with the mean (Cea *et al.*, 2007). Maximum/minimum threshold values were calculated as:

$$u_{min} = \bar{u} - \sqrt{2\ln(N)}\ \sigma_u$$

$$u_{max} = \bar{u} + \sqrt{2\ln(N)}\ \sigma_u$$

where u_{min} and $u_{\max}$ are the minimum and maximum longitudinal velocity thresholds, respectively, $\bar{u}$ is the mean longitudinal velocity, σ_u is the standard deviation of u, and N is the total number of data points. Data were filtered in the same way for lateral ($\bar{v}$) and vertical ($\bar{w}$) velocity measurements so that the mean velocity vector (V) could be calculated:

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

ArcGIS 10.1 (ESRI, Redlands, CA, USA) was used to produce mean velocity vector contour plots using spline interpolation.

4.4. Test species

4.4.1. Brown trout

Distributed throughout the UK, continental Europe, Scandinavia, and Iceland, and reaching 42° south (Harris and Milner, 2006), brown trout (Fig. 4.4) display a wide spectrum of life history traits, ranging from those that remain in freshwater for the duration of their lifecycle to full anadromy (Lucas and Baras, 2001). The anadromous form, commonly known as sea trout, spawn in freshwater, where surviving progeny remain for up to three years. After undergoing a series of physiological changes in preparation for transition into salt water, known as smoltification, juvenile sea trout (Fig. 4.5) migrate downstream and out to sea in the spring (Harris and Milner, 2006). After one or two winters at sea, fish return to freshwater predominately in the autumn to spawn. As an iteroparous species, trout may spawn several times in a lifetime (Harris and Milner, 2006). Amphidromous brown trout migrate between salt and freshwater for purposes other than spawning, such as feeding.

Fig. 4.4. An adult brown trout caught in the River Stiffkey, UK.

Fig. 4.5. A sea trout smolt (juvenile anadromous brown trout) caught in the River Blackwater, UK.

4.4.2. European eel

Distribution of the catadromous European eel, extends across the west European and North African coasts (Tesch, 2003). Mature adult eels spawn in the Sargasso Sea and then die. Surviving progeny, known as leptocephali, are transported up to 5000 to 6500 km by currents across the Atlantic Ocean. During this period, leptocephali transform into transparent glass eels, entering freshwater along the European coast in the spring (van Ginneken and Maes, 2005). After two to twenty-five years, adult eels, also known as yellow eels, undergo a number of physiological and morphological changes in preparation for the spawning migration back to the Sargasso Sea (Tesch, 2003). This transformation, known as silvering, is characterised by a change in pigmentation from brown to white-silver ventral and black dorsal surfaces distinctly separated along the lateral line (Tesch, 2003) (Fig. 4.6). Silver eels also exhibit large eye diameter and pectoral fin length to TL ratio, and darkened pectoral fins when compared to resident yellow eels (Tesch, 2003). Downstream migration typically occurs during the autumn (Boubée *et al.*, 2001).

Fig. 4.6. A silver European eel caught in the River Stiffkey, UK.

4.5. Fish capture

Two methods of fish capture were used to obtain wild trout and eels for tagging or transportation to the ICER flume facility.

4.5.1. Electric fishing

Electric fishing was used to capture adult brown trout and eels in the River Stiffkey, 1.0 to 6.0 km upstream of the tide gates (Chapters 5 and 6). During electric fishing, an anode and a cathode are submerged in the sampling water, creating a high voltage potential gradient typically using a direct current. The potential gradient induces galvanotaxis, causing fish to swim towards the anode as a result of involuntary muscular convulsions (Templeton, 2006). Fish encountering the electrical field near the anode become stunned, enabling them to be netted out of the water and into a holding container for recovery prior to tagging. Electrofishing is not harmful to fish when performed correctly (Templeton, 2006), and the frequency of the current can be adjusted to target eels and trout (Beaumont *et al.*, 2000). Although electric fishing is relatively ineffective in water with high conductivity (Beaumont *et al.*, 2005), tide gates precluded the majority of saline intrusion upstream. Hence electric fishing was effective in this area.

4.5.2. Fyke nets

Fyke nets were used to capture eels used for PIT tagging in the River Stiffkey from 0.5 to 1 km upstream from the tide gates (Section 6.3.2) (Fig. 4.7a). Sea trout smolts used for acoustic tagging were also caught with fyke nets 4.9 km upstream from the tide gates in the River Meon (Section 7.3.2), and during downstream migration in the River Blackwater for trout smolts used in the flume (Section 8.3.2). A fyke net consists of a series of tapering chambers with narrowing entrances which allow actively migrating fish to swim into the net but not out. Leaders or wings, approximately 5.0 m in length, acted like a funnel to guide fish towards the entrance. A 1 mm fine mesh box (height = 1.0 m, width = 0.5 m, length = 0.5 m) was attached at the distal end when targeting smolts due to their delicate exterior and propensity to migrate in high densities (Davis *et al.*, 1980) (Fig. 4.7b).

Fig. 4.7. Winged fyke nets with entrances facing upstream to catch (a) adult European eels 0.5 km upstream of Tide Gate 1 in the River Stiffkey, UK, and (b) sea trout smolts in the River Blackwater, UK, using a fine mesh catch box at the distal end.

Chapter 5

Impact of tide gates on the upstream movement of adult brown trout, *Salmo trutta*

5.1 Summary

Tide gates, used to regulate tidal flow as part of land reclamation programmes, temporally block fish movement by closing during the flood tide. Their impact on the upstream movement of brown trout has received little consideration. The River Stiffkey, UK, discharges into the North Sea via three top-hung tide gates, one counterbalanced (Gate 1), and two not (collectively referred to as Gate 2). Fifteen adult trout were caught between 0.5 and 6.0 km upstream from the gates on 20 separate days between July and December 2011 (total $n = 300$) and implanted with 23 mm half-duplex passive integrated transponder (PIT) tags before being released 15 m downstream from Gate 1 where PIT antennas were located on either side. Overall, gate attraction and passage efficiencies were 96.7% and 92.4%, respectively. The operation of an orifice, installed to improve connectivity for adult trout and juvenile eels, did not influence passage efficiency or delay. Of the fish that were released when the orifice was operational, 42.6 - 55.7% approached the orifice entrance and 70.6 - 92.3% of these passed through. Individuals that passed through the orifice were larger than those that did not. Movement past the tide gates took longer than subsequent passage through unimpeded reaches upstream. Duration of passage through the gates was predominately

influenced by the mean angle of gate opening during the time prior to passage, followed by water temperature. Overall, top-hung tide gates delayed the upstream movement of brown trout, potentially increasing risk of predation and energy expenditure and limiting access to essential habitat.

5.2. Introduction

Impoundments are one of the most prominent stressors to aquatic ecosystems (Heinz Center, 2002; Pielou, 1998). They disrupt natural discharge, sediment transport, and temperature regimes, reduce connectivity with floodplains (Poff *et al.*, 1997; Poff and Hart, 2002), and impact water quality, e.g. by increasing nutrient loads and causing algal blooms (Kondolf, 1997). Habitat fragmentation can reduce native species richness and abundance, including for diadromous fish that migrate between marine and freshwater to complete their lifecycles (Pess *et al.*, 2008; Pringle *et al.*, 2000). Compared to large infrastructure, the impacts of low-head dams and other intermittent barriers to migration, such as tide gated culverts used to help prevent tidal inundation as part of efforts to reclaim land, have received little attention (Garcia de Leaniz, 2008; Lucas *et al.*, 2009).

Tide gates open when hydraulic head differential is sufficient during the ebb tide, and close when minimised during the flood. As a result they temporally impede migrating fish, particularly those that utilise selective tidal stream transport to minimise energetic costs during river entry on the flood tide (adult Atlantic salmon, *Salmo salar*: Potter, 1988; Priede *et al.*, 1988; Russell *et al.*, 1998, juvenile American eels, *Anguilla rostrata*: McCleave and Kleckner, 1982). Further, when tide gates are open, migration may be restricted if apertures of entry are small, and by high velocities (Haro *et al.*, 2004), turbulence (Hinch and Rand, 1998), rapid changes in salinity (Zaugg *et al.*, 1985), abrupt temperature gradients (Jonsson, 1991), and/or the presence of overhead cover (Kemp *et al.*, 2005b).

Dikes and levees decrease floodplain productivity and overall system yield by limiting fluvial connectivity (Welcomme, 1995), with tide gates inhibiting fish species abundance, richness (Boys *et al.*, 2012; Pollard and Hannan, 1994) and movement (Doehring *et al.*, 2011). Interestingly, previous studies often fail to assess the effects of tide gates on diadromous species, including economically important adult salmonids. Impacts may include delayed migration and congregation of fish at structures which can increase risk of predation (Schilt, 2007), disease transfer (Garcia de Leaniz, 2008) and energy expenditure (Congleton *et al.*, 2002), thus influencing gonad production (Bernatchez and Dodson, 1987), egg viability (de Gaudemar and Beall, 1998), and decreasing the ability to reach spawning grounds (Bernatchez and Dodson, 1987).

Barrier removal is the most effective and efficient way to improve fish dispersal and production in rivers (Roni *et al.*, 2002). However, this is an unlikely option when considering schemes required to protect valuable land from tidal inundation. Instead, more affordable mitigation options have been developed, including the replacement of top-hung gates with side-hung doors or self-regulating valves that allow the structure to remain open wider for longer. Modification of existing gates with counterbalances, retarders or orifices that extend the period of connectivity is even more economical and thus attractive to river managers. The effectiveness of alternative mitigation options for improving migration has yet to be quantified.

In Europe, the socio-economically important brown trout, *Salmo trutta*, exhibits a wide spectrum of life history traits, ranging from individuals that remain in freshwater for the duration of their lifecycle to full anadromy (Lucas and Baras, 2001). Stocks of the anadromous form, commonly known as sea trout, have undergone serious declines throughout parts of Europe, including a number of regions in the UK (Harris and Milner, 2006) where the species is listed as threatened under the UK Biodiversity Action Plan (JNCC, 2010).

The present study aimed to identify the impact of top-hung tide gates and an orifice modification on the upstream passage efficiency and duration of adult brown trout. Passive Integrated Transponder (PIT) telemetry was used to determine: 1) the passage efficiency at a top-hung tide gate in the River Stiffkey, UK, when an orifice was either operational or non-operational, and 2) duration, also known as delay, taking into account the influence of other environmental factors.

5.3. Materials and methods

5.3.1. Study site

The River Stiffkey, North Norfolk, UK (52° 57' N; 0° 57' E; Fig. 5.1), is situated on a chalk aquifer and fed by a catchment of 141 km^2. From 5 July to 10 December 2011 mean (± SD) daily flow measured at Little Walsingham, 12.6 km upstream from the tide gates, was 0.09 (± 0.03) m^3 s^{-1} (equivalent to Q_{72} from 2009 - 2011). The river flows 33 km north from its source at Swanton Novers and through the Stiffkey Valley Site of Special Scientific Interest (SSSI) prior to discharging into the Blakeney Channel and the North Sea via two tide gates. Tide Gate 1 (Fig. 5.2) (width = 3.0 m, height = 2.1 m) is top-hung and counterbalanced by a weight allowing it to open wider for longer. The gate opens at the seaward end of a corrugated metal pipe culvert (length = 25.8 m), which is situated at the end of the main river channel, and through which the dominant proportion of river flow is discharged (Fig. 5.1). Tide Gate 2 (Fig. 5.3) consists of a pair of non-counterbalanced top-hung gates (width = 1.6 m, height = 1.5 m), each located at the seaward end of a smooth concrete pipe culvert (length = 25.8 m). Gates 1 and 2 opened for a mean (± SD) duration of 7.9 (± 0.8) h each tidal cycle at a median angle of 3.7^o (range = 0.7 - 35.8^o) and 6.4^o (0.7 - 23.4^o), which equated to a distance of 13.6 (2.6 - 129.1) cm and 16.8 (1.8 - 60.8) cm at the widest part of the aperture, respectively. Once the water level downstream from the gates started to rise, mean (± SD) duration to gate closure was 10.4 (± 7.0) min. The probability of flooding in the lower river is decreased by a carrier channel that increases storage capacity, ending 2.7 km inland from the tide gates (Fig. 5.1).

The River Stiffkey maintains a trout population, although the reported annual return of sea trout do not exceed single figures (Pawson, 2008). The tide gates are the only potential barrier to adult trout migration in the river (Beach, 2009). As part of a programme to increase sea trout returns the Environment Agency installed an orifice fish pass in Gate 1 (Fig. 5.2) (width = 0.5 m, height = 0.3 m) in May 2010. The orifice comprised of a bottom hinged door that, under the control of a float, closed at a set tide height. Once Gate 1 had closed, this modification extended the mean (± SD) period of connectivity between the estuary and river by 14.7 (± 8.2) min whilst maintaining flood protection and minimising saline intrusion upstream at high tide.

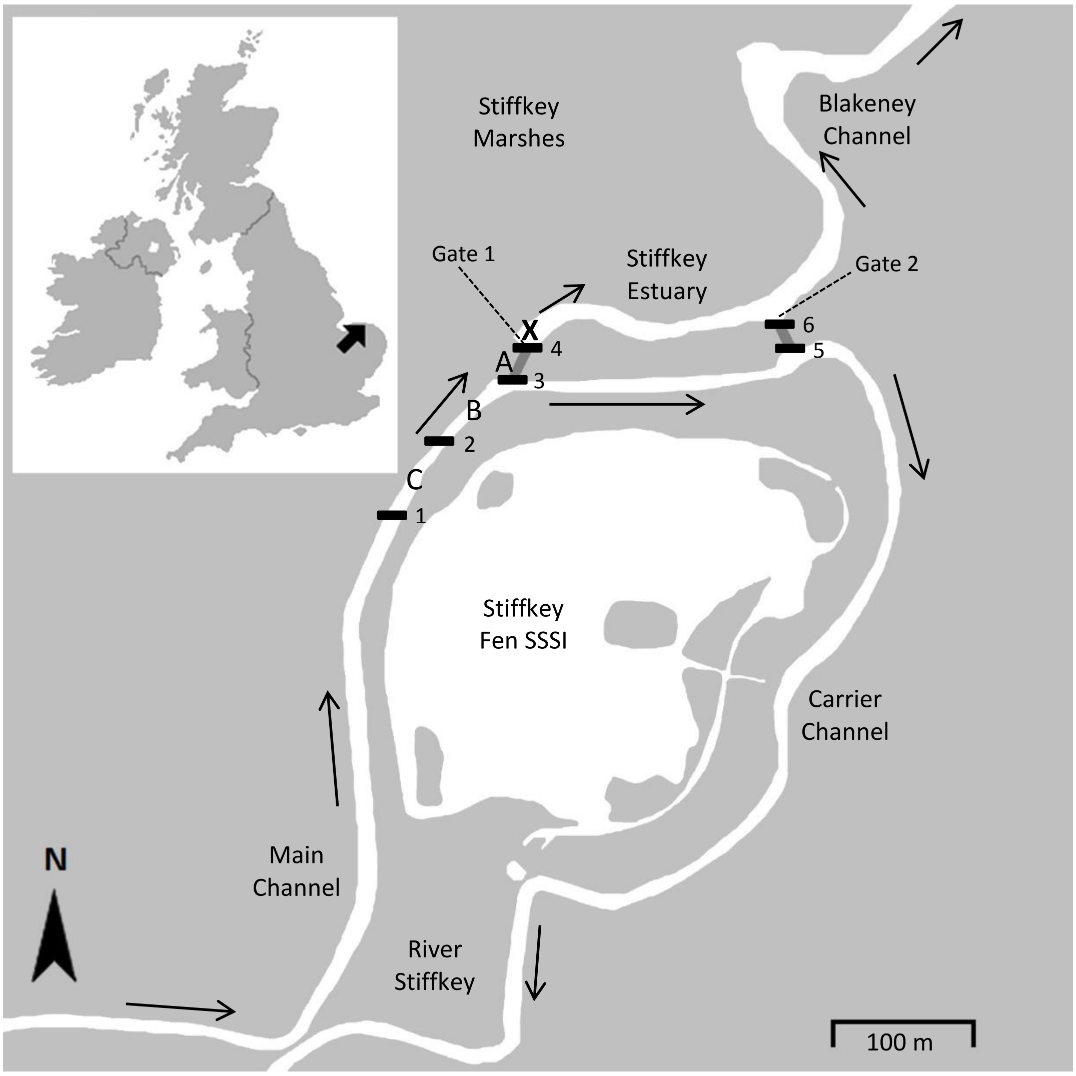


Fig. 5.1. The lower reaches of the River Stiffkey, North Norfolk, UK, showing release location (**X**) and direction of water flow (→) through Tide Gates 1 and 2. Four of the PIT loops (PLs, ▬), numbered in sequence from upstream to downstream, define limits of a reach containing Gate 1 and its culvert (A [between PLs 4 and 3]), and two control reaches containing no structures (B [between PLs 3 and 2] and C [between PLs 2 and 1]). Fish that passed Gate 2 (PLs 6 and 5) were excluded from further analysis.

Fig. 5.2. Left: Tide Gate 1 in the River Stiffkey, North Norfolk, UK, a counterbalanced top-hung gate. Right: An orifice fish pass installed in Gate 1.

Fig. 5.3. Tide Gate 2 in the River Stiffkey, North Norfolk, UK, consisting of two top-hung un-counterbalanced gates.

5.3.2. Fish capture and telemetry

Fifteen trout were caught on 20 separate days from July to December 2011 (total $n = 15 \times 20 = 300$) by electrofishing in the lower reaches of the River Stiffkey from Buxton Conservation (52° 57' 9.76" N; 0° 57' 20.85" E, 1.0 km from the tide gates) to Warham (52° 56' 12.84" N; 0° 54' 1.40" E, 6.0 km from the tide gates).

Trout were anaesthetised with MS-222 (80 mg l^{-1}; buffered to pH 7.0 with $NaHCO_3$), measured and weighed (mean fork length [FL] [± SD] = 255.2 [± 64.5] mm [range = 155.0 - 532.0 mm], mean mass [± SD] = 240.1 [± 218.9] g [range = 48.0 - 1495.0 g]), and implanted with a half-duplex passive integrated transponder (PIT) tag (Wyre Micro Design, Lancashire, England, UK; 2.0 mm diameter, 23.0 mm length, 0.61 g mass) via a ventral incision. Mean (± SD) tag length was 9.5% (± 2.1%) of FL (range = 4.3 - 14.8%), and mass was 0.4% (± 0.3%) of trout mass (range = 0.04 - 1.3%). Trout recovered from anaesthesia in an aerated water container for a maximum of 1 hour prior to release 15 m downstream from Gate 1 (Fig. 5.1) when the orifice installed in the gate was set to either ‘operational’ (operating as intended with its door closing only during high tide, $n = 150$), or ‘non-operational’ (orifice door clamped shut for the entire duration of the tidal cycle, $n = 150$). Status of orifice operation was alternated after every second tidal cycle. Median time from fish release to gate closure did not vary between the orifice being operational (4.83 [range = 2.68 - 7.03] h) or non-operational (6.23 [0.47 – 7.53] h) ($U = 9189.00$, $r = -0.02$, $P > 0.05$).

A separate sample of brown trout ($n = 13$, FL = 178.8 ± 51.7 mm [range = 146.0 - 344.0 mm], mass = 70.9 ± 41.7 g [range = 34.0 - 158.0 g]) were implanted with PIT tags and retained in a perforated plastic in-stream container receiving natural flow for 7 days to quantify tag retention and survival. Trout were fed daily with mealworm. Mean (± SD) PIT tag length was 13.5% (± 2.4%) of FL (range = 6.7 - 15.8%) and mass was 1.1% (± 0.5%) of trout mass (range = 0.4 - 1.8%) with 100% tag retention and survival.

Six half-duplex PIT Loops (PLs) (2.5 mm^2 cross sectional area insulated wire consisting of 50 strands of 0.25 mm diameter copper wire) were constructed on wooden frames (height = 1.8 m, width = 2.5 - 4.8 m) and installed in the lower reaches of the River Stiffkey (Fig. 5.1). Each PL was connected to a dynamic tuning unit (Wyre Micro

Design, Model: DTU), PIT reader (Wyre Micro Design) and external data logger (Wyre Micro Design, Model: Antilog), and powered by a 110ah 12v battery. PLs 3 to 6 (Gates 1 and 2) operated continuously from 5 July to the end of the study period on 10 December 2011, with the exception of PLs 5 and 6 (Gate 2) which did not operate from 23 September to 30 September and 6 October to 10 October 2011 due to logger failure. Logger malfunction also meant that PLs 1 and 2 operated from 27 October and 19 September 2011 to the end of the study, respectively.

Throughout the study period, tag detection range and efficiency was tested at different stages of the tidal cycle for each PL. Range (maximum distance of detection) was measured by individually passing three tags oriented at 90^o and 45^o to each PL, towards its centre, left, and right and recording the distance between the PL and the furthest position detection occurred. Range extended from 10 to 50 cm. Detection efficiency (percentage of tags detected within range of the PL) was quantified by passing three tags, each oriented at 90^o and 45^o to each PL, vertically and horizontally, through each PL at 20 cm intervals to cover its area. PIT tags were passed through PLs at speeds of 0.6 to 2.9 m s^{-1} to replicate the optimal and burst swimming speeds of trout at a range of water velocities and temperatures (Clough and Turnpenny, 2001). Tags tested at lower (0.6 - 1.6 m s^{-1}) and higher speeds (1.6 - 2.9 m s^{-1}) gave similar PL detection efficiencies of 100% (90^o), and 86.5% and 85.7% (45^o), respectively (Table 5.1). When the tide gates were open, efficiency for 90^o oriented tags was 98 - 100%. For 45^o oriented tags, efficiency was predominately 100% whilst the gates were open, decreasing to 71 - 93% immediately after the gates opened when water conductivity was high, before rapidly returning to 100%.

Table 5.1. Detection range and efficiency for 6 PIT loops (PLs) in the lower River Stiffkey, UK, tested with tags (*n* = 3) oriented at 90^{o} and 45^{o} to each PL across their area and at speeds 1 (0.6 - 1.6 m s^{-1}) and 2 (1.6 - 2.9 m s^{-1}). Ranges are reported in parentheses.

PL Number	Tag Orientation (^{o})	Range (cm)	Detection Efficiency		
			Area	Speed 1	Speed 2
1	90	50	98 (93 - 100)	100	100
	45	45	100	100	100
2	90	50	100	100	100
	45	45	100	100	100
3	90	35	100	100	100
	45	30	86 (71 - 100)	83	73
4	90	35	100	100	100
	45	10	90 (76 - 100)	78	85
5	90	40	100	100	100
	45	40	100	100	100
6	90	45	100	100	100
	45	45	100	100	100

5.3.3. Video data

When operational, the orifice was monitored by two infrared submersible cameras with integrated IR LEDs (Sony, Model: IR 37CSHR-IR 25m) from 19 September 2011 to the end of the study period. By fixing cameras at either side of the orifice, perpendicular to the flow, the entire area of entry was captured. The camera configuration provided an IR light source so that fish passage through the orifice could be recorded at night. Footage was captured on a digital video recorder powered by a 110ah 12v battery and downloaded at weekly intervals.

5.3.4. Environmental variables

Water conductivity, temperature, pressure and barometric pressure (Solinst, Georgetown, Ontario, Canada; Model LTC Levelogger Junior 3001 and Barologger Gold 3001) were logged at 5 minute intervals either side of Tide Gate 1 from 5 July to 12 December 2011. From these measurements, water depth and salinity were calculated (Fofonoff and Millard, 1983). Tri-axial static acceleration loggers recorded the opening angles of Gates 1 and 2 at 2 minute intervals over the same period (Onset, Bourne, Massachusetts, USA; Model UA-004-64), and were calibrated weekly using a tape measure. River discharge was recorded every 15 minutes at the Environment Agency gauging station at Little Walsingham. Dissolved oxygen (DO) was logged upstream from the gates every hour (YSI, Yellow Springs, Ohio, USA; Model 6600 V2-4) from 22 July to 10 November 2011. Velocities through the centre of the widest part of the opening aperture of Gate 1, the centre of its culvert at 60% water depth, and the centre of the orifice were sampled at low water fortnightly from July to October using an electromagnetic flow meter (Valeport, Totness, UK; Model 801).

5.3.5. Data analyses

5.3.5.1. Attraction and passage efficiency

Overall attraction efficiency of the gates was calculated as the number of fish detected at PLs 4 and 6 (downstream from the gates) as a percentage of those released. As this study aimed to assess the influence of orifice installation (in Gate 1 only) on passage efficiency and delay, fish that successfully passed through Gate 2 were excluded from further analysis. Passage efficiency at Gate 1 was calculated as the number of fish detected at PL3 (upstream) as a percentage of those detected at PL4 (downstream).

The number of approaches to Gate 1 were defined as the number of individual detections at PL4 > 5 min apart. Mann-Whitney (U) tests (including effect size, r) were used to assess variation in number of approaches with status of orifice operation.

Video footage recorded when the orifice was operational was manually reviewed between the times that trout were first detected at PLs 4 and 3 to identify any passage events. Where the time between detection at PLs 4 and 3 overlapped for more than one fish, it was not always possible to visually identify individuals. Therefore, the percentage of fish approaching the orifice was reported as a range, where the minimum value indicates the confirmed number of individuals identified, and the range (n = 8) represents fish that could not be identified as either individuals or the same fish making recurrent approaches. Where the passage time between first detection at PLs 4 and 3 did not overlap and individuals could be observed (*n* = 20), fish behaviour was defined as either (1) an *attempt*, or (2) a *rejection*, when a fish embarked on an upstream movement into, and then downstream out of, the orifice, and either remained within, or disappeared out of, the field of view, respectively. *Passage* (3) was deemed to have occurred when a fish moved upstream though the orifice after last detection at PL4 and was not seen again for the remaining duration of the video. For the few occasions where fish passage times between last detection at PL4 and first detection at PL3 overlapped, it was possible to visually identify individuals, thus the number of fish that passed through the orifice and their unique PIT tag code could be successfully identified. A Mann-Whitney test was used to compare the length of fish that passed through the orifice with those that did not.

5.3.5.2. Delay

The study site was divided into three reaches for analysis: (1) treatment reach A which included Gate 1, and (2) control reaches B (from 19 September 2011 when PL2 was operational) and (3) C (from 27 October 2011 when PL1 was operational) in which water control structures were absent (Fig. 5.1). The speed of migration (also known as net ground speed) was calculated for each reach as the quotient of the distance (m) separating upstream and downstream PLs, and duration (s) between first detection at each. Kolmogorov-Smirnov tests indicated that data were not normally distributed. Therefore, Wilcoxon signed-rank (T) and Friedman's ANOVA (X^2) were used to test for differences in speed of migration, Q_{fish}, and $Temp_{fish}$ (see definition below) between reach (treatment: A; controls: B and C). Bonferroni correction was applied when pairwise comparisons between multiple groups were made.

Mean angle of opening ($Angle_{fish}$), discharge (Q_{fish}), water temperature ($Temp_{fish}$) and percentage of time it was night (N%; defined as the proportion of time between sunrise and sunset), during passage through each reach (i.e. between first detection at the downstream and upstream PLs comprising each reach) were calculated for individual fish.

Time-to-event analysis was used to assess the influence of status of orifice operation (operational or non-operational) and environmental variables ($Angle_{fish}$, Q_{fish}, $Temp_{fish}$, N%) on delay in reach A. Fish that were known to have passed the gates (detection at PLs 3 to 1) but were not detected at either PL4 or PL3 ($n = 16$) were excluded from further analysis. A log-minus-log plot displaying duration of migration for each orifice status (operational or non-operational) with independent baseline hazard functions indicated that status of orifice operation violated the assumption of proportional hazards. Therefore, an extended Cox regression model (Ata and Sozer, 2007) was developed to include orifice status as a time dependent covariate in the form:

$$h(t) = [h_0(t)] \exp[B_1\text{*status} + B_2\text{*status*}t\_cov + B_3X_3 + B_4X_4 + B_5X_5 + B_6X_6]$$

where *h* is the probability or ‘hazard‘ of passage at time *t* given that an individual had not passed prior to time *t*, $h_0(t)$ is the baseline hazard function, *B* is the regression coefficient, *X* is the covariate value, and *t_cov* is time, used to generate orifice status as a time dependent covariate. Time to gate closure after release and FL had no independent relationship with speed of migration and were thus omitted from further analysis. Time from release to darkness was excluded from further analysis due to multicoliniarity with other covariates. Separate Cox regression models were created for each treatment: orifice operational and non-operational, in the same form as the extended model but excluding the status variable and time dependent covariate. Cox regression analyses were reported as unstandardized *B* coefficients and 95% confidence intervals (*CI*).

