UNIVERSITY OF SOUTHAMPTON

FACULTY OF ENGINEERING, SCIENCE & MATHEMATICS

School of Civil Engineering and the Environment

The Response of Eel, Lamprey and Brown Trout to Conditions Associated with Barriers to Up- and Downstream Movement Under Experimental Conditions in a Flume

by

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ABSTRACT

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Anthropogenic use of waterways is reducing connectivity at a rate faster than any time in geological history, sometimes causing serious declines in fish populations. Free passage of fish throughout the watercourse is necessary for species utilising different habitats for e.g. residing, spawning and feeding. Fish passes are employed to mitigate for impoundments, but are historically biased in design towards upstream migrating salmonids. Driven partly by more holistic environmental legislation, there is now an increasing interest in other species and life-stages, requiring development of fish passage criteria for multiple species during up- and down-stream migrations. To address these knowledge gaps this research programme undertook laboratory experiments with upstream migrant river lamprey, *Lampetra fluviatilis*, and downstream migrating European eel, *Anguilla anguilla*, and brown trout, *Salmo trutta*. The use of a large open-channel flume allowed control of the motivational state of, and stimuli encountered by the fish. The fish responses to a variety of model weirs and screens placed in the flume were assessed, allowing attainment of species and life-stage specific swimming capability and behavioural information. This research demonstrated that using large flumes where volitional swimming allows natural compensatory behaviours to be undertaken, provides more realistic swimming capability information for fish pass criteria than some traditional methods (i.e. confined swim chambers). Dependent on species and direction of movement, all structures tested had some level of impediment to migration, with small gauging weirs almost completely impeding movement of upstream migrant river lamprey under the conditions presented. Downstream migrant anguilliforms were seen to demonstrate structure oriented, thigmotactic behaviour compared to salmonids which responded to flow fields. Under high velocities, this lack of reaction to hydraulic cues may result in a higher probability of damage and mortality at facilities traditionally designed to protect salmonids. The information provided by this research, e.g. accurate swimming speeds and fish response to associated hydraulic conditions, will aid the production of effective multi-species fish pass facilities.

Contents

Abstract ... i

Contents ... iii

List of figures ... viii

List of plates ... x

List of equations ... x

List of tables ... xi

Glossary ... xii

A. Latin names of fish ... xii

B. Terms ... xiii

Declaration of authorship ... xv

Acknowledgements ... xvii

Chapter 1: Literature review 1

1.1 Introduction ... 1

1.2 Free passage of fish and barriers to migration ... 2

1.3 Protection and legislation ... 7

1.3.1 Salmonids ... 8

1.3.2 Anguilliforms ... 9

1.4 Restoring connectivity ... 12

1.5 Fish passage criteria and design: realising the ideal ... 14

1.6 Current state and trends in fish passage research ... 19

1.7 Summary ... 25

Chapter 2: Research aims 27

2.1 Hypotheses 29

2.2 Sub-aims 30

Chapter 3: General Research methodology 33

3.1 Why use flume based research? 33

3.2 Study species 34

3.2.1 European eel, *Anguilla anguilla* 34

3.2.2 River lamprey, *Lampetra fluviatilis* 36

3.2.3 Brown trout, *Salmo trutta* 38

3.3 Chilworth flume facility 39

3.4 Video analysis 41

3.5 Hydraulics 42

3.5.1 Flow measurements 42

3.5.2 Flow mapping and assessment 43

Chapter 4: Experimental quantification of the swimming performance and behaviour of spawning run river lamprey, *Lampetra fluviatilis* L., and European eel, *Anguilla anguilla* L. 45

4.1 Summary 45

4.2 Introduction 46

4.3 Materials and methods 49

4.3.1 Flume and weir structure 49

4.3.2 Fish and experimental trials 50

4.3.3 Swimming performance and behaviour 53

4.4 Results 54

4.5 Discussion 60

Chapter 5: Gauging weirs impede the upstream migration of adult river lamprey, *Lampetra fluviatilis* 65

5.1 Summary 65

5.2 Introduction 66

5.3 Materials and methods 70

  5.3.1 Experimental set-up 71

  5.3.2 Statistical analysis 74

5.4 Results 75

5.5 Discussion 85

Chapter 6: Response of downstream migrating European eels, *Anguilla Anguilla*, to bar racks under experimental conditions 91

6.1 Summary 91

6.2 Introduction 92

6.3 Materials and methods 95

  6.3.1 Experimental infrastructure 95

  6.3.2 Experiment 1 97

  6.3.3 Experiment 2 101

  6.3.4 Hydraulics 102

  6.3.5 Behaviour 102

6.4 Results 105

  6.4.1 Hydraulics 105

  6.4.2 Behaviour 107

6.5 Discussion 110

Chapter 7: Improving fish passage for multiple species: response of adult European eel, *Anguilla anguilla*, and brown trout, *Salmo trutta*, to accelerating flow at an orifice weir 115

7.1 Summary 115

7.2 Introduction 116

7.3 Materials and methods 120

7.3.1 Hydraulic conditions 121

7.3.2 Behaviour 122

7.3.3 Statistical analysis 124

7.4 Results 125

7.5 Discussion 138

Chapter 8: Disadvantages of group membership for those that are left behind: diminishing shoal integrity in the brown trout, *Salmo trutta* 145

8.1 Summary 145

8.2 Introduction 146

8.3 Materials and methods 150

8.4 Results 153

8.5 Discussion 159

Chapter 9: Conclusions and recommendations 165

9.1 Summary of key findings 165

9.2 General comments and recommendations 168

9.2.1 Key recommendations 168

9.2.2 Application of findings to nature 174

9.? Closing remarks 177

References 179

List of figures

2.1 Summary of aims and linkage of research areas 31

3.1 Life cycle of the European eel, *Anguilla anguilla* 35

3.2 Life cycle of the River lamprey, *Lampetra fluviatilis* 37

4.1 Water velocity vectors for an under- and over-shot weir 56

4.2 Mean time to first approach and pass time of upstream moving eel and lamprey at an undershot weir 57

4.3 Percentage of trials where upstream moving lamprey and downstream moving eel successfully passed and under- or over-shot weir 58

4.4 Mean pass time of downstream moving eel at an under- and over-shot weir 59

4.5 Mean time to first approach and pass time of downstream moving eel and lamprey at an undershot weir 60

5.1 Dimensions of a Crump and flat-v weir used to assess the ability of upstream migrant lamprey to pass under two discharge regimes 68

5.2 Water velocity vectors at a Crump and flat-v weir 78

5.3 Approach rate, time to first approach, time spent in observation zone, mean percentage of upstream approaches associated with the channel wall of upstream moving lamprey approaching a gauging weir 82

5.4 Percentage of total individual lamprey upstream approaches along the true left or right channel walls, and the attempts as a proportion of approaches when lamprey approached a Crump or flat-v weir 83

6.1 Basic setup for bar racks angled on horizontal plain 96

6.2 Basic setup for bar racks angled on vertical plain 97

6.3 Velocity profiles: 15° bar rack 100

6.4 Turbulence intensity profile: 30° angled bar rack 106

6.5 Turbulence intensity profile: High flow, 45° angled bar rack 107
6.6 Eel lateral approach position 108
7.1 Lateral approach position of downstream moving eels and trout on encountering an orifice weir 127
7.2 Approach depth of downstream moving eels and trout on encountering an orifice weir 128
7.3 Time taken and number of approaches made by eel and trout to a weir with a mid-column or channel floor oriented orifice 130
7.4 Time spent in and holding station in the observation zone for eel and trout at a mid-column or channel floor oriented orifice weir 132
7.5 Time taken by eel and trout to pass a weir with a channel floor or mid-column oriented orifice 133
7.6 Distance to orifice immediately prior to turning to positive rheotaxis and when closest to the orifice during a trout's first approach 135
8.1 Time to first approach to an experimental weir and orifice by downstream moving brown trout during individual and group trials 154
8.2 Number of downstream approaches to an experimental weir and orifice by individual and groups of brown trout 155
8.3 Number of rejections of an experimental weir and orifice by individual and groups of brown trout 156
8.4 Time taken to pass an experimental weir and orifice by downstream moving brown trout during individual and group trials 157
8.5 Time taken by downstream moving brown trout individuals (control) and individual group members (dependent on "position of passage" e.g.1st 2nd 3rd etc.) to pass the orifice weir 158

List of plates

1.1 Fish pass at Acaster Malbis 4

1.2 European eel mortalities due to screen impingement 5

1.3 Installation of eel friendly screens in Sweden 6

3.1 Eel rack on the River Stour 36

3.2 Chilworth flume facility 40

9.1 Flat-v weir at Kingsclere, UK 175

List of equations

7.1 Velocity gradient along fish body length calculation 123

List of tables

1.1 General fish passage criteria for total transparency of a structure 17

4.1 Main chapter objectives, and associated treatment conditions, to experimentally assess the swimming performance and behaviour of European eel and river lamprey 52

4.2 Hydraulic parameters associated with an under- and over-shot weir placed in the ICER flume facility, under three discharge regimes 55

5.1 Water depths associated with two experimental gauging weirs 71

5.2 Water velocities associated with a Crump and flat-v weir under experimental conditions 76

5.3 Results of two-way ANOVAs to determine the influence of discharge and weir type on the various dependent variables for upstream moving lamprey approaching a gauging weir 81

5.4 Behavioural traits demonstrated by groups (n = 30) of upstream migrating lamprey approaching a Crump or flat-v weir 84

6.1 Water velocities at experimental bar racks 99

7.1 Results of two-way ANOVAs to determine the influence of species and orifice orientation on the various dependent variables for downstream moving eel and trout approaching an orifice weir 126

7.2 Results of linear regressions to determine trout acclimate to the various dependent variables over successive approaches to an orifice weir 137

Glossary

A. LATIN NAMES OF FISH

COMMON NAME	LATIN NAME
American eel	*Anguilla rostrata*
American shad	*Alosa sapidissima*
Allis shad	*Alosa alosa*
Atlantic herring	*Clupea harengus*
Atlantic salmon	*Salmo salar*
Australian pilchards	*Sardinops sagax*
Barbel	*Barbus barbus*
Bluntnose minnow	*Pimephales notatus*
Brown trout	*Salmo trutta*
Burbot	*Lota lota*
Chinook salmon	*Oncorhynchus tshawytscha*
Chum salmon	*Oncorhynchus keta*
Coho salmon	*Oncorhynchus kisutch*
Common carp	*Cyprinus carpio*
European bullhead	*Cottus gobio*
European eel	*Anguilla anguilla*
Golden Shiner	*Notemigonus crysoleucas*
Guppy	*Poecilia reticulata*
Iberian barbel	*Luciobarbus bocagei*
Japanese eel	*Anguilla japonica*
Longfin eel	*Anguilla dieffenbachia*
Pacific lamprey	*Lampetra tridentata*
Pumpkinseed	*Lepomis gibbosus*
River lamprey	*Lampetra fluviatilis*
Sea lamprey	*Petromyzon marinus*
Sea trout	*Salmo trutta*
Shortfin eel	*Anguilla australis*
Smallmouth bass	*Micropterus dolomieu*
Sockeye salmon	*Oncorhynchus nerka*

B. TERMS

Anadromous: Life cycle with spawning in freshwater, feeding and growth at sea.

Anguilliform locomotion: A swimming motion used by eel like fish, which utilises the entire body length.

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

Bypass: A safe route of fish passage for downstream movement. Designed to prevent entrainment into e.g. hydropower turbines.

Catadromous: Lifecycle with spawning at sea, feeding and growth in freshwater.

Cavitation: The sudden formation and collapse of low-pressure bubbles in liquids by means of mechanical forces, e.g. from the rotation of a hydropower turbine.

Conspecifics: Of or belonging to the same species.

Critical swim speed (U_{crit}): The maximum that can be maintained for a specific time period (anything between 20 seconds and 200 minutes) (Brett, 1964). Usually measured in $m\ s^{-1}$ or body lengths s^{-1}.

Diadromous: Life cycle involves marine and freshwater stages (incorporates anadromous and catadromous life cycles).

Discharge: The volume rate of water flow. Units generally = $l\ s^{-1}$ or $m^3\ s^{-1}$.

Entrainment: The passage of fish through an intake structure, hydropower turbine or screening device.

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

Habitat connectivity: A measure of connectedness of landscape elements.

Hydraulics: The physical science of the behaviour of fluids.

Impingement: The entrapment of fish on the outer part of an intake structure or screening device during periods of intake water extraction/flow through.

K: See relative turbulence intensity

Maximum burst speed (U_{max}): The maximum swimming speed attainable and maintained for less than less than 20 seconds (Beamish, 1978). Usually measured in m s^{-1} or body lengths s^{-1}.

Potamodromous: Life cycle which involves large migrations between different habitats within the freshwater environment to access spawning, residential and feeding habitats.

Relative turbulence intensity (*K*): A dimensionless measure of turbulence calculated by dividing the standard deviation of velocity by the mean value.

Rheotaxis: Movement of an organism in response to a current of water.

Spillway: A channel for the overflow of water through e.g. a hydropower turbine.

Sub-carangiform locomotion: A powerful swimming motion used by salmonids, where the rear *ca.* two-thirds to half of the fish body length is used to provide propulsion.

Thigmotactic: Directed response of a motile organism to a continuous contact with a solid surface.

U_{crit}: See critical swim speed.

U_m: See velocity modulus.

U_{max}: See maximum burst speed.

Velocity modulus: The mean velocity vector (in cm s^{-1} or m s^{-1}) in three dimensions. Calculated from the three dimensional flow velocities attained using an Acoustic Doppler Velocimeter.

DECLARATION OF AUTHORSHIP

I, Iain Jamie Russon,

declare that this thesis entitled:

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and the work presented in it are my own and has 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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    1. i) Russon, I.J. & Kemp, P.S. (2011 early view). Experimental quantification of the swimming performance and behaviour of spawning run river lamprey *Lampetra fluviatilis* and European eel *Anguilla anguilla*. *Journal of Fish Biology*, doi: 10.1111/j.1095-8649.2011.02965.x.
    2. ii) Russon, I.J., Kemp, P.S. & Lucas, M.C. (2011). Gauging weirs impede the upstream migration of adult river lamprey *Lampetra fluviatilis*. *Fisheries Management and Ecology* **18,** 201–210.
    3. iii) Russon, I.J., Kemp, P.S. & Calles, O. (2010). Response of downstream migrating adult European eels (*Anguilla anguilla*) to bar racks under experimental conditions. *Ecology of Freshwater Fish* **19,** 197–205.

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Chapter 1: Literature Review

1.1 INTRODUCTION

Major declines in migratory fish stocks have been occurring Worldwide particularly with the diadromous (i.e. those with marine and freshwater stages during their life-cycle; McDowall, 1997) species (Porcher & Travade, 2002). Climate change, habitat loss, pollution, invasive parasite infestation, overfishing (in both the marine and freshwater phases), and reduced habitat connectivity due to the installation of anthropogenic barriers to migration have all been cited as possible causes of the observed declines (e.g. Feunteun, 2002; Porcher & Travade, 2002). In the majority of cases, significant declines are associated with increased development of many rivers for hydropower, river gauging purposes and water abstraction (Moser *et al.*, 2002a; Winter & Van Densen, 2001), and these causes have up to now masked others (Porcher & Travade, 2002).

There is a lack of understanding of the reasons for fish stock declines (Feunteun, 2002), making management decisions to protect and improve stocks difficult. A clearer understanding and further information concerning the fish response to the major causes of decline will aid in the implementation of suitable management plans to protect migratory fish stocks. The focus of this review concerns the passage of fish at anthropogenic barriers to migration.

1.2 FREE PASSAGE OF FISH AND BARRIERS TO MIGRATION

Free passage throughout the watercourse is of critical importance for many species of fish, particularly those undertaking long migrations between different habitats for e.g. spawning, feeding and residence. The range of spatial and navigational problems which may be encountered by different species, populations, individuals and life-history stages within the watercourse are extremely diverse (Odling-Smee & Braithwaite, 2003). Throughout Europe a large amount of river infrastructure has been built for the purpose of hydropower, flood defence, flow gauging, water abstraction and navigation (e.g. Haselbauer & Martinez, 2007; White *et al.*, 2006). In England and Wales alone there are *ca*. 2,500 obstructions identified that prevent or reduce migration of fish (both between the marine and freshwater environments, and entirely within freshwater), constraining access to suitable habitat (DEFRA, 2006). This anthropogenic utilisation of the waterways has significantly reduced connectivity in the associated systems at a rate faster than any time previously (Odeh, 1999; Pringle, 2003), so much so that dammed and regulated rivers are thought to be more common than continuous free flowing ones (Moss, 1998).

Continuous connectivity is necessary to maintain good ecological status within river networks (Weyand *et al.*, 2005). Discontinuous habitat connectivity on longitudinal, vertical, lateral and temporal levels can lead to local and regional extinctions in many animal populations (Jaegger *et al.*, 2005; Shepard *et al.*, 2008). For riverine fish (particularly diadromous populations) longitudinal connectivity is probably of most importance, with reduced connectivity leading to serious reductions in fish populations in both the long and short term, by reducing access to suitable spawning, feeding and residential habitat (Cote *et al.*, 2009; Lucas & Baras, 2001). The importance of continuous river connectivity is highlighted by the extinction of the Burbot, *Lota lota*, in the UK within the past *ca*. fifty years, which is thought to be partially due to the construction of anthropogenic barriers (Paragamian *et al.*, 2000).

Anthropogenic barriers to fish migration can cause delay, stress and injury to both downstream and upstream migrating life-stages (Larinier, 2002), may divert fish away from their natural migration route (McDowall, 1992) and hinder access to suitable habitat (Amoros & Bornette, 2002; Cote *et al.*, 2009). Where delay occurs there is often an accumulation of fish, and thus a greater predation pressure because of both an increased time for predation and predators learning where their prey accumulates (Peake *et al.*, 1997). For example river lamprey, *Lampetra fluviatilis*, are often observed accumulating in large numbers below small physical barriers during their night time migration (e.g. Plate 1.1). At these migratory bottlenecks predatory birds and mammals are regularly seen predating upon the lamprey with ease (Dr. Martyn Lucas, pers. comm.). Additionally, delay will lead to an overall increase in energy expenditure (Osbourne, 1961) and ultimately a reduction in reproductive success (Geen, 1975). A successful fish pass will completely alleviate these problems and requires the collaboration of biologists, ecologists and hydraulic civil engineers to create it (Castro-Santos *et al.*, 2009; Haselbauer & Martinez, 2007; Rice *et al.*, 2010).

Plate 1.1. Fish pass at Acaster Malbis on the Yorkshire River Ouse. A large number of river lampreys, *Lampetra fluviatilis*, are accumulated downstream (photo taken November 2008).

Of the potential barriers to migration, hydropower turbines are a major source of mortality for downstream migrating fish (Anderson, 1988; Winter *et al*., 2006, 2007). Turbine induced mortality can be due to blade strike from the moving parts, and sudden changes in pressure, cavitation and velocity (Larinier, 2008). Any mechanism that reduces entrainment of fish through turbines should aid the recovery of stocks. Most commonly physical barriers such as bar racks and screens are used to divert downstream migrating fish from the turbine intakes to bypass facilities (Larinier, 2008). However, it has been seen that poorly designed screens can lead to high mortalities due to impingement (Plate 1.2), and larger fish, e.g. downstream migrating adult European eels, *Anguilla anguilla*, are particularly susceptible (Calles *et al*., 2010).

Plate 1.2 European eel, *Anguilla anguilla*, mortalities due to impingement at the Ätrafors power plant screen on the River Ätran, Sweden, prior to replacing the screen in 2008 (photos courtesy of Simon Karlsson, taken 2007).

Calles *et al*. (2010) observed via telemetry studies at hydropower installations on the River Ätran, Sweden, a total of 18% of European eel approaches to a bar rack resulted in impingement, always leading to death. Some individuals undertook repeated upstream escapes, but 50% of these ended up dead on the rack at their last attempt. This impingement was size selective, with larger individuals being impinged. Of the smaller individuals that passed through the rack 44% died via turbine entrainment. Recent replacement of these screens with low sloping racks (Plate 1.3) designed based on information from previous studies (Larinier, 2008; Gosset *et al*., 2005), improved survival of the total fish tagged and released from 41% to 90% between 2007 and 2008 (Calles & Bergdahl, 2009). In addition, no impingement at this site occurred compared to 54% impingement in 2007 (Calles & Bergdahl, 2009). Although information of this nature is of great value to fish passage designers, it provides no details concerning the specific fine-scale behaviours of the fish when encountering screens, for which flume based studies are necessary to attain optimum passage efficiency (Rice *et al.*, 2010).

Plate 1.3 Replacement screens installed at the Ätrafors power plant on the River Ätran, Sweden during 2008 to improve safe passage of European eel, *Anguilla anguilla* (photos courtesy of Olle Calles, taken 2008).

To attain free passage of fish past navigational barriers, effective and safe fish mitigation measures are necessary, requiring detailed knowledge of both the physical capabilities and the behavioural responses of the species of interest to the various conditions (e.g. biotic, abiotic, hydraulic and physical) associated with the structure. Requirements for free movement of fish vary with species and life-history stage, making the development of effective fish passage facilities to accommodate multiple species and life-stages a major challenge.

1.3 PROTECTION AND LEGISLATION

With the implementation of international legislation such as the European Union's Water Framework Directive (WFD) 2000/60/EC (EC, 2000) and Habitats Directive 92/43/EEC (EC, 1992), and the USA's National Environmental Policy Act (NEPA, enacted as P.L. 91-190 on January 01, 1970) of 1969, it is necessary to protect all species utilising the watercourse within these regions. Concomitant with this is an increased dependency on hydropower, driven by e.g. the European Commission's Renewables Directive (2009/28/EC), requiring licensed electricity suppliers to source a specified and increasing proportion of electricity from renewables. Consequently, hydropower is an important component of the Europe's renewable energy policy. The UK Renewable Energy Strategy (UKRES) suggests the UK could see more than 30% of its electricity generated by renewables by 2020 (compared to 5.5% currently), of which hydropower will play an important role (DECC, 2009). Thus a major challenge for fisheries managers is to work within these conflicting legislative frameworks to minimise disruption to fish movement within the watercourse, concomitant with an increase in anthropogenic use of the waterways for power generation.

There is a major challenge to develop fish passage facilities that will efficiently pass multiple species and life stages. In addition to the general legislation already described, species in decline due to river infrastructure have recently received specific legislation protecting them, thus research concerning these poorly understood species is necessary to protect their stocks. The status and legislation related to some of these groups are described below.

1.3.1 SALMONIDS

Salmonids are an economically important group, posing a significant contribution to regional biodiversity, with significant importance to many native and regional cultures (Allan, 1995). However, major declines in many salmonid populations have been observed throughout their ranges. Significant declines in the Pacific salmonids have occurred in the North American Pacific, with the total Canadian salmon catch reaching an historic low in 1998 (Noakes *et al.*, 2000). Coho, *Oncorhynchus kisutch*, and Chinook, *O. tshawytscha*, salmon populations are particularly adversely affected (Brown *et al.*, 1994; Noakes *et al.*, 2000; Yoshiyama *et al.*, 1998) with Coho numbers being less than 6% of pre-1940 levels (Brown *et al.*, 1994). In the USA a number of salmonids are recognised as endangered including the Atlantic, *Salmo salar*, Chinook, *O. tshawytscha*, Coho, *O. kisutch*, Sockeye, *O. nerka*, and Chum, *O. keta*, salmon (U.S. Fish and Wildlife Service, 2010). This requires the Federal government to protect both the species and their habitat. In addition, a bill to protect and restore Pacific salmon strongholds in North America was introduced to the USA senate in April of 2009 (Cantwell *et al.*, 2009).

Similar declines in Atlantic salmonids (e.g. Atlantic salmon, *S. salar*, and brown trout, *S. trutta*) are occurring, with substantially reduced stocks due to anthropogenic destruction or interruption of access to their spawning habitats (Lundqvist *et al.*, 2006, 2008; Rivinoja *et al.*, 2001). Many of the European salmonid populations have thus lost their juvenile production and/or entire populace (Eriksson & Eriksson, 1993; Rivinoja *et al.*, 2001) in many of the regulated rivers. In the Baltic region there has been a reduction in wild salmon smolt recruitment of at least 25% since the 1970s (Eriksson & Eriksson, 1993). Atlantic salmon are protected under the EC habitats directive 92/43/EEC (EC,

1992) which has led to a number of regionalised river catchment based salmon action plans being created to improve their survival in England, Scotland and Wales. These action plans will be progressively integrated into the WFD (EC, 2000) planning cycle (Williams *et al.*, 2009). Further protection within the United Kingdom is provided through the Salmon and Freshwater Fisheries Act of 1975, controlling a number of conditions (e.g. fish pass construction and/or modification, fishing methods employed, and sale of salmon and trout) related to protection of salmonids.

1.3.2 ANGUILLIFORMS

1.3.2.1 Lamprey

Lampreys are economically and culturally important worldwide. Pacific lampreys, *L. tridentata*, in northwestern North America are important for food, medicinal and ceremonial purposes to the indigenous people (Close *et al.*, 2002; Moser & Butzerin, 2007). Within Europe, river, *L. fluviatilis*, (Plate 1.1) and sea, *Petromyzon marinus*, lamprey are consumed as food in e.g. Finland and Portugal (Maitland & Campbell, 1992). Historically, large lamprey fisheries were present in the UK, with their consumption even being attributed to the regicide of both King Henry I and King John (Kearn, 2004). Now, only a small fishery on the Yorkshire River Ouse is present, where catches are used as bait by anglers (Maitland, 2004).

Decline in the anadromous lamprey species (those that migrate from the marine to the freshwater environment as adults to spawn) has been occurring throughout the World. Populations of both anadromous lamprey species native to Europe (river and sea lamprey) have been declining over the past century

(Kelly & King, 2001; Masters *et al.*, 2006; Thiel *et al.*, 2009; Tuuainen *et al.*, 1980) and in extreme cases populations have been extirpated (e.g. river lamprey from Switzerland and the Rhine-Meuse hydro-system; Renaud, 1997). These species are now protected under the EC Habitats Directive 92/43/EEC (EC, 1992) and must be afforded Special Areas of Conservation (SAC) by member states (Bell & McGillivray, 2006).

A widespread decline in the numbers of the Pacific lamprey, *L. tridentata*, in the Columbia River has occurred since the 1960s (Beamish & Northcote, 1989) and in 2002 a petition was submitted to the U.S. Fish and Wildlife Service to list this species as a federally-endangered or threatened species (Close *et al.*, 2002). The reasons for the decline in numbers are not well understood, but population crashes appear associated with periods of most dam construction (Moursund *et al.*, 2001). Other potential factors involved in the observed declines are habitat loss, water pollution and oceanic conditions (Close *et al.*, 1995).