Mann-Whitney tests were used to assess variation in $\text{Angle}_{\text{fish}}$ and Q_{fish} with status of orifice operation. The relationships between duration of passage through reach A and estuary and river temperature and discharge at the time of release, and number of approaches, were explored using Spearman’s rho (r_s).

5.3.5.3. Environmental data

Environmental data for the full duration of the study period (5 July to 30 November 2011) could not be transformed to meet the assumption of normality (Kolmogorov-Smirnov tests: $P < 0.05$) and sample sizes were not equal. Therefore, independent samples Mann-Whitney tests were used to compare median and difference (Δ) in temperature, salinity and DO upstream and downstream of the gates when open and closed, and the relationship between orifice status and median and difference (Δ) in water temperature, salinity and depth between either side of the gates when closed, and gate angle and upstream depth between each orifice status when open.

5.4. Results

5.4.1. Attraction and passage efficiency

Of the 300 PIT tagged trout released downstream from Gate 1, 290 were detected by at least one of the PLs, giving an attraction efficiency of 96.7% (orifice operational: 94.7% [n = 142]; non-operational: 98.7% [n = 148]). Of these, 276 trout were detected at PLs 4 and 6 immediately downstream from the gates, two of which successfully passed through Gate 2 (without approaching Gate 1). Of the fish detected at PL4 (n = 274), 251 passed through Gate 1, giving a passage efficiency of 91.6% (orifice operational: 90.9% [n = 120]; non-operational: 92.3% [n = 131]). Fish passed the gate a median of 5.00 (0.02 - 9.02) h prior to gate closure, showing no distinct preference for passing during the flood or ebb tide. Trout made a median of 8 (1 - 154) approaches to the gate, which did not vary with orifice status (U = 7125.00, r = -0.08, $P > 0.05$; operational: 9 [1 - 60]; non-operational: 8 [1 - 154]). More fish passed at night (66.7%), and no individuals returned downstream after passing the gate. Twenty-one fish were detected at PL3 for the first time when the gates were closed, a median of 1.03 (0.12 - 4.08) h after closure.

Of 61 fish that passed Gate 1 (detection at PLs 4 and 3) when the orifice was operational and video cameras functional, 26 - 34 (42.6 - 55.7%) approached the orifice entrance and 24 successfully passed through (passage efficiency = 70.6 - 92.3%). For each individual that was identified, an average (± SD) of 1.65 (± 3.41) attempts and 0.90 (± 2.22) rejections were recorded. Trout that passed through the orifice were larger (median = 298.5, range = 201.0 - 487.0 mm) than those that passed Gate 1 when the orifice was open but did not use it (median = 249.0, range = 190.0 - 325.0 mm) (U = 255.50, r = -0.36, $P < 0.01$). Fish used the orifice a median of 3.54 (0.94 - 7.77) h prior to gate closure, when the gate was at a median angle of 2.2^{o} ($0.7 - 10.8^{o}$) which equated to a median distance of 8.1 (2.6 - 39.5) cm at the widest part of the aperture. Fish did not use the orifice when Gate 1 was closed.

5.4.2. Delay

Median duration from release to detection at PL4 was 1.05 (0.03 - 460.41) h. Median duration of passage through reach A containing the tide gates was 6.04 (0.03 - 197.75) h, with 31.1% of fish taking more than 12 h and 13.9% taking more than 24 h. Speed of migration through reach A was slower than for the two unimpeded reaches (B and C) immediately upstream (Fig. 5.4, Table 5.2). Median Q_{fish} was marginally lower in reach A than B (Table 5.2) when PL2 was functional (n = 125) but not PL1 (n = 43) (Table 5.2). Median $Temp_{fish}$ was higher in reach A than B (Table 5.2) when PL2 was functional (n = 125) but marginally lower when PL1 was operating (n = 43).

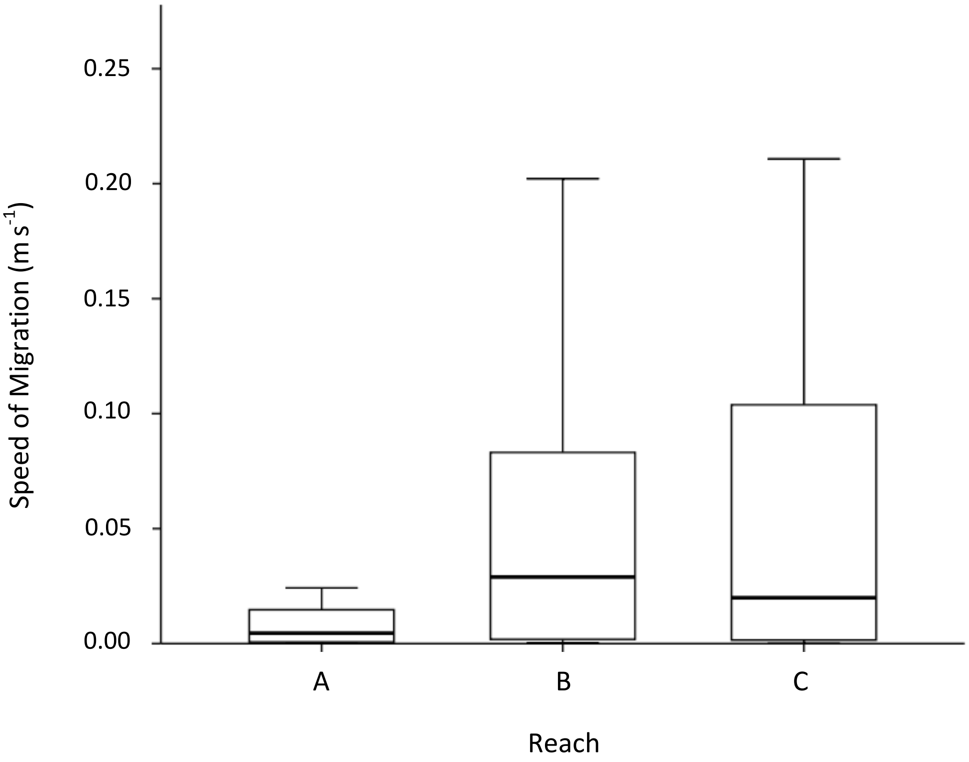


Fig. 5.4. Speed of migration of 43 brown trout through a river reach with a tide gate (A) and two reaches with no obstructions (B and C) in the lower River Stiffkey, UK, in November 2011. The box plots illustrate the median (horizontal line), interquartile range (boxes) and overall range up to 1.5 times the interquartile range (whiskers). Outliers > 1.5 times the interquartile range are not depicted.

Table 5.2. Wilcoxon signed-rank (*T*) with effect size (*r*) and Friedman's ANOVA (X^2) statistical analyses of median speed of migration, Q_{fish} and Temp_{fish} for PIT tagged brown trout moving upstream in the River Stiffkey, UK, through a reach with a tide gate (A [PL4 - PL3]) and two reaches with no structures present (B [PL3 - PL2] and C [PL2 - PL1]) during July - December 2011. Ranges are reported in parentheses.

	n	Reach			Statistical analysis	*P*
		A	B	C		
Speed (m s^{-1})	251	0.001 (0.00004 - 0.27)				
	125	0.002 (0.00007 - 0.09)	0.011 (0.00003 - 0.37)		$T = 1452.00$, $r = -0.55$	0.000^{**}
	43	0.005 (0.00009 - 0.09)	0.029 (0.00015 - 0.29)	0.020 (0.00004 - 0.21)	$X^2_2 = 19.02$	0.000^{**}
Q_{fish} (m^3 s^{-1})	251	0.08 (0.07 - 0.13)				
	125	0.09 (0.07 - 0.12)	0.09 (0.07 - 0.13)		$T = 1652.50$, $r = -0.30$	0.001^{*}
	43	0.09 (0.09 - 0.10)	0.09 (0.09 - 0.10)	0.09 (0.09 - 0.10)	$X^2_2 = 0.91$	0.634
Temp_{fish} (^{o}C)	251	15.04 (7.43 - 18.79)				
	125	13.24 (7.43 - 15.56)	12.00 (7.24 - 15.77)		$T = 1943.00$, $r = -0.44$	0.000^{**}
	43	7.75 (7.43 - 11.38)	7.99 (7.24 - 11.05)	7.72 (5.10 - 11.35)	$X^2_2 = 25.72$	0.000^{**}

* $P < 0.01$

** $P < 0.001$

Status of orifice operation did not influence median duration of passage (operational: 4.20 [0.17 - 197.75] h; non-operational: 7.27 [0.03 - 155.44] h) through Gate 1 (Fig. 5.5, Table 5.3). $\text{Angle}_{\text{fish}}$ had the most significant influence on duration of passage followed by $\text{Temp}_{\text{fish}}$. Cox regressions for both treatments individually revealed $\text{Angle}_{\text{fish}}$ was the sole influential parameter on duration when the orifice was non-operational, and $\text{Temp}_{\text{fish}}$ was the most influential covariate when operational. Median $\text{Angle}_{\text{fish}}$ and Q_{fish} were marginally higher for fish that were released when the orifice was non-operational ($\text{Angle}_{\text{fish}}$ = 4.0 [0.8 - 25.1]; Q_{fish} = 0.09 [0.07 - 0.13]) compared to operational ($\text{Angle}_{\text{fish}}$ = 3.0 [0.6 - 17.3]; Q_{fish} = 0.08 [0.07 - 0.11]) ($U = 3432.50$, $r = -0.49$, $P < 0.001$; $U = 3095.00$, $r = -0.52$, $P < 0.001$, respectively).

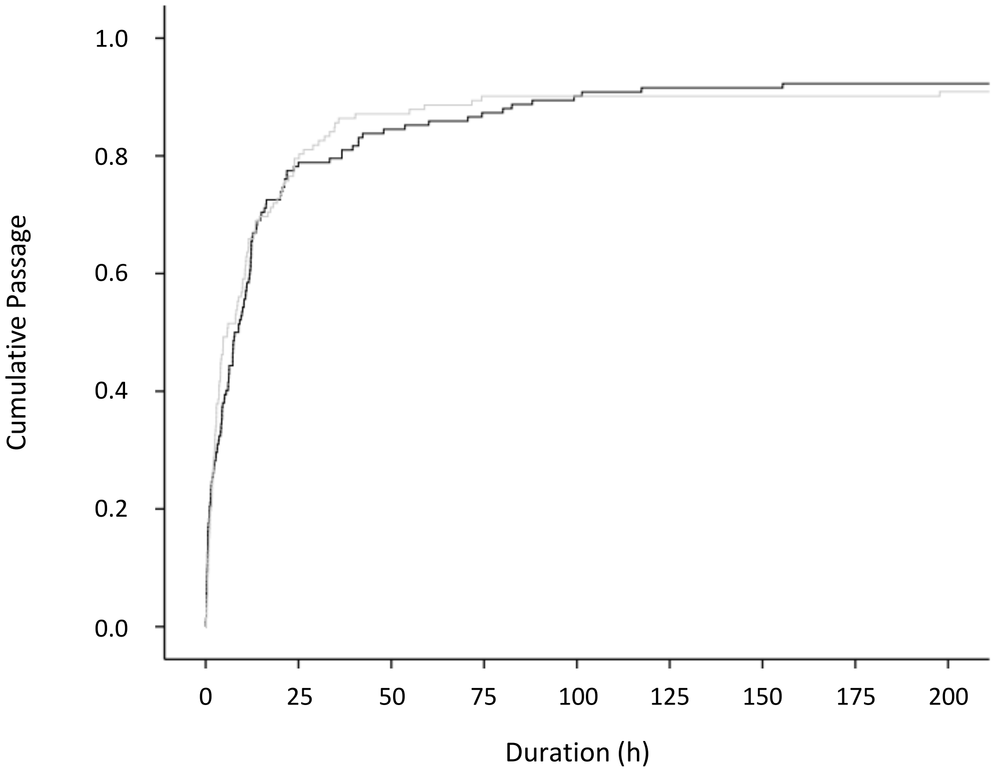


Fig. 5.5. Cumulative passage of upstream moving brown trout past tide gate 1 when an orifice was either operational (—) or non-operational (▬) at release.

Table 5.3. Results of an extended Cox proportional hazards regression that assessed the influence of orifice operation (operational or non-operational) combined with time (*t_cov*) to create a time dependent covariate, on duration of passage past the tide gate in reach A and Cox regressions on environmental covariates for each treatment for fish that passed, or were detected downstream of Gate 1 (PL4) but not upstream (censored).

	n		Variable	*B*	95% CI		Mean	*P*
	Passed	Censored			Lower	Upper		
Combined Data	251	23	Orifice Status	0.241	0.918	1.763	0.46	0.147
			Orifice Status * *t_cov*	-0.008	0.981	1.003	2.86	0.172
			Angle$_{\text{fish}}$ ($^{\circ}$)	0.163	1.116	1.242	3.66	0.000**
			Temp$_{\text{fish}}$ ($^{\circ}$C)	0.074	1.016	1.141	13.96	0.013*
			Q$_{\text{fish}}$ (m^{3} s^{-1})	-2.052	0.000	9441.996	0.09	0.720
			N%	-0.001	0.993	1.006	52.46	0.826
Non-operational	131	11	Angle$_{\text{fish}}$ ($^{\circ}$)	0.174	1.125	1.259	4.80	0.000**
			Temp$_{\text{fish}}$ ($^{\circ}$C)	0.082	0.999	1.179	13.69	0.054
			Q$_{\text{fish}}$ (m^{3} s^{-1})	2.172	0.000	2683094.317	0.09	0.736
			N% (%)	-0.002	0.989	1.007	52.71	0.639
Operational	120	12	Angle$_{\text{fish}}$ ($^{\circ}$)	-0.421	0.429	1.005	3.23	0.052
			Temp$_{\text{fish}}$ ($^{\circ}$C)	0.105	1.010	1.221	14.15	0.030*
			Q$_{\text{fish}}$ (m^{3} s^{-1})	3.401	0.000	3.750E+12	0.08	0.794
			N%	-0.004	0.987	1.005	50.25	0.353

* $P < 0.05$

** $P < 0.001$

Of the 274 fish included in the extended Cox regression models, 3 (1.1 %) were first detected at PL4 during a different status of operation from when they were released. Of the fish that passed Gate 1 during the study period (*n* = 251), 36 (14.3 %) were detected upstream at PL3 under a different status of orifice operation compared to release.

Number of approaches was positively correlated with duration of passage through reach A ($r_s = 0.58$, $P < 0.001$) and negatively related to $\text{Angle}_{\text{fish}}$ ($r_s = -0.14$, $P < 0.05$). Duration of passage through reach A was negatively related to estuary temperature ($r_s = 0.17$, $P = 0.01$), river temperature ($r_s = 0.16$, $P < 0.05$) and discharge ($r_s = -0.15$, $P < 0.05$) at the time of release.

5.4.3. Environmental data

Upstream and downstream median water temperatures were slightly higher when the gates were closed than when open (Table 5.4, Table 5.5, Fig. 5.6b). The difference in water temperature upstream and downstream from the gates was marginal when open, but greater when closed.

Table 5.4. Median and difference (Δ) in water temperature, salinity and dissolved oxygen (DO) upstream and downstream from Tide Gate 1 in the River Stiffkey, UK, when open and closed, or during periods of gate closure when the orifice was operational and non-operational, from 5 July to 30 November 2011, with ranges in parentheses.

	Location	Status	Temperature (^{o}C)	Salinity (PSU)	DO Sat (%)
Gate	Upstream	Open	14.06 (6.28 - 24.78)	0.49 (0.01 - 15.68)	68.22 (45.73 - 132.20)
		Closed	14.31 (6.49 - 19.94)	7.32 (0.32 - 16.32)	67.20 (49.43 - 131.77)
	Downstream	Open	14.10 (5.96 - 22.79)	0.83 (0.30 - 32.64)	
		Closed	14.91 (5.92 - 22.89)	27.40 (0.36 - 34.70)	
	Δ	Open	0.00 (-1.23 - 2.87)	0.33 (0.00 - 29.23)	
		Closed	0.63 (-1.59 - 4.37)	19.86 (0.00 - 31.52)	
Orifice	Upstream	Operational	14.77 (7.02 - 19.94)	7.19 (0.32 - 16.32)	67.33 (51.40 - 131.77)
		Non-operational	13.17 (6.49 - 19.72)	7.44 (0.33 - 14.68)	67.20 (49.43 - 119.60)
	Downstream	Operational	15.52 (6.99 - 22.89)	26.31 (0.41 - 34.70)	
		Non-operational	13.40 (5.92 - 20.72)	28.59 (0.36 - 34.08)	
	Δ	Operational	0.71 (-1.59 - 4.37)	19.07 (0.00 - 31.52)	
		Non-operational	0.55 (-1.13 - 3.72)	20.63 (0.00 - 30.73)	

Table 5.5. Mann-Whitney statistical comparisons of median and difference (Δ) in water temperature and salinity recorded over the full duration of the study (5 July to 30 November 2011) upstream and downstream of Tide Gate 1 in the River Stiffkey, UK, when open and closed, or during periods of gate closure when the orifice was operational and non-operational.

	Status	Location	Temperature			Salinity		
			U	*r*	*P*	*U*	*r*	*P*
Gate	Open vs Closed	Upstream	172969233.00	-0.04	0.000*	73239258.50	-0.50	0.000*
		Downstream	149863343.00	-0.15	0.000*	35670239.00	-0.67	0.000*
		Δ	60764879.00	-0.56	0.000*	33576144.50	-0.68	0.000*
Orifice	Operational vs Non-operational	Upstream	17482997.00	-0.29	0.000*	25950667.00	-0.01	0.396
		Downstream	17303089.50	-0.29	0.000*	22261547.00	-0.13	0.000*
		Δ	22843118.50	-0.11	0.000*	22251847.50	-0.13	0.000*

*$P < 0.001$

Upstream and downstream median salinity was higher when the gates were closed than when open (Table 5.4, Table 5.5, Fig. 5.6c). The difference in salinity upstream and downstream was minor when gates were open. Salinity upstream from the gate was considerably lower than downstream when it was closed.

Upstream DO was higher when the gates were open than closed ($U = 187042.00$, $r = -0.06$, $P < 0.001$) (Table 5.4, Fig. 5.6d). Mean (± SD) velocities measured at the bottom of the water column under Gate 1 through the centre of the widest part of its opening aperture and through the gate's culvert at low water were 0.50 (± 0.36) and 0.22 (± 0.20) m s^{-1}, respectively.

Status of orifice operation did not influence upstream median salinity over the period of study when the gates were closed (Table 5.4; Table 5.5) but was associated with variation in median difference in depth either side of the gates (operational: 82.12 [-2.59 - 244.56] cm; non-operational: 75.46 [-0.80 - 306.92] cm, $U = 24641490.00$, $r = -0.05$, $P < 0.001$), downstream salinity, and upstream and downstream temperature (Table 5.4; Table 5.5).

When the gates were open, Gate 1 angle (operational: 3.5^{o} [0.7 - 35.8 ^{o}]; non-operational: 4.3^{o} [0.7 - 29.4 ^{o}]; $U = 60748486.50$, $r = -0.19$, $P < 0.001$) and upstream depth (operational: 100.1 [94.8 - 164.4] cm; non-operational: 99.0 [94.8 - 158.8] cm; $U = 66806997.00$, $r = -0.13$, $P < 0.001$) were higher when the orifice was non-operational. Mean (± SD) velocity through the orifice at low water was 0.60 (± 0.31) m s^{-1}.

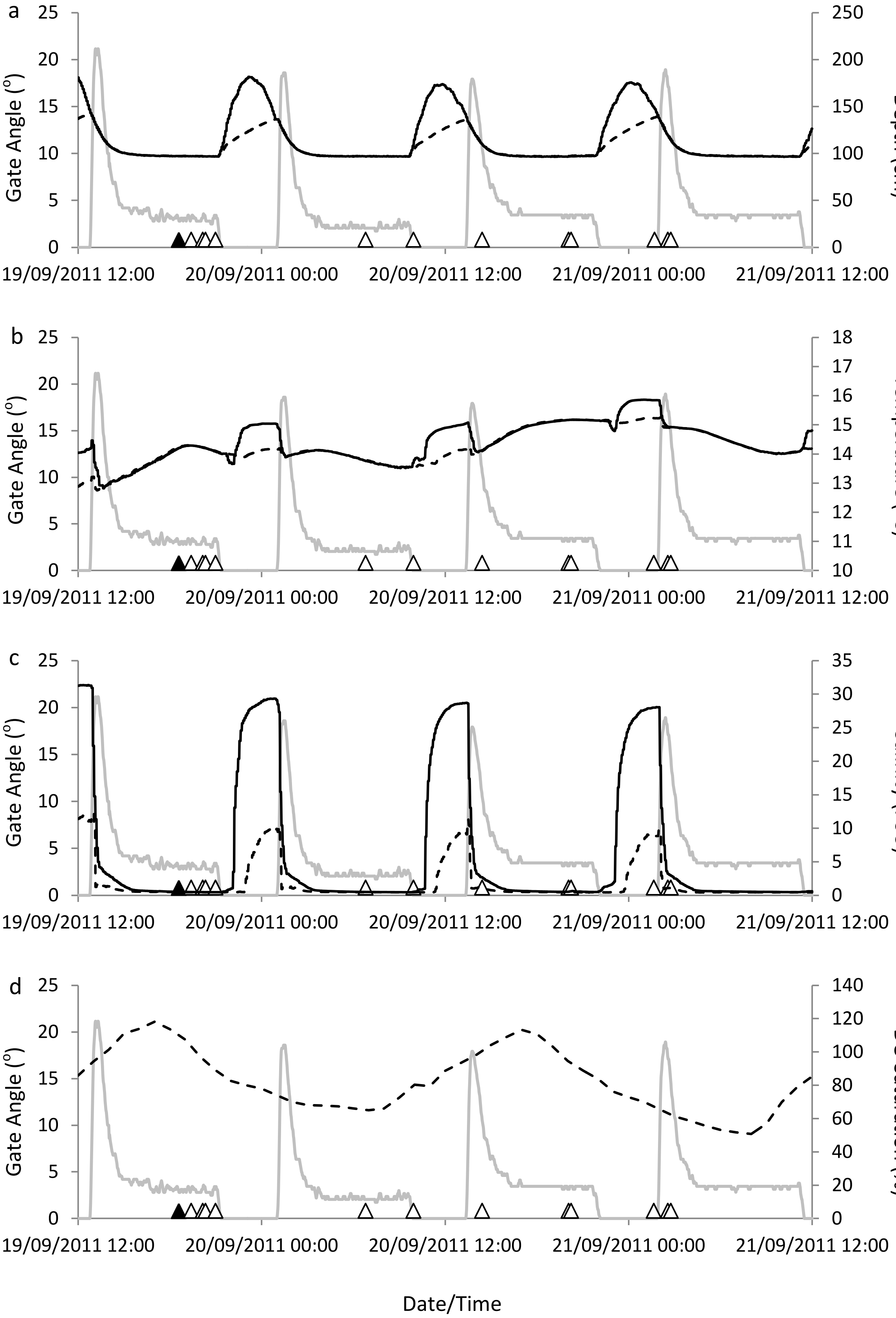


Fig. 5.6. An example of tidal and diel variation in gate angle (▬) and (a) depth (b) temperature and (c) salinity, and (d) dissolved oxygen (DO) upstream (- - -) and downstream (▬) of Tide Gate 1 in the River Stiffkey from 19 - 21 September 2011. Triangles indicate time of adult brown trout (*n* = 15) released downstream (▲) and passage upstream (detection at PL3) (Δ) of Gate 1 during this time.

5.5. Discussion

Despite being commonly installed to prevent tidal inundation of low-lying land in many regions of the world, the impact of tide gates on the movement of fish has received little attention. Although this study observed high attraction (96.7%) and passage efficiency (91.6%) in a small UK stream, tide gates delayed the upstream movement of adult brown trout. Installation of an orifice to increase the period of longitudinal connectivity during each tidal cycle did not improve attraction and passage efficiency, or reduce delay.

Information on how estuarine structures impact upstream movement of fish is scarce. Where evidence exists, attraction and passage tends to be considerably lower than that reported in the present study. For example, an average of 49% of acoustic tagged adult Chinook salmon, *Oncorhynchus tshawytscha*, passed tidal gates at an intertidal structure when other routes were blocked in the Sacramento Delta, USA, having been released 2.4 km downstream (Vincik, 2013). In the Wadden Sea, The Netherlands, 49% of radio tagged adult sea trout migrated upstream through sluices at an intertidal barrage (Bij de Vaate *et al.*, 2003). Interestingly, the same study found that fewer sea trout (14%) released along the south-west coast of The Netherlands chose to pass via sluices in another barrage when presented with a choice to migrate through a man-made canal (20%). Unfortunately, these studies fail to separate attraction and passage efficiency, and hence the impacts of the tidal structures themselves were not determined. In the UK, 73% of adult sea trout and Atlantic salmon tagged with combined acoustic and radio transmitters approached an intertidal barrage on the River Tawe, of which 42% successfully passed, predominately over tidally inundated weirs (Mee *et al.*, 1996). For downstream migrants, high passage efficiency at top-hung tide gates has been observed (adult European eel: Chapter 6; brown trout smolts: Chapter 7), although efficiency in the present study may reflect low site specific predator densities.

Delayed migration can increase risk of predation (Schilt, 2007), energy expenditure (Jonsson *et al.*, 1997), and susceptibility to (Schreck *et al.*, 1993), and transfer of (Garcia de Leaniz, 2008) disease where fish congregate. Although passage in this study was blocked at high tide when the gates were closed, fish did not initiate upstream movements immediately after opening on the ebb as might have been expected. A number of factors may have contributed to this. First, discharge through the gates would have been highest on opening, creating velocities that may have exceeded the swimming capabilities of the tagged fish (Clough and Turnpenny, 2001). Second, a chaotic hydrodynamic environment immediately downstream from the gate on opening may have caused behavioural avoidance. Turbulence is known to negatively impact fish swimming by increasing the energetic costs (Enders *et al.*, 2005) and reducing stability (Tritico and Cotel, 2010). Third, the trout may have avoided stark transitions in temperature (Berggren and Filardo, 1993; Boyd and Tucker, 1998; Jonsson, 1991), salinity (Zaugg *et al.*, 1985), and/or DO concentration (Richardson *et al.*, 2001) when the gates opened. Even after the initial release of flow through the gate had subsided and water velocities and opening aperture were sufficient for passage, trout did not tend to move through. Instead, they passed on average approximately 5 hours prior to gate closure (i.e. mid tidal cycle), after repeatedly approaching Gate 1 and exhibiting searching and milling behaviour as reported for salmonids at other structures (Croze *et al.*, 2008; Gowans *et al.*, 1999; Mee *et al.*, 1996). This recurrent avoidance behaviour was related to lower mean gate angles and led to longer passage times. Other studies suggest that the presence of overhead cover at culverts (Greenberg *et al.*, 2012; Kemp *et al.*, 2005b), and prevention of selective tidal transport caused by the gates (Aprahamian *et al.*, 1998; Potter, 1988), could contribute to the behavioural avoidance observed.

Delayed entry and ascent of rivers by adult salmonids has been associated with increased water temperature (Jonsson and Jonsson, 2002 for sea trout; Solomon and Sambrook, 2004, for Atlantic salmon). Similarly, duration of passage through the tide gate in this study was positively related to temperature. Longer durations of passage past structures at high water temperatures could negatively affect fish by decreasing DO concentration (Ozaki *et al.*, 2003), and increasing fish avoidance (Whitmore *et al.*, 1960), presence and transfer of disease and parasites in salmonids (Garcia de Leaniz, 2008), and the energetic costs of swimming (Enders *et al.*, 2005).

Previous studies have shown that adult salmonids will readily pass through orifices. At the Pitlochry Dam, Scotland, 100% of radio tagged adult Atlantic salmon that approached a pool and submerged orifice fish ladder successfully passed upstream (Gowans *et al.*, 1999). Further, 95% of mature male brown trout (average length = 27.3

cm) chose to pass upstream through a submerged orifice (0.2 x 0.1 m) in an experimental flume rather than over a weir with the same maximum water velocity (1 m s^{-1}) and turbulence (Guiny *et al.*, 2003). In this study, 70.6 - 92.3% of fish that located the orifice subsequently passed, which is high when compared to the efficiency of mitigation measures employed at other infrastructure (Noonan *et al.*, 2012). However, the orifice was ineffective at improving passage efficiency or decreasing delay, conceivably a result of the low number of fish that approached it (42.6 - 55.7%). To successfully attract fish, discharge emanating from fishways must be discernible from competing flows (Armstrong *et al.*, 2010), yet the dominant discharge at Gate 1 would have been associated with the aperture rather than the orifice. Adult salmonids often use selective tidal stream transport to migrate through unimpeded estuaries (Aprahamian *et al.*, 1998; Potter, 1988), yet trout in this study used the orifice on average approximately 3.5 h prior to gate closure, and no fish passed during the flood tide when Gate 1 was closed.

5.5.1. Conclusion

High passage efficiency was observed for adult brown trout at a top-hung tide gate in a small UK stream. However, migration past the gates was slower than for subsequent progression upstream through unimpeded reaches, and this was not mitigated by installation of an orifice that extended the period of connectivity. Under the configuration described, competing flows through the gate aperture likely limited the number of fish attracted to the entrance of the orifice, suggesting it is not a suitable mitigation option for adult salmonids. Trout did not use the orifice when the tide gate was closed, however the effect of extending the period of longitudinal connectivity during this time by increasing orifice door float arm length and/or ballast requires assessment. The effect of the orifice on other species and life stages (e.g. targets: salmonid smolts, juvenile eels; non-targets: adult European eel) and at sites with different tidal regimes should also be considered. Gate angle was the most significant correlate with delay. Consequently, modifications or replacements that enable gates to remain open wider and over a longer proportion of the tidal cycle, such as retarders, lightweight gates and self-regulating designs would likely be beneficial to the effective passage of adult salmonids.

Chapter 6

Impact of tide gates on the migration of adult European eels, *Anguilla anguilla*

6.1. Summary

Tide gates form a temporal barrier to fish migration, closing during the flood tide and opening during the ebb, primarily for flood prevention and land reclamation. Their impact on downstream adult migration of the critically endangered European eel, *Anguilla anguilla*, is unknown. The River Stiffkey, UK, has three top-hung tide gates (one counterbalanced, two not) through which it discharges into the North Sea. Adult eels of silver appearance (n = 118) were caught between 0.5 to 6.0 km upstream from the tide gates in Autumn 2011 and implanted with 23 mm half-duplex passive integrated transponder (PIT) tags. Tagged individuals were detected by PIT antennas located near the tide gates. Of the eels tagged, 80 were detected migrating downstream to the gates. Escapement past the gates was 98.3%. Speed of migration was slower near the gates than for an unimpeded upstream reach, and was positively and negatively related to mean degree of gate opening and mean light intensity, respectively. When the largest gate was modified through installation of an orifice intended to improve upstream passage of sea trout and juvenile eels, downstream migration was more rapid when it was operating. However, video analysis revealed that eels did not pass through the orifice, meaning that faster migration may have been a result of the gates being open on

more occasions when eels initially approached them, and/or the lower tides and upstream saline intrusion that occurred during these periods. Top-hung tide gates in the River Stiffkey delayed eel migration, potentially increasing the risk of predation and energy expenditure immediately prior to a 5000 - 6000 km migration to spawning grounds in the Sargasso Sea.

6.2. Introduction

European eel, *Anguilla anguilla*, recruitment has decreased by more than 90% since the early 1980s (Dekker, 2003; ICES, 2012) leaving the species endangered (Freyhof and Kottelat, 2008) and populations below sustainable conservation limits (Bult and Dekker, 2007). A number of factors have been attributed to the decline, including: (1) variation in oceanic currents which reduce the rate of return (Baltazar-Soares *et al.*, 2014) and food availability (Friedland *et al.*, 2007) for leptocephali, and alter adult spawning location (Friedland *et al.*, 2007); (2) over harvest (Moriarty and Dekker, 1997); (3) pollution (Knights, 1997; Robinet and Feunteun, 2002); (4) parasitism (Feunteun, 2002), and (5) impeded migration between essential habitats (Bruijs and Durif, 2009; Laffaille *et al.*, 2007; Winter *et al.*, 2006). In an attempt to reverse this decline, the EU Eel Recovery Plan (2007) (Council Regulation No: 1100/2007/EC) requires that all Member States develop strategies to meet silver eel biomass escapement targets of 40% relative to that expected in the absence of anthropogenic impacts (EC, 2007).

To date, eel escapement research has focused on: (1) assessing the barrier effects of structures on upstream migration of juveniles (Knights and White, 1998; Piper *et al.*, 2012), and (2) the impact of hydropower installations and success or failure of screening for downstream migrating adults (Calles *et al.*, 2013; Calles *et al.*, 2010; Pedersen *et al.*, 2012; Russon *et al.*, 2010). Intermittent barriers created by weirs, ramps, culverts, and tide gates, which are considerably more abundant than large structures such as dams (Lucas *et al.*, 2009), have received less attention.

Tide gates temporally obstruct migrating fish by closing under hydraulic pressure on the flood tide, and opening during the ebb (Giannico and Souder, 2005). Environmental conditions related to open gates, such as abrupt changes in salinity (Zaugg *et al.*, 1985) and temperature (Berggren and Filardo, 1993; Boyd and Tucker, 1998; Jonsson, 1991), accelerating water velocities (Haro *et al.*, 1998; Russon and Kemp, 2011a), continuous overhead cover created by associated culverts (Kemp *et al.*, 2005b), and a lack of tidal cues (Russell *et al.*, 1998) may cause stress and/or obstruct migration of some fish species. Although tide gates are used worldwide and are known to restrict fish species abundance and richness (Boys *et al.*, 2012; Pollard and Hannan, 1994), there has been little consideration of their impacts on the movement of diadromous fish, including eels. There are some exceptions. For example, fish passage is lower at gated culverts when compared to un-gated ones (for diadromous juvenile galaxiids, Doehring *et al.*, 2011). For eels, tidal structures, such as manually operated intertidal sluices, have been related to increased entrainment of downstream migrating adult eels at an abstraction intake (Piper *et al.*, 2013), while modifications to gates by maintaining connectivity through an aperture that remained open during the flood tide appeared to enhance upstream abundance of glass eels (Mouton *et al.*, 2011). The current lack of understanding of the impacts of tide gates on fish migration, including that for downstream moving eels, remains an area that requires further attention.

To date, knowledge of tide gate effects on diadromous fish migrations are largely based on assumption and or/qualitative observation. Where fish passage is thought to be sufficiently restricted, top-hung tide gates may be replaced with side-hung or self-regulating designs, or modified with counterbalances, retarders, orifices, or slots, all of which extend the period of connectivity between upstream and downstream. The ability of these modifications to improve diadromous fish passage at tide gates, as well as their impact on important non-target species and life stages, has not been fully quantified elsewhere.

This study assessed the impact of top-hung tide gates on the escapement and delay of actively migrating adult European eels, and the influence of an orifice modification, installed to assist the upstream movement of adult sea trout and juvenile eels past the gates. PIT telemetry was used to: (1) determine eel escapement past the top-hung tide gate structure, (2) quantify delay by measuring speed through unimpeded (control) and tide gate (treatment) reaches, whilst (3) assessing the influence of environmental variables and the orifice modification in the River Stiffkey, UK.

6.3. Materials and methods

6.3.1. Study site

Fed by a 141 km^2 catchment, the River Stiffkey, North Norfolk, UK (52° 57' N; 0° 57' E; Fig. 6.1) is sited on a chalk aquifer with a mean (± SD) daily flow (measured at Little Walsingham, 12.6 km upstream from the tide gates, over the study period from 23 September to 10 December 2011) of 0.09 (± 0.02) m^3 s^{-1} (equivalent to Q_{70} from 2009 - 2011). From its source at Swanton Novers the river flows north for 33 km through the Stiffkey Valley Site of Special Scientific Interest (SSSI) before discharging via tide gates into the Blakeney Channel and the North Sea. Tide Gate 1 (Fig. 5.2) is a top-hung design (width = 3.0 m, height = 2.1 m) opening at the seaward end of a corrugated metal pipe culvert (diameter = 2.9 m, length = 25.8 m). Located at the end of the main river channel, it discharges the majority of the river’s flow (Fig. 6.1). A weight at the top counterbalances the gate, extending the aperture of opening and the time it remains open. Tide Gate 2 (Fig. 5.3) comprises of a pair of top-hung gates (width = 1.5 m, height = 1.6 m), each located at the seaward end of a smooth concrete pipe culvert (diameter = 1.2 m, length = 25.8 m). Gates 1 and 2 opened for 7.89 ± 1.00 h (mean ± SD) each tidal cycle at a median angle of 3.5^o (range = 0.7 - 29.8 ^{o}) and 6.4^o (0.7 - 22.9 ^{o}), respectively. When the tide gates are closed, the carrier channel, which terminates 2.7 km inland from the tide gates, increases the storage capacity and therefore reduces probability of flooding (Fig. 6.1). In May 2010, the Environment Agency installed an orifice fish pass half way up Gate 1 (Fig. 5.2) (width = 0.5 m, height = 0.3 m), with a bottom hinged door that closed at a predetermined tide height under the control of a float. This modification was intended to aid the upstream movement of adult sea trout and juvenile eels past the gates by extending the period of connectivity between the estuary and river whilst maintaining flood protection and minimising saline intrusion upstream by closing at high tide.

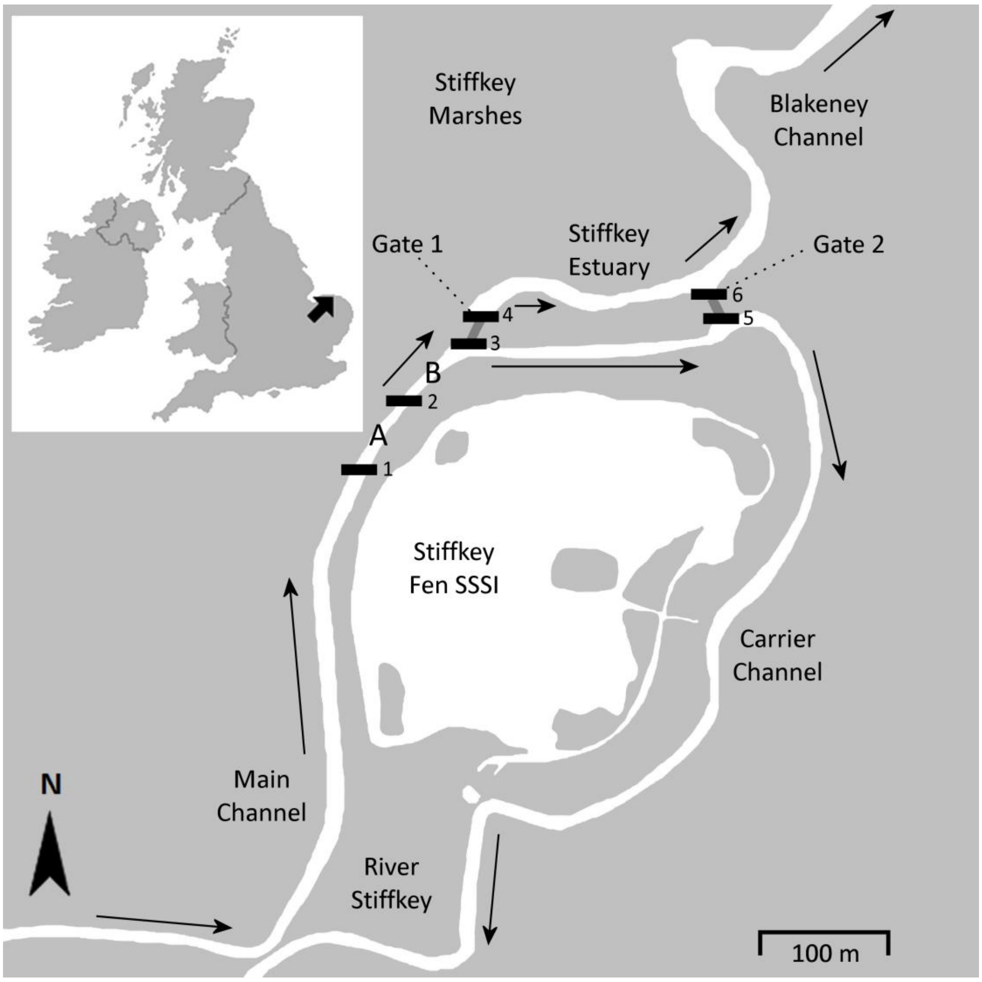


Fig. 6.1. The lower reaches of the River Stiffkey, North Norfolk, UK, showing direction of water flow (→) through Tide Gates 1 and 2. Six PIT loops (PLs, ▬) define limits of a control reach (A) containing no structures (between PLs 1 and 2), and a treatment reach (B) containing the tide gates (between PLs 2 and 4 or 6, dependent on the gate of exit). European eels (*n* = 118) tagged with PITs were released 0.5 - 6 km upstream from Gate 1 (not shown).

6.3.2. Fish capture and telemetry

The River Stiffkey maintains an established eel population (Pawson, 2008). The seaward spawning migration of European eels predominantly occurs during the autumn (Tesch, 2003). Therefore, adult eels were caught between July and December 2011 by a combination of electrofishing and trapping (fyke nets) in the River Stiffkey from Buxton Conservation (52° 57' 9.76" N; 0° 57' 20.85" E, 0.5 km upstream of the tide gates) to Warham (52° 56' 12.84" N; 0° 54' 1.40" E, 6.0 km upstream of the tide gates).

Adult eels were considered migratory if they exhibited the following characteristics when compared to resident yellow eels: (1) white-silver ventral and black dorsal surfaces distinctly separated along the lateral line; (2) large eye diameter to total length (TL) ratio; (3) large pectoral fin length to TL ratio; and (4) darkened pectoral fins (Tesch 2003).

Eels were anaesthetised with MS-222 (300 mg l^{-1}; buffered to pH 7.0 with $NaHCO_3$), measured and weighed (*n* = 118, TL [mean ± SD] = 384.1 ± 63.5 mm [range = 229.0 - 583.0 mm], mass [mean ± SD] = 113.8 ± 84.4 g [range = 40.0 - 591.0 g]), and implanted with a half-duplex passive integrated transponder (PIT) tag (Wyre Micro Design, Lancashire, UK; 2.0 mm diameter, 23.0 mm length, 0.61 g mass) via a ventral incision, in compliance with UK Home Office regulations under the Animals (Scientific Procedures) Act 1986. Mean (± SD) tag length was 6.1% (± 0.9%) of TL (range = 3.9 - 10.0%), and mass was 0.6% (± 0.2%) of eel mass (range = 0.1 - 1.5%). Eels recovered from anaesthesia in aerated water for a maximum of 30 minutes prior to release near the site of capture.

A separate sample of eels (10 silver eels, TL = 356.0 ± 20.1 mm [range = 328.0 - 389.0 mm], mass = 79.8 ± 18.1 g [range = 63.0 - 125.0 g]; 10 yellow eels, TL = 332.9 ± 18.9 mm [range = 312.0 - 382.0 mm], mass = 62.3 ± 14.9 g [range = 45.0 - 94.0 g]) were implanted with PIT tags and retained in an in-stream container receiving natural flow for 7 to 14 days to quantify tag retention and survival. Eels were fed daily with mealworm. Mean (± SD) PIT tag length was 6.7% (± 0.4%) of TL (range = 5.9 - 7.4%) and mass was 0.7% (± 0.2%) of eel mass (range = 0.5 - 1.4%) with 100% tag retention and survival.

Six half-duplex PIT Loops (PLs) (2.5 mm^2 cross sectional area insulated wire consisting of 50 strands of 0.25 mm diameter copper wire) were constructed on wooden frames (height = 1.8 m, width = 2.5 - 4.8 m) and installed in the lower reaches of the River Stiffkey (Fig. 6.1). Each PL was connected to a dynamic tuning unit (Wyre Micro Design, Model: DTU), PIT reader (Wyre Micro Design) and external data logger (Anticyclone Systems Ltd, Surrey, UK, Model: AntiLog RS232) and powered by a 110ah 12v battery. PLs 3 to 6 operated continuously from 5 July to 10 December 2011, with the exception of PLs 5 and 6 which did not operate from 23 to 30 September and 6 to 10 October 2011. PLs 1 and 2 operated from 27 October and 19 September 2011 to 10 December 2011, respectively.

The detection range and efficiency of all PLs were tested at different stages of the tidal cycle throughout the study. Range (maximum distance of detection) was assessed by individually passing three tags oriented parallel and at 45° to the direction of flow towards the centre, left, and right of the PL and measuring the distance between the PL and the farthest position detection occurred. Range varied from 10 to 50 cm. Efficiency (percentage of tags within range of the PL detected) was quantified by passing three tags, each oriented parallel and at 45° to the direction of flow, vertically and horizontally, through each PL at 20 cm intervals to cover its area. PIT tags oriented parallel (90° to the PL) and at 45° to the direction of flow were passed through PLs at speeds of 0.6 to 2.9 m s^{-1}, to encompass the optimal (Palstra *et al.*, 2008) and burst swimming speeds of adult eels (Blaxter and Dickson, 1959). Tags tested at lower (0.6 - 1.6 m s^{-1}) and higher speeds (1.6 - 2.9 m s^{-1}) returned similar PL detection efficiencies of 100% (90°), and 86.5% and 85.7% (45°), respectively (Table 5.1). Efficiency for 90° oriented tags was 98 - 100% when the tide gates were open. Efficiency for 45° oriented tags was 100% for the majority of the time the gates were open, decreasing to 71 - 93% immediately after the gates opened before rapidly returning to 100%.

6.3.3. Environmental variables

Water temperature, conductivity, pressure and barometric pressure (Solinst, Georgetown, Ontario, Canada; Model LTC Levelogger Junior 3001 and Barologger Gold 3001) were logged at 5 minute intervals immediately upstream and downstream of Gate 1 from July to December 2011. From these measurements, water depth and salinity were calculated (Fofonoff and Millard, 1983). Opening angles of Gates 1 and 2 were logged at 2 minute intervals over the same period via tri-axial static acceleration loggers (Onset, Bourne, Massachusetts, USA; Model UA-004-64), and calibrated weekly using a tape measure. Light intensity (Onset, Bourne, Massachusetts, USA; Model UA-002-64) and river discharge were recorded at 15 minute intervals at the tide gates and the Environment Agency gauging station at Little Walsingham (12.6 km upstream from the tide gates), respectively. Light intensity was 0 lux at night (between the hours of sunset and sunrise) and > 0 lux (median = 1550 lux; range = 2 - 63378 lux) during the day.

6.3.4. Video data

To assess the influence of the orifice installed in Gate 1 on the downstream migration of adult eels, the orifice was set to either ‘operational’, or ‘non-operational’ on alternate days throughout the study period. When operational, the orifice functioned as intended, remaining open at low water, and closing on average (± SD) 14.8 (± 8.0) min after the closure of Gate 1 during the flood tide. When non-operational, the orifice door was manually clamped shut for the entire duration of each tidal cycle.

During periods of operation, the orifice was monitored by two infrared (IR) submersible cameras with integrated IR LEDs (Sony, Model: IR 37CSHR-IR 25m). The cameras were mounted at either side of the orifice, perpendicular to the flow, to (1) observe the entire entry area, and (2) emit an IR light source from behind any fish using the orifice so that passage could also be viewed at night. The cameras operated throughout the study period (19 September - 30 November 2011), with the exception of the night of 25 November 2011, during which 1 tagged eel passed Gate 1. Video footage was recorded to a digital video recorder powered by a 110ah 12v battery and downloaded at weekly intervals. Footage recorded between the time of last eel detection at PL3 and first detection at PL4 was then manually reviewed to identify any orifice passage events.

6.3.5. Data analyses

6.3.5.1. Escapement

Eel escapement was assessed between 10 October and 10 December 2011 when PLs 2 to 6 were operational. Escapement was calculated as the number of fish detected at PLs 4 and 6 (downstream of the gates) as a percentage of those detected at PL2 (upstream of the gates).

6.3.5.2. Delay

The study site was divided into two reaches for analysis: (1) control reach A in which water control structures were absent (length = 55 m), and (2) treatment reach B which included the carrier channel and the tide gates (for fish exiting via Gate 1: length of reach = 85 m; Gate 2: length = 290 m) (Fig. 6.1). The speed of migration was calculated for each reach as the quotient of the distance (m) separating upstream and downstream PLs and duration or fish passage (s) between first detection at each. Data for 27 October 2011 onwards were square root transformed to comply with the assumption of normality (Kolmogorov-Smirnov test: $P > 0.05$). Eels were categorised based on their exit route as those that either initially passed Gate 1 or 2. A one-way repeated-measures ANOVA was used to compare speed of migration between reaches for the two groups. Independent *t*-tests were used to compare speed of migration through each reach for the two exit routes (Gate 1 or Gate 2).

Mean discharge (Q_{fish}), water temperature ($Temp_{fish}$), gate angle ($Angle_{fish}$) and light intensity ($Light_{fish}$) during passage through reaches A and B were calculated for individual fish. Although confounding data could not be transformed to comply with the assumption of normality (Kolmogorov-Smirnov test: $P < 0.05$), repeated-measures ANOVAs, which are robust to such deviations when sample sizes are equal (Harwell *et al.*, 1992), were used to compare Q_{fish}, $Temp_{fish}$, $Angle_{fish}$ and $Light_{fish}$ between reaches within exit route groups to identify any temporal differences in these variables experienced by eels. Where data were normally distributed, or parametric analysis was used, data were reported as means (± SD).

Multiple linear regression models were developed to explore the overall relationships between speed of migration and environmental variables (Q_{fish}, $Temp_{fish}$, $Angle_{fish}$ and $Light_{fish}$) in reaches A and B ($n = 32$) from 27 October to 10 December 2011 when all 6 PLs were functional. A Kolmogorov-Smirnov test indicated that standardised residuals were normally distributed ($P > 0.05$). To increase statistical power, an additional multiple linear regression model was used to explore the relationship between these variables for fish migrating through reach B between 10 October and December 2011 ($n = 58$) when PLs 2 to 6 were functional. Raw data were square root transformed to provide normally distributed standardised residuals (Kolmogorov-Smirnov test, $P >$

0.05). Release date, detection date and TL had no independent relationship with speed and were thus omitted from further analysis. Regression analyses were reported as unstandardized *B* coefficients and 95% confidence intervals (*CI*) with variance (R^2) indicated as percentages.

As data could not be transformed to meet the assumption of normality (Kolmogorov-Smirnov test: $P < 0.05$), Mann-Whitney (*U*) tests were used to assess the relationship (including effect size, *r*) between speed of migration through reach B and: (1) exit route (Gate 1 or Gate 2); (2) gate position (open or closed); (3) time of day (day or night); and (4) status of orifice operation (operational or non-operational) when fish entered treatment reach B ($n = 58$). Chi-square (X^2) was used to explore the relationship between gate position when eels entered reach B (open or closed) and route of exit (Gate 1 or Gate 2) and status of orifice operation (operational or non-operational).

Spearman's rho (r_s) was used to assess the relationship between (1) speed of migration between release and PL2 with distance and release date, and (2) gate angle at passage (detection at PLs 4 or 6) and duration of migration through the respective culvert (time between detection at PLs 3 or 5 and 4 or 6).

Mann-Whitney tests were used to compare the association between status of orifice operation (operational or non-operational) when fish entered reach B and Q_{fish}, $\text{Temp}_{\text{fish}}$, $\text{Angle}_{\text{fish}}$, $\text{Light}_{\text{fish}}$ and mean upstream depth ($\text{UDepth}_{\text{fish}}$), downstream depth ($\text{DDepth}_{\text{fish}}$), upstream salinity ($\text{USalinity}_{\text{fish}}$), and downstream salinity ($\text{DSalinity}_{\text{fish}}$) calculated for individual fish. Where data were not normally distributed and non-parametric analyses were used, results were reported as medians with ranges in parentheses.

The number of approaches immediately upstream from the gates and culverts (detection at PLs 3 and 5) was calculated. Each approach was defined as detection at PL3 or PL5 with an interval of > 5 min apart. A Wilcoxon signed-rank (*T*) test was used to compare downstream and upstream migration duration through the culverts for fish that re-entered the river.

6.3.5.3. Environmental data

Water temperature and salinity measurements, and their difference between upstream and downstream (Δ), collected over the entire duration of the study period were compared using Mann-Whitney tests to explore their relationship with tide gate position (open or closed).

When the gates were closed, Mann-Whitney tests were used to compare median and difference (Δ) in water temperature, salinity and depth between upstream and downstream for each orifice status (operational or non-operational), as well as to compare gate angle and upstream depth between each orifice status when the gates were open.

6.4. Results

6.4.1. Escapement

Of the 118 PIT tagged eels released, 67.8% (*n* = 80) were detected at PL2, 65 m upstream from Gate 1. Of these, 59 eels reached PL2 between 10 October and 10 December 2011 when PLs 2 to 6 were operational, 58 of which were detected at PLs 4 and 6 downstream of the tide gates by December 2011, giving a total escapement of 98.3% for those that approached the tide gates. More eels exited the river for the first time via Gate 1 (75.9%, *n* = 44) than Gate 2 (24.1%, *n* = 14). Nine eels (15.5%) re-entered the river once via Gate 1, predominately during the ebb tide, on average (± SD) 1.92 (± 1.39) h after the gates opened. No eels re-entered through Gate 2. Almost half of those that re-entered finally exited through Gate 2 (*n* = 4) rather than Gate 1 (*n* = 5), with a total of 69.0% of eels (*n* = 40) finally exiting via Gate 1 and 31.0% (*n* = 18) via Gate 2. Eels were less likely to re-enter the river if they exited for the first time through Gate 2 (*n* = 1) but there was no difference in TL (*U* = 159.00, *r* = -0.16, *P* > 0.05) between those that re-entered and those that did not. All eels that re-entered the river remained downstream from PL2.

6.4.2. Delay

The median duration and speed of migration of eels from the release locations (0.5 to 3.1 km upstream of the tide gates) to PL2 (*n* = 80) was 1.3 (0.1 - 69.3) days and 0.004 (0.0001 - 0.12) m s^{-1}, respectively. Speed of migration between these two points was related to distance from the release site to PL2 ($r_s = -0.23$, $P < 0.05$) and release date ($r_s = 0.52$, $P < 0.001$) (Fig. 6.2).

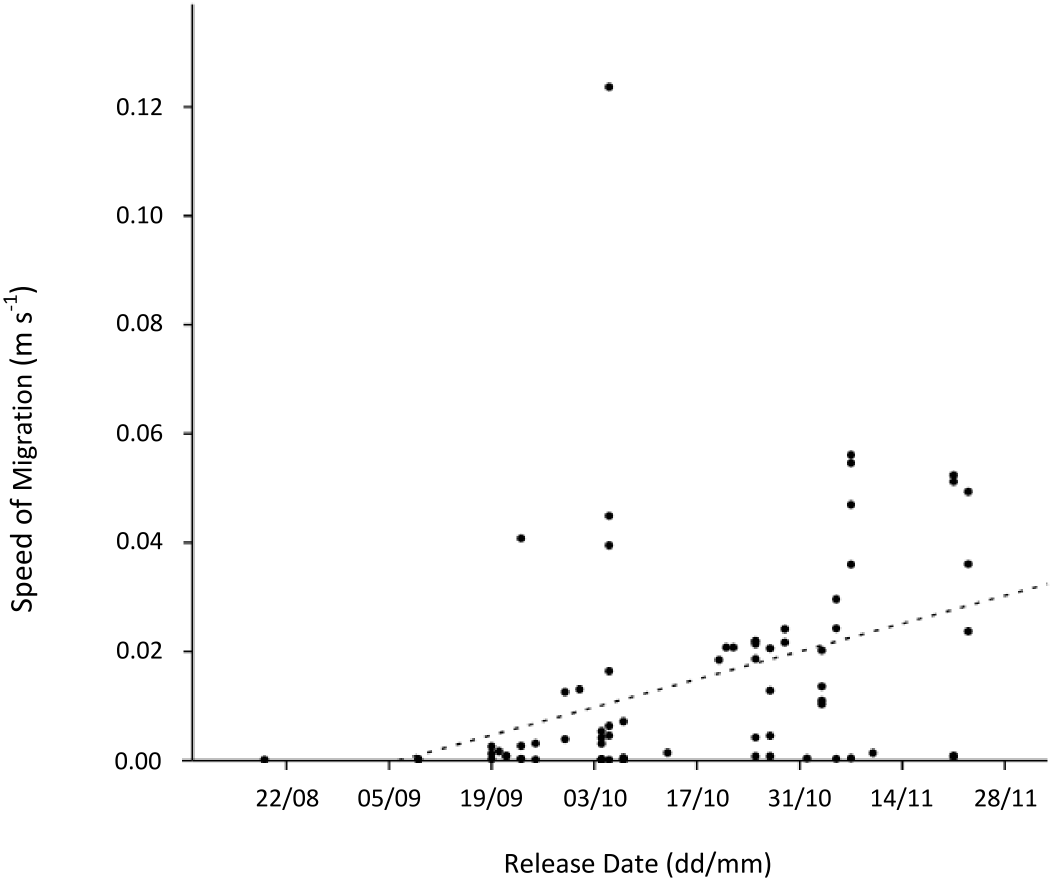


Fig. 6.2. Relationship between tagging release date and speed of eel (*n* = 80) migration from the release locations (0.5 to 3.1 km upstream of the tide gates) to PL2 in the River Stiffkey, UK, across the entire capture and study period (July to December 2011).