1.3.2.2 Eel

Worldwide eel stocks are in decline and are now suffering their lowest levels in recorded history (e.g. Haro *et. al.*, 2000a). There is a European wide decline of 90% in the recruitment of European eels, *A. anguilla*, (Bark *et al.*, 2007; Dekker, 2003) with glass eel abundance at less than 5% of pre-1980 levels (DEFRA, 2006; ICES, 2006). Recruitment of Japanese, *A. japonica*, (Han *et al.*, 2008), American, *A. rostrata*, (Aieta *et al.*, 2009; Haro *et al.*, 2000b), shortfin, *A. australis*, and longfin, *A. dieffenbachia*, (Jellyman *et al.*, 2002) eels have also significantly decreased.

Eels are a catadromous species, migrating downstream to the sea as adults to spawn. These spawning migrations can occur over vast distances with the European eel (Plate 1.2) migrating *ca*. 5000 km from Europe to the Sargasso Sea (Tesch, 2001, Van Ginneken & Maes, 2005). The details of this migration are relatively unknown but tagging via pop-up satellite archival transmitters (Aerstrup *et al*., 2009) is taking steps towards understanding European eel movements. Due to their elongated bodies and large size at the onset of their spawning run in freshwater, they are particularly susceptible to the deleterious effects of screen impingement and turbine entrainment, resulting in high mortality rates (Behrmann-Godel & Eckmann, 2003; Calles *et al*., 2010; Coutant & Whitney, 2000).

Although American eels are in decline there is no specific governmental legislation protecting them, however United States fisheries authorities are taking measures to protect stocks, with the Atlantic States Marine Fisheries Commission (ASMFC) implementing a fishery management plan for American Eel in 1999 (ASMFC, 2000; Taylor *et al*., 2008). The plight of the European eel has been recognised and it is now listed under appendix II of CITES, and is an IUCN critically endangered species (Freyhof & Kottelat, 2008). In addition, member states have developed eel management plans, due to implementation of the European Unions Eel regulations 1100/2007 (EC, 2007), in an effort to reduce anthropogenic mortalities so that a minimum of 40% silver-eel biomass (based on expected rates if there were no anthropogenic impediments) escapes to the sea.

1.4 RESTORING CONNECTIVITY

With the aforementioned negative impacts of river infrastructure on fish populations and the current legislation in mind, what connectivity restoration methods should be implemented at barriers that block fish dispersal? The main options are: a) not to build further river impoundments; b) do nothing and forget the fish; c) remove already installed infrastructure and d) mitigate via e.g. fish passes and/or screens. Of these options a) and b) are not viable due to the aforementioned legislation driving increases in renewable energy (via e.g. the EU Renewables Directive) concomitant with protection of all species utilising the watercourse through the WFD. However, restoration via options c) removal or d) mitigation, have led to some of the largest and fastest increases in fish abundance and production (Roni *et al.*, 2002). For example, Scully *et al.* (1990) observed an increase of 52% in steelhead and 72% in Chinook salmon parr within Idaho river systems due to the removal of barriers.

Although often having a pronounced positive effect, impoundment removal also has physical, biological and societal implications that must be accounted for (Leaniz, 2008). For example, the release of sediment accumulated behind larger dams will cause initially high sediment loads, negatively affecting egg and fry stages of salmonids and causing a lag in recolonisation and population rebuilding (Pess *et al.*, 2008). Some structures have high historical or societal value affecting the potential for removal (Leaniz, 2008). Additionally, many small impoundments, such as weirs, have potential use for low-head hydropower using e.g. water wheels, which is becoming more economically feasible with legislation (e.g. the EU Renewables Directive) increasing the need for renewables and more efficient new technologies (Muller & Kauppert, 2004). Thus, mitigation for the structures is often the only viable option. However, mitigation is not without its problems, the cost of which may make small hydropower schemes unviable (British Hydropower Association, 2009). There is also a lack of reliable fish passage criteria for multiple species and life-stages in both up- and down-stream directions based on swimming performance and behaviour (Kemp & O’Hanley, 2010) for application to designing effective mitigation measures.

1.5 FISH PASSAGE CRITERIA AND DESIGN: REALISING THE IDEAL

To enable free passage of fish a variety of passage facilities have been designed and implemented at barriers to migration (reviewed extensively by Clay, 1995, and Odeh, 1999). Despite advances in fish pass design over the past *ca.* fifty years (Roscoe & Hinch, 2010), fish passes often do not work as efficiently as expected and their presence does not guarantee fish passage. This is true in particular for non-salmonids e.g. American Shad, *Alosa sapidissima*, and sea lamprey, *P. marinus*, (Haro & Kynard, 1997), but also for the salmonids, for which passes are usually targeted, where potentially long delays and the cumulative effects of multiple barriers have led to unsuccessful migration (Naughton *et al.*, 2005).

The reasons for the low passage efficiencies experienced at fish passage facilities are due to a number of factors and biases in the research, many of which are raised in the following section 1.6, e.g. physical capabilities of the fish are taken into account more often than the behaviour during fish pass design. Many relevant biological parameters for fish passage remain poorly categorised, a major weakness in fish pass design and technology (Castro-Santos *et al.*, 2009). Swimming speeds obtained via the use of swim chambers and respirometers are the main biological components used in fish pass design (e.g. Tudorache *et al.*, 2008). However, the use of swim chambers does not allow for natural compensatory behaviours of the fish to be undertaken because of the confined conditions in which the fish are permitted to swim, thus conservative estimates of fish abilities are obtained. For example, volitional gait changes allow for an increased ability to pass velocity barriers (Farrell, 2007; Kemp *et al.*, 2008; Peake, 2004; Peake & Farrell, 2005;

Tudorache *et al.*, 2007) but can only be undertaken in less constricted conditions e.g. large open channel flumes. Peake (2004) undertook direct comparisons between forced swimming in a respirometer and volitional swimming in a 50 m flume of the swimming ability of smallmouth bass, *Micropterus dolomieu*. Critical swim speeds of 0.65 to 0.98 m s^{-1} were obtained in the respirometer, yet a high proportion of the fish could still swim the entire length of the flume against water velocities up to 1.20 m s^{-1}. This increased ability to pass a velocity barrier was possibly due to the fish being capable of undertaking an unsteady swimming gait characterised by accelerating sprints followed by passive glides resulting in rapid decelerations (burst and glide swimming). This unsteady gait has led to a significant increase in the mean ground speeds of fish compared to those swimming steadily (Peake & Farrell, 2004). Without the flume based volitional swimming studies, this behaviour may not have been observed, resulting in misleading and conservative estimates of swimming capabilities being obtained.

Although it could be assumed that conservative estimates of swimming capabilities will lead to more readily passable fish pass facilities with easily manageable flow velocities for the fish to swim through, there are associated problems with this concept. Fish pass entry is described as a two step process requiring 1) attraction and guidance towards the entrance and 2) the fish must detect and choose to enter (Bunt, 2001; Castro-Santos *et al.*, 2009). The problem with using conservative swimming speeds is that fish passes designed with this in mind may have a too low attraction flow, or will not stimulate fish passage even if they could easily pass through (Castro-Santos *et al.*, 2009). In fact, both salmonid (Naughton *et al.*, 2007) and non-salmonid species, e.g. Pacific lamprey, *L. tridentata* (Moser *et al.*, 2002b), have been observed to approach fish pass entrances but then not to enter, with subsequent adaptations to accommodate behaviour of these species increasing entry and passage efficiency. For example, by providing a smooth stainless steel plate material with a rounded edge over a bulkhead near a spillway entrance (where Pacific lamprey were known to have difficulty passing) Moser *et al.* (2002b) observed an increase in entry efficiency because the lamprey could remain attached as they moved around the obstacle and into the fish pass. However, entry efficiency did not necessarily increase through reduction of velocity (Moser *et al.*, 2002b).

Further highlighting the problem of conservative design of fish passes is the issue of multiple species and life-stage passage. It is often proposed that the maximum discharge or water velocity within a fish pass should not exceed the swimming capacity of the weakest swimming species (e.g. Peake *et al.*, 1997; Schwalme *et al.*, 1985). However, this may create a situation where a fish pass readily passes the weakest swimming fish, but species with higher swimming capabilities may not be attracted to the entrance, leading to low passage efficiencies. This again demonstrates the need for additional and more accurate and realistic information concerning the behaviour and performance of multiple species (both salmonids and non-salmonids) as they encounter fish passes and impediments to migration. It may be that a number of designs at a site would be more efficient at passing a variety of fish than a single all encompassing fish pass.

Obtaining conditions for the perfect fish pass design is further made difficult by what has been described as the “ideal fishway dichotomy” (Castro-Santos *et al.*, 2009). With this the biological needs of the fish populations must be balanced with the operational requirements of the structure being built. The ideal situation for fish is for passage to occur with minimal fitness costs, in effect being completely transparent to the movement of native species

(Castro-Santos *et al.*, 2009; Roscoe & Hinch, 2010) (Table 1.1). However, as already stated the operational requirements of the structure must also be met, i.e. minimise the costs and attain maximum efficiency (Table 1.1). Obviously the ideal situation for operational costs is not realistic; however minimisation of the costs for each of these criteria is the optimum.

Table 1.1. General criteria in river structures must possess for total transparency to fish and the ideal operational situation (adapted from Castro-Santos *et al.* (2009).

Passage criteria for total transparency of structure to fish	Criteria for ideal operation of a structure
1) Individuals of any native species wishing to move up- or down-stream must be able to do so with no delay.	1) Costs nothing to produce.
2) Entry leads to immediate passage success.	2) Requires no maintenance.
3) No temporal or energetic costs are incurred.	3) Uses no water, power, or other resources to operate.
4) No fitness-relevant costs e.g. stress, disease, injury, predation, must be incurred.	4) Free of licensing restrictions.

There is an obvious conflict between the operational and biological goals e.g. operational costs will be higher due to the necessity to construct and maintain a fish pass. Although there is the underlying conflict of interests, improvements in one area can potentially have mutual benefits in the other. Calles & Bergdahl (2009) found that adaptations to improve fish passage efficiency for downstream migrating European eels, *A. anguilla*, utilising angled screens at a hydropower facility, actually reduced the head loss from 7.5% to 4.0%, thus increasing the efficiency of and the flow through the turbines.

In addition to the problems of attraction, entry and passage through a fish pass (discussed above) the energetic costs of fish passage is of great concern. This is of an increased pertinence for species which do not feed during their migrations (e.g. the Pacific lamprey, *L. tridentata*, river lamprey, *L. fluviatilis*, and European eel, *A. anguilla*), thus have a finite amount of energy for migration, sexual maturation and spawning (Beamish, 1980; Mesa *et al.*, 2003; Quintella *et al.*, 2004). A successful fish pass will allow fish to reach their spawning habitat in a suitable condition and with sufficient energy reserves to spawn, and with iteroparous species (those that have multiple reproductive cycles during their lifetime) to return to their feeding habitats (Castro-Santos *et al.*, 2009).

To mitigate for the negative effects of fish passes on fitness, Roscoe & Hinch (2010) suggest further research examining the sub-lethal consequences, delayed mortality and fish physiology at passage facilities is required. Due to the uniqueness of each site, site-specific studies are regularly stated as necessary to fully attain this information and indeed other measures of efficiency and passage rates (Bunt, 2001; Sprankle, 2005). It cannot be certain a fish pass will work efficiently before implementation (Calles & Greenberg, 2007), thus it is necessary through effective long term monitoring to evaluate the function of each new pass after it is built, although currently long term monitoring is insufficient. Any increase in the understanding of generic fish behaviour and performance in response to the conditions associated with a variety of structures will lead to an increased likelihood of producing an effective fish pass from its initial construction.

1.6 CURRENT STATE AND TRENDS IN FISH PASSAGE RESEARCH

A number of historic trends and biases in research concerning the development of fish passage are widely recognised and will be covered in this section. Due, in part, to legislation for protection of multiple species utilising the watercourse only recently coming into effect (e.g. the WFD, 2000, and the Eel Regulations1100/2007), research concerning fish passage has focused on the economically, culturally and recreationally important anadromous salmonids (Calles & Greenberg, 2005; Clay, 1995; Enders *et al.*, 2009; Kemp & O'Hanley, 2010; Laine *et al.*, 1998; Larinier, 2008; Larinier & Travade, 2002a) with downstream migrating life-stages and non-salmonids being virtually ignored (Lucas *et al.*, 2000; Roscoe & Hinch, 2010). Roscoe & Hinch (2010) analysed much of the available literature between 1960 and 2008 concerning fish passage, finding 58% within this research area to be concerned with salmonids, and 45% being exclusively salmonid based. This has led to the majority of fish passes being designed exclusively for salmonids. In England and Wales alone there are approximately 380 fish passes, but almost all have been built exclusively for Atlantic salmon, *S. salar*, and Brown trout, *S. trutta* (Jungwirth *et al.*, 1998). Due to this species bias, the suitability of these fish passes for non-salmonids, which differ greatly in their abilities to pass physical and hydraulic barriers (e.g. lower maximum swimming speeds and an inability of European eel and river lamprey to jump large obstacles when compared to Atlantic salmon), is not well understood (Knaepkens *et al.*, 2006; Lucas & Frear, 1997).

Adults are the most studied life-history stage, largely because the majority of fish passes are designed to accommodate upstream migration (Odeh, 1999; Schilt, 2007), with a bias towards the anadromous salmonids.

Downstream fish passage technologies are less advanced than upstream ones because of the difficulty in engineering for downstream passage and the potential adverse effects of downstream migration only recently being recognised relative to upstream migration (Larinier & Travade, 2002a; Schilt, 2007). Historically it was assumed that downstream migration of fish was passive, however research over the past *ca*. 30 years has shown that there is an active component to this (Kemp & Williams, 2009; Thorpe *et al.*, 1981; Tytler *et al.*, 1978). For example, Kemp *et al.* (2005a, b) observed downstream migrating Pacific salmonid smolts avoid both rapid acceleration of flow and the presence of overhead cover. These experiments were undertaken in experimental flumes, allowing for fine scale observations of fish behaviour to be made when encountering the various conditions being examined.

A major concern of focusing solely on protecting upstream migrating life-stages is that if all individuals are efficiently passed upstream, but no adequate downstream passage is provided for the adult/juvenile stages (dependent on species) to reach suitable residential and feeding habitat, then an almost immediate extinction of the population could be incurred (Castro-Santos *et al.*, 2009). The need for improved downstream passage is of crucial importance and one of the most pressing requirements for protecting stocks. This requires the lack of knowledge concerning the motivation, orientation, sensory capacities and hydrodynamic preferences of downstream migrants to be urgently addressed (Castro-Santos *et al.*, 2009; Schilt, 2007).

A lack of consideration of fish behaviour partially accounts for the often observed lower than expected efficiency of fish passes (Anon, 1995). The opportunity for a fish to pass an obstacle can be assessed based on physical characteristics of the species and/or life-history stage in question, but whether they actually do so depends on their behavioural response (Winter & van

Densen, 2001). Behaviours vary among species, however, very little research concerning how and why this is the case is available (Castro-Santos *et al.*, 2009). Behaviour and sensory capacity influence passage success with response to flow velocity, acceleration and turbulence influencing rates of entry by fish into bypasses (Castro-Santos, 2004; Haro *et al.*, 1998; Kemp *et al.*, 2005a), affecting attraction towards and rejection of the entrance, dependent upon the species.

As previously stated, the majority of research concerns the salmonids. These tend to be strong swimmers with good leaping capabilities (Larinier, 1998). Other species that do not posses this capacity, yet still undertake similar migrations (e.g. the river lamprey, *L. fluviatilis*, and European eel, *A. anguilla*) must use alternative behavioural strategies to overcome the conditions involved. For example, fish move multiple fins to stabilise their bodies in turbulent flow (Liao, 2007) and pectoral fins are thought to be extremely important in maintaining stability of salmonids in complex flows associated with fish passes (Liao *et al.*, 2003; McLaughlin & Noakes, 1998). However, anadromous lamprey species do not posses pectoral fins and yet still undergo the long upstream migrations undertaken by anadromous salmonids. They must therefore undertake alternative strategies to move efficiently upstream.

There is little information concerning how weak swimmers cope with adverse flow conditions, but there are exceptions. Moser *et al.* (2002b) observed migration of Pacific lamprey, *L. tridentata*, in the field to be faster than expected from laboratory observations, possibly due to them taking advantage of the reduced water velocities near the substrate. Alternatively, under difficult passage conditions, Quintella *et al.* (2004) observed sea lamprey, *P. marinus*, to alternate between short bursts of intense activity and periods of motionless rest where they attach to suitable structures with their anterior sucker. This behaviour potentially allows the lamprey to cope with and overcome adverse conditions, such as high water velocities and turbulent flow. An alternative strategy for fish which do not possess the capacity to maintain station with paired fins (e.g. the eel) is that they will avoid such adverse conditions (Liao, 2007), however, research observing this is lacking.

A further simple behavioural trait rarely considered in the literature is where the fish swim in the water column. Fish passes for downstream migration are often designed on the principle that migrating fish are orientated in the upper reaches of the water column. However, although this is true for juvenile salmonid species (e.g. Arnekleiv *et al.*, 2007), Coutant & Whitney (2000) noted that non-salmonids will occupy different parts of the water column dependent upon species, life-stage and season. For example, downstream migrating juvenile lamprey swim low in the water column, thus have an increased potential for entrainment through hydroelectric turbines compared to the surface oriented downstream moving salmonid smolts (Moursund *et al.*, 2001). Understanding the behaviour of target fish species and life-stages is necessary to optimally design, locate and operate passage facilities, and is best observed with free-swimming fish in flumes retrofitted with natural or technical passage structures (Kynard, 1993; Kynard *et al.*, 2008). However, telemetry studies undertaken in the field are also useful, but they do not provide the fine-scale behavioural information achieved through direct observations obtained under experimental conditions (Rice *et al.*, 2010).

So far considered in this review are the influence of abiotic factors on the swimming ability and behaviour on fish, however, biotic factors also play a role. Many studies concerning fish passage utilise either groups or individual fish, but with no comparison of the differences in behaviour that are likely to occur between these treatments. This is obviously an unrealistic assumption because the presence of other individuals will have an over-arching influence on behaviour (Viscido *et al.*, 2005). Salmonid smolts often school during their downstream migrations (Haro *et al.*, 1998) and are likely to interact, influencing one another's behaviour. Studies assessing individual behaviours thus may not produce realistic information concerning group behaviour of the species in question. A number of studies have highlighted behavioural changes of individuals within groups to attain an energetic advantage (e.g. Herskin & Steffensen, 1998; Landa, 1998; Svendsen *et al.*, 2003) despite early arguments against this (Partridge & Pitcher, 1979).

Passage of fish can be inhibited by structures preventing the maintenance of school integrity (Bakshtansky *et al.*, 1993; Scruton *et al.*, 2005). Shad, for example, are known to move in shoals, and if fish passes are designed in such a way that the fish cannot pass through as a group, e.g. the traverse of a vertical slot fish pass is too narrow, then they will likely prefer to maintain school integrity and thus not enter the fish pass, or once entering will fall back to rejoin the group (Larinier & Travade, 2002b). Comparison studies of group and individual behaviours under controlled experimental conditions are needed to determine the influence of schooling behaviour not only for salmonids, but also all other species within the watercourse.

Roscoe & Hinch (2010) identified a strong regional bias for fish passage research, with the vast majority (52%) concerning North American, 30% European and only 18% South American and Australian species. A worrying trend within this regional bias is that only 4% of the North American studies examined the entire local fish community, even though the importance of multi-species fish passage has been highlighted (e.g. Bunt *et al.*, 2001; Odeh, 1999). However, the integrated knowledge of individual species specific behaviours for the various species within a local community is necessary to optimise the design of fish passage facilities to cater for multiple species. This approach is undertaken within the USA (Roscoe & Hinch, 2010) in contrast to Europe and tropical regions (with 38% and 94% of studies concerning the entire fish community respectively) which have legislation requiring holistic goals to optimise passage for all species (e.g. the WFD, EC 2000). However, there is still a need to study species specific behaviours to optimise fully passage facilities for each species present in the local community.

To optimise the effectiveness of fish protection schemes it has been suggested that site specific studies, in consideration of behaviour and swimming ability of target species, are necessary due to the structural and operational uniqueness of each structure (Scruton *et al.*, 2008). However, this also highlights the importance of identifying specific swimming performance and behavioural responses of fish to various conditions associated with impediments to migration, to aid fish pass engineers in producing mitigation that efficiently passes the target species from initial installation. This requires the design of laboratory experiments where both the motivational state of the fish and the stimuli they encounter are controlled, enabling studies designed for one system to be applied to others (Anderson, 1988).

A number of key gaps in the knowledge concerning fish passage operations have been highlighted above (i.e. lack of consideration of the swimming performance and behaviour of multiple species and life-stages), many of which are a consequence of the upstream migrating salmonid research bias. These gaps need to be addressed to provide fish pass engineers with the tools and criteria to design efficient and safe passage facilities for a broad range of species with equally diverse life-histories, during both up- and downstream migration.

1.7 SUMMARY

Throughout this review a number of trends and biases in fish passage research have been identified and must be addressed. International legislation requires that concomitant with increased anthropogenic use of the waterways (through e.g. Europe's Renewables Directive 2009/28/EC), there is a need to protect all species utilising them during all life-stages through e.g. the WFD and NEPA. However, there is a large bias in fish passage research towards upstream moving salmonids and particularly North American species (Roscoe & Hinch, 2010). Failure to provide adequate passage for multiple species (both diadromous and potamodromous) and life-stages poses a serious threat to the biological integrity of entire river networks (Meyer *et al.*, 2007). If major losses of global fish biodiversity are to be avoided, more information on the behaviour and potential of non-salmonid fish species, in addition to salmonids, to pass river infrastructure is required (Clay, 1995).

Optimising conditions for fish passes is one of the most critical and challenging problems of fish passage (Bunt, 2001). The main task of fisheries managers and fish pass engineers is to produce optimal designs taking into account the needs of the fish and the operational requirements of the structure, while incurring minimum costs. Thus, both further and more accurate information concerning swimming performance and behaviour of fish under a variety of conditions is required to produce effective mitigation measures for barriers to migration (Kemp & O'Hanley, 2010). Yet, basic knowledge such as swimming speeds is lacking for non-salmonids (Roscoe & Hinch, 2010) and information for all species may be inaccurate due to the use of confined swim chambers and respirometers prohibiting fish swimming to their full ability (Tudorache *et al.*, 2007). Thus there is a need to find alternative methods to attain fish passage criteria. The use of large open-channel flumes allows volitional compensatory swimming behaviours to be expressed and observed under controlled conditions. The establishment of generic rules of fish behaviour and swimming capacity for multiple species and life-stages will increase the efficiency of initial fish pass designs, reducing the number of structures that need retrofitting because of poor design and thus the biological and operational costs.

To address the issues raised in this review, the research presented in the following chapters aims to contribute to the knowledge of fish passage criteria for European species of non-salmonid fish during both up- and down-stream movement, by studying the very different swimming modes and abilities of anguilliforms. Research concerning salmonids during downstream movement is also presented, due to the relative lack of information on the behavioural responses at barriers gathered for this life-stage. An attempt to attain basic swimming performance and behaviour of fish will be made using methods allowing them to undertake natural behaviours (i.e. a large open-channel flume facility); thus attaining more accurate and realistic information than previously available through swim chamber tests or field studies where fine scale behaviours are difficult to observe. Finally, attempts to gather more detailed information of the fish response to other conspecifics (biotic variables) and the hydraulic conditions (abiotic factors) associated with barriers to migration will be made. The application of the observed generic responses to any fish passage scenario will aid the design and implementation of effective mitigation to migratory impediments, ultimately contributing to the protection of the biodiversity of our rivers.

Chapter 2: Research aims

The primary aim of this programme of research is to contribute towards a generic rule base of fish passage criteria for the under-researched diadromous anguilliform fish (European eel, *Anguilla anguilla*, and river lamprey, *Lampetra fluviatilis*) and a salmonid (*Salmo trutta*) during downstream movement. This will take a step towards addressing a number of the issues and biases raised in the literature review (chapter 1). To do this experiments quantifying the swimming abilities and behavioural responses of fish to model structures (and associated conditions) placed in a large open-channel flume facility were undertaken and presented in this thesis through five research chapters.

Chapter four, the first research chapter of this thesis, aims to show how the use of large open-channel flumes allows the attainment of basic swimming capabilities (i.e. swim speeds) which are more applicable to fish passage, compared to traditional methods where the fish can not undertake natural behaviour. The negative effect of small river infrastructure designed with the commonly researched salmonid behaviour in mind, on weak swimming anguilliforms will be highlighted through chapter five. Following on, chapter six aims to further demonstrate the potential negative effect that structures designed for downstream migrant salmonids to safely pass potential hazards (e.g. hydropower facilities) can have on anguilliforms which demonstrate very different behaviours. However, the research in chapter six also attempts to provide information of fish passage criteria to apply to bypass systems to improve passage efficiency and safety for this group. Direct comparisons of the behaviours of different target species are lacking for fish passage and chapter seven attempts to address this issue by directly comparing the response of downstream moving brown trout and European eels to conditions associated with an orifice weir. Further, building on chapter six where eels were seen to potentially respond to broad scale hydraulic conditions, an attempt to determine the response of the fish to specific hydraulic conditions was undertaken in chapter seven. This kind of information is vital to manipulate effectively hydraulic conditions to increase fish passage efficiency.

The aforementioned research chapters are mainly concerned with determining the effect of abiotic factors (e.g. hydraulic conditions) on fish swimming capabilities and behaviour, the final research chapter (eight) is the first where the influence of biotic variables (i.e. the presence of conspecifics) are assessed. This chapter attempts to demonstrate that fish passage criteria for the commonly researched salmonids is still lacking and anthropogenic river infrastructure can create conditions where certain biotic variables will reduce passage efficiency if they are not considered during construction.

2.1 HYPOTHESES

Specific hypotheses and objectives are presented in each research chapter (4-8) however, the following general hypotheses apply:

H1: Fish can attain higher swimming speeds when able to undertake natural behaviours, e.g. burst and glide, permitted in large flumes compared to traditional constrictive methods, i.e. swim chambers.

H2: Relatively weak swimming ability anguilliforms (i.e. have low maximum Burst swimming speeds) have difficulty passing structures designed with anadromous salmonids in mind.

H3: The ability of fish to pass a partial barrier is influenced by their behavioural response towards both the obstacles physical presence and associated hydraulic conditions.

H4: Anguilliforms demonstrate different strategies and capacities to deal with the conditions associated with barriers to migration compared to sub-carangiforms (salmonids).

H5: The break down of mono-species fish school integrity influences the level of adversity experienced by those left behind, more so than if they were simply lone individuals to start with.

2.2 SUB-AIMS

To meet the primary aim the following sub-aims were assessed via the relevant research areas/chapters (summarised in Fig. 2.1):

Sub-aim 1: Attain basic knowledge of fish swimming capabilities and behaviour

Sub-aim 2: Quantify the fish response to detailed hydraulics

Sub-aim 3: Attain fish passage criteria for less researched anguilliforms.

Sub-aim 4: Attain fish passage criteria for less researched downstream migration phases.