For the 32 eels detected while PL1 was functional, speed of migration was faster through the control (A) than the treatment (B) reach regardless of exit route (Fig. 6.3; Table 6.1). Speed of migration through reach A did not differ between eels that departed through Gate 1 or 2 ($t_{30} = -0.12$, $P > 0.05$), although those that escaped through Gate 1 did migrate more rapidly through reach B ($t_{29.4} = 2.34$, $P < 0.05$). When including eels ($n = 58$) that migrated earlier in the season (when PL1 was out of operation), median speed of migration (Gate 1: 0.04 [0.0001 - 0.37] m s^{-1}; Gate 2: 0.03 [0.0002 - 0.07] m s^{-1}) through reach B was not dependant on exit route ($U = 265.00$, $r = -0.10$, $P > 0.05$). Median duration of passage through reach B was 0.67 [0.06 - 406.61] h and 3.13 [1.24 - 360.32] h for eels ($n = 58$) that exited via Gates 1 and 2, respectively.

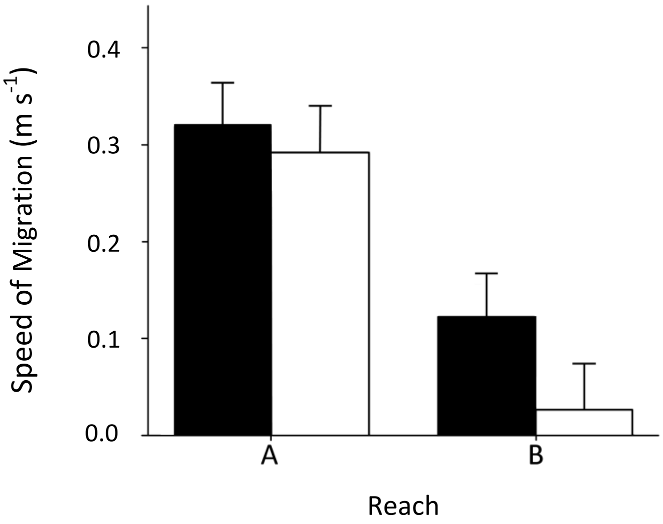


Fig. 6.3. Mean ± SE speed of migration of 32 adult European eels through a control reach with no structure (A) and a treatment reach with tide gates (B) in the lower River Stiffkey, UK, between October and December 2011. Eels exited the system via Tide Gate 1 (■) or Tide Gate 2 (□).

Table 6.1. Mean ± SD duration, speed of migration, Temp$_{\text{fish}}$, Q$_{\text{fish}}$, Light$_{\text{fish}}$, and Angle$_{\text{fish}}$ for 32 PIT tagged adult European eels migrating downstream in the River Stiffkey, UK, through a control reach with no structures (A) and a treatment reach (B) where eels could exit the system via Tide Gate 1 or Tide Gate 2, with results of repeated-measures ANOVAs comparing reaches A and B.

	Exit route	Reach		Repeated-measures ANOVA			
		A	B	*F*	*df*	*error*	*P*
Duration (h)	Gate 1	1.11 ± 4.65	66.24 ± 141.76				
	Gate 2	0.07 ± 0.05	53.34 ± 125.16				
Speed (m s^{-1})	Gate 1	0.32 ± 0.23	0.12 ± 0.13	21.67	1	23	0.000^{**}
	Gate 2	0.29 ± 0.13	0.03 ± 0.02	43.84	1	7	0.000^{**}
Temp$_{\text{fish}}$ (°C)	Gate 1	10.43 ± 2.05	10.06 ± 1.99	6.95	1	23	0.015^{*}
	Gate 2	10.81 ± 1.78	10.53 ± 1.75	0.78	1	7	0.406
Q$_{\text{fish}}$ (m^{3} s^{-1})	Gate 1	0.11 ± 0.03	0.10 ± 0.03	4.32	1	23	0.049^{*}
	Gate 2	0.12 ± 0.06	0.12 ± 0.05	2.65	1	7	1.148
Light$_{\text{fish}}$ (lux)	Gate 1	72.23 ± 353.83	291.87 ± 499.24	2.77	1	23	0.110
	Gate 2	0.00 ± 0.00	253.18 ± 473.08	2.29	1	7	0.174
Angle$_{\text{fish}}$ (°)	Gate 1	8.07 ± 9.02	9.64 ± 7.90	4.98	1	23	0.036^{*}
	Gate 2	1.29 ± 2.80	5.04 ± 2.64	5.41	1	7	0.053

$^{*}P < 0.05$

$^{**}P < 0.001$

$\text{Temp}_{\text{fish}}$, Q_{fish}, and $\text{Angle}_{\text{fish}}$ were greater in reach A than B for fish exiting via Gate 1 but not Gate 2 (Table 6.1). There was no variation in $\text{Light}_{\text{fish}}$ between reaches A and B for either route of exit.

Overall, Q_{fish}, $\text{Temp}_{\text{fish}}$, $\text{Light}_{\text{fish}}$ and $\text{Angle}_{\text{fish}}$ explained 24.1% and 57.0% of the variation in speed of migration through reaches A and B, respectively. The regression for reach A returned no significant correlates. $\text{Angle}_{\text{fish}}$ ($B = 0.007$, $CI = 0.002 – 0.012$, $P < 0.01$) had the most significant relationship with speed of migration through reach B followed by $\text{Light}_{\text{fish}}$ ($B = 0.000$, $CI = 0.000 – 0.000$, $P < 0.01$). In the regression model for 58 eels, Q_{fish}, $\text{Temp}_{\text{fish}}$, $\text{Light}_{\text{fish}}$ and $\text{Angle}_{\text{fish}}$ accounted for 60.5% of the variability in speed of migration, with $\text{Light}_{\text{fish}}$ being the most significant correlate ($B = -0.007$, $CI = -0.010 – -0.005$, $P < 0.001$) followed by $\text{Angle}_{\text{fish}}$ ($B = 0.065$, $CI = 0.030 – 0.100$, $P < 0.001$) and $\text{Temp}_{\text{fish}}$ ($B = -0.155$, $CI = -0.292 – -0.019$, $P < 0.05$).

Median speed of migration through reach B was faster if the gates were open when eels entered the reach ($n = 28$, 0.12 [0.0001 - 0.37] m s^{-1}) than when closed ($n = 30$, 0.01 [0.0001 - 0.23] m s^{-1}) ($U = 227.50$, $r = -0.39$, $P < 0.01$). If Gate 1 was open when entering reach B (detection at PL2), eels were more likely to exit through this route (89.3% versus 63.3% when closed, $X^2_1 = 5.33$, $P < 0.05$). All fish entered both reaches, and passed through the gates (detection at PLs 4 and 6) at night (0 lux). Eels passed the gates predominately during the onset of the ebb tide, a median of 39.7 (0.3 - 449.8) min after the gates opened. Duration of migration through the culverts (median = 74 s, range = 24 - 1381 s) was negatively related to gate angle at passage (i.e. detection at PL4 or PL6) (median = 16.8°, range = 2.1 - 27.8°) ($r_s = -0.36$, $P < 0.01$).

Eels migrated faster through reach B when the orifice was operational ($n = 28$, 0.07 [0.0001 - 0.37] m s^{-1}) compared to non-operational ($n = 30$, 0.01 [0.0001 - 0.33] m s^{-1}) ($U = 231.00$, $r = -0.39$, $P < 0.01$) (Fig. 6.4). However, video analysis revealed that eels did not pass through the orifice. Status of orifice operation was not associated with differences in Q_{fish}, $\text{Temp}_{\text{fish}}$, $\text{Angle}_{\text{fish}}$, or $\text{UDepth}_{\text{fish}}$ (Fig. 6.5a), but was related to lower $\text{USalinity}_{\text{fish}}$ (Fig. 6.5b), which was likely a result of lower $\text{DDepth}_{\text{fish}}$ (i.e. lower tides) (Fig. 6.5c), and $\text{DSalinity}_{\text{fish}}$ (Fig. 6.5d) when the orifice was operational. $\text{Light}_{\text{fish}}$ was also lower when the orifice was open at entry to reach B (Table 6.2) and the number of cases where Gate 1 was open when eels entered reach B was higher (X^2_1 = 5.56, $P < 0.05$).

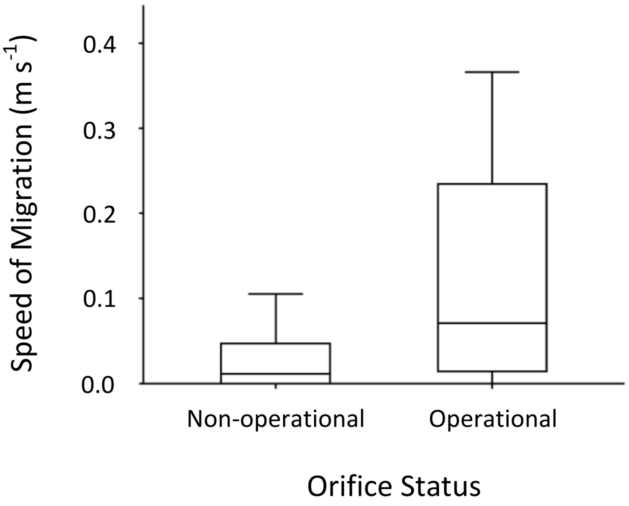


Fig. 6.4. Speed of migration of 58 adult European eels through the lower River Stiffkey, UK, when an orifice in Tide Gate 1 was non-operational or operational. The box plots illustrate the median (horizontal line), interquartile range (boxes) and overall range up to 1.5 times the interquartile range (whiskers). Outliers > 1.5 times the interquartile range are not depicted.

Table 6.2. Mann-Whitney statistical comparisons of Q_{fish}, $Temp_{fish}$, $Angle_{fish}$, $UDepth_{fish}$, $DDepth_{fish}$, $USalinity_{fish}$, $DSalinity_{fish}$, and $Light_{fish}$ for status of orifice operation (operational vs non-operational) during the passage of 58 adult European eels through reach B containing tide gates.

	Mann-Whitney		
	U	*r*	*P*
Q_{fish}	350.00	-0.14	0.276
$Temp_{fish}$	338.00	-0.17	0.202
$Angle_{fish}$	384.00	-0.07	0.575
$UDepth_{fish}$	275.00	-0.17	0.209
$DDepth_{fish}$	218.00	-0.31	0.023*
$USalinity_{fish}$	231.00	-0.28	0.041*
$DSalinity_{fish}$	238.00	-0.29	0.034*
$Light_{fish}$	302.00	-0.30	0.022*

$^*P < 0.05$

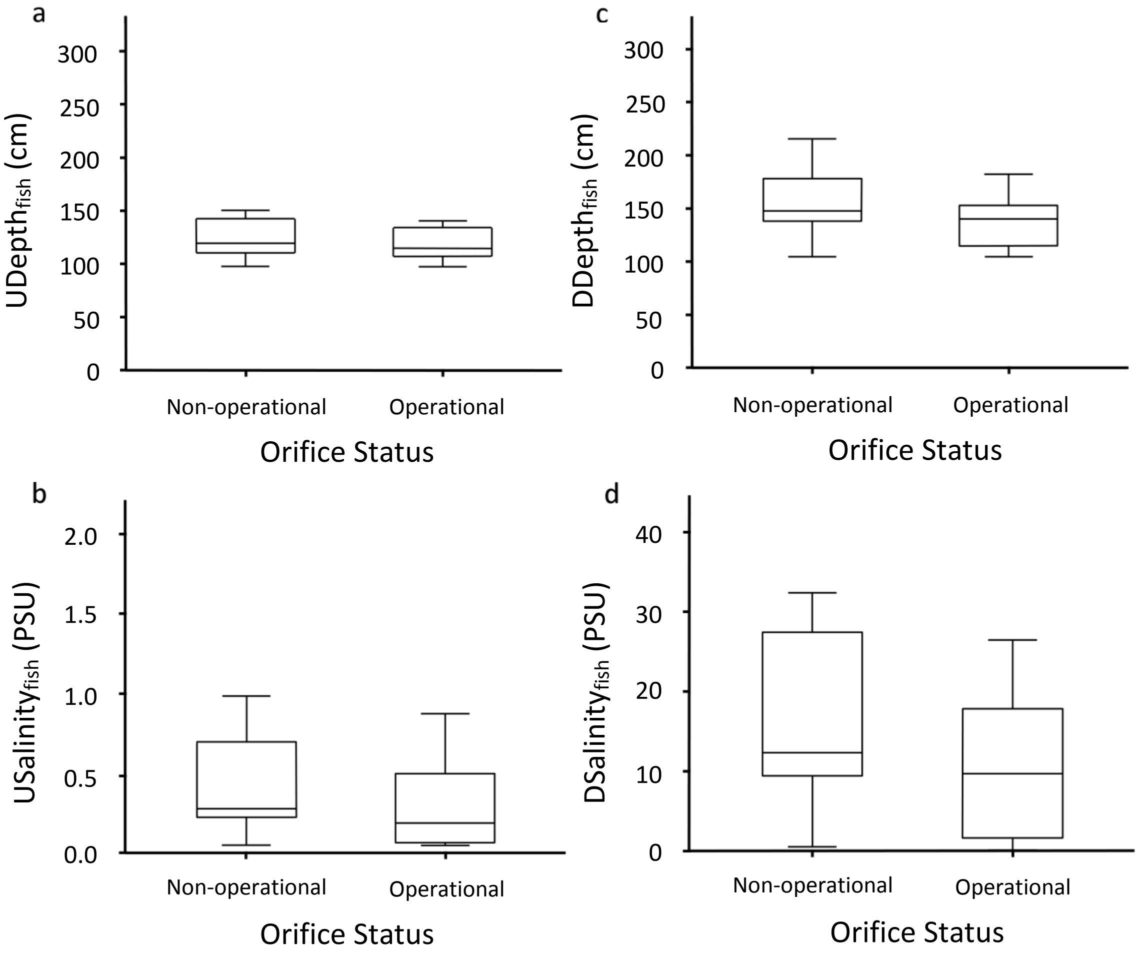


Fig. 6.5. (a) UDepth$_{fish}$, (b) USalinity$_{fish}$, (c) DDepth$_{fish}$, and (d) DSalinity$_{fish}$ for 58 adult European eels through the lower River Stiffkey, UK, when an orifice in Tide Gate 1 was non-operational or operational. The box plots illustrate the median (horizontal line), interquartile range (boxes) and overall range up to 1.5 times the interquartile range (whiskers). Outliers > 1.5 times the interquartile range are not depicted.

Fifteen eels (25.9%) explored the area upstream from one gate (detection at PL 3 or 5) before passing through the other (detection at PL 6 or 4, respectively). Twenty-two eels (37.9%) made more than one approach to the culverts (detection at PL3 or PL5, mean ± SD number of approaches = 4.0 ± 2.9) and the majority (89.7%, *n* = 52) remained in the area downstream from PL2 after entering reach B and prior to passage. Of the eels migrating (*n* = 58), 74.1% passed through reach B during the same period as one or more other tagged individuals, with a maximum of 7 being present at any one time. Eels that re-entered the river after first passage through the gates (15.5%, *n* = 9) took a median of 2.0 (1.0 - 22.1) days to pass downstream from the tide gates for the final time. There was no variation in the duration of passage through the culvert between downstream or upstream movement (T = 17.00, r = -0.15, $P > 0.05$).

6.4.3. Environmental data

Assessment of the relationship between the tide gates and environmental variables alone showed that upstream and downstream median water temperatures (Table 6.3) were marginally higher when the gates were closed than when open over the full duration of the study (Fig. 6.6a; Table 6.4). The difference in water temperature upstream and downstream from the gates was similar when open and more pronounced when closed (Table 6.4).

Table 6.3. Median and difference (Δ) in water temperature and salinity upstream and downstream of Tide Gate 1 in the River Stiffkey, UK, when open and closed, or during periods of gate closure when the orifice was operational and non-operational, from 23 September to 30 November 2011, with ranges in parentheses.

	Location	Status	Temperature (^{o}C)	Salinity (PSU)
Gate	Upstream	Open	10.76 (6.28 - 16.95)	0.54 (0.37 - 13.80)
		Closed	11.12 (6.48 - 17.14)	7.92 (0.33 - 13.38)
	Downstream	Open	10.77 (5.96 - 17.15)	0.90 (0.37 - 32.64)
		Closed	11.60 (5.92 - 18.76)	28.84 (0.41 - 34.70)
	Δ	Open	0.00 (-1.23 - 2.03)	0.37 (0.00 - 29.23)
		Closed	0.48 (-1.59 - 3.04)	20.80 (0.00 - 31.52)
Orifice	Upstream	Operational	11.45 (7.02 - 17.08)	7.89 (0.37 - 12.92)
		Non-operational	11.02 (6.48 - 17.14)	7.94 (0.33 - 13.38)
	Downstream	Operational	11.74 (6.99 - 18.63)	28.54 (0.41 - 34.70)
		Non-operational	11.48 (5.92 - 18.76)	29.02 (0.45 - 33.83)
	Δ	Operational	0.45 (-1.59 - 3.04)	20.50 (0.00 - 31.52)
		Non-operational	0.49 (-0.87 - 2.97)	20.90 (0.00 - 30.73)

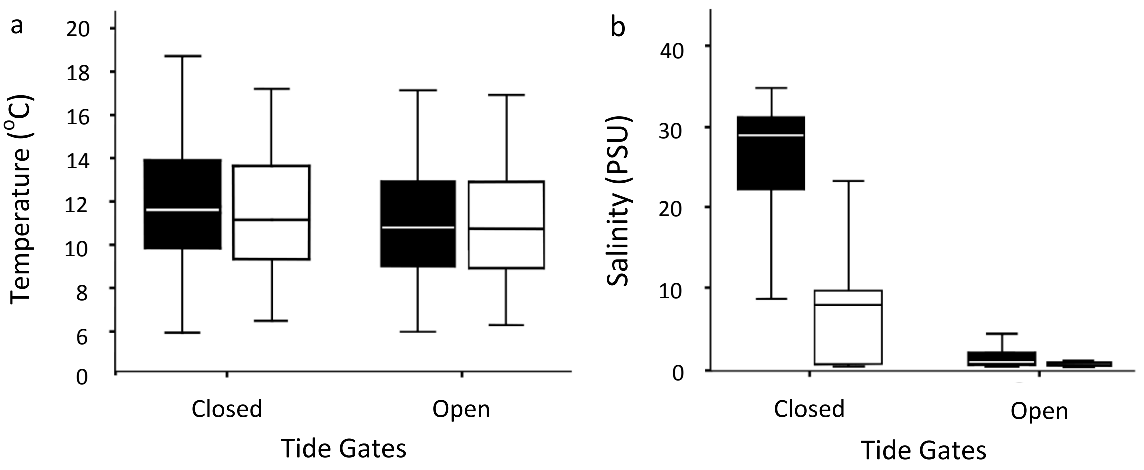


Fig. 6.6. (a) Water temperature and (b) salinity downstream (■) and upstream (□) of Tide Gate 1 in the River Stiffkey, UK, when the gate was open and closed from 23 September to 30 November 2011. Outliers > 1.5 times the interquartile range are not depicted.

Table 6.4. Mann-Whitney statistical comparisons of median and difference (Δ) in water temperature and salinity recorded over the full duration of eel movement during the study (23 September to 30 November 2011) upstream and downstream of Tide Gate 1 in the River Stiffkey, UK, when open and closed, or during periods of gate closure when the orifice was operational and non-operational.

	Status	Location	Temperature			Salinity		
			U	*r*	*P*	*U*	*r*	*P*
Gate	Open vs Closed	Upstream	954959441.50	-0.06	0.000*	416226210.00	-0.50	0.000*
		Downstream	845468032.50	-0.15	0.000*	207504262.50	-0.67	0.000*
		Δ	341361276.00	-0.56	0.000*	195576373.00	-0.68	0.000*
Orifice	Operational vs Non-operational	Upstream	126194307.00	-0.04	0.000*	132395311.50	0.00	0.600
		Downstream	128059556.50	-0.03	0.000*	126837062.50	-0.04	0.000*
		Δ	128426892.00	-0.03	0.000*	125782045.50	-0.04	0.000*

*$P < 0.001$

Upstream and downstream median salinity (Table 6.3) was substantially higher when the gates were closed than when open for the duration of the study (Table 6.4; Fig. 6.6b). There was a slight difference in salinity between upstream and downstream when the gates were open, and salinity became considerably higher downstream when closed.

Status of orifice operation did not influence upstream median salinity over the period of study when the gates were closed (Table 6.3; Table 6.4) and was not associated with variation in median ΔDepth (operational: 81.96 [-1.09 - 244.56] cm; non-operational: 83.36 [-0.80 - 306.92] cm, U = 131758485.50, r = -0.01, $P > 0.05$) even though downstream median salinity was higher when the orifice was non-operational. Median upstream water temperature also varied with status of orifice operation which likely resulted from differences in downstream temperature. When the gates were open, median Gate 1 angle (operational: 3.5^{o} [0.7 - 29.5^{o}]; non-operational: 3.5^{o} [0.7 - 29.5^{o}]; U = 279652651.00, r = -0.26, $P < 0.001$) and upstream depth (operational: 97.9 [94.8 - 158.1] cm; non-operational: 98.2 [94.8 - 158.4] cm; U = 376628644.50, r = -0.05, $P < 0.001$) were marginally higher when the orifice was non-operational.

6.5. Discussion

Despite the severe decline in European eel abundance over recent decades, little is known of how tide gates and other coastal infrastructure might impede their migration. In this study, escapement past tide gates in a small English stream was high (98.3%), but delay was substantial when compared to an unimpeded control reach, with speed of migration past Gates 1 and 2 being 2.7 and 9.7 times slower, respectively. An orifice fish pass installed to increase fluvial connectivity through the gates was associated with decreased delay, even though eels were not observed to pass directly through it.

As few studies have attempted to quantify the impact of estuarine infrastructure on seaward migrating adult eels, there is limited opportunity to compare results. In one exception, high (100%) escapement was observed for acoustic and PIT tagged silver eels that approached a complex of intertidal structures, which included tide gates but did not isolate their impact, on the River Stour, UK (Piper *et al.*, 2013). Further comparisons at present must be based on structures, such as undershot sluices at dams, which impose similar conditions to those encountered at the open top-hung tide gates of interest in this study. Based on the information available, efficiencies are highly variable. For example, on the River Ätran (Sweden), 15% of radio tagged silver eels passed Ätrafors hydroelectric plant via bottom fed spill gates (Calles *et al.*, 2010). Of interest, 74% of fish that eventually passed the dam via the turbines had first approached the spill gates, only to then reject this route of passage (see below discussion of avoidance behaviour). Conversely, at the Baigts hydroelectric facility in the Gave de Pau river (France), 76% of downstream moving radio and PIT tagged silver eels that explored alternate routes to the turbines (e.g. sluices, flap gates, and bypasses) subsequently passed via these structures (Travade *et al.*, 2010). Travade *et al.* (2010) and others (e.g. Breteler *et al.*, 2007; Jansen *et al.*, 2007) suggest that eels tend to escape via the route of dominant flow, an observation supported by the current study in which most eels (75.9%) exited through Gate 1 which discharged the highest volume.

Amphidromous behaviour has previously been observed for yellow eel, where mature adults migrate regularly between rivers and estuaries to feed (Thibault *et al.*, 2007). Although a number of eels ($n = 9$) re-entered the River Stiffkey after initially passing through the gates, these individuals exhibited physiological features reflecting their preparedness for marine migration (Tesch, 2003), and all eels subsequently passed downstream past the gates ≥15 days prior to termination of the study without returning upstream.

Tide gates have been shown to delay actively seaward migrating species (Chapter 7, for juvenile sea trout, *Salmo trutta*), but their influence on the downstream migration of adult European eel has not previously been reported. The role of behavioural avoidance is likely to be important in understanding the causes of delay at tide gates. While tide gates physically block migrating fish when closed, the narrow apertures through which water is discharged when open, and culvert entrances, may create a hydrodynamic barrier in the form of a rapid acceleration of flow which acts as a repellent (Pacific salmonid smolts: Enders *et al.*, 2009; Kemp *et al.*, 2005a, silver European eels: Piper *et al. in prep.*). Indeed, eels have been observed to exhibit non-passive exploratory behaviour at other riverine structures (silver American eels, *Anguilla rostrata*: Brown *et al.*, 2009a; Haro and Castro-Santos, 2000, silver European eels: Behrmann-Godel and

Eckmann, 2003; Travade *et al.*, 2010) during which they may reject an area approached, to either approach again, or find an alternative route (e.g. Brown *et al.*, 2009a). In this study, three key pieces of evidence suggest delay was at least in part a result of avoidance and exploration of conditions experienced at the tide gates. First, more than a third of the eels (37.9%) made more than one approach to the culverts, and a quarter (24.2%) approached the area upstream from one gate prior to exiting through another. Second, a positive relationship was observed between mean degree of gate opening and speed of migration through the treatment reach, which was the second most significant relationship after light. Third, a negative relationship between the degree of gate opening at the time fish passed and duration of culvert passage suggests a behavioural element of avoidance contributing towards delay. However, this could to some extent also be explained by lower water velocities within the culvert when the gate aperture was smaller. Avoidance may not have been solely induced by hydrodynamic stimuli. For example, continuous overhead cover, such as that associated with the culverts themselves, is known to induce avoidance in other fish species (e.g. Kemp *et al.*, 2005b for Pacific salmonids; Greenberg *et al.*, 2012 for juvenile sea trout), indicating the potential for multiple factors associated with complex river infrastructure to have confounding influences.

The downstream migration of eels is commonly considered to be predominantly nocturnal (e.g. Aarestrup *et al.*, 2008; Boubée and Williams, 2006) and partially triggered by low temperatures (Vøllestad *et al.*, 1986). In the present study, delay was elevated when temperatures were high, and eels passed the control reach and the gates only during periods of darkness. Greater delay was associated with increased light levels, suggesting that eels failing to pass the gates at night may have subsequently been inactive during the day (Davidsen *et al.*, 2011).

Delayed migration could be detrimental. During the silvering process, the alimentary tract degenerates (Pankhurst and Sorensen, 1984) and eels cease feeding (Olivereau and Olivereau, 1997). Thus successful migration is based on efficient utilisation of finite energy reserves. Delay extends the migratory period, while avoidance and exploration uses energy that might be otherwise allocated to gamete development (Van den Thillart and Dufour, 2009) or the 5000 to 6000 km oceanic migration to spawning grounds in the Sargasso Sea (Tesch, 2003). The impact of delay, acting through increased energetic expense, may be exacerbated for those eels already compromised through infection with the invasive parasite *Anguillicoloides crassus* (Höglund *et al.*, 1992) which may be present in up to 90% of the eel population in most European systems (Lefebvre and Crivelli, 2004). Further, due to accumulation of fish delayed at structures, the potential for parasite disease transfer is also enhanced (Garcia de Leaniz, 2008), as is the risk of predation by species such as cormorants, *Phalacrocorax carbo,* (Jepsen *et al.*, 2010; Keller, 1995) and otters, *Lutra lutra*, (Jenkins and Harper, 1980) both of which are known to frequent the study site.