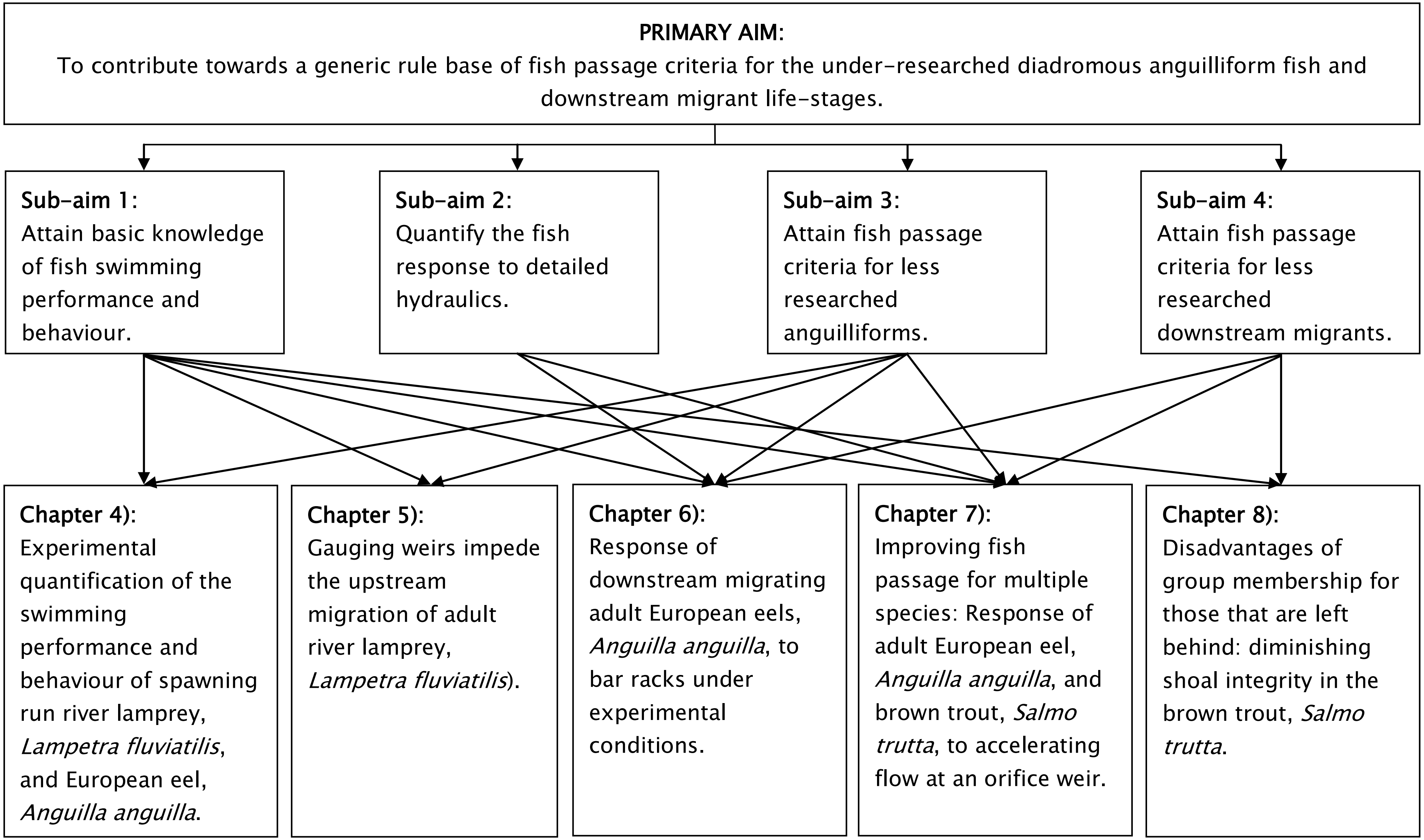

Fig. 2.1 Summary of the aims of this thesis and the research areas/chapters undertaken to meet these.

Chapter 3: General research methodology

The following chapter provides details of the general facilities, equipment, study species and software used during the research presented in this thesis, and reasoning as to why specific techniques were employed. More detailed methodologies are given in each appropriate research chapter (chapters 4-8).

3.1 WHY USE FLUME BASED RESEARCH?

Field studies using telemetry are regularly used to track fish movement and observe broad scale (ranging from *ca.* 1km to, more recently, 1 m accuracy; e.g. Brown *et al.*, 2009) behaviours throughout a catchment and/or at a barrier to migration (e.g. Brown *et al.*, 2009; Haro *et al.*, 2000a; Lucas *et al.*, 2009; Winter *et al.*, 2006). Although of great importance, telemetry studies do not provide the fine-scale behavioural information necessary to optimise passage efficiency and minimise mortalities at barriers to migration, which can be attained through direct observations under experimental conditions in a flume (Rice *et al.*, 2010). Brown *et al.* (2009) for example, observed downstream migrating European eels to return upstream on encountering a screen at a hydropower plant, through the use of three-dimensional acoustic telemetry that detects the fish position to an accuracy of *ca*. 1 m. However, whether the eels were responding to hydraulic conditions (and if so what specific conditions, e.g. velocity, turbulence intensity or shear stresses) or contacting the structure prior to demonstrating a response could not be ascertained using this technique, for which direct observations are necessary.

Knowledge concerning the fine-scale responses to conditions associated with barriers to fish migration (e.g. hydraulics) is necessary to determine e.g.

the fish response to specific flow conditions (e.g. water velocity and turbulence intensity) or to the physical presence of the structure. Larger flumes, such as the one used throughout this research programme, still permit natural compensatory swimming behaviours to be undertaken by the fish (Peake, 2004; Tudorache *et al.*, 2007), whilst providing conditions where the motivational state and the stimuli encountered are controlled for. Thus the fine-scale information provided through large flume based studies can be used to compliment the broader scale information gathered through telemetry studies in the field (and vice versa). This complimentary information can then be applied to provide suitable structural adaptations and/or manipulate flow conditions at barriers to create more efficient fish passes and reduce mortalities.

3.2 STUDY SPECIES

3.2.1 EUROPEAN EEL, *ANGUILLA ANGUILLA*

The European eel, *Anguilla anguilla*, is a catadromous species, maturing and residing in freshwater then undertaking a long spawning migration (*ca.* 6000 km) from European waters to a specific region of the North Atlantic (probably the Sargasso Sea), after which they die (Tesch, 2003). Ocean currents transport the juveniles (leptocephali) back to European coasts where they enter estuaries in the summer months, developing into elvers. Once in freshwater the eels grow and mature into yellow eels, which remain resident in freshwater for *ca.* 5-20 years before beginning their return to the spawning grounds as silver eels during the autumn (Fig. 3.1).

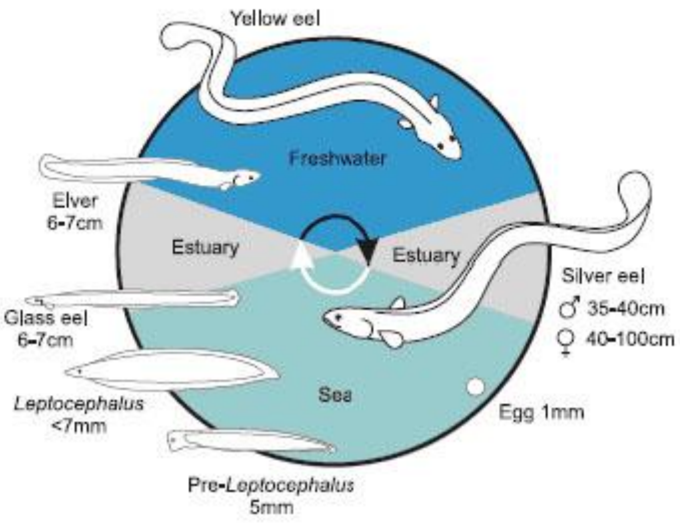

Fig. 3.1 Life cycle of the European eel, *Anguilla anguilla* (taken from www.cefas.gov.uk).

For this research programme, silver eels undertaking the start of their spawning migration were needed to assess the responses to conditions associated with migratory barriers during downstream movement. Fish were sourced from commercial trappers on the River Stour (Dorset, UK) and the River Test (Hampshire, UK) using permanently installed eel racks (Plate 3.1). Eel racks capture fish as they swim downstream, ensuring they are actively migrating.

Plate 3.1 Eel rack on the River Stour, Dorset UK (photo courtesy of Roger Castle, taken October 2008).

3.2.2 RIVER LAMPREY, *LAMPETRA FLUVIATILIS*

River lampreys are an anadromous species where spawning occurs in freshwaters and adults reside in the marine environment (Kelly & King, 2001). The juvenile phases spend *ca*. 3-8 years in buried in silty substrate as ammocoetes prior to metamorphosing into macrophthalmia, the downstream migration stage (Kelly & King, 2001) (Fig. 3.2). In the marine environment, young adults feed parasitically on other fish using their oral sucker. After 2-3 years the adults return to freshwater in the autumn, residing in freshwater for several months before spawning during late spring/early summer.

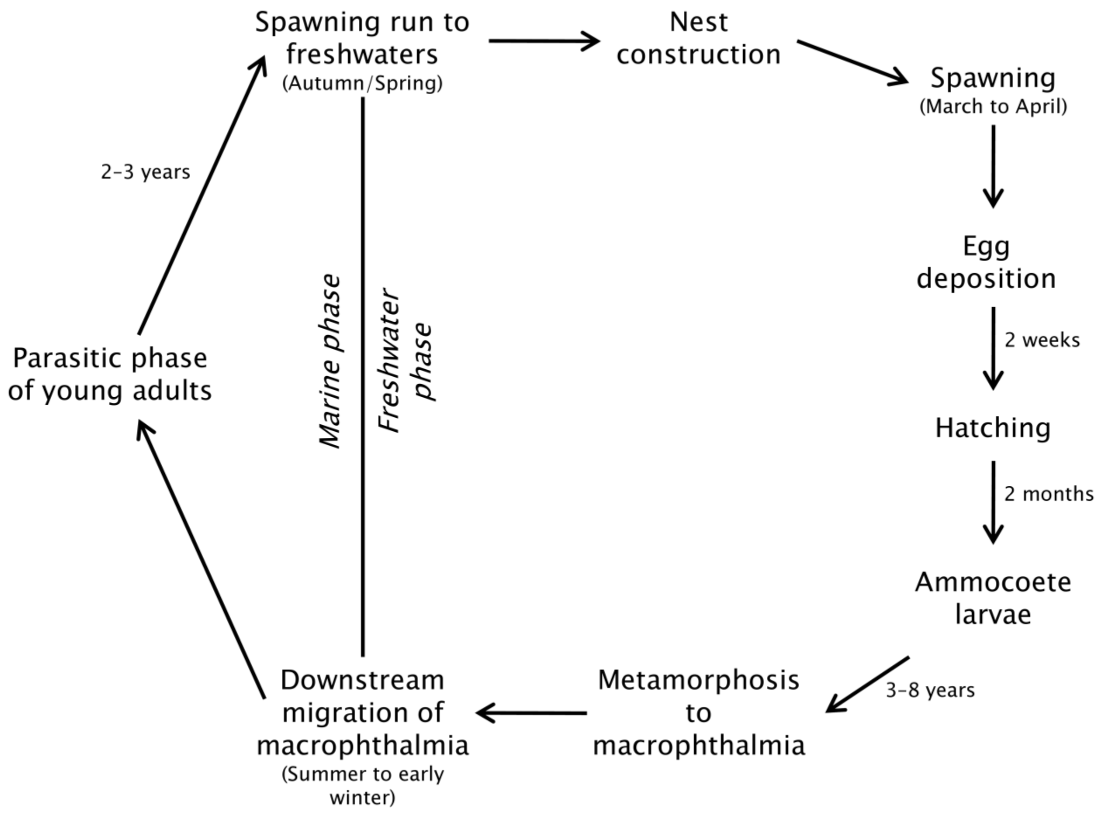

Fig. 3.2 Life cycle of the River Lamprey, *Lampetra fluviatilis* (adapted from Kelly & King, 2001).

As for eels, lampreys undertaking the freshwater stage of their spawning migration were needed to assess the swimming capabilities and behavioural response to barriers to migration during upstream movement. Actively upstream migrating adult river lampreys were collected from the tidal reaches of the River Ouse (North-east England) by a commercial trapper using two-funnel eel pots, for use in experimental trials.

3.2.3 BROWN TROUT, *SALMO TRUTTA*

Brown trout, *Salmo trutta*, have variable life-history strategies (Hindar *et al.*, 1991) ranging from anadromy (where the species is commonly referred to as sea trout), to potamodromy where the entire life-cycle is completed in freshwater but the fish still embark on considerable migrations e.g. of 40 km or more (Schulz & Berg, 1992) to access suitable spawning, residential or feeding habitat. Spawning occurs in the headwaters of streams during the autumn/winter, and the eggs hatch into alevins the following spring. After 3 years some populations of trout metamorphose into smolts and migrate to the sea during the summer, whereas other populations develop into sexually mature adults (at a slower rate and smaller size) while remaining in freshwater (Frost & Brown, 1967). Those fish migrating to the sea return to spawn in the freshwater after 1-2 years.

Although ideally wild fish during their migratory phase should be used during this research (as is the case for the European eel and river lamprey), these were not available and brown trout were sourced from a trout farm in Hampshire (UK). Maximum swimming speeds attainable by hatchery reared brown trout are generally lower (by approximately 25%) than for wild fish (Pedersen *et al.*, 2008). If permission to attain wild brown trout smolts was given, the method most commonly employed to capture fish for research is electro-fishing (Cowx & Lamarque, 1990). However, there is evidence to support that electro-fishing can reduce swimming performance and alter behaviours in fish (Bracewell *et al.*, 2004; Mitton & McDonald, 1994). Thus, the use of both electro-fished and farmed fish provides a compromise to direct observations in the field with wild fish that have not been interfered with (e.g. captured via electro-fishing and radio-tagged) when assessing swimming performance. However, observed behavioural responses to hydraulic conditions during downstream movement (see relevant research chapters 7 and 8) were similar to those observed for wild pacific salmonids presented with obstacles in a flume (Enders *et al*, 2009; Kemp *et al.*, 2005a), i.e. switching orientation on encountering a flow gradient rather than contacting the structure itself. In these studies the flume was based at a large hydropower facility (McNary Dam on the Columbia river, Washington, USA), and fish were taken directly from the juvenile bypass facility and placed into the flume without the use of electro-fishing or sedation (although forced swimming in the bypass facility may have reduced swimming performance; Mitton & McDonald, 1994). Thus, although being a compromise, observations of the farmed brown trout behaviour in response to hydraulic conditions are still applicable to fish passage, but inferences of swimming ability must take into account potential negative impacts, e.g. reduced swimming speeds and energy reserves, when compared to wild fish.

3.3 CHILWORTH FLUME FACILITY

All experiments presented in the following chapters 4-8 were conducted at the International Centre for Ecohydraulics Research flume facility (Southampton University) located at Chilworth, UK. The facility is a purpose built re-circulatory flume with glass sided walls and a steel base (Plate 3.2). It has a working length of 21.4 m, a width of 1.4 m, and a maximum depth of 0.6 m. Three electrically driven centrifugal pumps, with individual capacities of 90, 150 and 230 L s^{-1} drive water through the system. Discharge and depth are controlled by altering the number and combination of centrifugal pumps in use, the water flow through them (via adjustment of individual valve controls) and the height of an adjustable weir located at the downstream end of the flume.

Plate 3.2 Chilworth flume facility retrofitted with a model flat-v gauging weir.

Black plastic screens were installed along the outside of the channel walls. The screen height was 2 m on the true right of the flume (left side of Plate 3.2) where an elevated walkway was present. This reduced lateral illumination and disturbance to the experimental fish by the observers during experimental trials.

The flume was fitted with a number of different structures, e.g. a flat-v gauging weir (Plate 3.2), to create specific conditions associated with anthropogenic use of the waterways (see individual research chapters for descriptions of each structure type used).

3.4 VIDEO ANALYSIS

This research was undertaken during the hours of darkness, coinciding with the time of peak activity of the species being assessed (Kelly & King, 2001 for river lamprey: Calles *et al.*, 2010; Hadderingh *et al.*, 1999; Tesch, 2003 for European eel: Heggenes *et al.*, 1993 for brown trout). To assess fish movement and activity at the Chilworth flume facility during this period, trials were digitally recorded using overhead and side-mounted video cameras (see relevant chapter for position and number of cameras utilised). The cameras were capable of recording fish movement under low-light conditions under infra-red illumination. The addition of infra-red illumination units increased the clarity of the recordings.

From the video recordings a variety of behavioural and capability parameters were obtained, including depth and lateral position of approach, the number of approaches, successful passage of an obstacle and the timings of any event (see relevant chapter), manually by watching the play-back. For some experiments more detailed analysis of the recordings was necessary. A particle tracking programme designed using MatLab® 2009b (The Math Works, Inc., Natick, MA) was written by Dr Tony Lock (University of Southampton) and allowed the position of the fish as they demonstrated a response (e.g. rejection of the structure or changing orientation relative to the impediment) to be calculated to within 1 cm from the digital recordings. This more detailed information was then applied to hydraulic maps to assess fish response to the associated hydraulic conditions (see section 3.5 for more details).

3.5 HYDRAULICS

3.5.1 FLOW MEASUREMENTS

Water velocity at the Chilworth flume facility was measured using an electromagnetic flow meter (Valeport, 801-flat) calibrated to record over 10 seconds and present the mean velocity and standard deviation from the mean, along transects perpendicular to the flow at the channel floor, 40% depth and the surface. From the 40% depth transects (the average water velocity depth; Hamill, 2001) discharge could be calculated.

Where more detailed velocity measurements were necessary a Nortek Vectrino^{+} Acoustic Doppler Velocimeter (ADV) was used to provide high frequency velocity sampling. ADVs were developed in 1992/1993 for laboratory use, and are used to measure velocity profiles at sub-centimetre accuracy in 3D. Complete technical descriptions of the ADV are provided by Kraus *et al.* (1994) and Lohrmann *et al.* (1994). Advanced firmware was incorporated with this device allowing for sampling up to 200 Hz to be undertaken. However, sample frequency was set to a maximum of 50 Hz (the optimum frequency for the Nortek Vectrino^{+} ADV, above which measurement noise increases; Dr. Luke Myers, pers. comm.) in this research, with a sample volume of 0.31 cm^3. Sampling periods were set to 60 seconds, providing 3000 discrete velocity samples in 3D.

Spurious data and outliers were removed from the obtained ADV data using a velocity correlation filter as described by Cea *et al.* (2007) to reduce the doppler noise effect, one of the major sources of error in unfiltered ADV data. The velocity correlation filter is particularly recommended for highly turbulent flows (Cea *et al.*, 2007). From the filtered data the 3D mean velocity and relative turbulence intensity (*K*) were obtained. Other statistical parameters can also be calculated if necessary, including the Reynolds stresses, horizontal and vertical shear stresses, power spectrum and turbulent kinetic energy (Cea *et al.*, 2007). Statistical tests were then carried out to compare the behaviour of the fish (analysed via video analysis) to the flow conditions (e.g. water velocity and *K*) associated with the structure in question.

3.5.2 FLOW MAPPING AND ASSESSMENT

From the detailed flow measurements obtained via ADV, mapping of the various parameters calculated was undertaken for visualisation using SigmaPlot® (Systat Software Inc., London, UK). Allowing the routes selected by the fish during approaches to the structure in question to be compared to these hydraulic parameters. In addition to SigmaPlot® (Systat Software Inc., London, UK), a spline interpolation in ArcGIS™ 10's *Spatial Analyst* tool was used to map hydraulic conditions, i.e. velocity, for chapter 7 as described by Enders *et al.* (2009). By using the maps as tools, the interpolated velocities at the head and tail positions could be extracted by overlaying the position of a brown trout (attained via the particle tracking software in MatLab 2009b) turning from negative to positive rheotaxis for example, on the corresponding flow map. From the extracted velocity data it was possible to calculate a gradient of the hydraulic parameter in question along the length of the fish, making it possible to attain detailed information concerning the response of brown trout to specific changes in water velocity (see chapter 7), which can be utilised to manipulate hydraulic conditions at any situation, on any scale, to accommodate fish passage.

Chapter 4: Experimental quantification of the swimming performance and behaviour of spawning run river lamprey, *Lampetra fluviatilis* L., and European eel, *Anguilla anguilla* L..

4.1 SUMMARY

Limitations of traditional swim chamber tests to provide reliable estimates of fish swimming performance have been recognised. Inhibition of performance enhancing behaviour within confined conditions can result in conservative estimates, while the simplistic rectilinear flows provided inadequately recreate conditions experienced in nature. Furthermore, tests of fish swimming ability have tended to focus on the carangiform mode of locomotion, while other modalities are infrequently considered. As a result, alternative approaches are required to attain more realistic and accurate measures of fish swimming capability for multiple species and swimming guilds. Using a large-scale open channel flume, the swimming ability and behaviour of individual adult European eel, *Anguilla anguilla*, and river lamprey, *Lampetra fluviatilis*, species that exhibit anguilliform locomotion, was quantified under complex hydraulic conditions created by a 0.2–0.3 m high under- or overshot weir during one of 4 discharge regimes. Fish were allowed to approach the weirs from both up- and downstream. All fish passed the undershot weir, independent of discharge and direction of movement, and under high flow (mean ± S.E. 194.63 ± 6.48 l s^{-1}) swam upstream against velocities that ranged between 1.75–2.12 m s^{-1}, suggesting greater maximum swimming capability than previously reported. In

comparison, passage efficiency during upstream movement was lower for the overshot weir for both lamprey and eels. Downstream moving eels took longer to pass the over- than undershot weir. This study describes a methodology to attain realistic measures of swimming ability and behavioural performance required to develop multispecies fish passage criteria.

4.2 INTRODUCTION

Measures of fish swimming capability have historically been based on the performance of subjects forced to swim against unnatural rectilinear flows while confined within limited space provided by swim chambers (e.g. Brett, 1964; Van den Thillart *et al.*, 2007). Such methods have been criticised because forced swimming under highly artificial conditions can underestimate locomotory capacity that would otherwise be attainable in the field (Haro *et al.*, 2004; Mallen-Cooper, 1992; Peake, 2004; Peake & Farrell, 2004). Recent research has demonstrated that in both the field and large scale open-channel flumes, higher maximum swim velocities are attained when fish are allowed to exhibit volitional performance enhancing behaviours such as gait transition (e.g. “burst-and-glide” [Peake & Farrell, 2004; Tudorache *et al.*, 2007], or “burst-and-attach” in the case of lamprey [Kemp *et al.*, 2011]).

Peake (2004) compared the results of tests conducted in swim chambers with those performed in a 50 m flume to measure swimming capability of smallmouth bass, *Micropterus dolomieu* (Lacépède). Critical swim velocities (U_{crit}) of 0.65 to 0.98 m s^{-1} were obtained in the swim chamber, yet a high proportion of the fish could swim the entire length of the flume against water velocities up to 1.20 m s^{-1}. In a similar study, Tudorache (2007) observed a 20% increase in U_{crit} from between 0.60-0.80 m s^{-1} to 0.75-1.10 m s^{-1} for common carp, *Cyprinus carpio* L., with increasing flume length, likely as a result of exhibition of “burst-and-glide” swimming behaviour under less restrictive conditions. In recognition of this, increasingly efforts are made to attain more realistic estimates of swimming capabilities using open-channel flumes (e.g. Haro *et al.*, 2004; Kemp *et al.*, 2011; Peake, 2004; Tudorache *et al.*, 2007). Flume based studies also provide the opportunity to observe and obtain fine-scale behavioural information, e.g. how fish respond to the presence of river infrastructure (e.g. Russon *et al.*, 2010, for European eel, *Anguilla anguilla* L.) through direct observations under experimental conditions, compared with broad scale information provided from field studies, e.g. those that utilise telemetry (Rice *et al.*, 2010).

Past research to investigate locomotory performance of fish has tended to focus on few taxa and swimming modes, particularly the salmonids (Fisher & Hogan, 2007) and carangiform/sub-carangiform locomotion (Colgate & Lynch, 2004). Assessments of anguilliform swimming are less common and based predominantly on the results of swim chamber tests (e.g. Sébert *et al.*, 2009; Van den Thillart *et al.*, 2007). Kemp *et al.* (2011) provide a rare exception of a study of anguilliform swimming and behaviour using a large open channel flume. The authors found that adult river lamprey, *Lampetra fluviatilis* L., attained higher swimming velocities (>1.5 m s^{-1}) than had been previously observed. Generally, anguilliform locomotion is considered to be highly efficient when compared with the carangiform mode (van Ginneken & Maes, 2005), but is not as powerful, hence maximum burst swimming velocities tend to be lower (Dauble *et al.*, 2006).

Information on swimming performance is useful when applied to the development of criteria for fish pass and screening design, to divert and guide fish to alternative routes past river infrastructure. Compared to the salmonids, for which screening and fish passes have traditionally been designed, the lower burst swimming capacities of anguilliform fish, such as eels and lamprey, may limit the effectiveness of these facilities for multiple species. This is important because the impacts of reduced habitat connectivity are considered major contributory factors in declines of river lamprey and European eel populations over the past *c.* 20-50 years (Bark *et al.*, 2007; Dekker, 2003; Haro *et al.*, 2000a;- for eels: Lucas *et al.*, 2009; Masters *et al.*, 2006 - for lamprey). The development of passage and screening criteria for these species represents an important first step towards achieving restoration goals (e.g. as driven by legislation such as The EU Eels Regulation, no. 1100/2007), and thus realistic measures of swimming capability and behaviour are required. However, there are also large differences in the behaviours employed by anguilliforms to cope with challenging hydraulic conditions, e.g. lamprey attach to a suitable substrate using their oral sucker (Kemp *et al.*, 2011) and can rest to aid recovery from burst swimming (Quintella *et al.*, 2004), but eels do not have this capacity and must employ alternative strategies.

To provide realistic fish passage criteria for European eel and river lamprey, this study aims to quantify the swimming capacity and volitional behavioural response to velocity barriers created in a large open channel experimental flume. To achieve this aim, test fish were challenged to pass an over- or under-shot weir under varying discharge regimes. Specific objectives were 1) to attain maximum swimming velocities; 2) assess response to weir type as fish move in the direction of their natural migration for the specific life-stage of interest; and 3) assess response to accelerating flow. A sub-objective was to assess the differences in the behaviour of eel and lamprey. The methodology developed may help provide realistic information of swimming capabilities and behaviour for the development of effective multi-species fish passage and screening facilities.

4.3 MATERIALS AND METHODS

4.3.1 FLUME AND WEIR STRUCTURE

All experiments were conducted at the International Centre for Ecohydraulics Research (ICER) flume facility at the University of Southampton. Flow through a glass sided recirculatory flume (21.4 m long, 1.4 m wide and 0.6 m deep) was controlled by adjusting the number (maximum = 3) and combination of centrifugal pumps in operation, and the volume of water flowing through them. The height of a weir located at the downstream end of the flume was adjusted to maintain water depth. Dark plastic screens erected along the outside of both channel walls prevented lateral illumination and disturbance to the fish by the observer.

An 18 mm thick plywood weir, spanning the entire width of the channel, was placed in the centre of a 16 m long section of the flume. The weir was configured to represent either an over- or under-shot treatment. The water crested over the top of the weir during the overshot condition, and when undershot flowed through a 0.10 m gap at the channel floor. Four discharge regimes (termed low, intermediate, high, and very high) were selected to create a range of velocities and accelerations of flow. The height of the weir was 0.20 m under low and intermediate, and 0.30 m (to attain higher hydraulic head and associated velocities) under high and very high discharge treatments. To test maximum burst swimming (that which fish can maintain for just a few seconds; Crisp, 1996) performance, only the undershot treatment was presented during high and very high discharge. No control condition to observe fish movement and behaviour in the absence of a weir was deemed necessary because the aims of this study were to attain maximum swim speeds (challenging water velocities for the fish were only attainable through the insertion of constrictive structure within the flume channel) and compare the different behavioural responses towards two distinct weir types (under- and overshot). Velocity (and water depth) was recorded at five equidistant points along 10 transects perpendicular to the flow (between 1.0 m upstream and 2.0 m downstream of the weir) using an electromagnetic velocity meter with the probe positioned 20 mm above the channel floor as lamprey (Kemp *et al.*, 2011; Lucas *et al.*, 2009; Moser *et al.*, 2002b) and eels (Amaral *et al.*, 2003; Russon *et al.*, 2010) tend to move along the substrate during their spawning migrations.

4.3.2 FISH AND EXPERIMENTAL TRIALS

Actively downstream migrating adult European eels (mean total length (L_t) ± SE = 661 ± 7 mm; mean weight (M) ± SE = 483 ± 19 g) were captured at a commercial eel trap on the river Test, southern England (51°07′N, 01°52′W) on 11 October and 17 December 2007. The eels were placed in aerated and iced river water to minimise stress during transportation to the facility, where they were maintained in a 3000 L holding tank at a maximum stocking density of 9.97 kg m^{-3} for a minimum of 12 days before experiments commenced. The mean water temperature (± SE) was 15.10 ± 0.32°C prior to trials.

Upstream migrating adult river lamprey (L_t ± SE = 358.50 ± 3.38 mm; M ± SE = 82.04 ± 2.37 g) were collected in un-baited two-funnel commercial eel pots from the tidal reaches of the River Ouse, North-east England (53°54′N, 01°06′W) on 12 December 2007, and transported to ICER using the same method as for eels. Lamprey were maintained in a 900 L holding tank at a maximum stocking density of 4.06 kg m^{-3} for a minimum of 27 days prior to use in experimental trials. The mean water temperature (± SE) was 13.20 ± 0.42°C.

One-hundred and twenty four trials (Table 4.1) using individual fish were undertaken between 23 October 2007 and 21 January 2008. This period coincides with typical spawning migrations of eels (Haro, 2003; Tesch, 2003) and lamprey (Winter & Van Densen, 2001). Fish were acclimated for a minimum of one hour in porous black plastic containers within the flume before being released 8 m upstream or downstream of the weir (dependent on treatment, Table 4.1) and allowed to volitionally explore the channel. Although the eels were actively downstream migrating, in addition to determining behavioural responses to weir type and acceleration of flow during their natural direction of movement, trials were conducted where the fish were released downstream of the weir and volitional upstream movement permitted to attain burst swimming speeds (Table 4.1). Similarly, the spawning run river lamprey were naturally upstream moving, however, in addition to determining swim speeds during upstream movement, further trials where the fish were released upstream and allowed to volitionally move downstream through a velocity gradient were undertaken to assess their response to accelerating flow (to simulate conditions at e.g. water offtakes at power plant cooling facilities) (Table 4.1). Trials lasted a maximum of 0.5 hours, or until the entire body length of the fish successfully passed the weir. Species, weir type, release point, and discharge were alternated between trials. Mean water temperature (± SE) at the start of experimental trials was 12.63 ± 0.39°C.

Table 4.1. Main study objectives, and associated treatment conditions, to experimentally assess the swimming performance and behaviour of European eel and river lamprey.

Objective	Species	Direction of movement	Weir type	Discharge treatment & number of replicates (*n*)
1) Attain maximum swim velocity	European eel	Upstream	Undershot	Low (6), intermediate (6), high (3), very high (4)
	River lamprey	Upstream	Undershot	Low (6), intermediate (6), high (3), very high (4)
2) Response to weir type in natural direction of migration	European eel	Downstream	Under- & over-shot	Low (6), intermediate (6) Low (6), intermediate (6)
	River lamprey	Upstream	Under- & over-shot	Low (6), intermediate (6) Low (6), intermediate (6)
3) Response to accelerating flow	European eel	Downstream	Undershot	Low (6), intermediate (6), high (3), very high (4)
	River lamprey	Downstream	Undershot	Low (6), intermediate (6), high (3), very high (4)

4.3.3 SWIMMING PERFORMANCE AND BEHAVIOUR

Trials were conducted during the hours of darkness (17:00–03:00) to replicate the natural nocturnal spawning migration of river lamprey (Kelly & King, 2001) and European eel (Calles *et al.*, 2010; Hadderingh *et al.*, 1999; Tesch, 2003). Fish behaviour was recorded using a side-mounted and 2 overhead low-light cameras under infrared illumination (4 x 15 W units emitting light at 850 nm wavelength) when entering an observation zone extending from 2.0 m downstream to 2.0 m upstream of the weir.

The time (s) to first approach (when the entire body length of the fish entered the observation zone), percentage of successful passes (when the entire body length of the fish passed the weir), and the time (s) taken to pass were measured. Tests of normality and homogeneity of variance were performed using Shapiro-Wilk and Levene's tests, respectively. All data were normalised using natural log (L_n) transformation for statistical analysis.

Univariate two-way ANOVAs were used to assess the effect of 1) species and discharge on the time to first approach and pass an undershot weir during upstream movement; 2) discharge and weir type on the time taken by upstream moving lamprey and downstream moving eel to first approach and pass the weir and 3) species and discharge on time taken to first approach and pass an undershot weir during downstream movement.

4.4 RESULTS

Water velocity increased with discharge (Table 4.2), with highest mean values recorded between the weir and 0.4 m and 1.0 m downstream of the undershot and overshot treatments, respectively (Fig. 4.1). Directly downstream of the overshot weir the direction of currents tended to deviate from that of the bulk flow, as plunging flow over the weir produced helical vortices driving water along the substrate upstream towards the structure. During upstream movement all individuals of both species successfully negotiated a maximum velocity barrier (*ca.* 1 m long; Fig. 4.1) of 1.75–2.12 m s^{-1}, suggesting maximum burst velocities attainable by the fish to be at least 1.75 m s^{-1}. Eels first approached and passed the weir more rapidly than lamprey (univariate two-way ANOVA: $F_{1,16} = 8.99$, $P < 0.01$ and $F_{1,16} = 17.30$, $P = 0.001$, respectively) (Fig. 4.2). There was no effect of discharge (univariate two-way ANOVA: $F_{3,16} = 0.65$, $P > 0.05$ and $F_{3,16} = 0.49$, $P > 0.05$) and no interaction between the fixed factors (univariate two-way ANOVA: $F_{3,16} = 1.06$, $P > 0.05$ and $F_{2,16} = 1.18$, $P > 0.05$) for the time to first approach and the time taken to pass the weir, respectively.

Table 4.2. Hydraulic parameters associated with an under- and over-shot weir placed in the ICER flume facility, under three discharge regimes.

	Water depth (m)		Velocity ($m\ s^{-1}$) directly below (undershot) or above (overshot) weir			
Weir type & discharge	*1 m upstream of weir*	*1 m downstream of weir*	*Minimum*	*Maximum*	*Discharge ± S.E ($L\ s^{-1}$)*	*Hydraulic head (m)*
Undershot & low	0.31	0.29	0.53	0.61	60.99 ± 1.70	0.02
Overshot & low	0.31	0.29	0.51	0.61	60.99 ± 1.70	0.02
Undershot & intermediate	0.31	0.24	1.31	1.43	128.73 ± 6.53	0.07
Overshot & intermediate	0.35	0.25	0.62	0.69	128.73 ± 6.53	0.10
Undershot & high	0.37	0.26	1.45	1.73	163.57 ± 5.66	0.11
Undershot & very high	0.44	0.27	1.75	2.12	194.63 ± 6.48	0.17

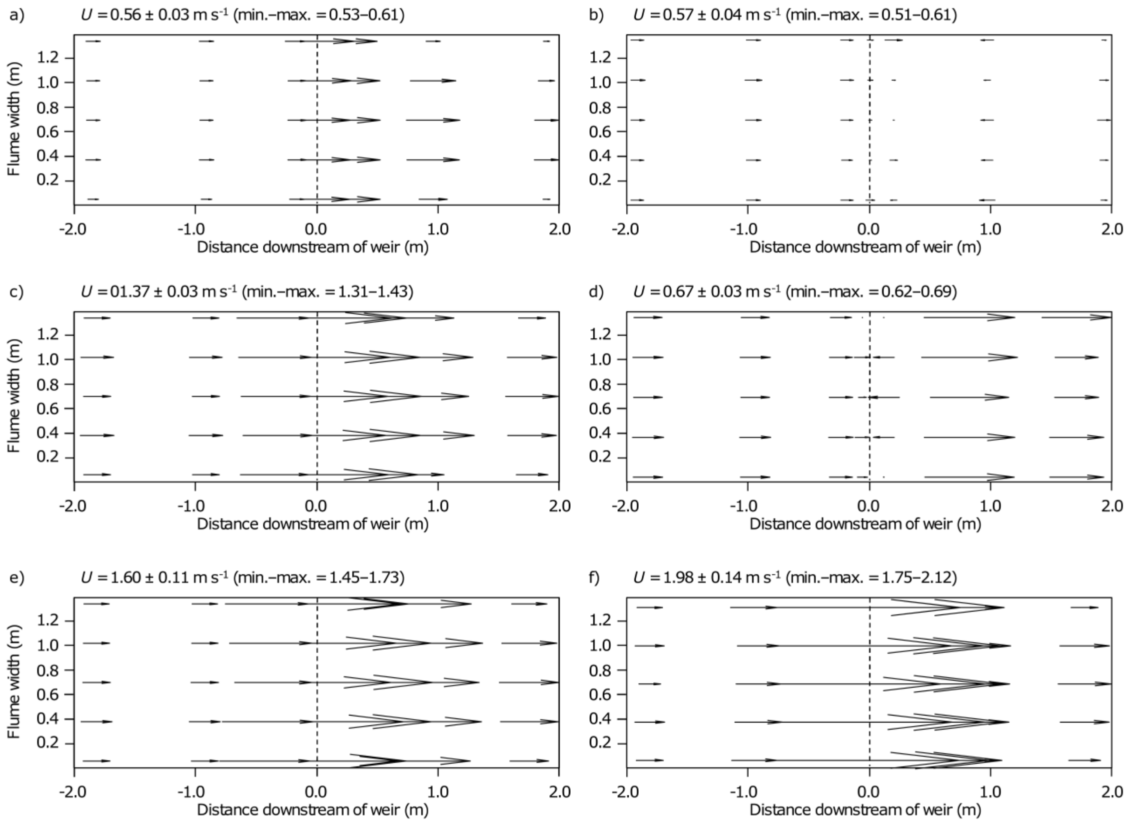

Fig. 4.1. Water velocity vectors 20 mm above the channel floor for the following weir type and discharge (a) undershot low, (b) overshot low, (c) undershot intermediate, (d) overshot intermediate, (e) undershot high and (f) undershot very high. Arrow length = relative velocity (m s^{-1}; scaled to the x axis). Dashed lines represent weir position. Mean velocity (*U*) directly above (overshot) or below (undershot) the weir are provided.

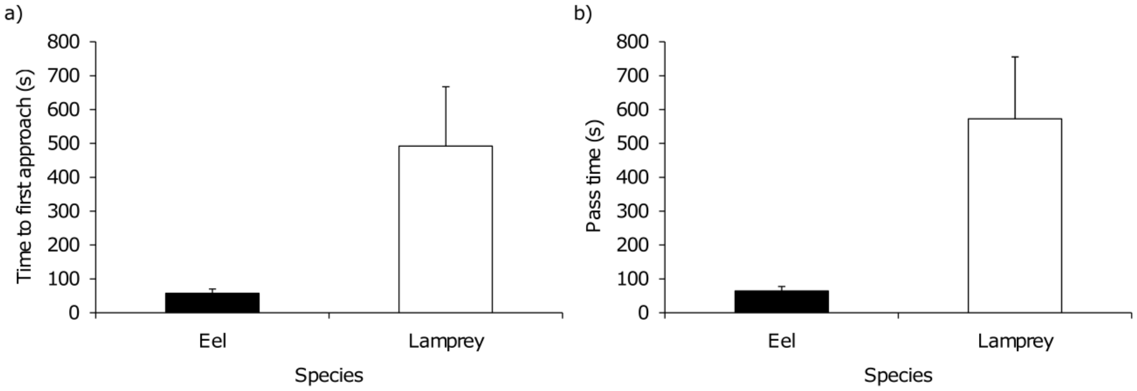

Fig. 4.2. (a) mean time to first approach and (b) mean pass time of upstream moving eel and lamprey at an undershot weir. Error bars represent the standard error of the mean.

All approaching fish successfully passed the undershot weir, regardless of discharge and direction of movement. During the fish's natural direction of movement, passage success for the overshot weir was 67 and 25% for upstream moving lamprey, and 71 and 83% for downstream moving eel under low and intermediate discharge respectively (Fig. 4.3). The time taken for upstream moving lamprey to first approach and to pass a weir was not affected by discharge (univariate two-way ANOVA: $F_{1,14} = 0.001$, $P > 0.05$ and $F_{1,9} = 0.12$, $P > 0.05$, respectively) and weir type (univariate two-way ANOVA: $F_{1,14} = 3.17$, $P > 0.05$ and $F_{1,9} = 0.03$, $P > 0.05$, respectively). There was no interaction between the fixed factors (univariate two-way ANOVA: $F_{1,14} = 0.12$, $P > 0.05$ and $F_{1,9} = 0.24$, $P > 0.05$, respectively).

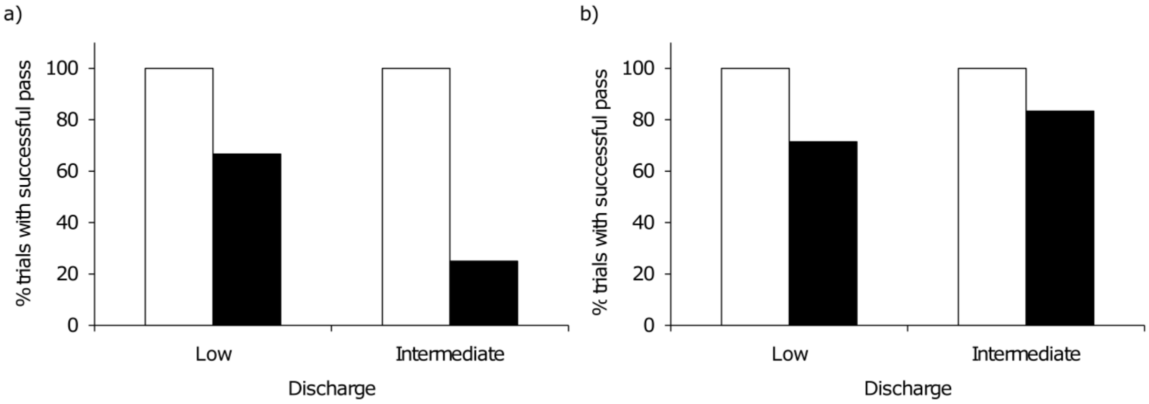

Fig. 4.3. Percentage of trials (omitting trials with no approaches) where (a) upstream moving lamprey and (b) downstream moving eel successfully passed an undershot (clear bars) or overshot (solid bars) weir.

Weir type did not influence the time to first approach of downstream moving eel (univariate two-way ANOVA: $F_{1,19} = 1.15$, $P > 0.05$), but eels passed the under- more rapidly than the over-shot weir (univariate two-way ANOVA: $F_{1,16} = 10.62$, $P < 0.01$) (Fig. 4.4). The time taken for downstream moving eel to first approach and to pass a weir was not affected by discharge (univariate two-way ANOVA: $F_{1,19} = 0.07$, $P > 0.05$ and $F_{1,}16 = 0.37$, $P > 0.05$, respectively). There was no interaction between the fixed factors (univariate two-way ANOVA: $F_{1,19} = 0.06$, $P > 0.05$ and $F_{1,16} = 0.35$, $P > 0.05$, respectively).

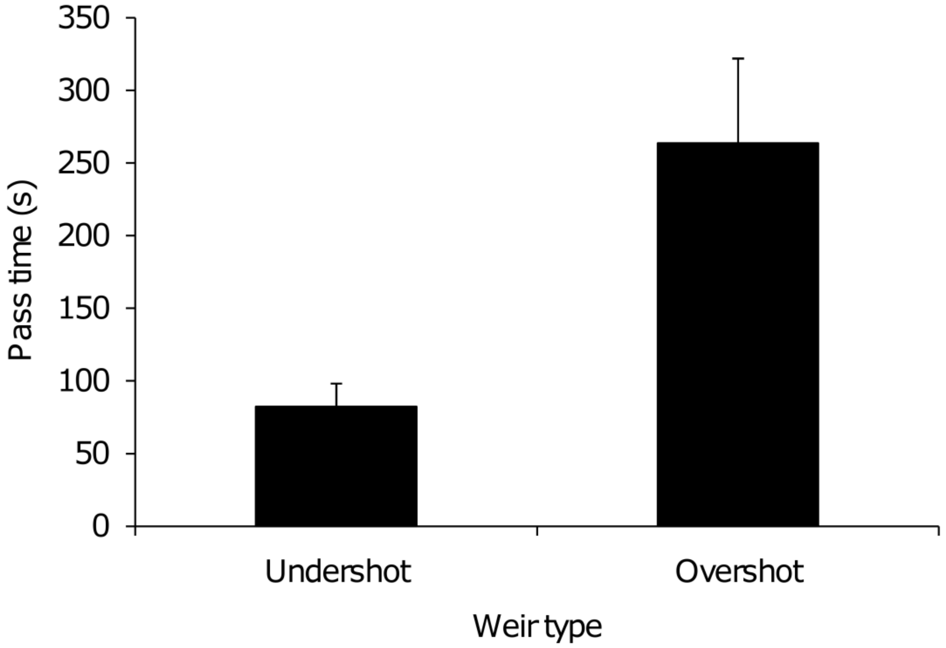

Fig. 4.4. Mean pass time of downstream moving eel at each weir type. Error bars represent the standard error of the mean.

In response to accelerating flow during downstream movement, all fish passed the undershot weir on their first approach (without repeated up- and down-stream movements in the locality of the weir). The majority of fish approached and passed head first (negative rheotactic orientation). Time to first approach (86.86 ± 20.56 s) and to pass (85.83 ± 20.65 s) the undershot weir was not affected by discharge (univariate two-way ANOVA: $F_{3,27} = 0.97$, $P > 0.05$ and $F_{3,27} = 0.50$, $P > 0.05$, respectively) or species (univariate two-way ANOVA: $F_{1,27} = 1.43$, $P > 0.05$ and $F_{1,27} = 1.72$, $P > 0.05$, respectively). There was no interaction between the fixed factors (univariate two-way ANOVA: $F_{3,27} = 0.59$, $P > 0.05$ and $F_{3,27} = 0.28$, $P > 0.05$, respectively) (Fig. 4.5).

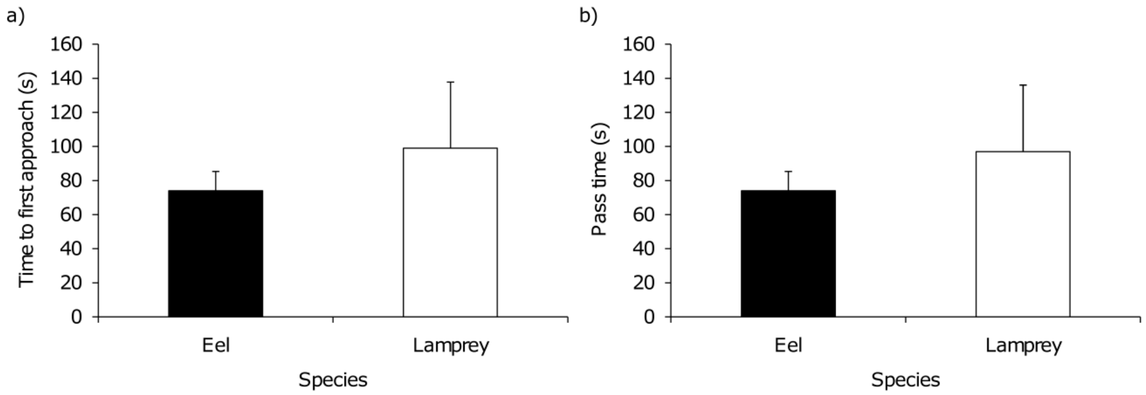

Fig. 4.5. (a) mean time to first approach and (b) mean pass time of downstream moving eel and lamprey at an undershot weir. Error bars represent the standard error of the mean.

4.5 DISCUSSION

The use of swim chambers to attain swimming velocities of fish can underestimate locomotory capacity attainable under more natural flows (Haro *et al.*, 2004; Mallen-Cooper, 1992; Peake, 2004; Peake & Farrell, 2004). Under the experimental conditions presented, all approaching eel and lamprey passed the undershot weir at peak discharge during voluntary upstream movement, attaining maximum burst velocities in the range of 1.75–2.12 m s^{-1}, based on the water velocities directly below the weir und very high discharge (Fig. 4.1f; Table 4.2). This is higher than previously reported. Lamprey have been observed to negotiate a velocity barrier at peak velocities of 1.66 m s^{-1} (Kemp *et al.*, 2011), and eels to attain burst velocities of *ca.* 1.35 m s^{-1} (Solomon & Beach, 2004). However, this is considerably slower than peak swimming velocities reported for the commonly studied adult salmonids, e.g. 3.87–8.08 m s^{-1} for Atlantic salmon, *Salmo salar* L., and 1.89–4.18 m s^{-1} for brown trout, *S. trutta* L. (Bell, 1986).

Maximum swimming velocities are the main biological component considered in the design of fish passes for upstream migration (e.g. Tudorache *et al.*, 2008). There is a trade-off between providing suitably low velocities within the fish pass to enable the majority of migrants to negotiate the structure (e.g. Peake *et al.*, 1997; Schwalme *et al.*, 1985), while providing sufficient flow to attract them to the entrance. Fish passes designed using conservative estimates of swimming velocity may allow fish to move upstream but fail to provide adequate attraction flow (Bunt, 2001; Castro-Santos *et al.*, 2009). Thus the design of fish passes should be based on realistic estimates of swimming performance to enable a balance between efficient attraction and passage to be achieved. In this study the period of maximum swimming velocity is only a few seconds and repeated bursts of speed will rapidly result in exhaustion (Beamish, 1978). Both water temperature and fish size also influence maximum attainable swimming velocities, generally increasing in absolute terms with rising temperature (Videler & Wardle, 1991; Wardle, 1980) and increased body length (Videler, 1993). Thus at common spawning migration water temperatures for *L. fluviatilis*, which are lower on average than those in the study flume (Masters *et al.*, 2006), maximum attainable swimming velocity may be lower than recorded in this study. In addition, the downstream migrating eels used in this study are larger than those moving upstream and river lamprey, thus having markedly greater absolute maximum swimming velocities.

Traditional fish passage facilities for downstream migration have frequently been designed to accommodate salmonid smolts, thought to move close to the surface (Arnekliev *et al.*, 2007; Johnson & Dauble, 2006). However, previous studies have shown that both upstream migrating lamprey (Kemp *et al.*, 2011) and downstream moving eels (Amaral *et al.*, 2003; Brown *et al.*, 2009; Russon *et al.*, 2010) tend to be predominantly substrate oriented. This study found all approaching eel and lamprey passed an undershot weir, but passage success was reduced when an overshot weir only 0.2m high was presented (Fig. 4.3 & 4.4). If this finding is replicated in the wild, the potential impact on migrating fish delayed at multiple structures could prove significant at a population level (e.g. Gowans *et al.*, 2003; Lucas *et al.*, 2009).

Fish frequently encounter water off-takes and screens during downstream migration through developed river systems. Unlike downstream migrating salmonids that avoid abrupt velocity gradients (e.g. Haro *et al.*, 1998; Kemp *et al.*, 2005a), eel and lamprey successfully passed the undershot weir on their initial attempt illustrating limited avoidance to the accelerating flow encountered under the experimental conditions described. This lack of avoidance to accelerating flow, if occurring in nature, could result in increased entry to off-take systems (Baumgartner *et al.*, 2009; King & O'Connor, 2007; Larinier, 2008) or impingement on screens, leading to damage and mortality (Baumgartner, 2005; Behrmann-Godel & Eckmann, 2003; Calles *et al.*, 2010 Larinier & Travade, 2002a). Consideration of the significance of alternative behavioural cues used by non-salmonid species is important if multispecies fish passes and screens are to be effective in the future.

Effective mitigation for the adverse effects of barriers to fish migration and water abstraction offtakes is essential to aid stock recovery, requiring realistic and accurate knowledge of fish swimming capabilities and behaviours of all affected species. By allowing volitional movement and natural compensatory behaviours to cope with difficult flow conditions to be undertaken by the fish, higher maximum swimming speeds than previously reported were measured, and the difficulty experienced by the thigmotactic channel floor oriented eels and lamprey as they encounter and attempt to pass a small overshot weir observed. In addition, the lack of response to different levels of accelerating flow during downstream movement at an orifice weir suggests a high susceptibility to water offtake entrainment if encountered during both eel and lamprey migrations. These observed results provide basic knowledge of swimming performance and behaviour for the anguilliform eel and lamprey used, as well as basic fish passage criteria (i.e. maximum burst swimming speeds of 1.75–2.12 m s^{-1}). The findings of this study support the recommendation that swimming estimates and understanding of behaviour obtained using large open channel flumes are more appropriate for developing fish passage design criteria than those based on traditional swim chamber tests (Haro *et al.*, 2004; Mallen-Cooper, 1992; Peake & Farrell, 2004). The use of alternative methodologies to obtain swimming performance and behaviour information for multiple species, such as those employed during this study, will help to provide realistic data that can be applied to creating efficient fish passage facilities, by manipulation of water velocity for example, that accommodate all target species.

Chapter 5: Gauging weirs impede the upstream migration of adult river lamprey, *Lampetra fluviatilis*.