Delay was lower when the orifice was operational. Eels did not pass through the orifice, which was situated half way up the gate, supporting the results of other studies which report eels to be principally benthic oriented during freshwater migration (Jonsson, 1991; Tesch, 2003) exhibiting a preference for undershot pathways (Gosset *et al.*, 2005; Russon and Kemp, 2011a; Russon and Kemp, 2011b). Reduced delay when the orifice was operational may have been due to the gates being open on more occasions when eels initially approached them, or the lower upstream salinity that may have resulted from the lower tides that occurred during these periods, as diadromous fish may need to adapt to abrupt salinity gradients (e.g. salmonid smolts: Otto, 1971). However, there is currently little evidence to suggest eels suffer adverse physiological consequences from stark transitions in salinity (Chan *et al.*, 1967; Maetz and Skadhauge, 1968; Rankin, 2008).

6.5.1. Conclusions

This study demonstrated that, although tide gates did not impact escapement, migratory delay was considerable. This may be costly in terms of energetic expenditure and predation risk. Tide gates are common throughout the range of the European eel in regions where large areas of land have been reclaimed for agricultural and other anthropogenic purposes. Coastal infrastructure required to manage water levels will become increasingly important as sea levels and flood risk rise (Nicholls *et al.*, 1999). Mitigation of the environmental impact of coastal infrastructure must be integrated as part of a wider design and planning process, which includes finding engineering solutions to protect migratory fish, such as the critically endangered European eel. Tide gate modifications designed to reduce migratory delay by opening wider for longer, whilst not compromising continued integrity of the tidal barrier, will provide a useful first step in the much needed development of sustainable infrastructure.

Chapter 7

Impact of tide gates on the migration of juvenile sea trout, *Salmo trutta*

7.1. Summary

As part of flood protection and land reclamation schemes, tide gates allow rivers to discharge to sea when open, and prevent salt water intrusion when closed. Their impact on diadromous fish migration between essential spawning and rearing habitats, and the effectiveness of mitigation measures, have received little consideration. The River Meon, UK, discharges to sea through four top-hung counterbalanced tide gates. In March 2012, the gates were replaced with new ones of the same design, but with an orifice installed in two of them partly to improve fish passage. Sixty downstream migrating juvenile sea trout, *Salmo trutta*, were trapped approximately 4.9 km upstream from the tide gates and tagged with acoustic transmitters in April 2011 (n = 30) and 2012 (n = 30). Tagged individuals were detected by acoustic receivers placed near the tide gates before (year 1) and after (year 2) orifice installation. Of the fish that approached the tide gates, 95.8% and 100.0% successfully passed in years 1 and 2, respectively. The speed of migration at the gates was slower than for upstream and downstream reaches, and was positively related to percentage of time the gates were open. Presence of the orifices did not influence delay. Overall, top-hung tide gates

delayed migration, potentially increasing the risk of predation and energy expenditure during the vulnerable juvenile life stage.

7.2. Introduction

Anthropogenic development has fragmented freshwater and estuarine environments, disturbing biogeochemical cycles and habitat structure via modified discharge and temperature regimes (Im *et al.*, 2011; Poff and Hart, 2002), and altered sediment and nutrient transport (Konrad, 2009). Infrastructure such as dams and barrages disrupt the movement of aquatic biota, including diadromous fish (Sheer and Steel, 2006) which migrate between marine and freshwater environments to spawn. The influence of estuarine obstructions on fish migration, particularly tide gated culverts used for flood prevention and land reclamation, has received substantially less consideration than river structures.

Tide gates form a temporal barrier to fish movement, closing when the tide floods and opening when hydraulic head differential becomes sufficient during the ebb (Giannico and Souder, 2005). Tide gates physically prevent fish migration when closed, whilst often increasing upstream water temperature (Giannico and Souder, 2005; Tonnes, 2007) and thus susceptibility of fish to disease (Dietrich *et al.*, 2014; Rees *et al.*, 2014), decreasing dissolved oxygen (Portnoy, 1991; Tonnes, 2007), and masking tidal cues (Russell *et al.*, 1998). When tide gates are open, associated conditions such as accelerating water velocities (Haro *et al.*, 1998; Russon and Kemp, 2011a), abrupt changes in salinity (Zaugg *et al.*, 1985), sudden temperature gradients (Berggren and Filardo, 1993; Boyd and Tucker, 1998; Jonsson, 1991) and overhead cover (Kemp *et al.*, 2005b) may cause stress and/or impede migration. This may explain why tide gates can limit fish abundance, richness (Boys *et al.*, 2012; Pollard and Hannan, 1994) and movement (Doehring *et al.*, 2011) when compared to un-gated channels. Previous studies have utilised nets (Boys *et al.*, 2012; Easton and Marshall, 2000; Kroon and Ansell, 2006; Mouton *et al.*, 2011; Pollard and Hannan, 1994; Roegner *et al.*, 2010), mark-recapture (Halls *et al.*, 1998) or Dual-frequency Identification Sonar (DIDSON) (Doehring *et al.*, 2011) techniques primarily to study estuarine species native to the southern hemisphere (Boys *et al.*, 2012; Doehring *et al.*, 2011; Easton and Marshall, 2000; Kroon and Ansell, 2006; Pollard and Hannan, 1994) and USA (Raposa, 2002; Ritter *et al.*, 2008; Rozas and Minello, 1998). Unfortunately, these methodologies cannot track individuals and fail to quantify the efficiency of tide gate structures to allow free passage of diadromous fish. Passage efficiency depends on: (1) attraction to an available route; (2) number of fish that pass as a proportion of those that approach; and (3) the time taken to pass, hereafter referred to as delay (Kemp and O'Hanley, 2010). Delayed migration and congregation of fish at structures can increase potential for predation (Schilt, 2007) and energy expenditure (Congleton *et al.*, 2002; Osborne, 1961), resulting in decreased fitness (Geen, 1975) and survival (Raymond, 1979).

Mitigation options for improving fish passage at river and estuarine infrastructure include fishways and bypass systems (Katopodis and Williams, 2012; Larinier, 2002). Unfortunately, many of these are unsuitable at tide gates due to the cost of traversing high levees. Top-hung gates can be replaced with side-hung doors and self-regulating valves that open wider for longer, but also at relatively high expense. A variety of alternative gate modifications have been proposed, including counterbalances and retarders that allow them to remain open for longer, and orifices that maintain connectivity and water mixing when they are closed. To date, the effectiveness of these modifications for improving fish passage efficiency and reducing delay has not been reported.

This study aimed to assess the impact of (1) top-hung tide gates and (2) modifications to them (orifice installation) on the downstream passage efficiency and delay of actively migrating juvenile sea trout (anadromous brown trout), *Salmo trutta*, commonly referred to as smolts. In the UK, stocks of socio-economically important sea trout have suffered serious declines in a number of regions (Harris and Milner, 2006). Therefore, sea trout provide a valuable model to study the impact of tide gates on the downstream migration of juvenile salmonids. Specific objectives were to use acoustic telemetry to determine smolt passage efficiency past top-hung tide gates pre and post orifice installation and to quantify and compare delay through unimpeded (control) and tide gate (treatment) reaches within a UK chalk stream. The results will help inform river managers of the impacts of tide gates on fish migration, and indicate how potential mitigation could be achieved.

7.3. Materials and methods

7.3.1. Study site

During the study period, the River Meon, located in Hampshire, UK (50° 49' N; -1° 14' E; Fig. 7.1), had a mean (± SD) daily discharge at Mislingford (13.0 km upstream of the tidal limit) of 0.85 (± 0.10) $m^3\ s^{-1}$ (April 2011) (equivalent to Q_{41} from 2002 - 2012) and 0.53 (± 0.22) $m^3\ s^{-1}$ (April 2012) (Q_{68}). Based predominately on a chalk aquifer, the river rises near East Meon and flows 31 km south to discharge into the Solent at Hill Head via four counterbalanced top-hung tide gates (each gate: height = 1.7 m, width = 2.3 m, Fig. 7.2a). The tide gates remained open for 5.2 ± 0.3 h (mean ± SD) and 5.1 ± 0.2 h each tidal cycle at an angle of $42.0^o \pm 9.8^o$ and $45.3^o \pm 10.3^o$, which equated to a distance of 1.2 ± 0.3 m and 1.3 ± 0.3 m at the widest part of the aperture in April 2011 and 2012, respectively. At Fishers Hill, approximately 4.9 km upstream from the tidal limit, the ‘Natural Channel’ bifurcates into a man-made ‘Canal’. The river is designated a Site of Importance for Nature Conservation, a Site of Special Scientific Interest (SSSI) at Titchfield Haven Nature Reserve (Fig. 7.1), and has an established annual sea trout smolt run during March and April (Environment Agency, *pers. comm.*). In March 2012, the Environment Agency replaced the tide gates with those of the same design, and added a 300 mm diameter circular orifice in gates 1 and 4 (Fig. 7.2b) to prevent avian disease from *Clostridium botulinum* toxins by increasing tidal incursion upstream (Jubilo and Lamarque, 1999), and to aid diadromous fish passage. The orifices remained fully open throughout each tidal cycle.

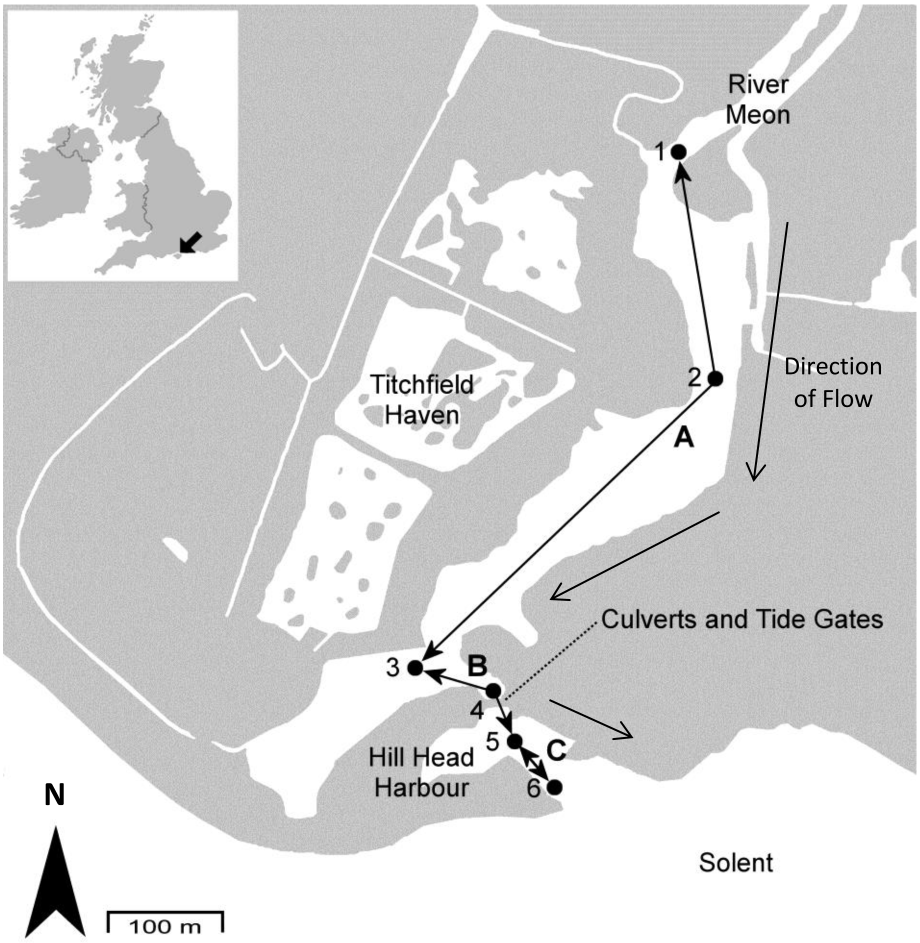


Fig. 7.1. The lower River Meon in Hampshire, UK, flowing through Titchfield Haven into the Solent. Acoustic receivers 1 – 6 (●) were deployed to assess the passage efficiency and delay of seaward migrating juvenile sea trout (smolts) released approximately 4.9 km upstream from receiver 1 at Fishers Hill (not shown). The speed of migration through control reaches A (receivers 1 - 3) and C (receivers 5 - 6) in April 2011 and 2012 were compared with those through the treatment reach B (receivers 3 - 5) containing 4 tide gates, with the addition of 2 orifices in year 2.

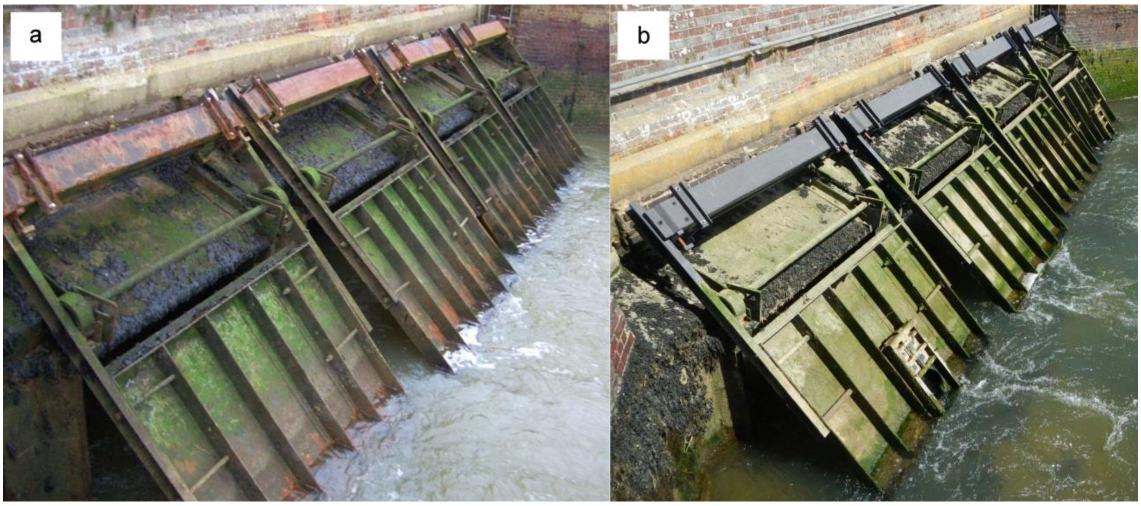


Fig. 7.2. (a) Four counterbalanced top-hung tide gates on the River Meon at Hill Head, Hampshire, UK, in 2011 (year 1), pre installation of orifices; (b) orifices were installed in two of the gates in 2012 (year 2).

7.3.2. Fish capture and telemetry

Actively migrating wild smolts were caught at Fishers Hill during five nights between 6 and 12 April 2011 (year 1) and three nights between 3 and 5 April 2012 (year 2). Winged fyke nets with a fine mesh (1 mm) catch box (height = 1.0 m, width = 0.5 m, length = 0.5 m) at the distal end were deployed in the Canal and Natural Channel during darkness between 2100h and 0300h British Summer Time (BST) and checked every hour. In both years, a total of 30 smolts were retained for tagging, 10 and 11 from the Natural Channel and 20 and 19 from the Canal in years 1 and 2, respectively.

Smolts were held in aerated water at ambient river temperature for a maximum of 1 hour prior to being anaesthetised with MS-222 (100 mg l^{-1}; buffered to pH 7.0 with $NaHCO_3$). Mass and fork length (FL) were measured (n = 30, FL [mean ± SD] = 195.3 ± 14.8 mm [range = 170.0 - 232.0 mm], mass = 77.3 ± 17.4 g [range = 51.0 - 125.0 g] in year 1; n = 30, FL = 202.0 ± 14.0 mm [range = 179.0 - 233.0 mm], mass = 78.7 ± 14.9 g [range = 55.0 - 97.0 g] in year 2). Smolts were then tagged with an acoustic transmitter (Vemco, Nova Scotia, Canada; Model V7-2L, 7 mm diameter, 18.5 mm length, 1.6 g mass, 0.75 g weight in water, 30 second pulse rate) via a ventral incision sutured with 5-0 coated Vicryl absorbable sutures (Ethicon, New Jersey, USA), in compliance with UK

Home Office regulations under the Animals (Scientific Procedures) Act 1986. Mean (± SD) transmitter mass was 2.2% (± 0.5%) of smolt body mass (range = 1.3 - 3.1%) in year 1, and 2.1% (± 0.3%) (range = 1.6 - 2.9%) in year 2. Mean (± SD) transmitter length was 9.5% (± 0.7%) of FL (range = 8.0 - 10.9%) in year 1 and 9.2% (± 0.6%) of FL (range = 7.9 - 10.3%) in year 2. After surgery, smolts recovered from the effects of anaesthesia in an aerated water container for a maximum of 1 hour before being released downstream from the respective capture net during the hours of darkness.

To assess the impact of the tagging procedure on survival and to quantify tag retention, a separate sample of smolts (*n* = 20, FL = 193.2 ± 11.0 mm [range = 177.0 - 220.0 mm], mass = 75.9 ± 15.0 g [range = 56.0 - 117.0 g] in year 1; *n* = 12, FL = 204.5 ± 12.0 mm [range = 191.0 - 233.0 mm], mass = 81.6 ± 16.9 g [range = 65.0 - 128.0 g] in year 2) were implanted with ‘dummy tags’ (inactive tags with equivalent dimensions, mass and shape to the transmitters - Vemco, Model V7-2L) using the same method for active tagging. Smolts implanted with dummy tags were held in in-stream containers with a through-flow of river water for seven days and fed with mealworm once daily. Mean (± SD) dummy tag mass was 2.2% (± 0.4%) of smolt body mass (range = 1.4 - 2.9%) in year 1, and 2.0% (± 0.3%) (range = 1.3 - 2.5%) in year 2. Mean (± SD) dummy tag length was 9.6% (± 0.5%) of smolt FL (range 8.4 - 10.5%) in year 1, and 9.1% (± 0.5%) (range = 7.9 - 9.7%) in year 2. Dummy tagged fish showed 100% tag retention (*n* = 32) and 3.1% mortality (*n* = 1).

Six stationary acoustic receivers (Vemco, Model VR2W, 69 kHz) were anchored to the river bed in Titchfield Haven Nature Reserve and Hill Head Harbour (Fig. 7.1), from 4 April to 23 August 2011 and 3 April to 25 June 2012. Floats were used to orientate the hydrophone upwards in the water column, except for Receiver 5 which was attached to a buoy and allowed to rise and fall with the tide whilst facing the river bed.

Detection range and efficiency were tested under the prevailing environmental conditions at all six receivers during the first week of April in both years. Range was defined as the maximum lateral (across the river width) and longitudinal (upstream to downstream) detection distance of tags submerged at approximately 30% and 60% water depth. Range testing was conducted at regular intervals from each receiver whilst noting time and GPS coordinates. Lateral range extended to the river banks adjacent to each receiver. Maximum longitudinal detection radius was 118 m in year 1 and 125 m in year 2 (Table 7.1). Because fish may have actively swum past the receivers (Davidsen *et al.*, 2005; Svendsen *et al.*, 2007) tags submerged at approximately 30% and 60% depth were towed behind a motor boat at 1 m s^{-1}, similar to the sustained swimming speed of a 150 mm brown trout (1.17 m s^{-1} at 10^{o}C) (Clough and Turnpenny, 2001). Detection efficiency, defined as the proportion of tags identified within maximum range of each receiver, was 100% at all receivers except receiver 4 where towed tags were not detected at the furthermost bank. Detection efficiency of tagged fish was 100% at all receivers in both years with the exception of receiver 3 where efficiency was 95.7% in year 1 and 91.7% in year 2.

Table 7.1. The maximum tag detection range of 6 acoustic receivers deployed in the lower River Meon, UK, in April 2011 (year 1, pre orifice installation) and April 2012 (year 2, post orifice installation) with inaccessible areas (-).

Receiver No.	Maximum Longitudinal Detection Range (m)			
	Year 1		Year 2	
	Upstream	Downstream	Upstream	Downstream
1	106	90	106	90
2	118	94	125	106
3	94	-	94	-
4	75	15	75	15
5	38	62	38	75
6	56	-	63	-

7.3.3. Environmental variables

Water conductivity, temperature, pressure and barometric pressure were logged (Solinst, Ontario, Canada; Models LTC Levelogger Junior 3001 and Barologger Gold 3001) at 10 minute intervals either side of the tide gate structure from 1 April to 25 June 2012. Due to logger malfunction, these variables were only recorded downstream of the gates from 1 April to 23 August 2011. Angle of tide gate opening was logged at 2 minute intervals during the same period using tri-axial static acceleration loggers (Onset, Massachusetts, USA; Model UA-004-64), and calibrated against manual angle measurements using a tape measure at low tide each week throughout April 2011 and 2012. Discharge in the River Meon was recorded at 15 minute intervals at the Environment Agency gauging station at Mislingford.

7.3.4. Data analyses

7.3.4.1. Passage efficiency

Passage efficiency was calculated as the number of fish detected at receiver 5 as a percentage of those recorded at receivers 3 and 4 (Fig. 7.1).

7.3.4.2. Delay

The lower River Meon was divided into control reaches A and C, respectively upstream and downstream from treatment reach B that contained the tide gates (Fig. 7.1). The speed of migration was calculated for each reach as the quotient of the distance (m) separating upstream and downstream receivers (reach A = distance between receivers 1 and 3; B = receivers 3 and 5; C = receivers 5 and 6) and duration (s) between first detection at each (reach A = duration from first detection at receiver 1 to first detection at receiver 3; B = duration between first detection at receivers 3 and 5), with the exception of reach C where duration between first detection at receiver 5 and last detection at receiver 6 was used. When tags were not detected at receiver 3 (n = 3), first detection at receiver 4 was used to calculate speed of migration through reaches A and B. Mean discharge (Q_{fish}) and water temperature ($Temp_{fish}$) during passage through each reach were calculated for individual fish. Data from year 2 revealed that temperatures recorded upstream and downstream of the tide gates were highly correlated (Spearman's rho, $r_s = 0.92$, $P > 0.05$). Therefore, $\text{Temp}_{\text{fish}}$ was calculated from data recorded downstream of the tide gates in both years due to upstream logger malfunction in year 1.

Kolmogorov-Smirnov tests indicated that speed of migration, Q_{fish}, and $\text{Temp}_{\text{fish}}$ were not normally distributed. Due to being robust to deviations from normality when sample size is equal (Harwell *et al.*, 1992), mixed-measures ANOVAs with Greenhouse-Geisser correction (F) were used to test for differences in speed of migration, Q_{fish}, and $\text{Temp}_{\text{fish}}$ between reach (controls: A and C; treatment: B) and year (year 1: pre modification; year 2: post modification). Levene's test indicated that variance was homogenous between years ($P > 0.05$). Bonferroni correction was applied when making pairwise comparisons between multiple groups.

Because the size of apertures did not vary considerably between gates, or throughout the period of opening, gates were classed as open or closed. The percentage of time gates were open (GO%) during passage through each reach was calculated for individual fish. Similarly, the influence of diurnal periodicity was considered by calculating the percentage of time it was night (N%) during the migration of individual fish through each reach.

To increase statistical power, data from both years were aggregated in multiple regression models developed to explore the relationships between speed of migration and the confounding variables (FL, Q_{fish}, $\text{Temp}_{\text{fish}}$, GO%, N%) in reaches A and B. Additional multiple regression models used data from each year separately to assess these relationships within years. Year and date/time of detection were omitted from regressions due to colinearity with discharge (Pearson's r: $r > 0.9$). FL did not vary between years ($t_{46} = -1.61$, $P > 0.05$), had no independent relationship with speed, and was thus excluded from further analysis. Where Kolmogorov-Smirnov tests indicated that standardised residuals were not normally distributed ($P < 0.05$), regressions with outliers removed corroborated the results. Regression analyses were reported as unstandardised B coefficients and 95% confidence intervals (CI) with variance (R^2) indicated as percentages.

Independent *t*-tests were used to assess the influence of tide gate position (open or closed) and the time of day (day or night) when fish entered the treatment reach (B) (first detection at receiver 3 or 4) on the speed of migration, and to compare conductivity and water temperature up and downstream from closed tide gates in year 2.

7.4. Results

7.4.1. Passage efficiency

In total, 25 of the 30 tagged smolts were detected in Titchfield Haven in both years. Of these, one individual in year 1 exhibited anomalous detections indicating likely mortality and was excluded from further analysis. Of the fish caught and released in the Natural Channel, 90.0% ($n = 9$) in year 1 and 84.8% ($n = 10$) in year 2 reached the acoustic receivers at Titchfield Haven. For fish caught and released in the Canal, 75.0% ($n = 15$) in year 1 and 82.3% ($n = 14$) in year 2 were detected at Titchfield Haven. Passage efficiency at the tide gates was 95.8% and 100.0% in years 1 and 2, respectively.

7.4.2. Delay

Speed of migration was greater through the control reaches (A and C) than the treatment (B) (Table 7.2) ($F_{2, 74} = 15.13$, $P < 0.001$), with no difference between the control reaches within both years ($P > 0.05$) (Fig. 7.3). Speed of migration through each control reach did not differ between years ($F_{1, 46} = 0.18$, $P > 0.05$). After entry into reach B (first detection at receiver 3 or 4), 60.9% and 62.5% of smolts were detected by receivers upstream, with 28.6% and 66.7% of these being detected as far upstream as receiver 1 in years 1 and 2, respectively.

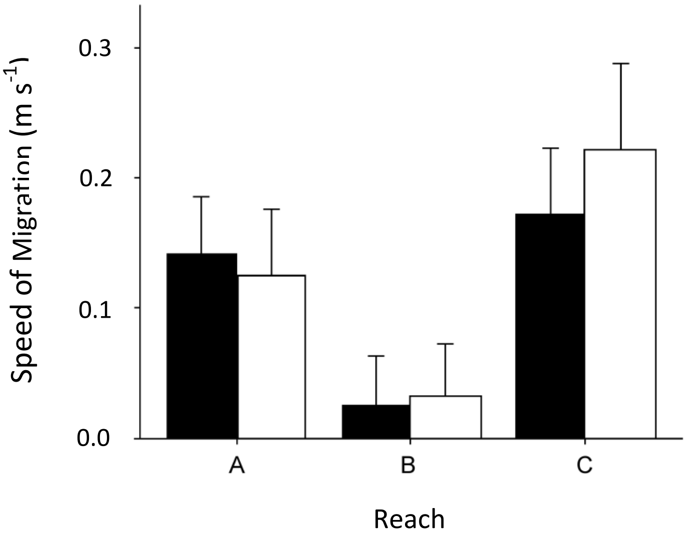


Fig. 7.3. Mean ± SE speed of migration of 23 sea trout smolts in year 1 (pre orifice installation) (■) and 25 smolts in year 2 (post orifice installation) (□) through two control river reaches with no obstructions (A and C) and one treatment reach with tide gates (B) in the lower River Meon, Hampshire, UK, in April 2011 and 2012.

Mean (± SD) Q_{fish} did not differ between reaches ($F_{1,\ 60} = 1.68$, $P > 0.05$) but did differ between years ($F_{1,\ 46} = 1743.09$, $P < 0.001$) with year 1 (0.88 [± 0.04] $m^3\ s^{-1}$) being higher than year 2 (0.42 [± 0.04] $m^3\ s^{-1}$) (Table 7.2). Mean (± SD) $Temp_{fish}$ was lower in reach A (11.49 [± 1.79] ^{o}C) than reach B (11.81 [± 2.02] ^{o}C) ($F_{2,\ 72} = 4.08$, $P < 0.05$) and differed between years ($F_{1,\ 46} = 72.71$, $P < 0.001$) with year 1 (13.25 [1.68] ^{o}C) being higher than year 2 (10.33 [± 0.86] ^{o}C) (Table 7.2).

Table 7.2. The mean ± SD speed and duration of migration, Q_{fish} and $Temp_{fish}$ for acoustic tagged sea trout smolts migrating downstream in the River Meon, Hampshire, UK, in year 1 (pre orifice installation, *n* = 23) and year 2 (post orifice installation, *n* = 25) through two reaches with no structures present (A and C) and one reach with tide gates (B) in April 2011 and 2012.

Year	Reach	Distance (m)	Structures	Speed (m s^{-1})	Duration (h)	Q_{fish} (m^3 s^{-1})	$Temp_{fish}$ (^oC)
1	A	581	None	0.15 ± 0.15	4.06 ± 4.89	0.88 ± 0.04	13.06 ± 1.29
	B	125	Tide gates	0.02 ± 0.04	6.48 ± 9.16	0.88 ± 0.05	13.38 ± 1.80
	C	50	None	0.17 ± 0.17	2.88 ± 11.99	0.88 ± 0.05	13.32 ± 1.94
2	A	581	None	0.12 ± 0.20	5.39 ± 4.47	0.43 ± 0.04	10.04 ± 0.45
	B	125	Tide gates	0.04 ± 0.09	23.74 ± 34.03	0.42 ± 0.03	10.36 ± 0.70
	C	50	None	0.22 ± 0.24	2.85 ± 8.65	0.42 ± 0.04	10.58 ± 1.20

When data from both years were aggregated, Q_{fish}, $Temp_{fish}$, GO% and N% accounted for 19.8% of the variance in speed of migration through reach A and 40.8% through reach B, with GO% being the only significant correlate (reach A: $B = 0.002$, $CI = 0.000 – 0.003$, $P < 0.05$; reach B: $B = 0.001$, $CI = 0.000 – 0.002$, $P < 0.001$), with the exception of N% in reach B ($B = 0.000$, $CI = 0.000 – 0.001$, $P = 0.05$).