5.1 SUMMARY

The ability of individual and groups of 30 migrating adult river lamprey, *Lampetra fluviatilis* L., to pass a Crump or flat-v gauging weir under two discharge regimes (moderate and low) was assessed in an experimental channel. Despite repeated attempts by the lamprey, the Crump weir remained impassable during all trials. Lamprey passage over the flat-v weir occurred only during group trials at low discharge (5.73 ± 0.19 L s^{-1}) and only as a single burst swimming event via the deeper water (2.1 cm compared to 0.4 cm for the crump weir) at the centre of the weir face. Where successful passage occurred, the maximum water velocity at the centre of the weir face was 1.50 m s^{-1}, but fish did not pass under moderate discharge (68.06 ± 2.41 L s^{-1}) when maximum velocity was 2.08 m s^{-1}, yet the water deeper (5.3 cm) than at low discharge conditions. Lampreys generally approached the weirs along the channel walls and particularly favoured the true right wall associated with elevated velocities during low discharge and reverse currents at moderate discharge. Time spent immediately below the weir was lower than expected compared to further downstream. Rate of weir approach, attempts to pass (absolute number and as a proportion of the total approaches), and time spent immediately downstream of the weir were highest for the Crump weir at low discharge and the flat-v weir at moderate discharge. The present study

suggests that gauging weirs may severely impede the movements of migrating adult river lamprey under low to moderate discharges.

5.2 INTRODUCTION

Over the past century, populations of anadromous lamprey species have declined in the United Kingdom (Masters *et al.*, 2006), the Baltic countries (Thiel *et al.*, 2009; Tuunainen *et al.*, 1980), France, Switzerland, the Czech and Slovak republics (Kelly & King, 2001) and in the U.S.A. (Beamish & Northcote, 1989). In extreme cases, populations have been extirpated, e.g. the river lamprey, *Lampetra fluviatilis* L., from Switzerland and the Rhine-Meuse hydrosystem (Renaud, 1997). Of current concern in several European countries is the status of river lamprey (Masters *et al.*, 2006), which, as a species listed under the EC Habitats Directive 92/43/EEC (EC, 1992), must be afforded Special Areas of Conservation by member states (Bell & McGillivray, 2006).

The decline of lamprey populations has been attributed to multiple factors, including commercial fishing (Masters *et al.*, 2006; Tuunainen *et al.*, 1980), pollution (Renaud, 1997), adverse oceanic conditions (Close *et al.*, 1995), and in particular reduced access to, and loss of, key habitat because of river engineering (Close *et al.*, 2002; Lucas et al., 2009; Nunn *et al.*, 2008; Oliveira *et al.*, 2004; Renaud, 1997; Tuunainen *et al.*, 1980). The river lamprey typically enters European rivers in the late summer and autumn (Winter & Van Densen, 2001) after which they can spend several months in fresh waters prior to spawning between March and May (Kearn, 2004; Kelly & King, 2001). This makes them particularly susceptible to the negative effects of river infrastructure (e.g. dams, sluices, weirs and hydropower plants) during this time. No feeding takes place during the upstream migration phase thus, energy reserves are depleted and death inevitably follows spawning (Kearn, 2004).

During the 20th century, an estimated 45,000 large dams (head > 15 m), capable of impeding the movements of migratory fish (Lucas & Baras, 2001), were constructed in 140 countries [WCD (World Commission on Dams), 2000]. Although the impacts of smaller low-head barriers (e.g. triangular profile gauging weirs) are less often considered, it is suggested that they are probably two to four orders of magnitude more abundant (Lucas *et al.*, 2009), potentially having a greater cumulative negative impact on populations of migrating fish than a single larger structure (Jungwirth *et al.*, 1998). Lucas *et al.* (2009) noted 98% of lamprey spawning habitat in the River Derwent, England, occurred more than 51 km upstream. However, only 1.8% of spawners were recorded there because of the presence of multiple, small-scale barriers to migration, including gauging weirs.

There are increased demands for hydrological information (Butterworth *et al.*, 2000) to monitor flood risk and the maintenance of minimum acceptable discharges (e.g. the U.K. Water Resources Act; OPSI, 1963, 1991). This has led to the installation of hydrometric gauging weirs throughout Europe (White *et al.*, 2006) and other regions (e.g. South Africa, Wessels & Rooseboom, 2009). In England and Wales alone, there are estimated to be more than 800 gauging structures, with 550 being flat-v and two-dimensional Crump weirs (White *et al.*, 2006), the majority (*ca.* 375) being Crump weirs (Servais, 2006). Crump weirs have a triangular profile with 1:2 and 1:5 slopes on the upstream and downstream sides, respectively, whereas flat-v weirs possess the same triangular profile, with cross slopes along the crest of between 1:10 and 1:40 that meet at the lowest point at the centre (Fig. 5.1).

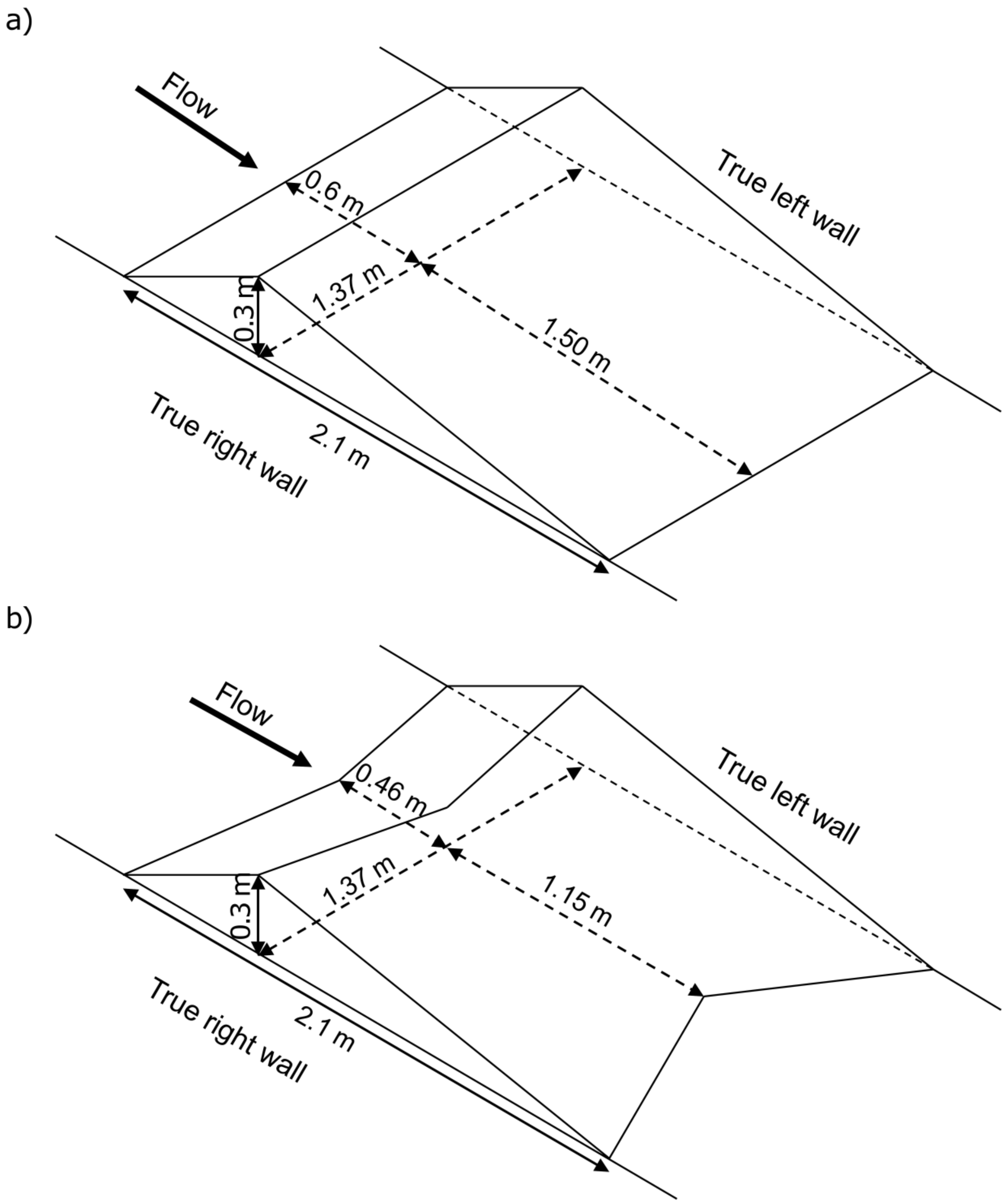

Fig. 5.1. Dimensions of (a) Crump and (b) flat-v weir used in experiments to assess the ability of upstream migrating lamprey to pass under two discharge conditions. Upstream slope = 1:2, downstream slope = 1:5, cross slope of flat-v weir = 1:10, height at centre of flat-v = 0.23 m.

Gauging weirs can have negative impacts on upstream fish passage (White *et al.*, 2006) if water velocities are higher than swimming capabilities, if depths are insufficient to allow swimming over the weir and if the hydraulic jump (caused by an abrupt change in velocity from high super-critical on the weir face to low sub-critical at the base of the structure) that forms at the base provides an additional barrier due to increased turbulence disorienting the fish (Beach, 1984; Boiten, 2002). Thus, weirs are often only passable under a limited range of environmental conditions (Lucas & Frear, 1997). The concentration of flow at the centre of flat-v weirs may produce velocities in excess of the swimming capabilities under high discharge conditions and result in disorientation due to the presence of side eddies (Armstrong *et al.*, 2004; Beach, 1984). Conversely, the deeper water at the mid-point of the weir face may allow passage at low discharges. However, for some species, including lamprey, gauging weirs may be passable under high discharges, when fully submerged, and this is particularly the case when the lateral extremities of the weir are overtopped (Lucas *et al.*, 2009). However, under low discharge conditions, gauging weirs are likely to impede the movement of fish because depths are insufficient to allow free swimming (e.g. Nunn *et al.*, 2008). This problem may be exacerbated in the future as the frequency and intensity of extreme low discharge events are predicted to increase (Hulme *et al.*, 2002), e.g. frequency of events with the intensity of the current 100-year droughts may occur every 10-50 years by the 2070s (Lehner *et al.*, 2006).

The aim of the present study was to assess the passage efficiency of traditional Crump and flat-v gauging weir design under low discharge scenarios to lamprey under experimental conditions. Weir type and associated hydrodynamics are predicted to influence the approach behaviour exhibited by lampreys because of some deterrent effect that would ultimately impede upstream progress. Under low discharge scenarios, a flat-v weir may be easier for lampreys to pass because of the presence of deeper water at the centre, which would facilitate swimming.

5.3 MATERIALS AND METHODS

Experiments were conducted in a glass-walled recirculatory flume (21.4 m long, 1.4 m wide, 0.6 m deep). Discharge and depth were controlled by adjusting the number of centrifugal pumps in use (maximum of three), volume of water flowing through them and height of an adjustable weir at the downstream end of the flume. Dark plastic screens were erected outside of the flume along both channel walls to prevent observer disturbance of the experimental animals and to block lateral illumination.
Two test gauging weirs (flat-v and Crump, constructed from 18 mm plywood and coated with a grey textured masonry paint to mimic the surface of concrete) were alternately installed within the flume (Fig. 5.1). The weirs spanned the entire channel width and were designed to the British Standards Institution criteria (BS ISO 4377 2002, for flat-v; BS 3680-4B 1986, for Crump). The downstream slope of the Crump weir was 1:5 and the upstream slope 1:2, with a maximum height of 0.30 m. The flat-v weir was built to the same specifications with cross slopes of 1:10. No condition without a weir was tested because the aim of this study was to assess behavioural and passage efficiency differences in lamprey between two commonly used gauging weir types.

Two relatively low discharge (± SE) treatments (low = 5.73 ± 0.19 L s^{-1}; moderate = 68.06 ± 2.41 L s^{-1}) were selected to recreate the potential low discharge scenarios that will more frequently prevail in the future (Lehner *et al.*, 2006). Water velocities over the weirs and 1.00 m downstream of the weir/channel floor interface were maintained below the maximum recommended (3.50 and 0.30 m s^{-1}, respectively) in the U.K.'s National Fish Pass Manual (Armstrong *et al.*, 2004). A shallow depth of water constantly flowed over the downstream weir face, which was never fully submerged by the downstream water level. Mean water depths varied with discharge and weir type (Table 5.1).

Table 5.1. Water depths (cm) associated with two experimental gauging weirs. Depths were recorded at the centre of the channel (unless stated otherwise).

		Water depths by location				
Weir	Discharge category	3.50 m downstream of crest	On crest at centre	On crest at channel walls	0.05 m downstream of crest (weir face)	0.60 m downstream of crest (weir face)
Crump	Low	15.5	1.6	1.6	0.6	0.4
	Moderate	18.0	7.0	7.0	3.2	2.3
Flat-v	Low	15.0	3.4	0.0	2.9	2.1
	Moderate	16.0	9.2	3.3	8.4	5.3

5.3.1 EXPERIMENTAL SET-UP

A total of 180 actively migrating adult river lamprey of 347 ± 3 mm mean total length (L_t ± SE) and 76 ± 2 g mean wet weight (M ± SE) were collected in unbaited, two-funnel, commercial eel pots from the tidal reaches of the River Ouse in Yorkshire (53°54′N, 01°06′W) on the 12 December 2007. The lampreys were gently removed from the nets and placed in tanks with aerated and iced river water to minimise stress during transportation to the facility. The lampreys were maintained in a 900 L holding tank at a maximum stocking density of 4.06 kg m^{-3} for a minimum of 63 days before experiments commenced to replicate the length of time (several months) that they remain resident in fresh water prior to spawning (Kelly & King, 2001). The mean holding tank water (± SE) temperature was 13.4 ± 0.3 °C.

To mimic conditions that occur in nature, both individuals and groups of spawning run lamprey were used during the hours of darkness, replicating the nocturnal migration (Kelly & King, 2001). Forty eight (n = 12 per treatment: low and moderate discharge; Crump and flat-v weir) 1 h trials using individual lamprey were conducted between 15 February and 3 March 2008. Four (n = 1 per treatment) 3 h trials were undertaken on 22 February (Crump weir) and the 3 March (flat-v weir) 2008 with groups of 30 lampreys to assess whether presence of conspecifics influences passage. Lampreys were used in one trial only to avoid pseudo-replication. Lampreys were acclimated for a minimum of 1 h at the downstream end of the flume in porous black plastic containers prior to use. Lampreys were released 7 m downstream of the weir crest and allowed to volitionally explore the channel. Discharge was alternated between trials. Weir treatment was alternated from Crump to flat-v mid-way (14 days) through the trials because of installation time. Daily mean (± SE) flume water temperature at the start of experimental trials was 13.4 ± 0.7 °C. Water temperature increased during trials because of the actions of centrifugal pumps. A maximum rise in water temperature of 2 °C was tolerated before trials were stopped.

Lateral velocity profiles were obtained by recording mean and standard deviation velocities at nine equidistant points, along 12-18 (dependent on discharge and weir) transects perpendicular to the flow (between 1 m upstream to 2 m downstream of the weir base) using an electromagnetic velocity meter

(Valeport, 801-flat). Velocities were recorded 20 mm above the channel floor as lampreys tend to be substratum oriented during their upstream migration (Kemp *et al.*, 2011; Lucas *et al.*, 2009; Moser *et al.*, 2002b). Vector plots of point velocities were created using SigmaPlot®: Systat Software Inc., London, UK.

Trials were conducted during the hours of darkness (18:00-03:00), and fish behaviour recorded digitally for later analysis using two overhead, low-light cameras (Swann C-510R) under infrared illumination (4 x 15 W units emitting light at 850 nm wavelength) when they entered the observation zone (from the weir crest to 2 m downstream). Cameras and lights were suspended 2.1 m above the channel floor.

Records for individual lamprey trials were taken of the time to first approach (when the entire body length of the fish entered the observation zone) after release, total number of approaches and total time spent within the observation zone (between entry and either returning downstream, or passing over the weir crest) during each approach. Lamprey position relative to the channel walls was recorded during their approach to the weir. Channel wall approaches were deemed to have occurred when lampreys were within 0.2 m of the flume walls, because in practice, fish approaching within this area were in constant contact with the channel walls. The attachment time (when a lamprey was attached to the channel floor or weir face for a minimum of 3 s), attempts to pass (when a lamprey moved over the weir face above the level of the downstream water surface) and the number of successful upstream passage events were also recorded.

The total number of approaches, attachment events, number of attachments as a proportion of approaches, attempts to pass, number of successful passes, and the route of successful passage taken were recorded for group trials.

5.3.2 STATISTICAL ANALYSIS

Tests of normality and homogeneity of variance were performed using Shapiro-Wilk and Levene's tests, respectively, and where necessary non-parametric data were natural-log transformed. Where attempts to normalise the data failed, non-parametric tests were used. All proportions were arcsine square-root transformed. The variation in velocities between treatments was assessed using Friedman's non-parametric analysis of variance test on ranked data. Two-sample Wilcoxon signed-rank tests (T) were used *post hoc* to identify sources of significant difference. A Bonferroni correction was applied, so all effects are reported at $P = 0.01$ level of significance. Variation in lateral velocity profile (divided into three categories: true left 0.2 m, true right 0.2 m and central 1.0 m) was assessed using a one-way parametric analysis of variance (ANOVA) for each treatment. A Tukey *post hoc* test was performed to identify sources of significant difference. The influence of discharge and weir type (fixed factors) on the dependent variables: (1) approach rate (number of approaches per minute); (2) time taken to first approach; (3) time spent in the observation zone prior to passing; (4) percentage of channel wall approaches; (5) attachment time; (6) attempt to pass rate (attempts per minute) and (7) attempts to pass as a proportion of approaches, were analysed using a two-way ANOVA. One-sample t-tests were used to determine if: (1) approaches made along each channel wall were equal by assessing the number that approached the right channel to a t-value of 0.5, and (2) expected time spent in the observation zone (having controlled for differences in area with treatment) and in the section downstream were different from actual observations. Results for group trials were descriptively analysed.

5.4 RESULTS

Treatment had a significant effect on velocity (Friedman's test: $\chi^2(3) = 19.40$, $P < 0.001$; Table 5.2), which was significantly higher for the Crump weir during moderate discharge than both the Crump (Wilcoxon: $T = 287.50$, $r = -0.37$) and flat-v (Wilcoxon: $T = 426.50$, $r = -0.36$) weirs under low discharge. There were no significant differences in velocities between: (i) the Crump weir at low discharge and the flat-v regardless of discharge; (ii) the flat-v weir at either discharge and (iii) the two weirs during moderate discharge.

Table 5.2. Mean water velocities (m s^{-1} ± SE (min.–max.) associated with a Crump and flat-v weir under experimental conditions. Low and moderate discharge (± SE) was 5.73 ± 0.19 L s^{-1} and 68.06 ± 2.41 L s^{-1}, respectively.

Weir	Discharge category	*Water velocities by location*				
		Entire area of measurements (*n* = 99–153)	Observation zone (*n* = 63–108)	Weir face, in observation zone (*n* = 18–63)	Downstream of weir, in observation zone (*n* = 54)	3.5 m downstream of weir crest (*n* = 9)
Crump	Low	0.05 ± 0.01 (−0.07–0.24)	Insufficient depth	Insufficient depth	0.05 ± 0.01 (−0.07–0.24)	0.04 ± 0.02 (−0.03–0.16)
	Moderate	1.04 ± 0.07 (−0.49–2.30)	1.11 ± 0.08 (−0.49–2.30)	1.78 ± 0.05 (1.19–2.30)	0.44 ± 0.07 (−0.49–1.25)	0.22 ± 0.05 (0.02–0.43)
Flat-v	Low	0.16 ± 0.05 (−0.29–1.50)	0.18 ± 0.05 (−0.29–1.50)	1.06 ± 0.08 (0.59–1.50)	0.03 ± 0.02 (−0.29–0.54)	0.04 ± 0.06 (−0.14–0.34)
	Moderate	0.77 ± 0.08 (−0.43–2.08)	0.82 ± 0.09 (−0.43–2.08)	1.45 ± 0.08 (0.09–2.08)	0.40 ± 0.10 (−0.43–1.64)	0.31 ± 0.19 (−0.37–0.96)

Velocities over the flat-v weir varied across the lateral profile under both the moderate (one-way ANOVA: $F_{2,\,96} = 30.94$, $P < 0.001$) and low (one-way ANOVA: $F_{2,\,96} = 7.19$, $P = 0.001$) discharge (Fig. 5.2). The highest velocity (mean = 0.70 ± 0.08 m s^{-1}) occurred along the channel centre under moderate discharge rates, and velocity direction differed from that of the bulk flow (mean = −0.26 ± 0.02 m s^{-1}) along the true right wall. Under low discharge, velocity direction differed from the bulk flow (mean ± SE = −0.07 ± 0.01 m s^{-1}) along the true left wall with no difference between the right wall and channel centre (mean ± SE = 0.08 ± 0.03 m s^{-1}).

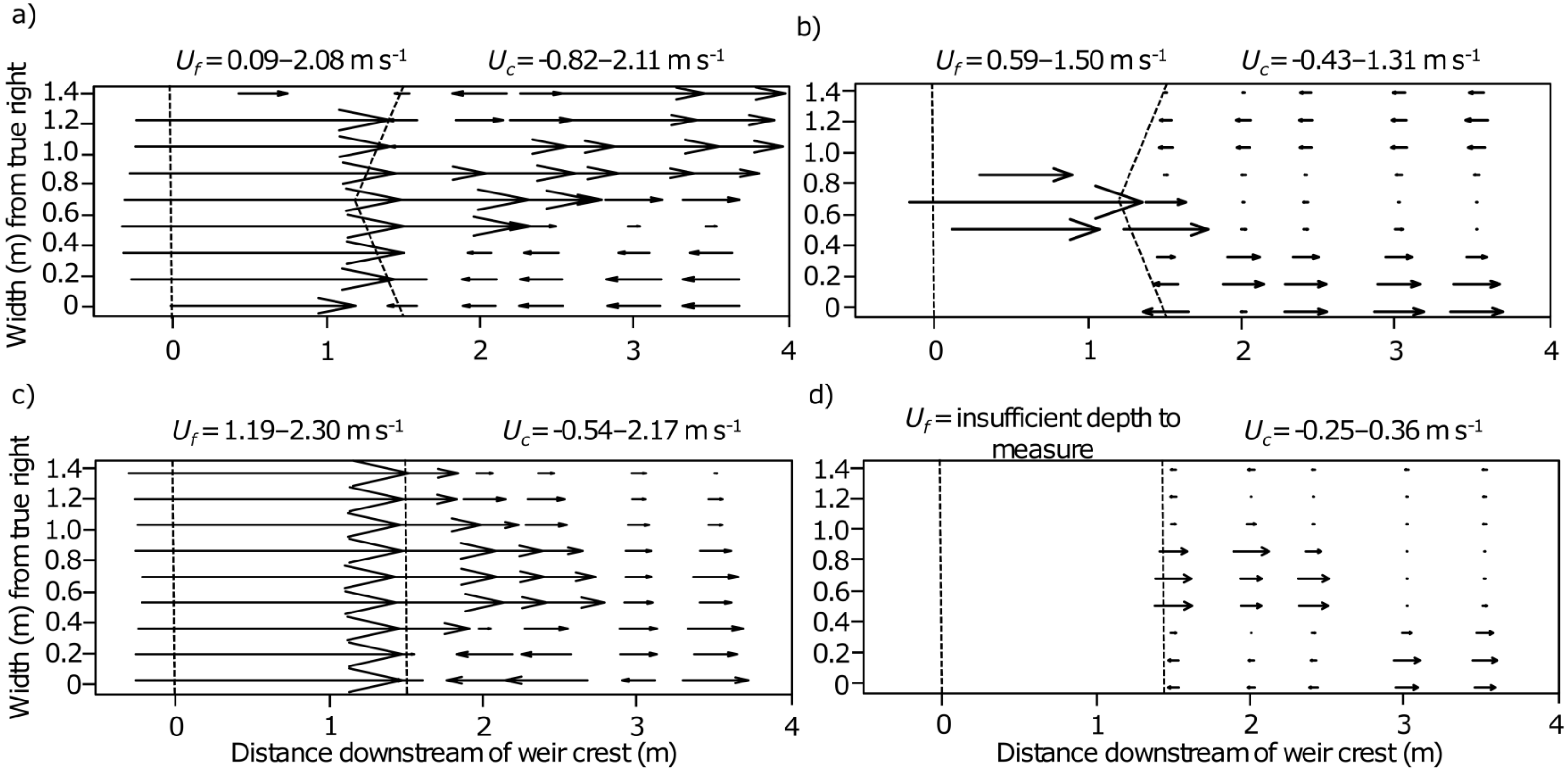

Fig. 5.2. Water velocity vectors 20 mm above the channel floor or weir face for a flat-v weir at (a) moderate and (b) low discharge, and a Crump weir at (c) moderate and (d) low discharge. Arrow length = relative velocity (m s^{-1}; scaled to the x axis). Dashed lines represent weir crest (0 m) and the downstream weir-channel floor interface. U_f and U_c = minimum and maximum velocity over the weir face and channel floor, respectively.

Velocity varied significantly across the lateral profile of the Crump weir at both moderate (one-way ANOVA: $F_{2, 96} = 56.38$, $P < 0.001$) and low (one-way ANOVA: $F_{2, 96} = 18.67$, $P < 0.001$) discharge (Fig. 5.2). Highest velocities were associated with the channel centre under both moderate (mean ± SE = 0.58 ± 0.05 m s^{-1}) and low (mean ± SE = 0.09 ± 0.01 m s^{-1}) discharge. Under moderate discharge, velocity direction differed from that of the bulk flow (mean ± SE = –0.23 ± 0.06 m s^{-1}) along the true right wall. There was no significant difference in velocity between the true left and right channel walls at low discharge (mean ± SE = –0.01 ± 0.01 m s^{-1}).

In the individual trials, an interaction between discharge and weir type was apparent for rate of approach (Table 5.3), which was higher and lower for the Crump and flat-v weir under low and moderate discharge, respectively (Fig. 5.3a). Overall, rate of weir approach was higher under low discharge, and there was no effect of weir type. Lamprey took longer to make an initial approach to a flat-v than a Crump weir under low discharge (Fig. 5.3b). Discharge had no influence overall and there was no interaction between discharge and weir type.

Total time spent in the observation zone was higher for the Crump than the flat-v weir under low discharge (Table 5.3). Under moderate discharge, this relationship was reversed (Fig. 5.3c). Time spent in the observation zone was highest for both weir types under low discharge, but under all treatments was less than expected (t_{11} for all treatments, $P < 0.001$) if the lamprey had used the entire downstream section of the channel equally.

The percentage of weir approaches associated with the channel walls was lower for the Crump weir and under moderate discharge (Table 5.3; Fig. 5.3d). A higher percentage of approaches were associated with the true right than true left walls under all treatments (t_{28} for the Crump weir under moderate discharge $P < 0.05$, and $P < 0.001$ for all other treatments; Fig. 5.4a, b).There was no relationship between discharge and weir type on period of attachment (mean ± SE = 23.87 ± 6.80 s). Of 985 weir approaches recorded during all individual trials, only 33 attachment events were observed, the majority (18) of which occurred under the flat-v low discharge treatment; of these 18, 11 occurred during a single 1-hr trial.