Q_{fish}, $Temp_{fish}$, GO% and N% explained 34.8% and 49.3% of the variation in speed of migration through reach A, and 46.9% and 64.8% through reach B, in years 1 and 2, respectively. GO% was the most significant correlate in reach B in both years (year 1: $B = 0.001$, $CI = 0.000 – 0.001$, $P < 0.05$; year 2: $B = 0.002$, $CI = 0.001 – 0.003$, $P < 0.01$) and reach A in year 2 ($B = 0.004$, $CI = 0.002 – 0.007$, $P < 0.01$). Speed of migration was positively related to N% through reach A in year 1 ($B = 0.002$, $CI = 0.000 – 0.004$, $P < 0.05$) and reach B in year 2 ($B = 0.001$, $CI = 0.000 – 0.002$, $P < 0.05$).

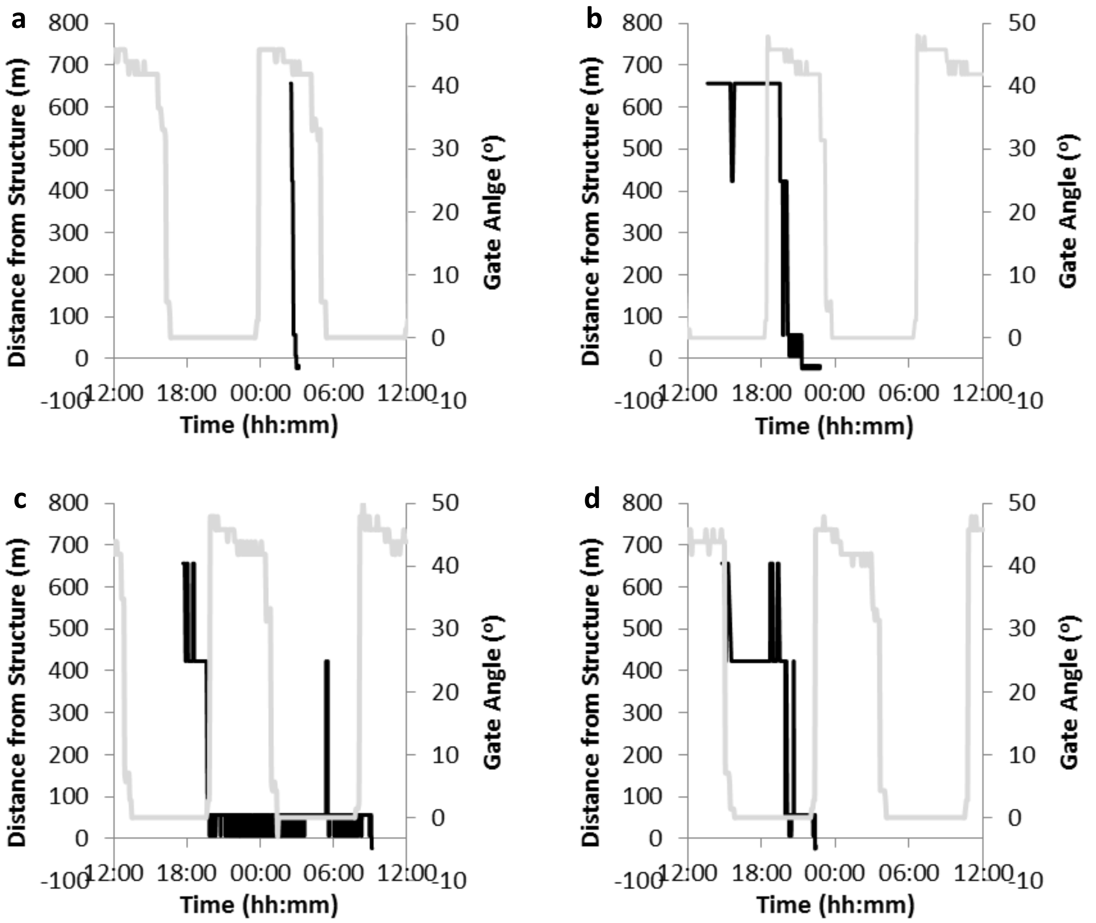
There was no difference in speed of migration through reach B between fish entering during day or night (year 1: $t_{13.2} = -1.34$, $P > 0.05$; year 2: $t_{11.2} = 1.58$, $P > 0.05$), or when the gates were open or closed (year 1: $t_{8.3} = -1.72$, $P > 0.05$; year 2: $t_{13.0} = -1.84$, $P > 0.05$). Four smolts (17.4%) that entered reach B at night whilst the tide gates were closed subsequently passed during the day.

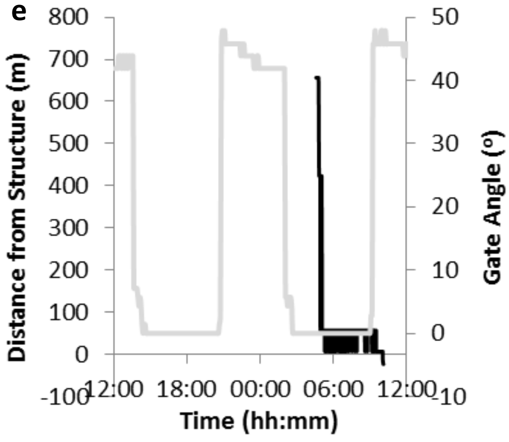
When closed, mean (± SD) water temperature upstream from the tide gates in year 2 did not differ from downstream (10.2 ± 1.0 ^{o}C, $t_{3130} = -0.31$, $P > 0.05$). Mean (± SD) conductivity upstream from closed gates in year 2 (29.9 ± 10.4 mS cm^{-1}) was marginally lower than downstream (31.6 ± 10.3 mS cm^{-1}) ($t_{3130} = -4.53$, $P < 0.05$).

In year 2, more fish were first detected immediately upstream of the tide gates (detection at receiver 4) when they were open (84.0%) compared to year 1 (60.9%) (Table 7.3; Fig. 7.4). Fish that first approached when the gates were open were more likely to take longer than one tidal cycle to pass in year 2 (66.7%) than in year 1 (28.6%). When including fish that initially approached the tide gates when they were closed, the mean (± SD) time from first detection immediately upstream once the gates had opened (detection at receiver 4) to passage downstream (detection at receiver 5) for all fish was 4.73 (± 9.36) h in year 1, and 22.63 (± 34.25) h in year 2.

Table 7.3. Sea trout smolt delay before passage through the tide gate structure in the River Meon, UK, in year 1 (April 2011, pre orifice installation) and year 2 (April 2012, post orifice installation) and gate position when first detected at receiver 4 (immediately upstream of the tide gates).

Category	Gate Position	Delay Before Passage	Fig.	Number of Fish	
				Year 1	Year 2
1	Open	< 1 h	7.4a	7	4
2	Open	1 h to end of tidal cycle	7.4b	3	3
3	Open	> 1 tidal cycle	7.4c	4	14
4	Closed	< 1 h	7.4d	6	1
5	Closed	1 h to end of tidal cycle	7.4e	2	1
6	Closed	> 1 tidal cycle	7.4f	1	2





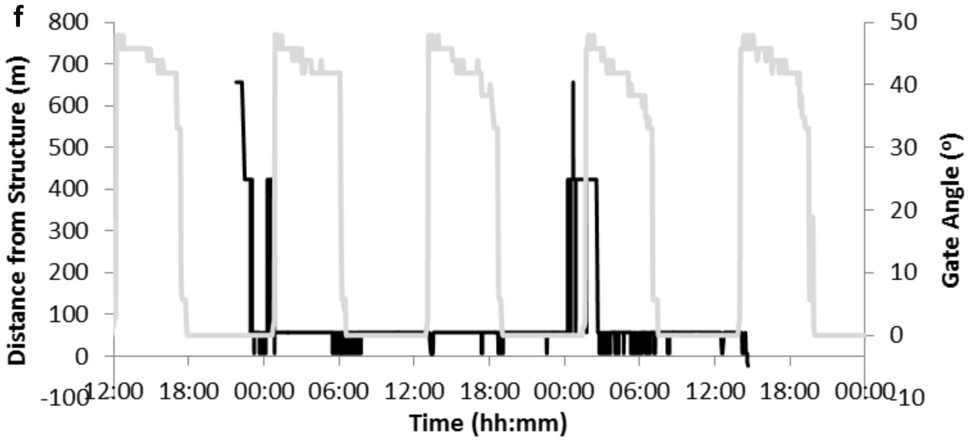


Fig. 7.4. Sea trout smolt movements (▬) during approach to, and passage through, the top-hung tide gate structure in the lower River Meon, Hampshire, UK, during gate angles (▬) that vary with the tidal cycle. Smolt movement patterns were classified into 6 groups, each demonstrated by an individual fish: (a) minimal delay before passage (within 1 h) with gate open on approach to structure (detection at receiver 4); (b) intermediate delay (passage after 1 h and within the same tidal cycle) with gate open; (c) extensive delay (passage after more than one tidal cycle) with gate open; (d) no delay before passage with gate closed on approach; (e) intermediate delay before passage with gate closed; (f) extensive delay before passage with gate closed.

7.5. Discussion

Although tide gates are used worldwide (e.g. Belgium, Mouton *et al.*, 2011; North America, Giannico and Souder, 2005; Australia, Kroon and Ansell, 2006; New Zealand, Doehring *et al.*, 2011), this study is the first to quantify their impact on salmonid smolt passage efficiency and delay. While passage efficiency was high in both years (95.8% - 100.0%), sea trout smolts experienced considerable delay at the tide gates, and this was not reduced by installation of orifices designed to increase fluvial connectivity.

Mitigation of obstructions to fish passage is a key fisheries management challenge (Kemp and O'Hanley, 2010). While evaluation of the effectiveness of various mitigation measures, i.e. different fish pass and screen designs, are relatively common (e.g. Noonan *et al.*, 2012), the impact of unmitigated infrastructure on downstream salmonid migration is seldom quantified (see Aarestrup and Koed, 2003, for an exception). Instead, assumptions of impact tend to be accepted based on anecdote or broad-scale qualitative observation of changes in abundance and diversity of target species. In this study, the passage efficiency at temporal barriers to fish migration created by tide gates was high.

Passage via small-scale weirs and sluices at dams may represent an appropriate analogue with which to compare the results obtained, although comprehensive quantification of these structures is also scarce. Where such studies have been conducted, passage efficiencies are variable. For example, at the Hunderfossen dam in south-east Norway, 100% of radio tagged hatchery-reared sea trout smolts passed via bottom and surface release spill gates (Arnekleiv *et al.*, 2007). For wild and stocked sea trout smolts, respectively, the passage efficiencies of low-head weirs ranged from 46 to 90% (low flows) and 92 to 100% (standard flows) on the River Tweed, UK (Gauld *et al.*, 2013), and 29 to 82% for stocked sea trout smolts in two Danish rivers (Aarestrup and Koed, 2003). Even fewer studies consider salmonid passage efficiency at temporal estuarine barriers. In one example, 100% (1994) and 78.3% (1995) of Atlantic salmon, *Salmo salar*, and sea trout smolts passed the Tawe barrage, UK (Moore *et al.*, 1996). As with tide gates, opportunities for fish to pass the barrage via a navigation lock or over weirs and a fish pass were intermittent. The high passage efficiencies recorded in the current study may to some extent be explained by the relatively large mean apertures of the gates when open (1.2 - 1.3 m). Lower passage efficiencies may be expected for alternative tide gate designs, including other top-hung gates that only open wide during the early stages of the ebb tide.

Despite high passage efficiency, smolts were substantially delayed at the tide gates. The temporal functioning of the gates exerted the greatest influence on speed of migration in both the upstream control and treatment reaches. Tide gates physically block the movement of fish when closed whilst modifying tidal migratory cues (Russell *et al.*, 1998), flow velocities, and thermal and salinity gradients (Giannico and Souder, 2005), all of which may influence speed of migration. Changes in flow regimes (Arnell, 2004), increasing demand for abstraction (Weatherhead and Knox, 2000; Wilby *et al.*, 2006), and sea level rise (Nicholls *et al.*, 1999) will likely cause tide gates to remain closed for longer in the future (Walsh and Miskewitz, 2013).

Speed of migration in the present study was greater at night, supporting the results of a number of smolt studies (e.g. sea trout, Moore *et al.*, 1998a; Atlantic salmon, Thorstad *et al.*, 2012). It is proposed that nocturnal migration may be an adaptive strategy to avoid visual predators (McCormick *et al.*, 1998) and UV radiation damage (Zagarese and Williamson, 2001) in the absence of increased water depths and turbidity. A number of fish that approached closed tide gates at night were delayed until they were able to subsequently pass the open structures the following day.

Even when tide gates were open, the majority of smolts did not pass immediately, reflecting the influence of migratory behaviour. Salmonid smolts actively avoid continuous overhead cover (Greenberg *et al.*, 2012; Kemp *et al.*, 2005b) and accelerating flow (Haro *et al.*, 1998; Kemp *et al.*, 2005a), features commonly created at tide gates. Further, larger scale site specific characteristics may have been influential. Changes in direction of flow and water levels, as the tide gates open and close, may have the potential to cause disorientation.

Delay can have a number of negative impacts, such as increasing predation risk, particularly from piscivorous birds (Koed *et al.*, 2006; McKay *et al.*, 2003; Stewart *et al.*, 2005) such as those which inhabit Titchfield Haven Nature Reserve. Delay can also increase energy expenditure (Congleton *et al.*, 2002), susceptibility to disease (Plumb *et al.*, 2006), and cause mismatch between the onset of oceanic feeding and productivity (Jonsson and Jonsson, 2004) decreasing post smolt survival (Budy *et al.*, 2002).

Modification of tide gates through installation of the orifices did not increase speed of migration. However, river discharge varied between years, and therefore further assessment should be carried out to establish the orifices' impact under a wider range of hydrological conditions. Saline intrusion upstream from the gates was high post modification. Enhanced opportunity for gradual acclimation to sea water upstream from tide gates will likely be advantageous, reducing the potential for osmotic shock when fish encounter an abrupt salinity transition, a condition that may reduce swimming performance (Brauner *et al.*, 1994; Brauner *et al.*, 1992), ability to evade predators (Handeland *et al.*, 1996) and overall survival (Otto, 1971).

7.5.1. Conclusions

In this study, the first to fully quantify the impact of tide gates on salmonid smolt passage efficiency and delay, the following was found:

- Sea trout smolt passage efficiency at tide gates was high.
- Gates delayed smolt migration.
- The period of gate closure was the most significant factor in migratory delay, suggesting that smolts would benefit from the installation of modifications or gates that remain open for a longer proportion of the tidal cycle, such as retarders, side-hung doors, or self-regulating gates.
- Even in the vicinity of open gates, smolt migration was delayed, illustrating the influence of a behavioural component.
- The installation of orifices into tide gates to extend the period of connectivity and extent of saline intrusion did not reduce delay.
- Further research is needed to assess the impact of tide gates on other life stages and species. Assessment of the orifices would benefit from supplementary study across a variety of hydrological regimes, and fine-scale investigation into fish

behaviour at tide gates is also required to improve development of appropriate environmental impact mitigation technology.

Chapter 8

Behavioural response of downstream migrating juvenile sea trout, *Salmo trutta*, to model tide gates under experimental conditions

8.1. Summary

Tide gates provide flood protection by closing during high water, temporarily preventing longitudinal movements of fish between essential habitats. When gates open during the ebb, downstream migration may be impeded or delayed if environmental conditions encountered induce avoidance behaviours. Tide gates have been modified in an attempt to improve passage and minimise delay, but quantification of the effectiveness of these changes has been limited. This experimental study assessed the impact of a top-hung tide gate and associated modifications that allowed it to open wider and for longer on the behaviour of downstream migrating wild juvenile sea trout, *Salmo trutta*, in a flume. Discharge was maintained at 0.08 $m^3 s^{-1}$ under three treatments comprising a top-hung gate mounted at different angles (30^o, 19^o, 14^o) and a control (no gate). Fish were more likely to exhibit avoidance (switch in orientation from negative to positive rheotaxis, increased tail beat frequency, retreat upstream) in the vicinity of a gate with a smaller angle and passage aperture. Individuals approaching the gate slowed more when a higher number of avoidance responses were exhibited. Initial avoidance responses occurred at 1.40 (± 1.24) body lengths upstream from the gate and in the absence of visual cues. Fish reacted at the same spatial velocity gradient (0.9 ± 0.2 cm s^{-1} cm^{-1}) along their body regardless of treatment, although this was greater for fish exhibiting positive rheotactic orientation. This study indicated that modifying top-hung tide gates so that they open wider and for longer could reduce behavioural avoidance in actively migrating juvenile salmonids.

8.2. Introduction

River and estuary infrastructure, such as dams, weirs and barrages, fragments critical habitat and obstructs the migration of diadromous fish (Pess *et al.*, 2008; Pringle *et al.*, 2000). Fishways and bypass systems have been installed at many sites in an effort to mitigate for the impact of such impediments on the movements of fish. Considerable focus has been directed at upstream migrating life stages, where passage success is dictated by the fishway's capacity to: (1) attract fish to the entrance, (2) permit entry, and (3) enable successful ascent. To achieve this, the fishway must provide hydrodynamic conditions (velocities and turbulence) suitable for fish passage without disorientation (Beach, 1984; Tritico and Cotel, 2010). Further, the environment encountered should not induce avoidance behaviours that result in delay (Jansen *et al.*, 2007; Jepsen *et al.*, 1998) or conditions that favour predators (Agostinho *et al.*, 2012).

With some notable exceptions (e.g. Aarestrup and Koed, 2003; Kemp *et al.*, 2008; Moore *et al.*, 1998b) fish passage for downstream migrating life stages is less often considered than for those migrating upstream (Katopodis and Williams, 2012). As for upstream moving fish, behaviour is an important determinant of passage efficiency as clear attraction to the entrance of a preferred route, such as a bypass, and the absence of conditions that induce disorientation, avoidance and associated delay are important (Johnson and Moursund, 2000; Svendsen *et al.*, 2011).

Provision of fish passage facilities are commonly considered for large riverine infrastructure (e.g. Arnekleiv *et al.*, 2007; Coutant and Whitney, 2000; Johnson and

Dauble, 2006; Schilt, 2007), rather than smaller but more abundant intermittent barriers to migration such as weirs, ramps, and tide gates (Lucas *et al.*, 2009). Tide gates discharge water on the ebb and close under hydraulic pressure on the flood tide to prevent tidal inundation, thus restricting abundance, richness (Boys *et al.*, 2012; Pollard and Hannan, 1994) and movement (Doehring *et al.*, 2011) of estuarine dwelling fish. Recent research using telemetry shows that tide gates delay the movement of downstream migrating adult European eel (Chapter 6) and sea trout smolts (Chapter 7) in English streams. Delay was primarily related to the duration of gate closure. Migration after gate opening was not instantaneous, and may have been a result of factors such as: (1) the absence of strong tidal cues that facilitate migration (Russell *et al.*, 1998), (2) disorientation due to changes in upstream flow direction, and (3) avoidance of abrupt shifts in salinity (Zaugg *et al.*, 1985), sudden temperature gradients (Berggren and Filardo, 1993; Boyd and Tucker, 1998; Jonsson, 1991), and/or overhead cover created by culverts associated with gates (Greenberg *et al.*, 2012; Kemp *et al.*, 2005b). Further, accelerating (Kemp *et al.*, 2005a, for wild Pacific salmonids; Haro *et al.*, 1998, for wild Atlantic salmon, *Salmo salar*; Piper *et al*., under review for European eel, *Anguilla anguilla*) and/or decelerating current velocities (Enders *et al.*, 2012, for Chinook salmon, *Oncorhynchus tshawytscha*) commonly found at river infrastructure may impede downstream migration at tide gates by inducing avoidance of hydrodynamic gradients. Researchers frequently struggle to quantify the influence of environmental variables on fish behaviour in the field due to the difficulty in isolating confounding factors and manipulating those of interest, while being restricted by limitations of equipment on recording fine-scale fish behaviour (Rice *et al.*, 2010). There is, therefore, a need to take an experimental approach using physical models to identify the mechanisms contributing to migratory delay at obstructions such as tide gates and to establish appropriate mitigation via both field and experimental flume-based methods (Rice *et al.*, 2010).

In an effort to improve fish passage efficiency and reduce delay, traditional top-hung tide gates have been replaced or modified with side-hung doors, self-regulating valves, lightweight gates, counterbalances or retarders that decrease the hydraulic head differential required to open them for longer and wider. Another option is to install an orifice in the gate, which extends the period of connectivity without increasing the aperture or duration of gate opening. To date, orifice installation has not benefitted upstream moving adult brown trout (Chapter 5), or downstream migrating smolts (Chapter 7) establishing a requirement for other mitigation options to be developed. The effectiveness of mitigation measures that decrease hydraulic head differential to improve fish passage has not yet been reported.

This study aimed to assess the fine-scale impact of tide gates on the downstream migration of juvenile sea trout (anadromous brown trout) smolts under controlled experimental conditions. Sea trout have suffered declines throughout Europe (e.g. Borsuk *et al.*, 2006), including the UK (Harris and Milner, 2006), where the species is listed as threatened under the UK Biodiversity Action Plan (JNCC, 2010). The movements of downstream moving sea trout smolts in an experimental flume were analysed to establish the effectiveness of open top-hung tide gates and modifications designed to allow them to open wider and for longer.

8.3. Materials and methods

8.3.1. Experimental flume arrangement

Experiments were performed using an indoor recirculatory flume (length = 21.40 m, width = 1.37 m, depth = 0.60 m) at the International Centre for Ecohydraulics Research, University of Southampton, UK. An opaque acrylic plastic model top-hung tide gate (length = 1.16 m, width = 0.11 m, depth = 0.73 m) was attached 0.13m above the maximum water level of the flume (Fig. 8.1a). Upstream from the gate, wooden panels (length = 9.76 m, width = 0.16 m, depth = 0.61 m) constricted the flume to replicate a smooth box culvert (Fig. 8.1b). To assess the influence of modifications that allow tide gates to open wider for longer, four experimental setups were used: (1) control (no gate); (2) treatment 1 (gate fixed open at an angle of 31^o to the vertical); (3) treatment 2 (gate fixed open at 19^o), and (4) treatment 3 (gate fixed open at 14^o) (Fig. 8.1a).

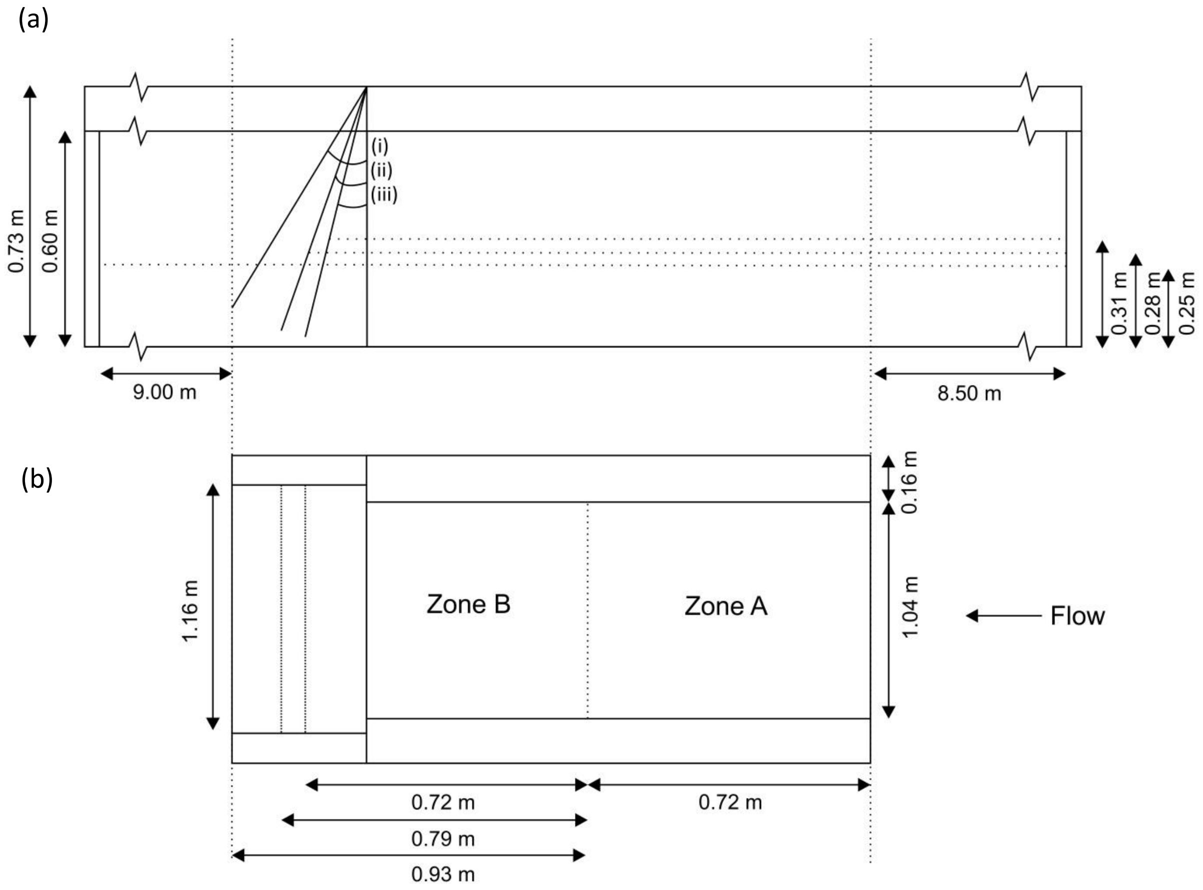


Fig. 8.1. (a) Schematic profile of the experimental flume channel used to assess the behaviour of downstream migrating wild sea trout smolts at a model tide gate set to one of three angles: (i) 31^{o} (treatment 1), (ii) 19^{o} (treatment 2), and (iii) 14^{o} (treatment 3) compared with a control (no gate). (b) Plan view of the observation area divided into zones A and B for behavioural analysis.

Discharge through the flume was maintained at 0.08 $m^3 s^{-1}$ for all setups. Mean water depths upstream from the gate were 25.0, 25.0, 27.6 and 31.0 cm for the control and treatments 1 to 3, respectively (Fig. 8.1a). Mean water depth downstream from the gate (25.0 cm) did not vary between setups.

An Acoustic Doppler Velocimeter (ADV) (Model: Vectrino+, Nortek, Nova Scotia, Canada) was used to measure mean longitudinal ($\bar{u}$), lateral ($\bar{v}$) and vertical ($\bar{w}$) water velocities at 50 Hz (sample volume 0.31 cm^3) at the bottom, middle, and top (80%, 50%, and 20% depth, respectively) of the water column and at 4 to 10 cm intervals across the length and width of the observation area. Over a duration of 60 s, 3000 velocity readings were recorded for each sampling point. ADV data was then processed in Microsoft Excel using a minimum/maximum threshold filter according to Cea *et al.* (2007). The mean velocity vector (V) was then calculated as:

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

At 50% water depth and 1.40 m upstream from the gate, V was 0.30, 0.28, 0.26, and 0.21 m s^{-1} for the control and treatments 1 to 3, respectively. ArcGIS 10.1 (ESRI, Redlands, CA, USA) was used to produce mean velocity vector contour plots using spline interpolation.

The observation area was monitored by an overhead infra-red camera, illuminated by infra-red LED panels and was split into two zones for analysis purposes (Fig. 8.1b) based on changes in longitudinal velocity increase and decrease (Table 8.1): (A) velocity gradient absent and (B) velocity gradient present.

Table 8.1. Longitudinal velocity increase/decrease through zones A (0.55 to 1.27 m upstream of the gate's apex) and B (bottom of the gate to 0.55 m upstream of the apex) in an experimental flume at three top-hung gates angles, and a control with no gate, assuming a linear gradient.