No lamprey passed the weir during individual trials. The attempt rate and the attempts as a proportion of approaches were higher and lower for the Crump weir than the flat-v under low and moderate discharge, respectively (Table 5.3; Fig. 5.4c and d). Overall attempt rate was lower under moderate discharge and weir type had no effect. There was no relationship between attempts as a proportion of approaches and discharge or weir type.

Table 5.3. Results of two-way ANOVAs to determine the influence of discharge and weir type (fixed factors) on the various dependent variables for upstream moving individual lampreys approaching a gauging weir.

		Discharge		*Weir type*		*Interaction*	
Dependent variable	d.f.	*F*	*P*	*F*	*P*	*F*	*P*
1) Approach rate	1, 44	26.99	< 0.001	0.43	> 0.05	10.11	< 0.01
2) Time to first approach	1, 44	0.31	> 0.05	10.58	< 0.01	2.06	> 0.05
3) Time spent in observation zone prior to passing	1, 44	26.63	< 0.001	0.78	> 0.05	6.98	< 0.05
4) Percentage of channel wall approaches	1, 44	11.31	< 0.01	6.63	< 0.05	13.75	$= 0.001$
5) Attachment time	1, 14	0.22	> 0.05	0.65	> 0.05	0.58	> 0.05
6) Attempt to pass rate	1, 44	4.33	< 0.05	2.18	> 0.05	12.92	$= 0.001$
7) Attempts to pass as a proportion of approaches	1, 34	1.77	> 0.05	0.31	> 0.05	4.40	< 0.05

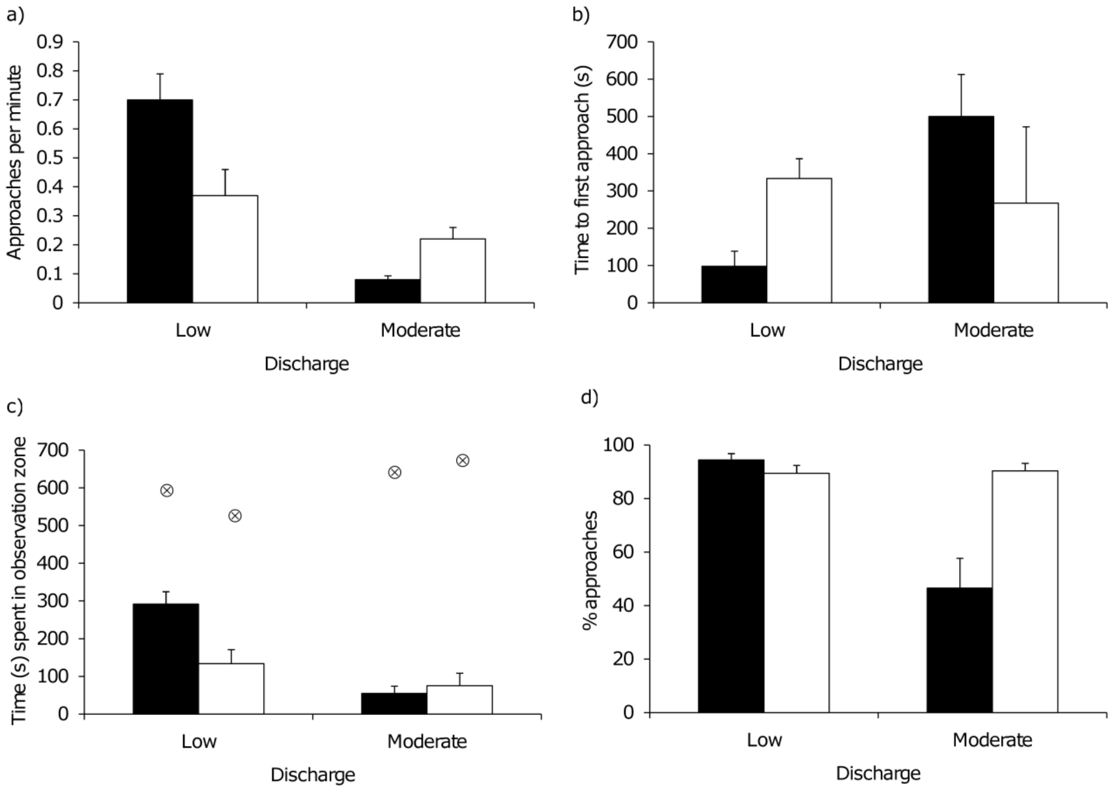

Fig. 5.3. Mean and standard error (bars) for individual lamprey at a Crump (solid bars) and a flat-v (clear bars) weir: (a) frequency of approach, (b) time to first approach, (c) time spent in an observation zone (2.00 m x 1.37 m) downstream of the weirs and (d) mean percentage of upstream approaches in association with the channel wall. ⊗ = expected time spent in the observation zone if lampreys spent equal time distributed along the length of the downstream section of the flume.

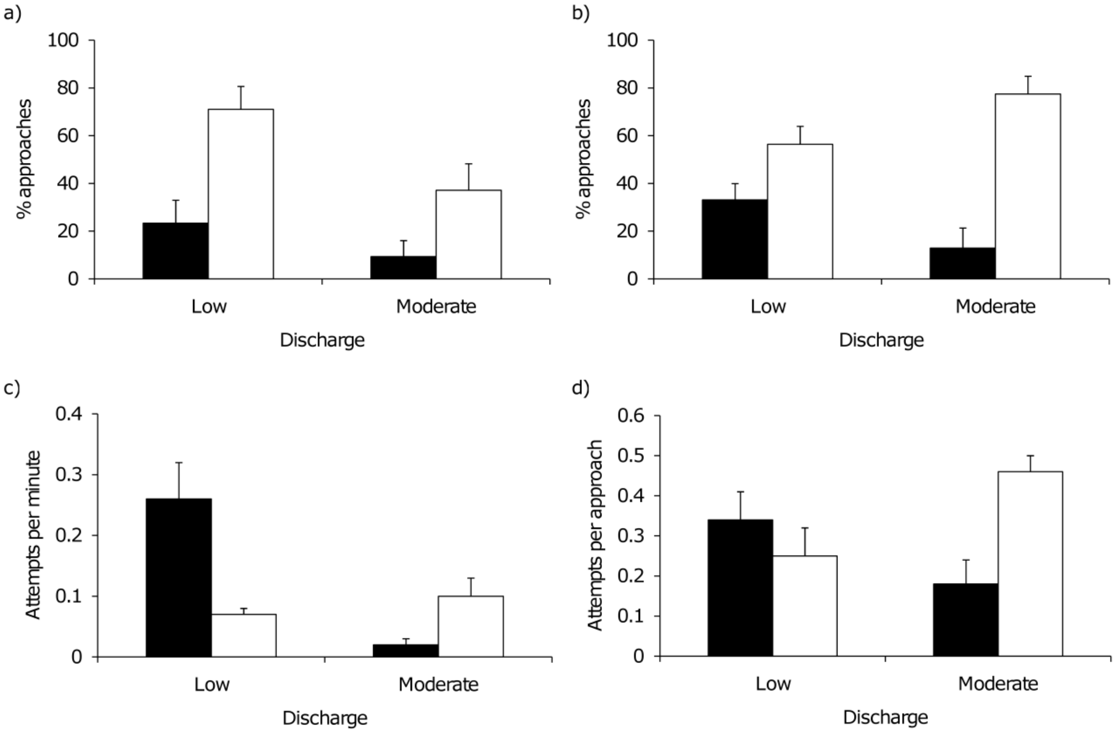

Fig. 5.4. Mean and standard error (bars) for the percentage of total individual lamprey upstream approaches along the true left (solid bars) or right (clear bars) channel walls to the (a) Crump weir and (b) flat-v weir, as well as the (c) attempt rate and (d) number of attempts as a proportion of upstream approaches of individual lamprey to a Crump (solid bars) and flat-v (clear bars) weir.

In the group trials, a total of five lampreys passed upstream of the weir crest, all under the flat-v low discharge treatment (Table 5.4). During three successful passes, the lampreys attached (for 45, 57 and 434 s) to the downstream weir face at the centre with the head section above the water surface. The two remaining successful lampreys did not attach to the weir face but approached along the channel walls and moved to the centre having passed the submerged weir face. On detachment, or reaching the centre, the lamprey swam over the weir crest in a single burst movement.

Table 5.4. Behavioural traits demonstrated by groups (*n* = 30) of upstream migrating adult lamprey approaching and passing two types of gauging weir under experimental conditions.

Weir	Discharge category	*Trait* Total approaches	Total attempts	Total attachments	Attachments per approach	Total passes
Crump	Low	1346	648	189	0.14	0
	Moderate	771	226	206	0.27	0
Flat-v	Low	1181	345	103	0.09	5
	Moderate	964	346	124	0.13	0

5.5 DISCUSSION

Considerations of fish passage at gauging weirs, as with other river infrastructure (Roscoe & Hinch, 2010), have focused on the requirements of salmonids (Beach, 1984). Current design criteria, however, may create conditions that prove challenging for other species (Armstrong *et al.*, 2004), e.g. barbel, *Barbus barbus* L., (Lucas & Frear, 1997) and European bullhead, *Cottus gobio* L., (Knaepkens *et al.*, 2006). In the present study, the upstream movement of river lamprey was severely impaired by model gauging weirs under moderate discharge, with no passes during any individual trial. The gauging weirs and/or associated hydraulic conditions impeded upstream progress by deterring approach to the structure (Fig. 5.3). The low number of lampreys passing the flat-v weir under low discharge in group trials (Table 5.4) occurred despite the velocities encountered being much lower (maximum = 1.50 m s^{-1}; Table 5.2) than the maximum recommended (< 3.5 m s^{-1}) for the United Kingdom (Armstrong *et al.*, 2004). Water depths over the weir (Table 5.1) were also likely insufficient to allow free swimming, causing a further impediment to the lampreys. In nature, groups of lamprey are more likely to occur at migratory barriers than individuals during mass spawning migrations (e.g. see Fig. 1.1), and passes only occurred when fish were in a group. Potentially, this could be due to there being more fish and thus a greater chance that some will successfully pass, or speculatively through social facilitation (where the presence of conspecifics has either a negative or positive effect on the ability of others; Guerin, 1993) the lamprey were more “confident” and likely to pass.

Although flume studies can not fully replicate natural conditions, they do provide the opportunity to control for confounding variables, and the observed responses improve understanding of events occurring in the wild. Based on the results of the present study, it is likely that lamprey passage over gauging weirs and similar small-scale structures will become increasingly difficult with increased probability of prolonged periods of low discharge (Hulme *et al.*, 2002; Kemp *et al.*, 2011; Lehner *et al.*, 2006), as depth will more frequently become insufficient to allow upstream progress past these points. Delays to migration at barriers can adversely affect individual fitness by increasing energetic costs (Hinch & Rand, 1998), predation risk (Peake *et al.*, 1997), and physiological stress and susceptibility to disease (O'Brien, 1999). Interruptions to river lamprey migrations at gauging weirs under low discharges may impact reproductive success because of a reduction in energy available for allocation to gonad development and secondary sexual characteristics (e.g. spawning behaviours) (Geen, 1975; Mesa *et al.*, 2003; Quintella *et al.*, 2004).

Rates of approach (Fig. 5.3), attempts (Fig. 5.4) and time spent in the observation zone (Fig. 5.3) by lampreys were lower at the Crump than the flat-v weir under moderate discharge, possibly reflecting a behavioural response to high velocities created downstream of the Crump weir. At low discharge, these parameters were higher for the Crump than the flat-v weir, suggesting an increased negative impact on lamprey passage for the Crump weir with increasing discharge. In all cases, lampreys spent a lower proportion of time in the immediate vicinity relative to sections further downstream suggesting associated hydraulics, e.g. shallower depths and higher velocities, had a repellent effect.

The lack of paired fins, elongated body morphology and relatively weak swimming ability demonstrated by lamprey in comparison with salmonids might be expected to result in high energy expenditure in challenging complex hydraulic environments (Liao, 2007; Liao *et al.*, 2003; McLaughlin & Noakes, 1998; Mesa *et al.*, 2003). To move upstream efficiently, lamprey exhibit alternative strategies. Attachment using the oral disk may conserve energy in turbulent flow (Kemp *et al.*, 2011), but was rarely observed during the present study, although it may have occurred downstream of the observation zone. Lamprey also tend to migrate close to the substratum where velocities are lower (Kemp *et al.*, 2011) and may use reduced discharge and/or reverse flow conditions to facilitate upstream migration. Faster than expected movement upstream has been observed for Pacific lamprey, *L. tridentata* (Richardson), (Moser *et al.*, 2002b) and sockeye salmon, *Oncorhychus nerka* (Walbaum), (Hinch & Rand, 1998) in the field, possibly as a result of selecting areas of low velocity and reverse flow near the substratum and along the shore. The asymmetry in lateral velocity profiles observed (Fig. 5.2), possibly due to imperfections in the weir or flume, although unintended allowed an interesting observation to be made. Although speculative, the tendency to approach the flat-v weir along the true right wall at moderate discharge (Fig. 5.4), where velocity vectors were in directions that deviated from the bulk flow (Fig. 5.2), possibly reflected selection of an energetically less costly route.

The exhibition of intermittent locomotion to enhance efficiency and conserve energy has been described for several species (Kemp *et al.*, 2009). Many species use “burst-and-glide” swimming modes (Jayne & Lauder, 1996; Peake & Farrell, 2004; Tudorache *et al.*, 2007), whereas sea lamprey, *Petromyzon marinus* L., (Quintella *et al.*, 2004, 2009) and river lamprey (Kemp *et al.*, 2011) have been observed to “burst-and-attach-to-rest”. In the present study, attachment prior to burst swimming was observed with a small number of lampreys when they attempted to pass the flat-v weir. Unlike Pacific lamprey, which are capable of negotiating sloping (Reinhardt *et al.*, 2008) or vertical (Kemp *et al.*, 2009) barriers, no evidence was provided to suggest that river lamprey are able to climb over such barriers. Further research is needed to rule out the climbing ability of river lamprey, however, if they prove unable to climb, or at least to move on a smooth substrate in high velocity water without releasing and being washed downstream, adaptations that improve climbing lamprey species passage efficiency will be ineffective. For example, by exploiting the climbing ability of Pacific lamprey Moser *et al.* (2002b) increased fish pass entry efficiency by providing a smooth stainless steel plate material with a rounded edge over a bulkhead near a spillway entrance (where Pacific lamprey were known to have difficulty passing).

Adequate mitigation of human alterations to watercourse morphology is necessary to improve and maintain ecological status as required under current EU legislation, e.g. the Water Framework Directive (EC, 2000). Under the experimental conditions described, relatively small gauging weirs can have a significant impact on the upstream movements of river lamprey. The relatively deeper water at the centre of the flat-v weir (2.1 cm, compared to 0.4 cm for the Crump weir) facilitated the passage of some lampreys at low discharge, and thus, a flat-v may be a slightly better option than a Crump weir if low discharge conditions frequently prevail. However, the depth of water over the Crump weir under moderate discharge was deeper (2.3 cm) than where lamprey passage occurred (2.1 cm), and it is likely that water velocity played a larger role in preventing fish passage. Water velocities on the Crump weir face during moderate discharge (mean ± S.E. = 1.78 ± 0.05 m s^{-1}; maximum = 2.30 m s^{-1}) were higher than under conditions where some passage occurred (Table 5.2), and may have been in excess of the swimming capabilities of lamprey, where maximum burst speeds attained during chapter 4 of this thesis were in the region of 1.75 – 2.12 m s^{-1}. Thus, there is a need for further research to develop appropriate modifications, such as baffle systems for Crump weirs (Rhodes & Servais, 2008), to improve multispecies fish passage at these structures by e.g. reducing velocities while maintaining sufficient depth to allow swimming of fish on the weir face.

Chapter 6: Response of downstream migrating adult European eels, *Anguilla anguilla* L., to bar racks under experimental conditions.

6.1 SUMMARY

The behavioural response of downstream migrating non-salmonid fish to hydraulic conditions associated with river infrastructure is poorly understood. The response of downstream migrating adult European eels, *Anguilla anguilla*, to bar racks (12 mm bar spacing) angled on the vertical and horizontal planes under different flow regimes and during periods of darkness was assessed. Eels predominantly moved along the channel floor and wall, tending to follow routes where turbulence intensity was high. Time taken to approach the racks was greater than expected if fish had moved passively with the flow. Eels did not exhibit clear avoidance behaviour prior to encountering the racks, instead marked changes in behaviour occurred only after physical contact was made with the structure. No impingement or passage through the racks occurred, and passes per approach were high (98%), when vertical racks were angled at 15°, 30°, or 45° relative to the flow. Impingement and passage through the racks only occurred when horizontally inclined racks were placed perpendicular to the flow. Time eels were impinged on the racks was negatively related to discharge when angled at 30° relative to the channel floor, and positively related when upright. Frequency of impingement was higher under low discharge (132.9 ± 16.6 L s^{-1}) where maximum velocity was 0.73 m s^{-1}. Impinged eels escaped from racks at approach velocities of 0.90 ± 0.05 m s^{-1}.

Passage through the upright rack was common under high discharge (278.9 ± 36.2 L s^{-1}) at water velocities up to 1.02 m s^{-1}. The information presented will improve current fish passage criteria for European eels that are required to develop more effective fish passage facilities.

6.2 INTRODUCTION

Worldwide, eel stocks are considered to be at their lowest levels in recorded history (e.g. Haro *et al.*, 2000a). A 90% decline in the recruitment of European eels, *Anguilla anguilla*, (Bark *et al.*, 2007; Dekker, 2003) with glass eel abundance less than 5% of pre-1980 levels (DEFRA, 2006; ICES, 2006) has resulted in their designation as critically endangered by the International Union for Conservation of Nature (IUCN) (Freyhof & Kottelat, 2008). Concurrently, recruitment of Japanese, *A. japonica* (Han *et al.*, 2008), American, *A. rostrata* (Aieta *et al.*, 2009; Haro *et al.*, 2000b), shortfin, *A. australis*, and longfin, *A. dieffenbachia* (Jellyman *et al.*, 2002), eels have significantly decreased.

In an attempt to halt further decline, international legislation designed to protect eels has been implemented. In Europe, the EU Eels Regulation (Council Regulation No. 1100/2007 establishing measures for the recovery of European eel stocks) requires that member states aim to meet escapement targets of 40% eel biomass (EC, 2007). These efforts are reinforced by the EU Water Framework Directive 2000/60/EC, necessitating consideration of all species utilising watercourses (EC, 2000). Elsewhere, fisheries authorities are making concerted efforts to better manage and protect stocks (e.g. United States, ASFMC 2000; Canada, CEWG 2007; New Zealand, Jacques Boubée pers. comm.). The European eel is listed under appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

Management of eel stocks is made difficult due to the lack of understanding of the causal factors for their decline, although climate change, habitat loss, parasite infestation, overfishing and barriers to migration have been suggested (Feunteun, 2002). On rivers developed for hydropower, passage through turbines is associated with high levels of mortality (Anderson, 1988; Calles *et al.*, 2010; Montén, 1985; Winter *et al.*, 2006, 2007) due to blade strike, abrupt changes in pressure, cavitation, and sudden acceleration or deceleration of flow (from e.g. 3–5 m s^{-1} at the turbine entrance to 10–30 m s^{-1} within the wheel) (Larinier, 2008). Larger fish (Coutant & Whitney, 2000), and especially those with elongated morphologies, such as eels (Behrmann-Godel & Eckmann, 2003; Larinier & Travade, 2002a), are particularly susceptible to damage and mortality due to blade strike. Screening systems have been employed to reduce fish entrainment through turbines and/or to divert downstream migrants to bypass facilities. At high velocities, however, fish can become impinged on poorly designed racks and screens, resulting in significant mortality. In a recent study, mortality of large eels ($L_t > 680$ mm) that encountered a bar rack at a Swedish hydropower plant was 100% (Calles *et al.*, 2010). The high susceptibility of eels to become impinged on screens and bar racks was attributed to their elongated bodies and relatively weak burst swimming capabilities (maximum *c.* 1.35 m s^{-1}, Solomon & Beach, 2004, versus 1.95 m s^{-1} for Atlantic salmon, *Salmo salar*, smolts, Peake & McKinley, 1998). In recognition of considerable impacts of poorly designed screening systems on local eel populations, efforts are currently underway to improve their efficiency to block and divert fish in line with EU regulations. Screen and rack design criteria are required, but current understanding is limited and based on swimming capability. The influence of behaviour has, until now, been largely ignored. It is now recognised, however, that the design of screening and fish passage facilities requires adequate species-specific criteria based on swimming capability and behaviour (Rice *et al.*, 2010).

Downstream migrating eels have previously been assumed to drift passively with the current (Tesch, 2003). However, recent research employing telemetry techniques at hydropower plants indicates that eels exhibit active searching (Brown *et al.*, 2009) for areas of highest discharge (e.g. Jansen *et al.*, 2007). However, telemetry studies, while useful, do not provide the fine-scale behavioural information achieved through direct observations obtained under experimental conditions (Rice *et al.*, 2010). The few behavioural studies that have investigated eel response to screens and bar racks have been conducted during the day (see Adam *et al.*, 1999; Amaral *et al.*, 2003), despite the tendency for eels to be primarily nocturnally active (Edel, 1975; Hadderingh *et al.*, 1999; Tesch, 2003; Vøllestad *et al.*, 1986).

This chapter assessed the behavioural response of European eels to bar racks in a large-scale experimental flume during nocturnal periods to provide the information needed to improve the efficiency of these structures at hydropower plants. Two experiments utilising racks at different angles on either the horizontal plane relative to the flow or the vertical plane relative to the channel floor were undertaken. Velocities were selected which were typical of hydro-power plant forebays (Amaral *et al.*, 2003). It was hypothesised that rack efficiency would increase (greater bypass passage and reduced impingement and passage through the racks) under low rack angles relative to the flow or the channel floor and low discharge.

6.3 MATERIALS AND METHODS

6.3.1 EXPERIMENTAL INFRASTRUCTURE

Two experiments were conducted in a glass-walled recirculatory flume (21.4 m long, 1.4 m wide, and 0.6 m deep) at the International Centre for Ecohydraulics Research (ICER) facility during September and October 2007 (experiment 1) and January 2009 (experiment 2) during the hours of darkness. Discharge and depth were controlled by altering the number of centrifugal pumps in use (maximum of three), the water flow through them, and the height of an adjustable weir at the downstream end of the flume.

Fish behaviour was recorded using a combination of overhead and side-mounted cameras (Fig. 6.1 and 6.2) capable of recording fish movement under low-light with infra-red illumination. Four 15.0 W infrared illumination units emitting light at 850 nm wavelength were used to illuminate the flume. This is outside the spectral sensitivity of reproductively mature European eels (λ_{max} = 482 nm, Archer *et al.* 1995; Hope *et al.* 1998; range from c. 300 to 600 nm, Andjus *et al.* 1998) and humans (λ_{max} = 577 nm, Bowmaker & Dartnall 1980; Marks *et al.* 1964; range from c. 400 to 700 nm, Smith & Pokorny 1972). As visible light intensity during trials was at levels below which observers could see it was assumed that this was also true for the test fish.

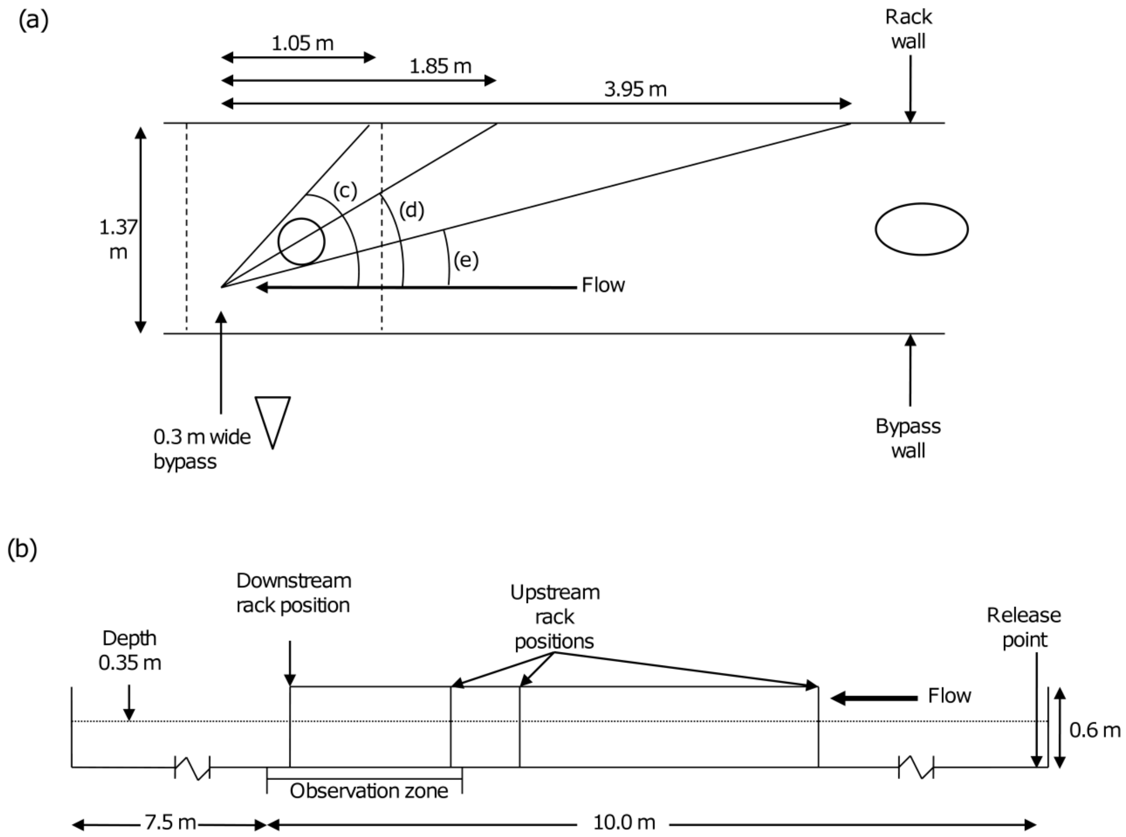

Fig. 6.1. Flume layout for experiment 1: (a) plan view with observation zone represented between the dashed lines, (b) elevation view, (c) 45° angle rack (length = 1.5 m), (d) 30° angle rack (length = 2.15 m), (e) 15° angle rack (length = 4.1 m) relative to the flow. Rack height = 0.6 m. Triangle = side mounted camera, circle = overhead camera directly above observation zone, oval = overhead camera angled downstream providing an overview image.