Channel Location	Setup	Gate Angle	Increase or Decrease in Velocity (m s^{-1})	
			Zone A	Zone B
Centre	Control	No Gate	0.00	-0.01
	Treatment 1	31^o	0.00	-0.06
	Treatment 2	19^o	-0.01	-0.06
	Treatment 3	14^o	0.00	-0.04
Walls	Control	No Gate	0.00	0.00
	Treatment 1	31^o	0.00	0.06
	Treatment 2	19^o	0.01	0.07
	Treatment 3	14^o	0.00	0.13

Flow velocity in zone A for treatment 1 replicated those through gated culverts in the River Meon, UK, at low water during the ebb tide measured over a period of a week in April 2012 (0.34 [± 0.02] m s^{-1}) and were similar to those recorded at other tide gated culverts (e.g. Gate 1, River Stiffkey, UK, 0.22 [± 0.20] m s^{-1}).

8.3.2. Fish capture and maintenance

Actively migrating wild sea trout smolts (*n* = 120) were trapped during the hours of darkness on 30 and 31 March 2012 in the River Blackwater, Hampshire, UK (50° 57' 3.69" N; 1° 30' 53.74" W), using a winged fyke net with a fine mesh (1 mm) catch box (height = 1.0 m, width = 0.5 m, length = 0.5 m) at the distal end. Smolts were transported in aerated containers to the ICER experimental facility where they were held in two tanks totalling 4000 L capacity (stocking density =2.2 kg m^{-3}). Mean (± SD) fork length (FL) (194.7 ± 14.6 mm) and mass (72.1 ± 17.7 g), and did not vary between setups (univariate ANOVA, FL: $F_{3, 106} = 0.29$, $P > 0.05$; weight: $F_{3, 106} = 0.33$, $P > 0.05$). A filtration system aerated the tanks and along with 10% water changes twice weekly ensured high water quality ($NH_3 = 0$, $NO_3 < 50$ mg l^{-1}, $NO_2 < 1$ mg l^{-1}) was maintained. Mean (± SD) tank temperature was 11.9 (± 1.2) ^{o}C.

8.3.3. Experimental protocol

Between 7 and 15 April 2012, a total of 12 trials were performed during the hours of darkness (22:00 to 04:00 h British Summer Time) when sea trout smolts are most active (Moore *et al.*, 1998a). Three separate trials were conducted for each setup (control and treatments 1 - 3). For 1.0 h prior to each trial, fish (*n* = 10) were held at the location of release (9.76 m upstream of the gate) in a perforated container in the flume to acclimatise. At the start of each trial, fish were released and allowed to move downstream volitionally. After an hour each trial was terminated and fish measured and weighed. Setups were randomly assigned between trials to avoid bias related to capture date and/or fluctuations in temperature. Temperature was logged every 5 minutes throughout each trial (Onset, Bourne, Massachusetts, USA; Model UA-002-64), with average temperature varying by a maximum of 0.6^{o}C between setups.

8.3.4. Fish behaviour

Fish behaviour was recorded during passage through the observation area (length = 1.4 to 1.7 m, width = 104.0 m, Fig. 8.1b), and assessed in two parts: (1) as a population, and (2) as individuals. During population analysis smolts could pass through the gate multiple times. Over the 1 hour duration of each trial, the number of times each of the following behavioural traits occurred per approach to the gate were quantified: (1) *orientation switches* (changing from positive to negative rheotaxis); (2) *increased tail beat frequency* and *holding* (maintaining station for > 5 s), and (3) *rejections* (moving upstream from zone A). Orientation during passage past the gate was also assessed.

For individuals, behaviour was recorded during final passage through the observation area (Fig. 8.1b) prior to passing the tide gate for the first time, but before any fish from that trial that had passed the gate moved upstream again. Duration and rheotaxis during passage through each zone in the observation area and past the gate were recorded. A side-mounted infra-red camera recorded the exact time of passage past the gate, and approximate depth in the water column at which an initial reaction occurred (top, middle, or bottom) through a glass panel in the flume wall. During passage through the observation area, the following behavioural traits were assessed: (1) orientation switch; (2) increased tail beat frequency; (3) holding (maintaining station for > 5 s).

When a behavioural response was observed, head and tail coordinates, and total fish length, were attained using video tracking software (Logger Pro v3.8.2, Vernier Software, Beaverton, OR, USA). Coordinates were transferred to ArcGIS and overlaid onto a velocity profile of the corresponding setup and depth at which the reaction occurred (top, middle, or bottom). Reaction velocity (R_V) at the point of response was calculated, in addition to spatial velocity gradient along the fish's body (R_{VG}), as described by Enders *et al.* (2009):

$$R_{VG} = \frac{(V_{US} - V_{DS})}{L}$$

where V is the velocity at the head or tail position upstream (US) and downstream (DS), and L is the fish's total length. Coordinates for DS also enabled the distance of reaction upstream from the gate (R_D) to be measured, expressed as fish body lengths, BL.

8.3.5. Data analyses

For population analysis, univariate ANOVA (F) with Bonferroni corrected post hoc tests were used to compare behaviour (orientation switches, increased tail beat frequency and holding, and rejections per approach). For individual analysis, duration of passage through zones A and B were converted to speed to account for the greater length of zone B in treatments 1 and 2. The speed of movement was calculated for each zone as the quotient of the distance (m) separating upstream and downstream extents of the zone and duration (s) between first observation of the entire fish's body at each. Speed data were square route transformed to comply with the assumption of normality (Shapiro-Wilk: $P > 0.05$). Repeated-measures ANOVAs were used to test for differences in speed between zones for each setup.

All remaining data were normally distributed (Shapiro-Wilk: $P > 0.05$) with homogenous variance (Levene's tests: $P > 0.05$). Univariate ANOVA (F) with Bonferroni corrected post hoc tests were used to compare speed, behaviour (orientation switch, increased tail beat frequency, holding), and physical data recorded at time of initial response for individuals (R_V, R_D, R_{VG}) between setups. Pearson chi-square (X^2) tests were used to compare orientation (positive or negative rheotaxis) through zones A, B or under that gate, or the probability of orientation switch between setups. Independent t-tests compared R_V, R_D, and R_{VG} between orientation (positive or negative rheotaxis) and direction of the velocity gradient (accelerating or decelerating). Pearson's r was used to assess the relationship between speed through the observation area and the number of instances a behavioural response was initiated.

8.4. Results

8.4.1. Population level analysis

Fish were more likely to switch orientation when the gate was present (treatments 1 - 3) compared to absent (control) ($F_{3,8} = 4.97$, $P < 0.05$; Fig. 8.2). Increased tail beat frequency and holding behaviours occurred more at lower gate angles (treatments 2 and 3, 19^o and 14^o, respectively) ($F_{3,8} = 18.84$, $P < 0.01$; Fig. 8.3) and the number of rejections per approach, where fish moved upstream out of the observation area, were greater in treatment 3 ($F_{3,8} = 9.48$, $P < 0.05$; Fig. 8.4).

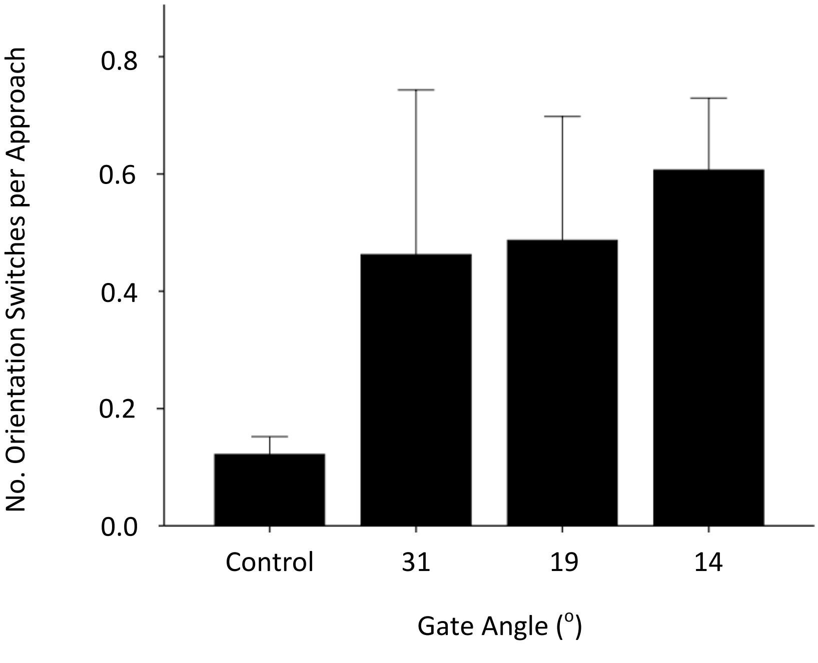


Fig. 8.2. Mean (± SE) number of orientation switches by downstream moving sea trout smolts during per approach to a tide gate opened at three different angles or no gate (control) in an experimental flume.

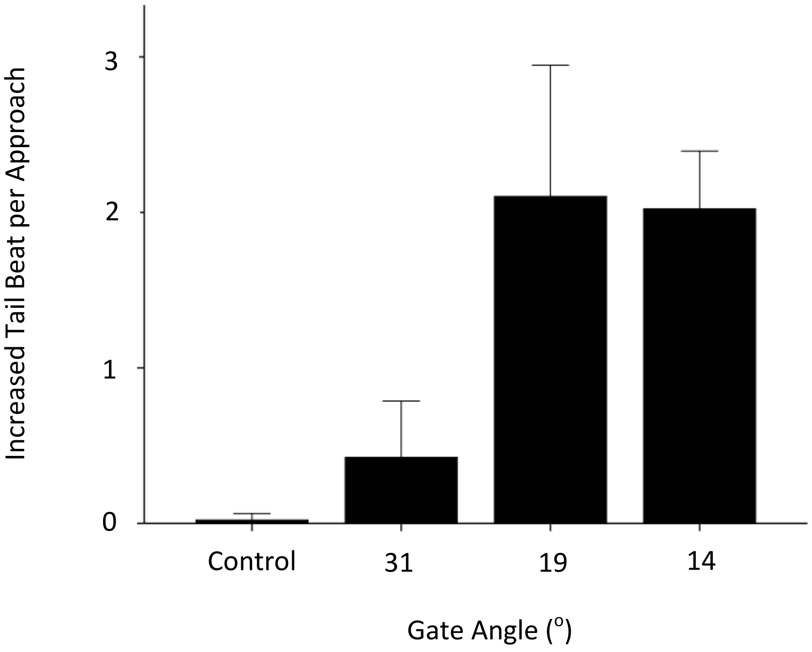


Fig. 8.3. Mean (± SE) number of times downstream moving sea trout smolts increased tail beat frequency and holding per approach to a tide gate opened at three different angles or no gate (control) in an experimental flume.

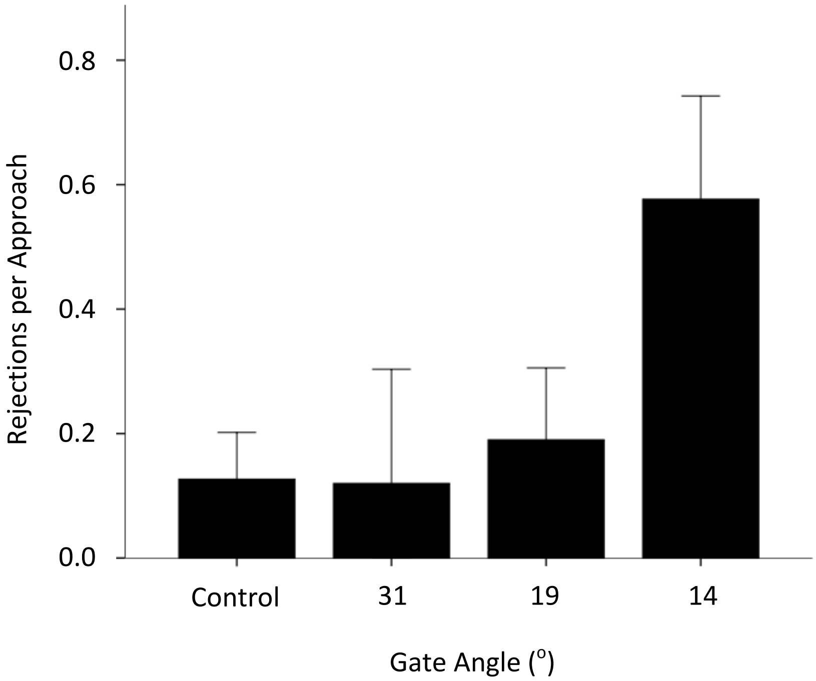


Fig. 8.4. Mean (± SE) number of rejections for downstream moving sea trout smolts per approach to a tide gate opened at three different angles or no gate (control) in an experimental flume.

8.4.2. Analysis of individuals

During their final time in the observation area, smolts travelled faster through zone A than B in all setups except the control (Fig. 8.5; Table 8.2). Speed of movement downstream did not differ between setups for zone A (velocity gradient absent) ($F_{3, 71}$ = 1.31, $P > 0.05$), but did for zone B (velocity gradient present) ($F_{3, 71}$ = 4.70, $P < 0.01$), with treatment 3 (14°) slower than the control ($P < 0.001$) and treatment 1 (31°) ($P < 0.05$).

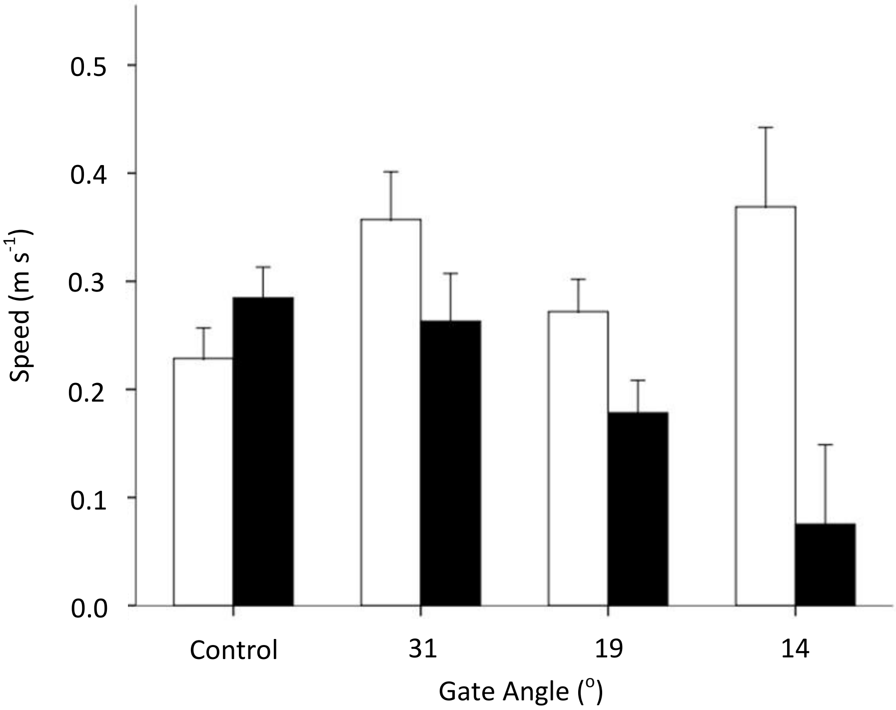


Fig. 8.5. Mean (± SE) speed of downstream movement during final passage through the observation area comprising of zones A (□) (velocity gradient present) and B (■) (velocity gradient absent) (0.7 to 1.4 m and 0.0 to 0.7 m upstream from the gate, respectively) for 75 sea trout smolts encountering three different gate angles or no gate (control) in a flume.

Forty-seven and 41% of smolts exhibited a positively rheotactic orientation when passing through zones A and B, respectively. There was no difference in fish orientation through zone A (X^2_3 = 2.74, $P > 0.05$) or B (X^2_3 = 1.03, $P > 0.05$) between setups. Smolts moved downstream faster when facing downstream (zone A: $F_{7, 67}$ =

11.31, $P < 0.001$; zone B: $F_{7, 67} = 11.64$, $P < 0.001$), for all setups except treatments 2 and 3 for zone B ($P > 0.05$). Speed was negatively related to the mean total number of avoidance reactions exhibited by fish ($r = -0.59$, $P < 0.01$).

Table 8.2. Mean ± SD duration and speed of downstream movement for 75 sea trout smolts through an observation area comprising of zones A (velocity gradient absent, 0.55 m to 1.27 m upstream of the gate's apex) and B (velocity gradient present, bottom of the gate to 0.55 m upstream of the apex) and before encountering a tide gate opened at three different gate angles or no gate (control) in an experimental flume. Repeated-measures ANOVAs compared speeds within each setup.

Setup	Gate angle	*n*	Duration (s)		Speed (m s^{-1})		Repeated-measures ANOVA			
			A	B	A	B	*F*	*df*	*error*	*P*
Control	No gate	18	22.32 ± 46.24	13.19 ± 30.69	0.23 ± 0.18	0.28 ± 0.21	3.18	1	17	0.092
Treatment 1	31	22	6.57 ± 13.53	97.66 ± 290.74	0.36 ± 0.33	0.26 ± 0.24	6.75	1	21	0.017^{*}
Treatment 2	19	18	4.37 ± 3.94	27.58 ± 52.81	0.27 ± 0.20	0.18 ± 0.19	8.07	1	17	0.011^{*}
Treatment 3	14	17	3.62 ± 3.16	44.31 ± 93.79	0.37 ± 0.29	0.08 ± 0.08	27.56	1	16	0.000^{**}

$^{*}P < 0.05$

$^{**}P < 0.001$

Smolts were more likely to switch orientation prior to passage when gate angles were low ($X^2_3 = 20.24$, $P < 0.001$) (Fig. 8.6). Reacting fish switched orientation if negatively rheotactic on approach to the gate, or increased tail beat frequency if positively rheotactic. All switches were from negative to positive rheotaxis, and smolts were more likely to face upstream whilst passing through gates with lower angles ($X^2_3 = 22.67$, $P < 0.001$) (Fig. 8.7). The number of times fish exhibited increased tail beat frequency increased with decreasing gate angle ($F_{3, 71} = 6.15$, $P < 0.01$) (Fig. 8.8), with differences between the control and treatments 2 ($P < 0.05$) and 3 ($P < 0.01$). There was no difference in the number of times smolts exhibited holding, or duration of holding, between setups ($F_{3, 71} = 1.29$, $P > 0.05$; $F_{3, 71} = 1.18$, $P > 0.05$, respectively).

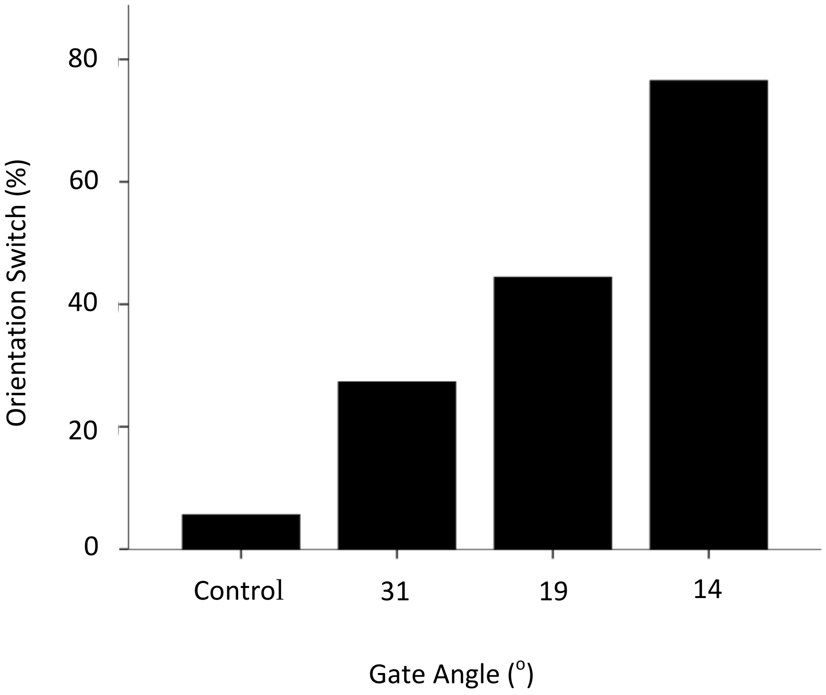


Fig. 8.6. Percentage of sea trout smolts ($n = 75$) that switched orientation to positive rheotaxis prior to passing a tide gate at three different angles or no gate (control) in an experimental flume.

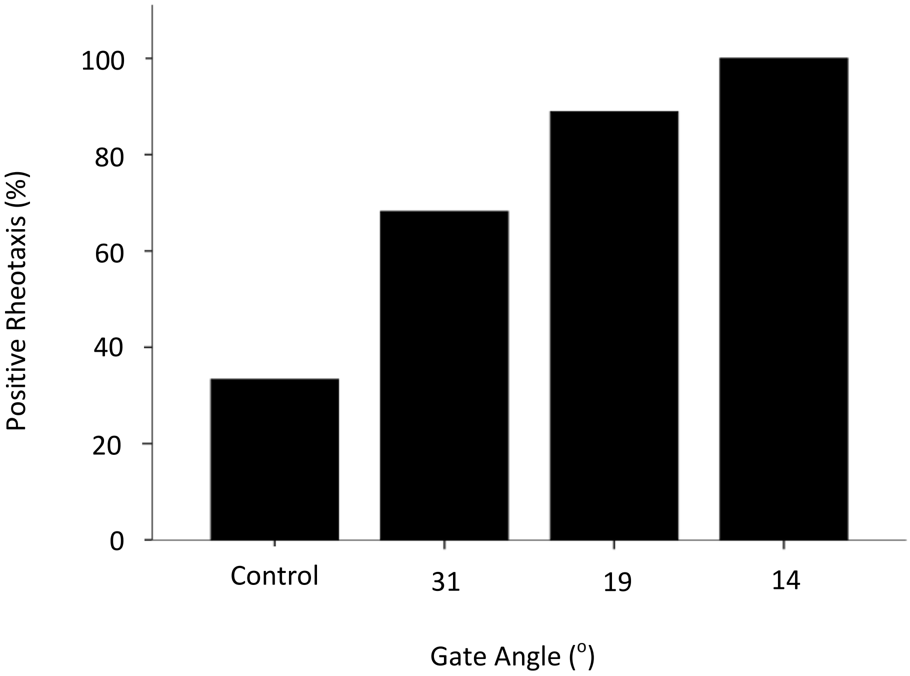


Fig. 8.7. Percentage of sea trout smolts exhibiting positive rheotaxis when passing a gate at three different angles or no gate (control) in an experimental flume.

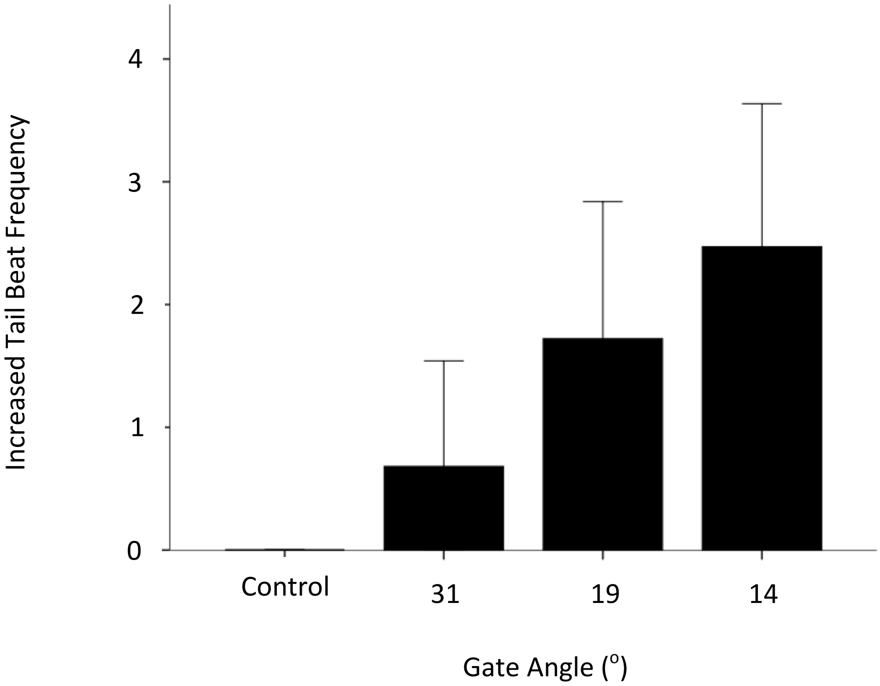


Fig. 8.8. Mean (± SE) number of times increased tail beat frequency was exhibited by 75 sea trout smolts encountering three different gate angles or no gate (control) in an experimental flume.

Initial avoidance responses occurred 1.40 (± 1.24) BL upstream from the gate. R_V was greater in the control and treatments 1 and 2 than 3 ($F_{3,42} = 6.34$, $P < 0.01$; Table 8.3; Fig. 8.9) but R_D ($F_{3,42} = 1.34$, $P > 0.05$) and R_{VG} ($F_{3,42} = 0.271$, $P > 0.05$) did not vary between setups (Table 8.3). Mean (± SD) R_V was greater for positively (0.27 [± 0.04] m s^{-1}) than negatively rheotactic fish (0.24 [± 0.04] m s^{-1}) ($t_{44} = -2.58$, $P < 0.05$), as was R_{VG} (positive rheotaxis: -0.16 [± 0.24] cm s^{-1} per cm; negative rheotaxis: -0.02 [± -0.14] cm s^{-1} per cm; $t_{29.3} = -2.34$, $P < 0.05$), whilst R_D was unaffected ($t_{44} = -0.41$, $P > 0.05$). R_{VG} of fish reacting to accelerating flow did not differ from those reacting to decelerating flow ($t_{44} = 1.721$, $P > 0.05$).

Table 8.3. Mean ± SD initial avoidance response velocity (R_V), distance from gate (R_D) (reported as body lengths, BL) and spatial velocity gradient (R_{VG}) of smolts during final passage through the observation area whilst encountering three different gate angles (treatments 1, 2, and 3; 31°, 19°, and 14°, respectively) or no gate (control) in an experimental flume.

Setup	*n*	R_V (m s^{-1})	R_D (BL)	R_{VG} (cm s^{-1} cm^{-1})
Control	2	0.28 ± 0.01	0.78 ± 1.10	-0.04 ± 0.00
Treatment 1	13	0.27 ± 0.03	1.76 ± 1.67	-0.10 ± 0.20
Treatment 2	14	0.26 ± 0.05	0.93 ± 0.88	-0.09 ± 0.29
Treatment 3	17	0.22 ± 0.03	1.58 ± 1.08	-0.08 ± 0.12

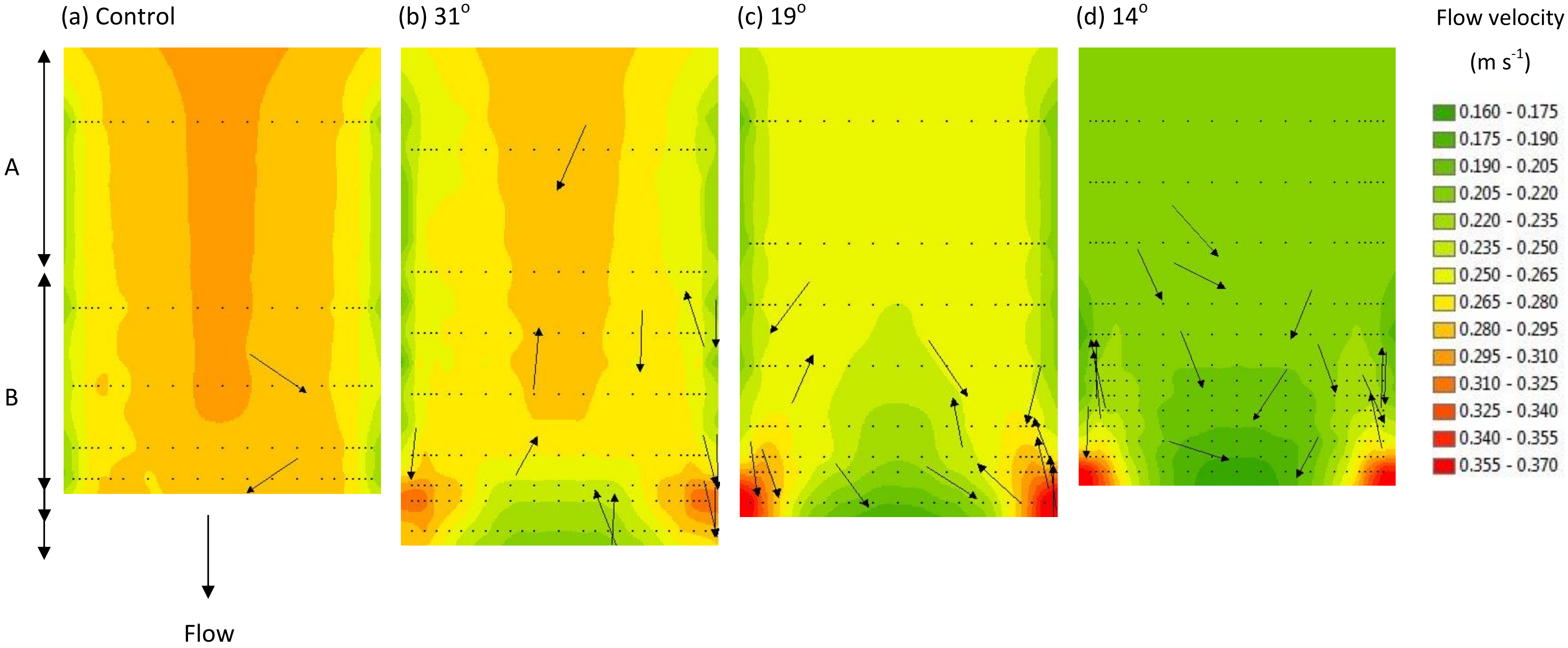


Fig. 8.9. Flow velocity profiles of the observation area with sampling locations (•) measured at 50% depth for a control setup with no gate (a) and treatments 1 to 3 with different gate angles (31° [b], 19° [c], and 14° [d], respectively), split into zones A (velocity gradient absent) (0.55 m to 1.27 m upstream of the gate's apex) and B (velocity gradient present) (bottom of the gate to 0.55 m upstream of the gate's apex). Arrows represent sea trout smolts that initiated an avoidance reaction (Table 8.3), indicating their length, orientation and location immediately prior to their initial response to switch orientation if negatively rheotactic or increase tail beat frequency if positively rheotactic.

8.5. Discussion

Tide gates delay downstream migrating sea trout smolts in the field (Chapter 7). Studies of fish in their natural environment, however, often fail to provide fine-scale information on behaviour needed to understand the mechanisms that explain responses observed (Rice *et al.*, 2010). In this study, downstream migrating wild sea trout smolts encountered areas of accelerating and decelerating flow velocity created by a model tide gate under experimental conditions. Small gate angles and narrow apertures created abrupt velocity gradients which induced behavioural avoidance and delayed downstream progress.

Active migration was observed in the present study, where smolts passed through zone A at the same speed independent of setup. During passage through this zone, smolts exhibited both positive and negative rheotaxis, contrary to the findings of others where smolts would swim predominately head-first (Enders *et al.*, 2009; Kemp *et al.*, 2005a; Swanson *et al.*, 2004 for Pacific salmonids) or tail-first (Johnson *et al.*, 2000, for Pacific salmonids; Haro *et al.*, 1998, for Atlantic salmon). Variances in orientation may result from differences in species (Thorpe, 1982), genetics (Aarestrup *et al.*, 1999; Nielsen *et al.*, 2001), origin (hatchery or wild: Marchetti and Nevitt, 2003), and flow velocity (Enders *et al.*, 2009), although the different velocities between setups in the present study (0.21 to 0.30 m s^{-1}) had no effect. Migration through zone A was faster for fish oriented downstream head-first, a finding corroborated by Pacific salmonids diverted at the McNary Dam, USA, into an experimental flume (Kemp *et al.*, 2005a).

Delay can increase energy expenditure (Congleton *et al.*, 2002), predation risk (Schilt, 2007), and disease transfer where congregation occurs (Garcia de Leaniz, 2008). Movement through zone B, where steep velocity gradients were localised, was slower at smaller gate angles and negatively correlated with the mean number of avoidance responses (switching orientation, increased tail beat frequency, holding, and/or retreat) exhibited by smolts. Negatively rheotactic fish that displayed an avoidance response switched orientation, a behaviour documented for salmonids encountering accelerating or decelerating flows at other structures (e.g. orifices: Enders *et al.*, 2012; Enders *et al.*, 2009; Russon and Kemp, 2011a, screens: Enders *et al.*, 2012, constrictions: Kemp *et al.*, 2005a; Vowles and Kemp, 2012; surface bypasses: Johnson *et al.*, 2000). Negatively rheotactic smolts switched orientation regardless of the velocity gradient direction. Switching to, and maintaining, positive rheotaxis enables fish to control their progression downstream, extend exposure to environmental stimuli and avoid deleterious consequences from disorientation, which could increase vulnerability to predation or passage into dangerous locations (Kemp *et al.*, 2005a). This is supported by positively rheotactic fish in the present study only reacting by increasing tail beat frequency or holding station. These responses increased with lower gate angles. Conversely, Haro *et al.* (1998) found that positively rheotactic Atlantic salmon, smolts would switch orientation. This behavioural variation could be a result of higher velocities experienced at their experimental weirs' crests (2.00 and 3.00 m s^{-1}) when compared to the present study (maximum velocity at the gate = 0.37 m s^{-1}).

For hatchery-reared brown trout, Russon and Kemp (2011a) found that the duration of holding station increased in the presence of a benthic orifice weir when compared to a mid-column orifice. Interestingly, the duration of, and the number of times smolts exhibited, holding behaviour in the present study did not differ between setups, meaning that active searching behaviour was higher at small gate angles. Similar behaviours have been reported at dams or weirs that create steep velocity gradients (Croze and Larinier, 1999; Johnson and Moursund, 2000).

Variation in water velocity is detected along a fish's mechanosensory lateral line (Bleckmann, 1994). Smolts in the present study responded at a discrete spatial velocity gradient along their body of approximately 0.9 cm s^{-1} cm^{-1} irrespective of gate angle or direction of velocity gradient (accelerating or decelerating), similar to those reported for Chinook salmon smolts (accelerating flow: ~0.1 cm s^{-1} cm^{-1}, Enders *et al.*, 2009; ~1.2 cm s^{-1} cm^{-1}, Enders *et al.*, 2012; decelerating flow: ~1.0 cm s^{-1} cm^{-1}, Enders *et al.*, 2012). For Atlantic salmon, smolts avoided passage at a sharp-crested weir (2 m s^{-1} m^{-1}), but not an adapted weir (1 m s^{-1} m^{-1}) (Haro *et al.*, 1998), suggesting that a spatial velocity gradient threshold of approximately 1 cm s^{-1} cm^{-1} exists, reflecting the optimum swimming speed of fish and minimisation of energetic costs (Enders *et al.*, 2012). By contrast, hatchery-reared juvenile brown trout responded to lower spatial velocity gradients (~0.4 cm s^{-1} cm^{-1}) (Vowles and Kemp, 2012) which could reflect the influence of origin (hatchery or wild) on experience, swimming capabilities (Pedersen *et* *al.*, 2008) and costs (Enders *et al.*, 2004). Positively rheotactic smolts in the present study, which responded with increased tail beat frequency, reacted at a higher spatial velocity gradient in agreement with the findings of Enders *et al.* (2009). This is presumably another result of upstream orientation allowing more controlled descent, time to process mechanosensory information and quicker propulsion upstream and away from potentially harmful conditions. Although distance of initial avoidance response from the gate did not vary with gate angle, Vowles and Kemp (2012) found that the distance of reaction upstream from a constriction increased during illuminated trials that allowed juvenile hatchery brown trout to experience visual stimuli. This could impact the migration of smolts that approach closed tide gates at night, which subsequently open to allow passage during daylight hours (Chapter 7).

8.5.1. Conclusions

Understanding the mechanisms which contribute to delay at tide gates is crucial for successful fisheries management. This study demonstrated that smaller apertures resulting from traditional, heavy, and unmodified top-hung tide gates could accentuate passage avoidance and increase energetic costs by increasing tail beat frequency and other avoidance behaviours. As a result, modifying gates to increase the angle of opening, by the addition of retarders or counterbalances, or refitting with lightweight gates, side-hung doors or self-regulating gates could be beneficial.

Chapter 9

General Discussion

Habitat fragmentation is a fundamental concern in conservation biology (Meffe and Carroll, 1997). Discontinuity in the spatial distribution of resources and unique environments can limit habitat use, reproduction, and survival of a diversity of species (Franklin *et al.*, 2002). As a result, the contribution of organisms to important ecosystem services may be reduced or inhibited. Diadromous fish provide protein and other nutrients to consumers, transfer energy between marine, freshwater and terrestrial environments (Schindler *et al.*, 2003) and support the recreational and commercial activities of humans (Environment Agency, 2003). Unfortunately many diadromous species are undergoing population declines (Limburg and Waldman, 2009). Anthropogenic infrastructure in rivers and estuaries has contributed to this (e.g. Naughton *et al.*, 2005), reducing the ability of diadromous fish to fulfil ecosystem services. Fluvial obstructions contribute to habitat loss by altering the local environment and influencing connectivity between essential habitats in terms of ease, distance and/or duration of passage (Poff and Hart, 2002). Although the impact of riverine infrastructure on habitat fragmentation is relatively well recognised, potential obstructions to migration in the estuarine environment have received comparatively little consideration (see Chapter 2).

Estuaries and coasts form a vital nucleus for human activity, providing access for shipping, reliable water supplies, fertile alluvial agricultural land and productive waters supporting numerous fish and shellfish species (Edgar *et al.*, 2000). Human populations will continue to depend on this valuable resource. As sea level and flood risk continue to rise (Nicholls *et al.*, 1999) the integrity of many of these services will depend on maintenance or even installation of new coastal and estuarine infrastructure. This thesis aimed to identify the impact of tide gates, one of the most tidally restrictive anthropogenic estuarine modifications, on the migration of diadromous fish. This chapter summarises and considers the key findings of this research while outlining recommendations for management and future study.

9.1. Key findings and recommendations for management and further research

An index for quantifying longitudinal connectivity for fish in river systems developed by Cote *et al.* (2009) highlighted that the furthest downstream stages of fragmentation impact connectivity most because fewer alternate routes, if any, exist. As a result, decreased connectivity caused by tide gates could have serious impacts on habitat availability for diadromous fish. In this thesis, passage efficiency of upstream moving adult brown trout, *Salmo trutta*, and downstream migrating juvenile sea trout, *Salmo trutta,* and adult European eel, *Anguilla anguilla* past top-hung tide gates was high (Table 9.1). Although little information on the impact of tide gates on diadromous fish passage exists elsewhere, structures that may create analogous conditions to open gates showed wide variations in passage efficiency for different species. For juvenile salmonid smolts, passage efficiency at combined bottom and surface release gates (Arnekleiv *et al.*, 2007) and a temporally passable estuarine barrage (Moore *et al.*, 1996) were exceptionally high (100%). Conversely, European eel passage efficiency ranged from 100% at a complex of intertidal structures (Piper *et al.*, 2013) to 15% at undershot spill gates (Calles *et al.*, 2010). Combined attraction and passage efficiency of upstream migrating adult salmonids at estuarine sluices (Bij de Vaate *et al.*, 2003) and tide gates (Vincik, 2013) ranged from 14 - 49%. These diverse results highlight the variation that can occur in the ability of structures with seemingly marginal differences in design, operational regimes, hydraulic conditions, and environments to pass migratory fish. Although passage efficiencies reported in this thesis indicated relatively little impact of top-hung tide gates on diadromous fish movement, care must be taken when considering the effects of other gates at different sites. The complexity created by variations in gate design, weight, buoyancy, hinge type and resistance, culvert elevation, location in relation to the natural tidal limit, tidal and fluvial regime, modifications and site specific predator densities means that gates at other locations could fragment habitat more severely at some sites. Further research is required to fill this gap in knowledge. Temporal variation in conditions within sites over an extended period of time (i.e. many years) are also important, and future studies should be planned to assess this.

Table 9.1. Summary of passage efficiencies and mean (± SD) or median (range) durations reported in Chapters 5 - 7 for adult and juvenile brown trout, *Salmo trutta*, and adult European eel, *Anguilla anguilla*, passing through a reach containing tide gates in the Rivers Stiffkey (Chapters 5 and 6) and Meon (Chapter 7).

Direction	Species	Life stage	Chapter	Passage Efficiency (%)	Duration (h)
Upstream	Brown trout	Adult	5	91.6	6.0 (0.03 - 197.8)
Downstream	European Eel	Adult	6	98.3	66.2 (± 141.8)
	Brown trout	Juvenile	7	95.8	6.5 (± 9.2)
				100.0	23.7 (± 34.0)

This thesis showed that top-hung tide gates facilitated multi-species and life stage passage for adult eel and juvenile and adult brown trout. The impact of tide gates should also be considered for other species in the future. For example, river lamprey abundance has declined over the last century, leading to protection under Annexes II and V of the EC Habitats Directive 92/43/EEC (EC, 1992) and being classified as a priority species under the UK Biodiversity Action Plan. However, few acoustic and radio tagged adult river lamprey, *Lampetra fluviatilis*, passed upstream through a barrage at the mouth of the River Derwent, UK, when sluices were operating normally (i.e. closing at high tide) (Lucas *et al.*, 2009). In contrast, 67% of the lamprey that did pass in 2005 - 2006 did so during high flow events when the sluices were atypically kept open over a number of tidal cycles. Similar effects could be expected at tide gates, suggesting that the passage efficiencies of species investigated in this thesis may not occur in all species.

Delay at structures can increase energy expenditure (Congleton *et al.*, 2002), predation risk (Schilt, 2007), fitness (Geen, 1975) and survival (Raymond, 1979). Prior to the research presented in this thesis, the extent of delay at temporal estuarine barriers, including tide gates, was unknown (Chapter 2). Downstream migrating adult eels, juvenile sea trout, and upstream moving adult trout experienced delay at tide gates (Table 9.1). Delays have been infrequently quantified for structures that may create similar conditions to tide gates. At substantially larger structures often considered to have greater impacts on fish, such as dams, similar passage times have been recorded (7.9 - 33.4 h) (Naughton *et al*., 2005), although a small percentage of fish could take > 5 days (Keefer *et al.*, 2004; Naughton *et al*., 2005) or several weeks (Caudill *et al*., 2007; Keefer *et al*., 2004) to pass. River managers must identify the measures required to best improve the riverine environment, including prioritisation of barrier remediation. Prioritisation is based on numerous factors, such as the impact of structures on fish passage (ideally from quantifying efficiency and delay), habitat accessibility/availability, financial budget, ease of implementation, public perception, and location within the river network (Keefer *et al*., 2013a; Kemp and O'Hanley, 2010). In this context, the need to improve fish passage at tide gates, a barrier through which the majority of diadromous fish must pass, may deserve higher or equal priority to structures upstream, where fish experience more delay but modifications would potentially provide less habitat and require more expensive remediation measures. Assessment for prioritisation must also consider the need for flood and saline intrusion prevention, and maintaining agricultural land and wetlands intact. Numerous small-scale obstructions can also cause greater adverse effects than an individual structure of greater scale (Jungwirth *et al.*, 1998) by accumulating the negative effects of delay at multiple obstacles, potentially leading to unsuccessful migration (Jackson and Moser, 2012; Naughton *et al.*, 2005).

Gate designs and site specific characteristics that cause tide gates to open for shorter periods and/or with smaller apertures may also lead to greater migratory delay compared to that reported in this thesis. This is an area for further research. In addition, the post passage effects of delay should be considered to identify biologically significant impacts (Roscoe and Hinch, 2009). Large-scale acoustic telemetry tracking programmes such as the Pacific Ocean Shelf Tracking array (Welch *et al.*, 2008) are beginning to make this possible for downstream migrants. This also includes considering the impact of gates on downstream migrating kelts (spent salmonids), which are generally larger and more fecund than one-sea-winter individuals.

Temporal functioning and aperture angle of top-hung tide gates had the most significant relationship with delay for adult eels and juvenile and adult brown trout. Sea level rise (Nicholls *et al.*, 1999), changes in flow regimes (Arnell, 2004) and increasing abstraction demands (Weatherhead and Knox, 2000; Wilby *et al.*, 2006) could extend the duration of top-hung gate closure each tidal cycle in the future (Walsh and Miskewitz, 2013). Downstream migrating smolts and adult eels in this thesis were more active at night. Eels failing to pass the tide gates at night are likely to be sedentary during the day (Davidsen *et al.*, 2011) exacerbating the duration of delay. For trout smolts that initially approached at night when the gates were closed, a number subsequently passed during the day when risk of predation by visual predators was greater (McCormick *et al.*, 1998). Tide gates modified or replaced with designs that open wider and for longer, such as retarders, counterbalances, lightweight gates, side-hung doors or SRTs would therefore be beneficial for decreasing delay and predation risk of different species and life stages.

Increased water temperature is related to delayed entry and ascent of rivers by adult salmonids (Jonsson and Jonsson, 2002; Solomon and Sambrook, 2004). In this thesis, duration of adult trout passage through Tide Gate 1 in the River Stiffkey was positively related to temperature (Chapter 5). Climate change predictions suggest that global temperatures will increase, and summer and autumn flows will reduce (Ficke *et al.*, 2007). For example, air temperatures in the south east of England have been predicted to increase by 2.0 - 6.4^{o}C by 2080, while precipitation across the UK could decrease by 17 - 23% (DEFRA, 2009). High water temperatures decrease DO concentration (Ozaki *et al.*, 2003), which can adversely affect fish and increase avoidance behaviour (Whitmore *et al.*, 1960). High temperatures can also amplify the presence and transfer of disease and parasites (Garcia de Leaniz, 2008), and the energetic costs of swimming

(Enders *et al.*, 2005). This may particularly affect larger, more fecund adult salmonids that have been observed to approach and enter rivers earlier in the migratory season than smaller individuals (Niemelä *et al.*, 2006).

Riverine barrier removal can increase fish abundance and productivity over a relatively short timescale by economically viable means (Scully *et al.*, 1990; Roni *et al.*, 2002). This is often not possible at structures used for flood defence or regulating water levels (Garcia de Leaniz, 2008). Mitigation measures used at riverine infrastructure e.g. fish ladders, locks and lifts, (Katopodis and Williams, 2012; Larinier, 2002) may be unsuitable for improving fish passage at tide gates due to the costs of traversing high dikes, highlighting a need for effective mitigation measures unique to tide gates. The impact of modifications on water levels and saline intrusion must be considered before implementation, sometimes limiting those that can be used. An orifice modification installed in Tide Gate 1 in the River Stiffkey did not influence saline intrusion upstream (Chapters 5 and 6). High passage efficiencies have previously been observed for adult salmonids at orifices (Gowans *et al.*, 1999; Guiny *et al.*, 2003). The orifice in Tide Gate 1 was ineffective at improving passage efficiency or decreasing delay for adult brown trout with the float configuration tested. However, a large trout (*c.* 500 mm) was observed in the Stiffkey estuary at low water during August 2011 immediately downstream from Tide Gate 2 when it was open but its aperture was too narrow to facilitate passage (*pers. obs.*). Tide Gate 2 was the first potential route of passage into the River Stiffkey encountered by trout migrating upstream from the sea, suggesting that a submerged orifice modification may have been more beneficial there. Alternatively, Gate 2 could be modified or refitted with designs that would allow wider apertures. A key advantage of the orifice installed in Gate 1 was to extend the period of fluvial connectivity once the gate had closed, while maintaining integrity of the tidal barrier to prevent saline intrusion by closure of a flap regulated by a float. Salmonids have been observed to utilise selective tidal stream transport when migrating through estuaries and entering rivers (Priede *et al.*, 1988). In this thesis, trout did not use the orifice under the door and float configuration tested when the gate was closed. Pilot flume studies on the duration of opening of a flapped SRT orifice revealed that fluvial connectivity could be extended by increasing float arm length and/or ballast in the orifice door (*pers. obs.* in association with Aquatic Control Engineering Ltd at ICER flume facility). Therefore, testing of flapped orifices using increased float arm lengths and amounts of ballast, under varying hydrological conditions and at different sites is recommended.

Adult eels have been observed to be benthic oriented during freshwater migration (Jonsson, 1991; Tesch, 2003) displaying a preference for undershot routes (Gosset *et al.*, 2005; Russon and Kemp, 2011a; Russon and Kemp, 2011b). In this thesis, silver eels migrated faster through Reach B in the River Stiffkey (containing the tide gates) when the orifice was operational. Video analysis revealed that eels did not pass through the orifice, which was situated half way up the gate. This suggests that environmental factors such as the number of occasions gates were open when eels approached them, and/or the lower upstream salinity that may have resulted from the lower tides that occurred during these periods, could have been influential instead. However, there is currently little evidence to suggest that eels suffer adverse physiological consequences in response to encountering stark transitions in salinity (Chan *et al.*, 1967; Maetz and Skadhauge, 1968; Rankin, 2008).

Upstream migrating glass eels are weak swimmers (Clough and Turnpenny, 2001) that utilise selective tidal stream transport to migrate through estuaries (White and Knights, 1997a). In the Yser River, Belgium, tide gates that remained open by 100 mm during the flood tide significantly improved the upstream passage of glass eels by a factor of > 200 (Mouton *et al.*, 2011). Orifices may provide similar benefits and should be investigated further. This thesis indicated that orifices do not negatively affect passage efficiency or delay adult eels and brown trout and therefore remain a potentially viable option for improving juvenile eel passage.

An orifice that remained open for the entire duration of the tidal cycle in the River Meon did not reduce the downstream speed of migration of sea trout smolts (Chapter 7). Saline intrusion upstream from the gates was high after modification, potentially increasing the opportunity for gradual acclimation to saltwater upstream of the tide gates. This could reduce the potential for osmotic shock when transitioning through a salinity gradient. Indirect effects of osmotic shock may include decreased swimming performance (Brauner *et al.*, 1994; Brauner *et al.*, 1992), ability to evade predators (Handeland *et al.*, 1996) and overall survival (Otto, 1971). Further research into the post passage impact of unmodified and modified or refitted tide gates that alter upstream saline intrusion would be beneficial.

Even when tide gates were open, the species and life stages studied in this thesis did not pass straight through. Adult eels and adult and juvenile trout showed recurrent behaviour, investigating potential routes of passage before selecting to pass through another (Chapter 6), making a number of attempts before passage (Chapter 5), and rejecting passage to return upstream (Chapter 8). Fish may actively avoid continuous overhead cover (Greenberg *et al.*, 2012; Kemp *et al.*, 2005b), accelerating flow (Haro *et al.*, 1998; Kemp *et al.*, 2005a), abrupt changes in temperature (Berggren and Filardo, 1993; Boyd and Tucker, 1998; Jonsson, 1991), salinity (Zaugg *et al.*, 1985), and/or DO concentration (Richardson *et al.*, 2001). Temporal operation of gates in the River Stiffkey caused differences in temperature, salinity and DO between upstream and downstream, and when open and closed (Chapters 5 and 6). For upstream migrants, flow velocities through gates may exceed swimming capabilities. Tide gates modified or replaced with designs that open wider and for longer would increase mixing at the estuarine/freshwater interface and decrease the period of river impoundment, minimising the extent of these gradients and decreasing velocities.

Telemetry allows spatial and temporal assessment of movements by individual fish (Cagnacci *et al.*, 2010; Castro-Santos *et al.*, 2009). Such broad-scale information has been successfully used to identify the impact of obstructions on migratory fish to a maximum resolution of approximately 50 cm (Brown *et al.*, 2009a). Combination of telemetry with a high resolution acoustic imaging system (i.e. DIDSON) could be used to track and identify the depth of fish approaching structures. Pilot studies in the River Stiffkey revealed that infrastructure often associated with tide gates such as wing walls and culverts limit DIDSON positioning, preventing effective use (*pers. obs.*). To further investigate the mechanisms underlying downstream fish passage at tide gates with different apertures, Chapter 8 utilised flume-based methods. Open channel flumes enable fine-scale observation of fish behaviour while providing a high degree of control over confounding variables that would not be possible in the field (Rice *et al.*, 2010). Tide gates created areas of accelerating and decelerating flow velocity, which were accentuated by smaller gate angles and apertures. Downstream migrating sea trout smolts displayed avoidance responses (orientation switches, increased tail beat frequency, and rejection by moving upstream) when encountering velocity gradients created by lower gate angles. Similar effects have been reported for downstream moving salmonids at other structures (e.g. orifices: Enders *et al*., 2012; Enders *et al*., 2009; Russon and Kemp, 2011a, screens: Enders *et al*., 2012, constrictions: Kemp *et al*., 2005a; Vowles and Kemp, 2012; surface bypasses: Johnson *et al*., 2000). Three-dimensional acoustic telemetry has shown that adult eels also reject routes with constricted flow in the field (Brown *et al.*, 2009a); reacting when encountering increases in velocity of > 0.05cm s^{-1} (Piper *et al*., *in prep.*). Gradual increases in velocity towards constrictions are recommended for improving fish passage (Clay, 1995; Larinier and Travade, 2002). This was achieved in Chapter 8 by opening the model gate wider, which was related to a decreased probability of passage rejection and returning upstream by smolts.

Low-head and intermittent barriers, including tide gates and culverts, are thought to be 2 to 4 orders of magnitude more abundant than larger barriers such as dams (Lucas *et al.*, 2009). However, an asset management database created by the UK Environment Agency neglects to include tide gates and culverts (Environment Agency, 2010). Although attempts have been made on a regional scale to quantify these structures (Environment Agency, *pers. comm.*), there still remains a need to record gate design, dimensions, duration and aperture of opening, presence of any modifications, and environmental characteristics at each site. By following similar guidelines, results from peer-reviewed literature would allow a wider application of findings. Standardised terminology would also make information more accessible (Chapter 2). By using telemetry, this thesis has demonstrated a methodology that can be used at other sites to assess the impact of various tide gate designs on diadromous fish, under different environmental conditions. Obtaining this information for an increasing number of sites would enable better fisheries management decisions to be made based on the physical data in the asset management database.

This thesis also presents a cost effective alternative to acoustic methods traditionally used for tracking the movements of fish in tidal waters. Saline water dissipates the electromagnetic field of Passive Integrated Transponder (PIT) Loops (PLs), often preventing the use of this type of telemetry in brackish environments (but see Adams *et al.*, 2006; Meynecke *et al.*, 2008). Dynamic tuning units enabled HDX PLs to automatically retune every few minutes, maximising the detection range and efficiency of 23 mm tags throughout the tidal cycle and under a range of environmental conditions (Chapter 5, Section 5.3.2). The PLs also detected smaller 12 mm HDX tags (*pers. obs.*) that could be used to study smaller species and life stages, although rigorous quantification of detection range and efficiency of these was outside the scope of this thesis.

9.2. Conclusions

Anthropogenic infrastructure fragments fluvial connectivity, impacting populations of environmentally, economically and socially important diadromous fish that must migrate between essential habitats. Regulation requires the impacts of all anthropogenic infrastructure to be minimised (e.g. EU Management Plans, Water Framework Directive). Low-head and intermittent obstructions to fish passage are thought to be more abundant than larger infrastructure (Lucas *et al.*, 2009), yet their impact on diadromous fish, particularly for temporal estuarine barriers, has received comparatively little attention.

Previous research has identified that tide gates can limit fish species abundance, richness and movement. However, the studies presented in this thesis are the first to quantify the impact of tide gates on diadromous fish by identifying passage efficiency and delay. Passage efficiencies of downstream migrating adult European eels, juvenile sea trout, and upstream moving brown trout were high, but delays were experienced prior to passage. Smaller gate apertures created steeper velocity gradients, causing fish to be more likely to exhibit passage avoidance. Removal may not be possible for structures used for flood defence or regulating water levels (Garcia de Leaniz, 2008), highlighting a need for unique mitigation methods applicable to tide gates.

The results presented in this thesis indicate that migratory delay and the adverse environmental conditions created at gates would be improved by refitting or modifying gates with designs that enable them to open wider and for longer, such as retarders, lightweight gates, side-hung doors and SRTs. Although orifice modifications studied in this thesis did not influence passage efficiency or delay of the diadromous fish studied, their suitability for facilitating multiple species and life stage movement past gates at different sites, particularly for glass eels and lamprey, remains an area for supplementary research.

Asset management databases used in the UK currently neglect to include tide gates and culverts (Environment Agency, 2010). It is recommended that the physical characteristics of such infrastructure are detailed in these databases, and complemented by data obtained on the impact of fish passage. This thesis provided a first step towards achieving this, demonstrating a methodology that could be used in studies at other sites and for different fish species. Inclusion of this information will enable river managers to understand the impacts of tide gates on fish in relation to catchment-wide concerns, and thus to balance the requirements of fisheries with water resource management.

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