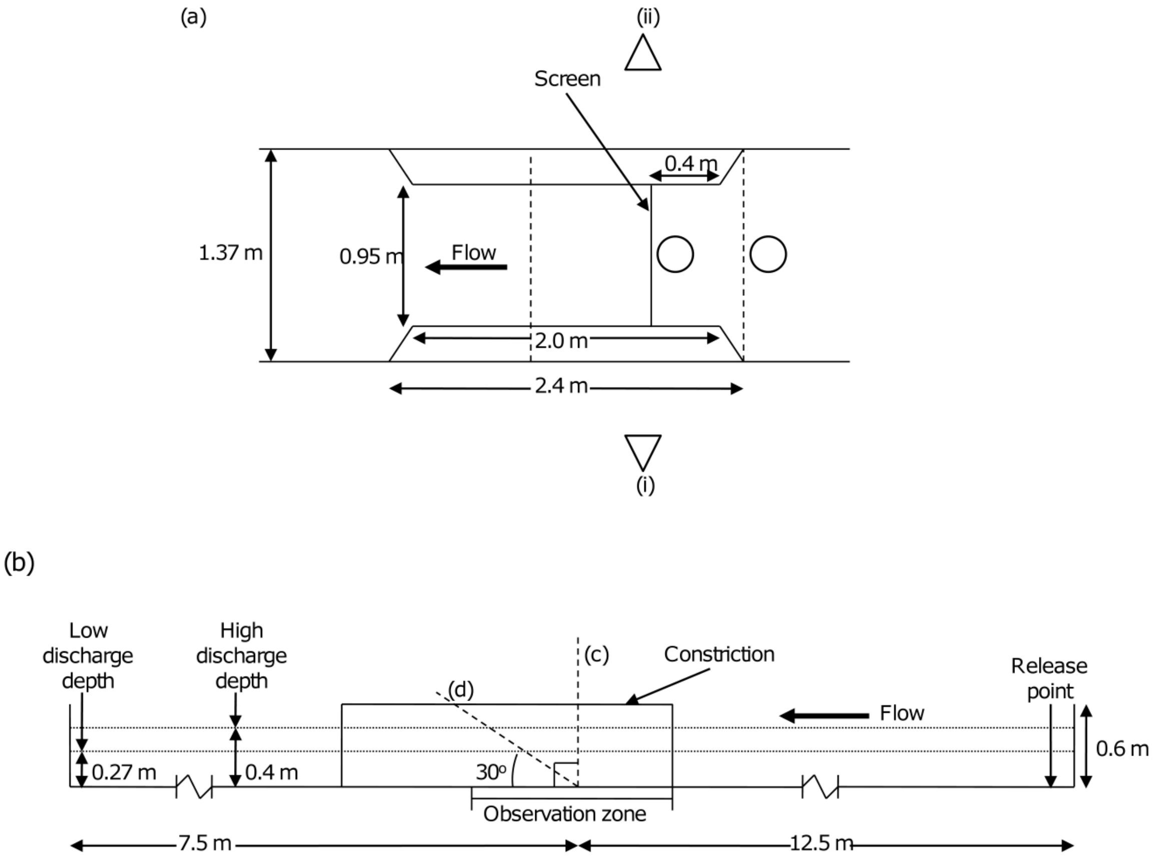

Fig. 6.2. Flume layout for experiment 2: (a) plan view with observation zone represented between the dashed lines, (b) elevation view. The bar rack was angled at (c) 90° and (d) 30°. Triangles = side mounted cameras ((i) = true left, (ii) = true right), circles = overhead cameras directly above observation zone.

6.3.2 EXPERIMENT 1

A stainless steel bar rack (6 mm diameter vertical cylindrical bars interspersed by 12 mm gaps), commonly used in the UK to block and divert fish movement at intakes and hydro-plants (EA, 2009), was placed vertically in the flume at one of three angles, 15°, 30° and 45° relative to the flow (Fig. 6.1). Rack angle and discharge (high: 237.3 ± 35.8 L s^{-1}; low: 138.1 ± 13.6 L s^{-1}) were alternated between trials, with depth maintained at 0.35 m. The gap between the downstream end of the rack and the channel wall was termed the “bypass entrance" which extended the entire depth of the water column. A 30 cm gap width was selected based on guidelines provided by Turnpenny *et al.* (1998).

Channel floor velocities, measured 2 cm above the channel floor, were recorded along transects perpendicular to the flow 5.0 m upstream (referred to as the "approach velocity") and at the bypass entrance using an electromagnetic flow meter (Valeport, 801-flat). Velocities (Table 6.1) were selected to allow fish to exhibit volitional exploratory behaviour and escape from the racks, yet were similar to those encountered at hydro-electric plants in the field. Velocity gradients to the bypass entrance (e.g. Fig. 6.3) were similar to those described by Amaral *et al.* (2003). The proportions of the total discharge flowing through the bypass were 23.85 ± 0.30 %, 27.24 ± 2.61 %, and 32.57 ± 1.02 % for the 45°-, 30°-, and 15°-angled racks respectively.

Table 6.1. Mean channel floor water velocities. Upstream of bar rack = 5.0 m upstream of the bypass entrance (experiment 1); upstream of constriction = 2.0 m, and within constriction = 0.2 m, upstream of the rack-channel floor interface (experiment 2); "mean water" relates to the combined upstream and downstream velocities accounting for acceleration of flow from the release point to the bypass entrance (experiment 1) or the rack-channel floor interface (experiment 2).

	Mean channel floor velocity, m s^{-1} ± SD (min.-max.)		
Treatment	Upstream of rack/constriction.	At bypass entrance/within constriction.	Mean water
Expt. 1, low flow	0.29 ± 0.03 (0.24-0.32)	0.35 ± 0.06 (0.29-0.45)	0.30 ± 0.01 (0.24-0.45)
Expt. 1, high flow	0.49 ± 0.07 (0.41-0.58)	0.65 ± 0.12 (0.51-0.77)	0.53 ± 0.03 (0.41-0.77)
Expt. 2, low flow	0.36 ± 0.04 (0.29-0.41)	0.58 ± 0.17 (0.39-0.73)	0.34 ± 0.19 (0.29-0.73)
Expt. 2, high flow	0.50 ± 0.04 (0.46-0.54)	0.90 ± 0.12 (0.77-1.02)	0.48 ± 0.27 (0.46-1.02)

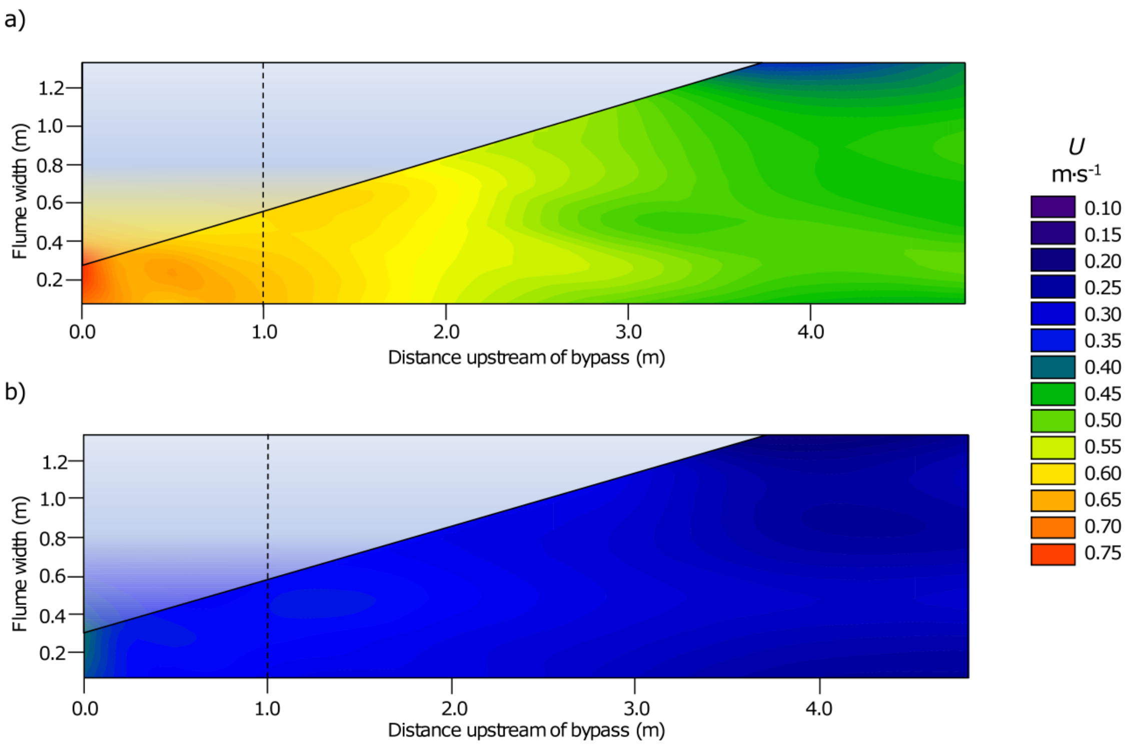

Fig. 6.3. Velocity (U) plots along the channel floor at a 15°-angled bar rack under (a) high and (b) low discharge. The observation zone is downstream of the dashed line.

Actively migrating adult European eel (mean total length (L_t) 660 ± 47 mm, min.–max. = 583–806 mm; mean mass (M) 544 ± 142 g, min.–max. = 300–1121 g) were locally sourced from a commercial trapper on the River Test (Hampshire, UK) in late September 2007 and maintained at ambient temperature in a 3,000 L tank. Water quality was maintained via constant circulation with a 10,500 L capacity pond pump, through a 12,000 L capacity pond filter.

Sixty 1-hr trials, each using a single eel, were conducted. Prior to the start of each trial, eels were held in perforated containers placed at the centre of the channel at the upstream end of the flume to acclimate for a minimum of one hour. An eel was netted from the container and each trial commenced on the immediate release of the eel 10.0 m upstream of the bypass entrance. At the end of each trial, fish were removed and L_t and M measured.

6.3.3 EXPERIMENT 2

To assess eel response to a bar rack placed perpendicular to the flow at high velocities the channel was constricted by approximately 30% to 0.95 m (Fig. 6.2). The inclusion of a constriction and the omittance of a bypass were necessary to attain higher approach velocities within the channel. This meant that there was an overlap of water velocity between the high and low flow conditions for experiments 1 and 2, respectively. The maximum velocity upstream of the constriction for low flow was the same (0.41 m s^{-1}) as the minimum water velocity upstream of the rack for experiment 1 during high flow (Table 6.1). The rack was maintained at either 90° or 30° on the horizontal plane relative to the channel floor, and spanned the entire water depth (Fig. 6.2). Velocities (Table 6.1) were selected for and measured as described for experiment 1, at transects 0.2 m and 2.0 m upstream of the rack-channel floor interface, providing values within and outside of the constriction. Rack angle and discharge (high: 281.0 ± 21.2 L s^{-1}; low: 132.9 ± 16.6 L s^{-1}) were alternated between trials. Maximum water depth varied from 0.40 to 0.27 m under high and low discharge respectively.

Actively migrating adult European eels (L_t 567 ± 9 mm, min.-max. = 443-706 mm; M 306 ± 164 g, min.-max. = 87-590 g) were locally sourced from a commercial trapper on the River Stour (Dorset, UK) in November 2008, and maintained as described for experiment 1.

Twenty 1-hr trials, each using a single eel were conducted. Eels were acclimated and released in the flume as described for experiment 1. Each trial commenced on the release of an eel 12.5 m upstream of the rack. At the end of each trial, fish were removed and L_t and M measured.

6.3.4 HYDRAULICS

For experiment 1, detailed velocities were recorded along the channel floor using a Nortek Vectrino+ Acoustic Doppler Velocimeter (ADV) set to sample at 50 Hz with a sample volume of 0.31 cm^3. Sampling duration was 60 s providing 3000 discrete velocity measurements in three dimensions. Spurious data and outliers were removed using a velocity correlation filter as described by Cea *et al*. (2007). Relative turbulence intensity (K) was calculated in the downstream direction by dividing the standard deviation of the velocity by the mean. The variation in turbulence intensity across the channel was assessed using a one-way ANOVA and contour plots of K created using SigmaPlot®.

6.3.5 BEHAVIOUR

Video recordings were analysed to describe eel response to racks during hours of darkness. The field of view, referred to as the observation zone, for experiment 1 extended from 0.3 m downstream to 1.0 m upstream of the bypass entrance. A second overhead camera covered an area from 0.0–6.0 m upstream of the bypass entrance. For experiment 2 the observation zone extended from 0.6 m upstream to 0.7 m downstream of the rack-channel floor interface. This covered the entire area within the constriction zone in which fish could move. The following behavioural parameters were recorded:

6.3.5.1 *Bar rack approach*

The depth and lateral position of the eel as it entered the observation zone was recorded. Depth was defined as surface (upper third of the water column), mid-column, or channel floor (lower third of the water column). Lateral position was determined in relation to being within 20% (because in practice, all fish approaching within this region were in contact with the channel wall) of channel width of the bypass or rack walls (experiment 1), the true left or right walls (Fig. 6.2, experiment 2), or the central channel (remaining 60% of channel width). An approach was deemed to occur when the entire body length of the eel entered the observation zone. The mean velocity (m s^{-1}) of the eel from point of release to the bypass (experiment 1) or rack-channel floor interface (experiment 2) was compared with the mean channel floor water velocity. Pearson chi-square tests and a univariate two-way ANOVA were used to assess the effect of discharge and bar rack angle (fixed factors) on the position and time taken (dependent variables) for eels to approach the rack, respectively. A one-sample *t*-test was used to determine if an equal (i.e. 0.5) proportion of approaches were made along each channel wall.

6.3.5.2 *Rejection*

A rejection was deemed to occur when an eel returned upstream after approaching within 0.1 m of either the bypass entrance in experiment 1 (bypass rejection), the rack-channel floor interface (rack rejection) for both experiments, or the narrowest point of the constriction (constriction rejection) in experiment 2. The total number of rejections was recorded and a Pearson chi-square tests used to assess the effect of angle and discharge on bypass, rack, and constriction rejections.

6.3.5.3 *Passage efficiency and bar rack impingement*

Time taken from the point of release until total body length passed through the bypass entrance, and the total number of passes as a proportion of the total number of approaches were recorded for experiment 1. For experiment 2, impingement was deemed to occur when more than approximately half of total body length maintained contact with the bar rack for a minimum of 5 s prior to escape upstream or passage through the gaps of the rack. Number of impingements and passes through the rack, and mean impingement time, were recorded. A univariate two-way ANOVA was used to determine the influence of discharge and rack angle (fixed factors) on time taken to pass the bypass and duration of impingement (dependent variables). A Pearson chi-square test was used to investigate the influence of discharge and rack angle on passage through the bar rack.

6.4 RESULTS

6.4.1 HYDRAULICS

During low discharge, K was highest along the rack wall ($F_{2,\,39} = 4.27$, $P < 0.05$) (e.g. Fig. 6.4). Under high discharge, K was higher along the bypass wall (e.g. Fig. 6.4), although this was not significant ($F_{2,\,39} = 1.15$, $P > 0.05$). An exception was that high K was created through the channel centre (Fig. 6.5) when the rack was angled at 45°, but this was not significant ($F_{2,\,11} = 1.81$, $P > 0.05$).

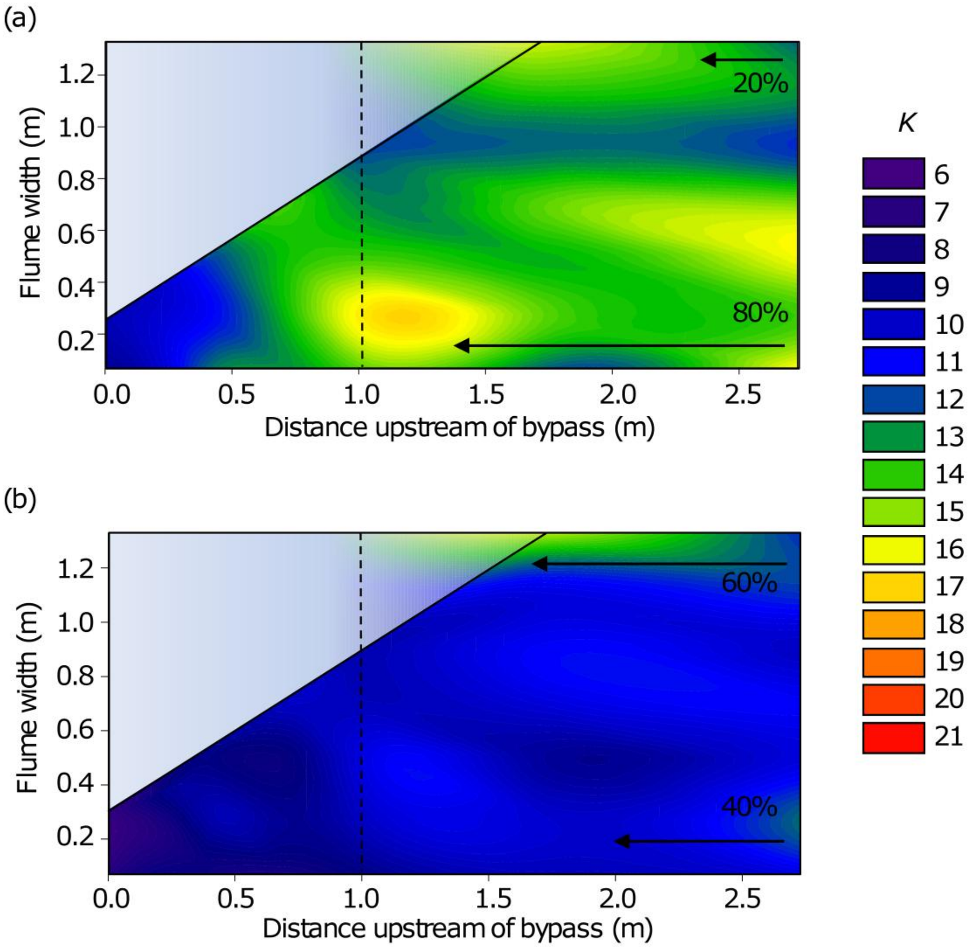

Fig. 6.4. Turbulence intensity along the channel floor at a 30° angled bar rack under (a) high and (b) low discharge. The observation zone is downstream of the dashed line. Arrow position and length represent the location and percentage of eel approaches respectively.

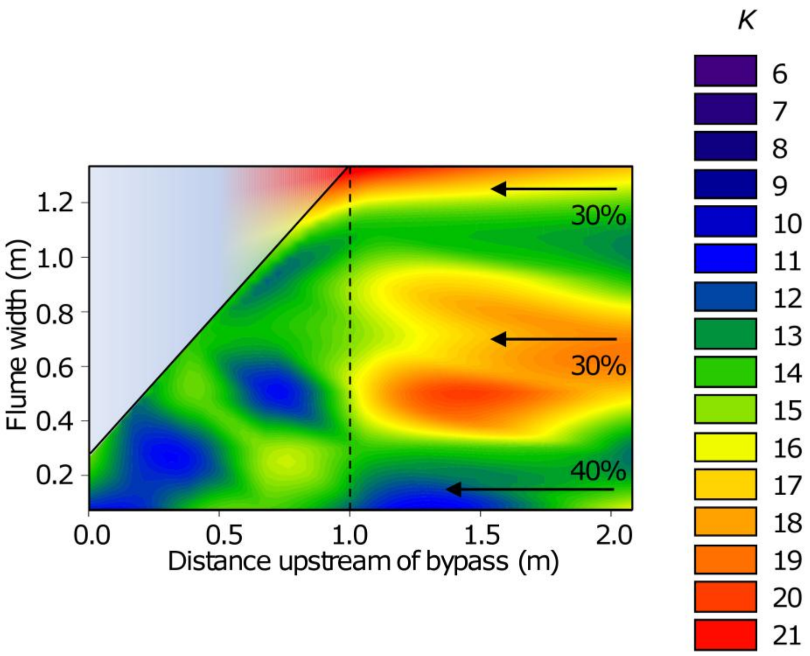

Fig. 6.5. Turbulence intensity along the channel floor, at 45° angled bar rack under high discharge. The observation zone is downstream of the dashed line. Arrow position and length represent the location and percentage of eel approaches respectively.

6.4.2 BEHAVIOUR

6.4.2.1 *Bar rack approach*

Experiment 1: During sixty trials, fifty-nine fish approached the bypass entrance, with one fish approaching twice. The majority of approaches (n=36) were associated with the channel floor (91.7%) and walls (95%) against which eels tended to maintain regular contact. The few central channel approaches were associated with areas of high velocity and *K* under high discharge with the rack angled at 45° (Fig. 6.6).

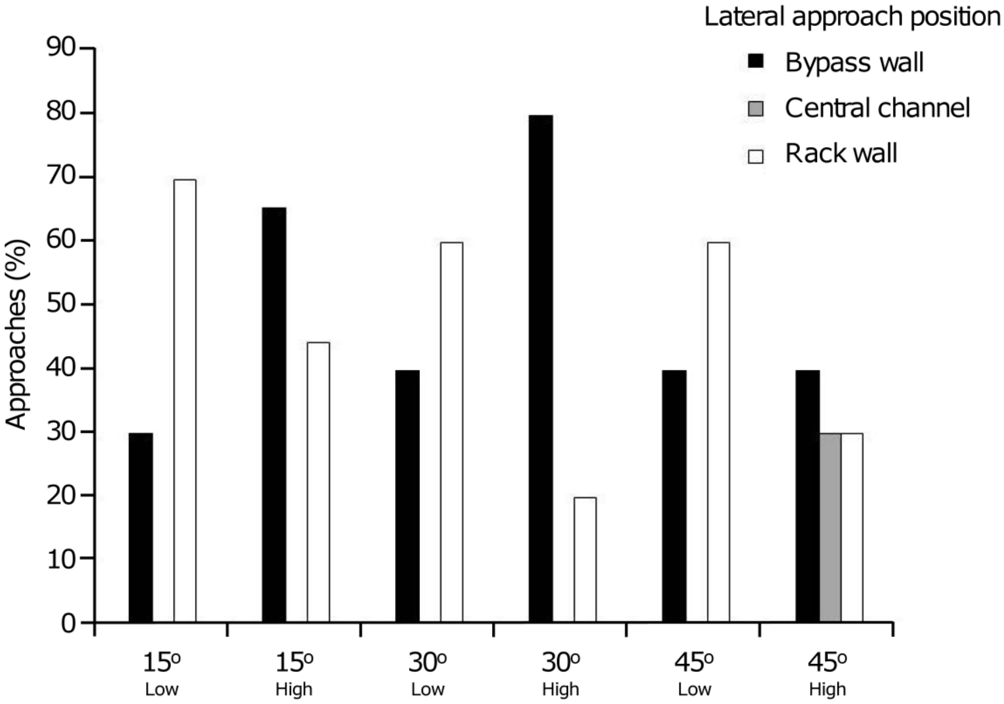

Fig. 6.6. Percentage of eel approaches at each lateral position, dependent on treatment, for experiment 1.

The mean eel velocity (0.04–0.11 m s^{-1}) was lower than the mean channel floor water velocity from the release point to the bypass entrance (0.29–0.55 m s^{-1}) under all discharge and rack angle treatments.

Discharge influenced lateral approach position ($\chi^2(2) = 7.84$, $P < 0.05$). The majority of approaches (63.33%) were associated with areas of highest K at the rack wall under low discharge ($t^{0.5}(29) = 12.67$, $P < 0.001$), and the bypass wall (58.62%) under high discharge ($t^{0.5}(28) = 7.97$, $P < 0.001$). Rack angle and discharge had no effect on approach depth, time to first approach, or eel velocity.

Experiment 2: All 139 approaches during 20 trials were channel floor oriented, and 84.2% were associated with the channel walls with which the eels maintained regular contact. The mean eel velocity (0.03–0.16 m s^{-1}) was lower than the mean channel floor water velocity (0.34–0.48 m s^{-1}) under all discharge and rack angle treatments. Rack angle and discharge had no effect on approach depth, lateral approach position, or time to first approach.

6.4.2.2 *Rejection*

Experiment 1: No rejections occurred.

Experiment 2: Rack and constriction rejection was uncommon (3.6% and 4.3% of approaches respectively). Avoidance behaviour was usually exhibited only after physical contact with the rack. Rack angle had a significant effect on rejection of the bar rack ($\chi^2(1) = 7.69$, $P = 0.01$) and constriction ($\chi^2(1) = 4.83$, $P < 0.05$), with the majority occurring at 30°. Discharge had no effect on either parameter.

6.4.2.3 *Passage efficiency and impingement*

Experiment 1: All but one fish passed the bypass, with the majority (98.3%) passing on the first approach. Eels did not become impinged on the rack, nor did they pass through the bars.

Experiment 2: Impingement for more than 5 s before escape occurred in 46.8% of approach events and was most frequently associated with the vertical rack (66.7% of approaches) and low discharge (60.6% of approaches). An interaction ($F_{1, 62} = 5.07$, $P < 0.05$) indicated impingement time was positively and negatively related to discharge at 90° and 30°, respectively. All but those fish passing through the rack escaped from impingement at mean approach velocities within the constriction of 0.90 ± 0.12 m s^{-1}.

The majority of eels passing through the racks did so under high discharge ($\chi^2(1) = 4.00$, $P < 0.05$) with no effect of rack angle. Four eels passed through the vertical rack under high and one under low discharge, and one eel passed the 30° angled rack at high discharge. Those that passed continued to demonstrate normal searching behaviour downstream of the bar rack. The entrained fish were slightly smaller than the overall mean fish size with mean $L_t = 526.67 \pm 98.12$, min.–max. 443–687 mm, and $M = 235.5 \pm 168.44$, min.–max. 87–500 g.

6.5 DISCUSSION

The design and placement of racks and screens at hydropower turbine intakes must minimize damage to downstream migrating adult eels if management plans driven by EU Eel Regulations are to prove effective. Poorly designed screens and racks can result in high levels of eel mortality (Calles *et al.*, 2010) because an elongated body morphology increases the probability of impingement and relatively weak swimming performance reduces ability to escape. This chapter illustrates the importance of behaviour when considering the design of racks and screens. Unlike juvenile salmonids that avoid areas of rapid acceleration of flow (Haro *et al.*, 1998; Kemp *et al.*, 2005a), eels did not avoid abrupt changes in the hydrodynamic environment created as a result of fluid–structure interactions, only rejecting racks after direct contact with them and thus increasing the potential for impingement. At the relatively low velocities experienced (range = 0.77 –1.02 m s^{-1}; Table 6.1), eels were able to escape the racks. Under high velocities such as those that may be encountered at hydropower intake racks (e.g. *ca*. 1.47-1.85 m s^{-1} at the Ätrafors hydropower plant, Sweden; Calles *et al*., 2010). However, the probability of mortality due to impingement can be considerable (e.g. Calles *et al*., 2010).

Downstream moving eels tended to associate with physical structure (channel floor and walls) as previously described based on the results of both laboratory (Amaral *et al*., 2003 for American eels) and field (Brown *et al*., 2009; Gosset *et al*., 2005) studies. Of interest is the finding that trajectories switched from the rack to the bypass-channel wall as discharge changed (Fig. 6.6), resulting in consistent association with areas of highest relative turbulence intensity (Fig. 6.4). Elevated turbulence intensity under some conditions may reduce the energetic cost of swimming and thus be attractive to fish (Cheong *et al*., 2006) and provide a means to locate structure. Previous research has indicated that brown trout, *Salmo trutta*, account for levels of turbulence when selecting habitat (Cotel *et al*., 2006). The influence of turbulence on selection of migratory routes of fish has received relatively limited attention (but see Kemp & Williams, 2008), but may provide the basis for interesting future interdisciplinary research to understand how fluid dynamics influences fish behaviour (Rice *et al*., 2010).

Eels moved downstream more slowly than if they had been passively displaced, possibly because they held position on release and/or actively swam back upstream prior to entering the observation zone. Avoidance in response to some factor associated with bar racks has been observed in the field, in which downstream migrating eels hesitate and adopt recurrent searching behaviour on encountering conditions associated with trash racks (Behrmann-Godel & Eckmann, 2003; Brown *et al*., 2009; Jansen *et al*., 2007).

The negative impacts of racks and screens on migratory eels can be reduced by altering the angle. Vertical racks perpendicular to the flow resulted in the highest probability of impingement, and will likely prove difficult to escape from when velocities are high (as observed by Adam *et al.*, 1999). Conversely, horizontally inclined racks resulted in lower impingement and higher guidance efficiencies (supporting findings of Amaral *et al.*, 2003).

Impingement only occurred during experiment 2 when racks were placed perpendicular to the flow. Discharge influenced probability of impingement, reflecting frequent repetition following easy escape at low flows. Length of impingement was positively related to discharge when the rack was vertical, but negatively related when sloping. It is not clear why this should be the case, although the eels may have been more capable of escaping from the sloping than the vertical racks at higher flows. Suggesting, speculatively, that utilisation of angled racks on the horizontal plane relative to the channel floor (Fig. 6.2) will permit escapement of fish at higher through velocities if the rack were vertical. These angled racks may also direct the thigmotactic channel floor oriented eels to surface-oriented bypasses, which are often used to accommodate downstream salmonid smolt passage (Arnekleiv *et al.*, 2007; Brown *et al*, 2009).

The results of this chapter provide important information to improve the design of racks and screens for downstream migrating eels. Eels, that tend to move along the channel floor, exhibit different behaviours to surface-oriented downstream migrating salmonids for which current screening and passage facilities are most frequently designed (Arnekleiv *et al.*, 2007; Johnson & Dauble, 2006; Long, 1968). Under the experimental conditions created, eels tended to exhibit behavioural avoidance only after encountering physical structure, while Atlantic (Haro *et al.*, 1998) and Pacific salmon (Kemp *et al.*, 2005a) smolts are known to avoid abrupt velocity gradients. If eels exhibit similar behaviour under higher velocities, then the impact of impingement at racks and screens and/or entrainment through turbines may be substantial. The results presented clearly indicate the advantage to using angled racks, as opposed to those placed vertically and perpendicular to the flow, for enhancing guidance efficiency and reducing probability of impingement. Bar racks placed at angles <45° on the vertical or horizontal planes will likely prove most effective at diverting downstream migrating eels to bypass channels. Probability of impingement would be higher at more acute angles as through would exceed sweeping velocities. These results indicate that eels were able to escape racks when approach velocities were as high as 0.9 m s^{-1}, thus it may be possible to utilise more extreme angles at lower velocities, but further research is necessary to determine whether this is the case. This also suggests that guidelines proposing velocities at screening facilities should not exceed 0.5 m s^{-1} (Adam *et al.*, 1999; ICES, 2007) may be conservative, although lack of effective bypass facilities may result in prolonged impingement and increased rates of mortality.

Chapter 7: Improving fish passage for multiple species: response of adult European eel, *Anguilla anguilla*, and brown trout, *Salmo trutta*, to accelerating flow at an orifice weir.

7.1 SUMMARY

Historically, fish passage facilities developed to mitigate for adverse environmental impacts focused predominantly on the upstream migration of a limited number of families, primarily the Salmonidae. Driven partly by more holistic environmental legislation, it is now necessary to develop passage criteria for multiple species and life-stages. To do so, fish behaviour in response to conditions encountered at passage facilities should be quantified. The behavioural response of downstream moving European eel, *Anguilla anguilla*, and brown trout, *Salmo trutta*, to a hydraulic gradient created by a weir and orifice placed in a flume facility was evaluated. The orifice (20 x 20 cm) was located either on or 15 cm above the channel floor. Eels tended to passively move downstream along the channel floor and walls, initiating a response after physical contact with the weir. Conversely, brown trout predominantly moved downstream head first and exhibited a switch to positive rheotaxis on encountering the velocity gradient without contacting the structure. Trout spent longer than eels in the area immediately upstream of the channel floor orifice weir, although time taken to pass was similar. Trout spent less time than eels associated with the mid-column orifice weir, despite taking longer to pass. Both species took longer to pass the mid-column orifice. Eels

passed the orifice head first on the initial encounter with no rejections, whereas trout passed tail first. The position at which trout first switched to positive rheotaxis occurred closer to a channel floor than mid-column orifice, as was the closest position to the orifice reached during first approach. However, velocity gradient along the body length did not differ with orifice treatment for both position metrics. Trout did not appear to acclimate to the hydraulic gradient by moving closer to the orifice with successive approaches. The behavioural difference between species observed illustrates the challenges faced in developing multi-species fish passes.

7.2 INTRODUCTION

Development of rivers, e.g. for hydropower, flood defence, and water abstraction, has significantly altered and reduced habitat connectivity (Odeh, 1999; Pringle, 2003). Fluvial discontinuity (Ward & Stanford, 1983) can cause populations of aquatic biota, e.g. fish, to decline by impeding access to habitats that are essential for feeding, reproduction, and growth (Cote *et al.*, 2009). To enable fish to pass river infrastructure, a range of fish passage facilities have been developed (e.g. juvenile bypass systems, fish ladders, lifts and locks). However, previous attention was focused on relatively few species, driven primarily by their economic, recreational and cultural importance. As a result, the majority of fish passage research has concentrated on upstream migrating adult salmonids (Calles & Greenberg, 2005; Clay, 1995; Enders *et al.*, 2009; Larinier, 2008; Larinier & Travade, 2002; Roscoe & Hinch, 2010). Despite this bias, current legislation (e.g. the EU Water Framework Directive [WFD; 2000/60/EC] and the US National Environmental Policy Act [NEPA] 1969) has advanced interest in progressing the development of fish passage (and screening) criteria for multiple species throughout their life-history (e.g. see Kemp *et al.*, 2010, and Lucas *et al.*, 2009, for river lamprey, *Lampetra fluviatilis*; Quintella *et al.*, 2009, for sea lamprey, *Petromyzon marinus*; Guiny *et al.*, 2003, for mature brown trout, *Salmo trutta*, and Atlantic salmon parr, *S. salar*; Russon *et al.*, 2010, for European eel, *Anguilla anguilla*; Lucas & Frear, 1997, for barbel, *Barbus barbus*; Silva *et al.*, 2010, for Iberian barbel, *Luciobarbus bocagei*).

Due to the attention directed at upstream migrating life-stages, swimming performance has been a key consideration in fish passage design. This is important in determining when velocities are likely to exceed the endurance (e.g. for culverts) or burst (e.g. for orifice and weir fish ladders) swimming capabilities of the target species. It is known that swimming ability and behaviour varies with age/maturity status (Williams & Brett, 1987), species (Videler, 1993), body length (Beamish, 1978; Brett, 1964), physiological condition (Farlinger & Beamish, 1978) and past experience (Goodwin, 2007, but see Hammer 1995 for a review of further influential factors). Behaviour has perhaps been less often the focus of fish passage research than swimming performance, but for downstream migrating life-stages is usually of greater significance. For example, juvenile salmonids (e.g. Moore *et al.*, 1998; Peake & McKinley, 1998) and adult eels (e.g. Behrmann-Godel & Eckmann, 2003; Jansen *et al.*, 2007) appear to utilise regions of high flow, presumably as a means to conserve energy during migration, but actively avoid rapid velocity gradients when viewed at fine-resolution scales (for salmonids: Haro *et al.*, 1998; Kemp & Williams, 2008; Kemp *et al.*, 2005a), or exhibit recurrent milling behaviour on encountering conditions associated with in-river structures such as at dams (e.g. Croze & Larinier, 1999; Goodwin *et al.*, 2006; Johnson & Moursund, 2000; Venditti *et al.*, 2000; for salmonids; and Behrmann-Godel & Eckmann, 2003; Brown *et al.*, 2009; Jansen *et al.*, 2007; Winter *et al.*, 2006 for eels).

Descriptions of potential mechanisms that might explain observed behavioural avoidance at bypass systems have been described. In presenting a numerical fish surrogate model, Goodwin *et al.* (2006) proposed that as a downstream migrating juvenile salmon approaches a physical structure that obstructs the flow field, it will experience a free-shear flow gradient, characterised by both increasing hydraulic strain (steady-state acceleration, Hudspeth, 1989) and velocity. The fish are able to use this information to differentiate between structures that induce form and friction (wall-bounded flow gradients) resistance, the latter suggested to be associated with increasing hydraulic strain, but decreasing velocity. It is hypothesised that a behavioural response will be induced as the fish perceives the “just noticeable difference” (Weber, 1846) between the stimuli (hydraulic factor) and background levels. The position of this critical threshold varies with the individual depending on antecedent experience (level of acclimation to the stimuli). On encountering a free-shear flow gradient, Goodwin *et al.* (2006) hypothesised that an avoidance response will be elicited in which the fish swims towards decreasing water velocity or against the flow vector. Indeed, this suggestion is to some extent supported by experimental observation in which juvenile salmonids that encountered a free-shear flow gradient created by a constriction frequently switched orientation from negative to positive rheotaxis, and on occasion rejected the condition by swimming upstream against the flow (Kemp *et al.*, 2005a). It is predicted that after repeated encounter and continued exposure to the hydraulic gradient, the fish will become acclimated to the stimuli, at which point avoidance is no longer exhibited and downstream progress ensues. Understanding how hydraulic variables induce avoidance behaviour, and how this might be reduced, may help the development of more efficient bypass systems for downstream migrating fish.

To construct meaningful fish passage criteria, there is a need to develop metrics that quantify both swimming capability and behaviour for the target life-stages of the multiple species of interest. This study concentrates on advancing understanding of the behaviour of downstream moving fish by comparing two species, brown trout and European eel, which differ in both life-history strategy, locomotory mode, and body morphology. The fish encountered two different acceleration gradients created by an experimental weir with an orifice in one of two positions. Based on the work of Goodwin *et al*. (2006), it is predicted that the hydraulic gradient created by the orifice treatments would induce behavioural avoidance, and that acclimation would occur after repeated exposure. The aim of the experiment is to identify interspecific variation in behaviour between the two species, and test two key hypotheses. First, that a more abrupt velocity gradient (stronger stimuli) would induce a more marked avoidance response, indicated by a greater period of acclimation (and as consequence greater delay to downstream movement), and exhibition of an avoidance response (demonstrated by a switch in orientation) at a greater distance from the orifice. The second hypothesis is that during the period of acclimation the fish would incrementally sample conditions increasingly closer to the orifice until passage occurred.

7.3 MATERIALS AND METHODS

An orifice weir (1.8 x 50 x 140 cm) was installed perpendicular to the flow in a glass-walled recirculatory flume (21.4 m long, 1.4 m wide, and 0.6 m deep) at the International Centre for Ecohydraulics Research (ICER) experimental facility (University of Southampton). The orifice (20 x 20 cm) was centred midway along the width of the weir either at the base of the channel (floor orifice treatment) or 15 cm above the floor (mid-column orifice treatment). Manipulation of the volume of water passing through the centrifugal pumps and the height of an adjustable weir at the downstream end allowed discharge and depth to be controlled. Screens were erected along the channel walls to prevent disturbance to the fish by the observer.

Fish behaviour was digitally recorded using 2 overhead (2.1 m above the channel floor) and 2 side-mounted (one on each wall, placed 0.5 m upstream of the weir) low light cameras under infra-red illumination (4 x 15 W units emitting light at 850 nm wavelength) to provide a field of view termed “the observation zone” which extended from 0 to 2 m upstream of the weir.

Actively migrating adult European eels (mean total length (L_t) = 586 ± 12 mm; mean wet weight (M) = 383 ± 23 g) were captured using a permanently installed eel-rack on the River Stour (Dorset, UK) on 3 November 2008. The eels were placed in aerated and iced river water during transportation to the ICER facility, where they were maintained in a 900 L holding tank (mean temperature prior to trials = 14.25 ± 0.40°C; maximum stocking density = 17.02 kg m^{-3}) for between 14 and 23 days prior to use in trials. Twenty-one months old brown trout (L_t = 238 ± 3 mm; M = 231 ± 3 g) were obtained from a local trout farm and transported to the ICER facility in aerated tanks on 12 November 2008. Trout were maintained in a 3000 L holding tank (mean temperature = 14.35 ± 0.26°C; maximum stocking density = 2.03 kg m^{-3}) for between 5 and 14 days prior to use in trials. The farmed origin of the brown trout could potentially influence their behaviour (e.g. increasing risk taking; Huntingford & Adams, 2005) and swimming capabilities (e.g. reduced maximum swimming speeds; Pedersen *et al.*, 2008) compared to wild populations. However, the results of this study do not suggest this to be problematic for this research (see discussion).

Eighty trials (n = 40 per treatment per species), lasting 2-hours or until the entire body length of the fish passed through the orifice, using individual fish were conducted between 17 and 26 November 2008. Trials were undertaken during the hours of darkness (17:00–03:30) to replicate the nocturnal migration in European eel (Tesch, 2003; Calles *et al.*, 2010; Hadderingh *et al.*, 1999) and brown trout (during late autumn and winter: Heggenes *et al.*, 1993). Fish were acclimated for a minimum of 1.5 hours at the upstream end of the flume prior to release from a point 10 m upstream of the weir. Species and treatment were alternated every 1 and 2 trials, respectively. Mean flume water temperature at the start of experimental trials was 14.70 ± 0.50°C.

7.3.1 HYDRAULIC CONDITIONS

Detailed velocities of the two weir configurations were measured using a Nortek Vectrino^{+} Acoustic Doppler Velocimeter (ADV) set to sample at 50 Hz with a sample volume of 0.31 cm^3. Sampling period was 60 s providing 3000 discrete velocity measurements in three dimensions. To remove spurious measurements and outliers, the data were filtered using a velocity correlation filter as described in Cea *et al.* (2007). Velocities were measured at 40% depth along a transect perpendicular to the flow 2 m upstream of the weir. The mean velocity along this transect was termed the approach velocity, based on being the velocity the fish experienced when approaching the weir travelling in the downstream direction. Mean discharge was 58.44 ± 3.07 L s^{-1}, with approach velocities of 0.09 ± 0.01 and 0.12 ± 0.00 m s^{-1} at the mid-column and channel floor orifice weirs, respectively. Depth upstream of the weir and maximum velocity at the orifice were 0.45 and 0.37 m, and 1.50 ± 0.00 and 1.65 ± 0.03 m s^{-1} at the mid-column and channel floor oriented orifices, respectively. Assuming constant one-dimensional motion, acceleration of water over 2 m was 0.56 m s^{-2} for the mid-column and 0.68 m s^{-2} for the channel floor treatments.

Detailed measurements of flow characteristics were obtained using an ADV at between 7-11 (more recordings were taken nearer the structure) equidistant points along 10 transects perpendicular to the flow (from 0.05 m to 2.00 m upstream of the weir, at 0.16 m depth). The mean velocity modulus in three dimensions (u_m, in m s^{-1}) was calculated as described by Nikora *et al.* (2003). Maps of u_m were created for the two orifice orientations using spline interpolation in ArcGIS™ 10's *Spatial Analyst* tool. The derived maps of u_m were used as tools from which interpolated values from specific locations could be obtained (see section 7.3.2).

7.3.2 BEHAVIOUR

At the point of entering the observation zone from upstream, the lateral position (recorded at 20 cm intervals relative to the channel walls) and depth (recorded at 9 cm intervals) of the fish was recorded. Time to first approach (when the entire body length of the fish entered the observation zone), total number of approaches per trial, time spent in the observation zone per approach, and time spent holding station per approach were registered for each trial. The number of times the fish made physical contact with the weir (reported as a proportion of the total number of approaches) and whether fish made contact with the weir prior to demonstrating a switch in rheotactic orientation was monitored. Successful passage through the orifice, and time taken from point of release to do so, was documented. Fish orientation (positive or negative rheotaxis) was recorded as the fish both entered the observation zone and passed through the orifice.

Behavioural response (defined as a switch from negative to positive rheotaxis) to hydraulic gradient was described for trout (eels exhibited limited response to hydraulic gradients instead responding predominantly to structure, see results). The position of head and tail when a response was first elicited and at the closest point to the orifice reached during each approach were attained using a particle tracking programme (designed in MatLab® 2009b, The Math Works, Inc., Natick, MA) written by Dr Tony Lock (University of Southampton), from which the distance to the centre of the orifice was calculated to the nearest 1 cm. Trout that made contact with the structure prior to exhibiting a response were excluded from further analysis. These positions were superimposed on the corresponding u_m map and the u at the head and tail extracted and used to calculate the velocity gradient (uG) along the length of the fish at the point of response using the following formula:

Equation 7.1: $$uG = \delta u \; / \; L_\mathrm{t}$$

7.3.3 STATISTICAL ANALYSIS

Tests of normality and homogeneity of variance were performed using Shapiro-Wilk and Levene's tests respectively. Attempts to normalise non-parametric data were made but were unsuccessful, thus non-parametric tests were used for these parameters.

The influence of species and treatment on the dependent variables: 1) lateral approach position; 2) depth of approach; 3) time to first approach; 4) total number of approaches per trial; 5) time spent in the observation zone per approach; 6) time spent holding station per approach and 7) time to pass, were analysed using univariate two-way ANOVA. A Kruskal-Wallis test was performed to determine the effect of species and treatment on the number of weir contacts per approach.

The influence of treatment on distance (and corresponding *uG*) from the orifice of position of response and closest point reached by trout during the first approach per trial was assessed using a Kruskal-Wallis test. To test the hypothesis that during acclimation fish would incrementally sample conditions closer to the orifice with each approach, linear regressions were performed for each treatment to assess whether the dependent variables: position of response, closest point reached, and corresponding *uG* were influenced by approach number (the predictor variable). Prior to performing linear regressions, one-way ANOVAs were undertaken to determine if treatment influenced the slopes of the lines (*b* values) obtained for each trial, and where no effect was found data were pooled.

7.4 RESULTS

Species influenced lateral position and depth of approach (Table 7.1) to the weir as the vast majority of eels moved downstream along the channel wall (98.2% versus 43.9% for trout; Fig. 7.1) and at a depth of between 0-9 cm from the channel floor (96.4%; Fig. 7.2). Trout approached higher in the water column, with the majority (61.8%) of approaches occurring between 9-18 cm from the channel floor (Table 7.1; Fig. 7.2). Orifice treatment did not influence lateral approach position but affected depth of approach, with a greater proportion of trout approaching a mid-column oriented orifice higher in the water column compared to the channel floor (Table 7.1; Fig. 7.2). No interactions between species and treatment occurred with either metric (Table 7.1).

Table 7.1. Results of two-way ANOVAs to determine the influence of species and orifice orientation (fixed factors) on the various dependent variables for downstream moving eel and trout approaching an orifice weir.

		Species		*Orifice treatment*		*Interaction*	
Dependent variable	d.f.	*F*	*P*	*F*	*P*	*F*	*P*
1) Lateral approach position	1, 404	4.48	< 0.05	0.14	> 0.05	0.10	> 0.05
2) Depth of approach	1, 380	179.96	< 0.001	8.03	< 0.01	2.24	> 0.05
3) Time to first approach	1, 76	98.95	< 0.001	0.02	> 0.05	4.56	< 0.05
4) Total number of approaches per trial	1, 76	3.45	> 0.05	60.22	< 0.001	1.06	> 0.05
5) Time spent in observation zone per approach	1, 406	1.18	> 0.05	0.24	> 0.05	6.81	< 0.01
6) Time holding station in observation zone per approach	1, 76	0.09	> 0.05	0.00	> 0.05	10.23	< 0.01
7) Time to pass orifice	1, 71	9.42	< 0.01	22.74	< 0.001	0.00	> 0.05

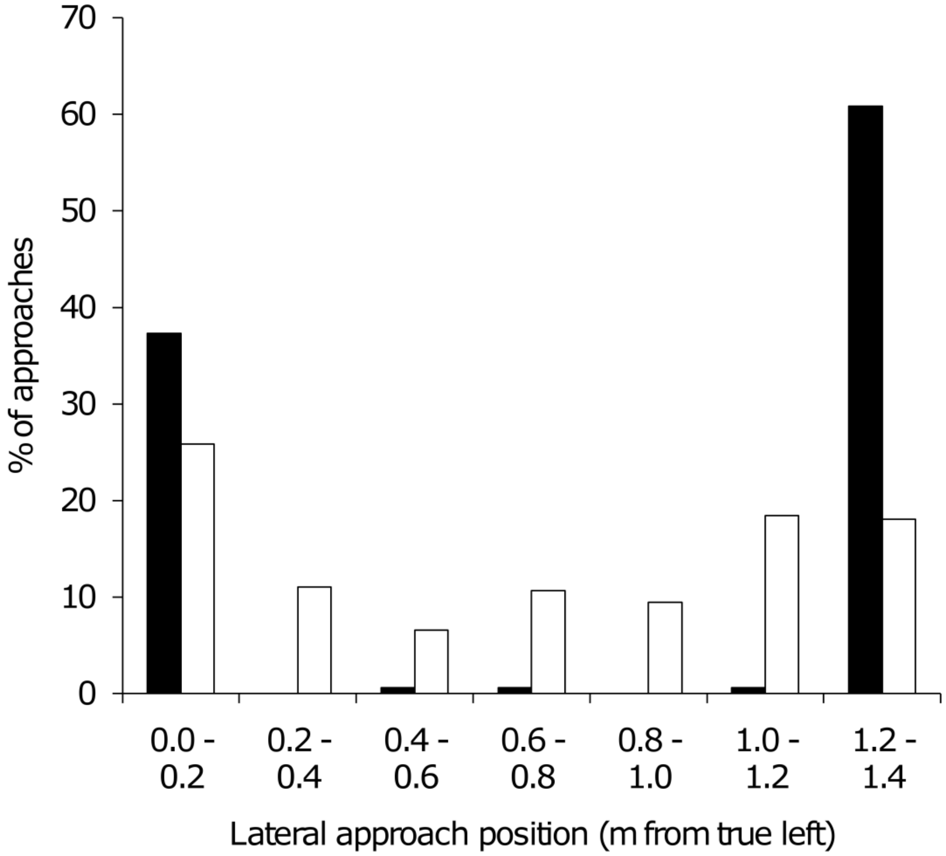

Fig. 7.1 Proportion (%) of approaches by eels (solid bars) and trout (clear bars) at each lateral approach position. Flume width = 1.4 m.

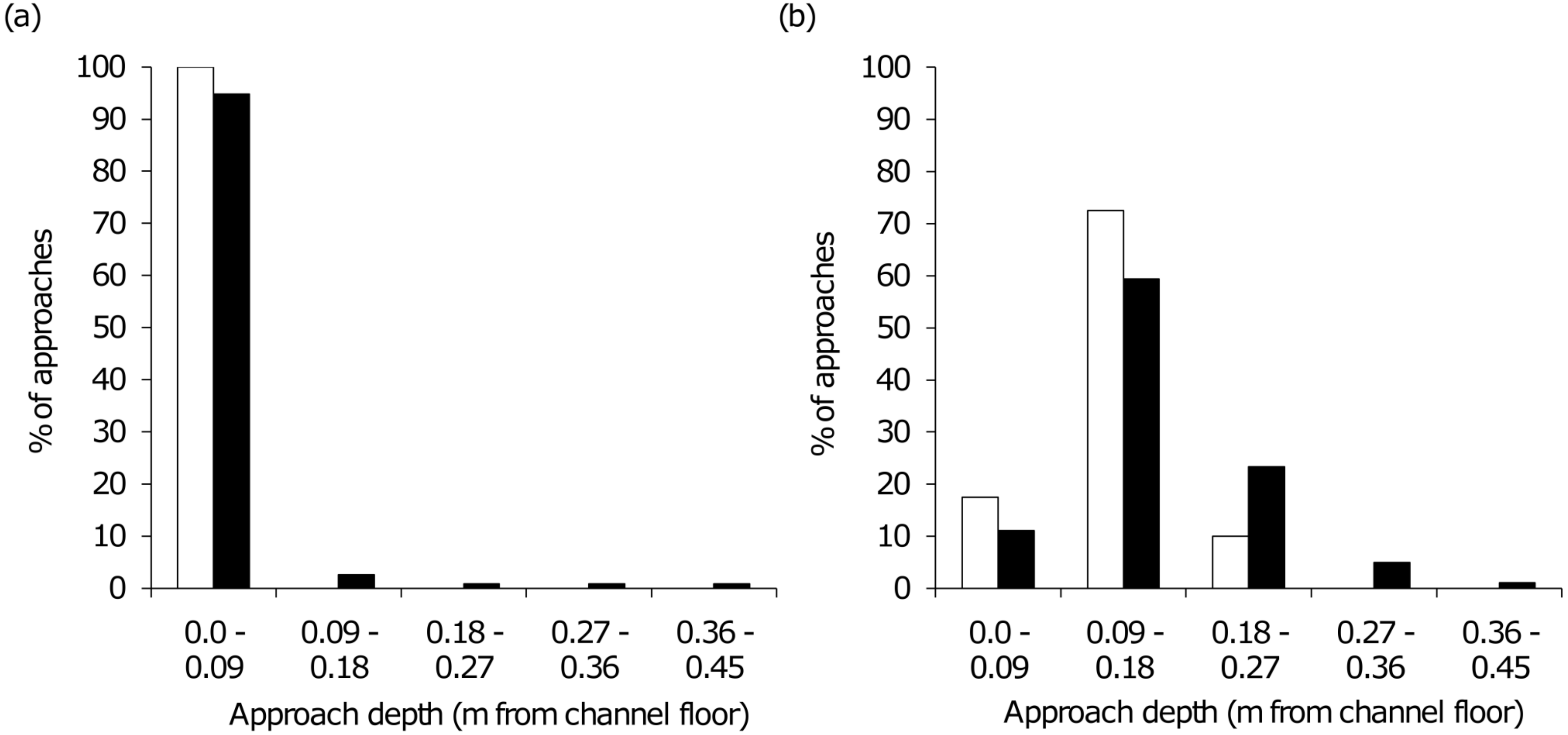

Fig. 7.2 Proportion (%) of approaches by (a) eels and (b) trout to a channel floor (clear bars) or mid-column (solid bars) orifice at each approach depth. Water depth = 0.45 and 0.37 m at the mid-column and channel floor oriented orifices, respectively.

An interaction indicated time to first approach was higher and lower for the mid-column compared to the channel floor treatment for trout and eels respectively (Fig. 7.3a). Eels approached the weir more quickly than trout, but orifice treatment had no effect (Table 7.1). The total number of approaches per trial was greater for the mid-column orifice treatment (Fig. 7.3b). Species had no effect and there was no interaction between species and treatment (Table 7.1).

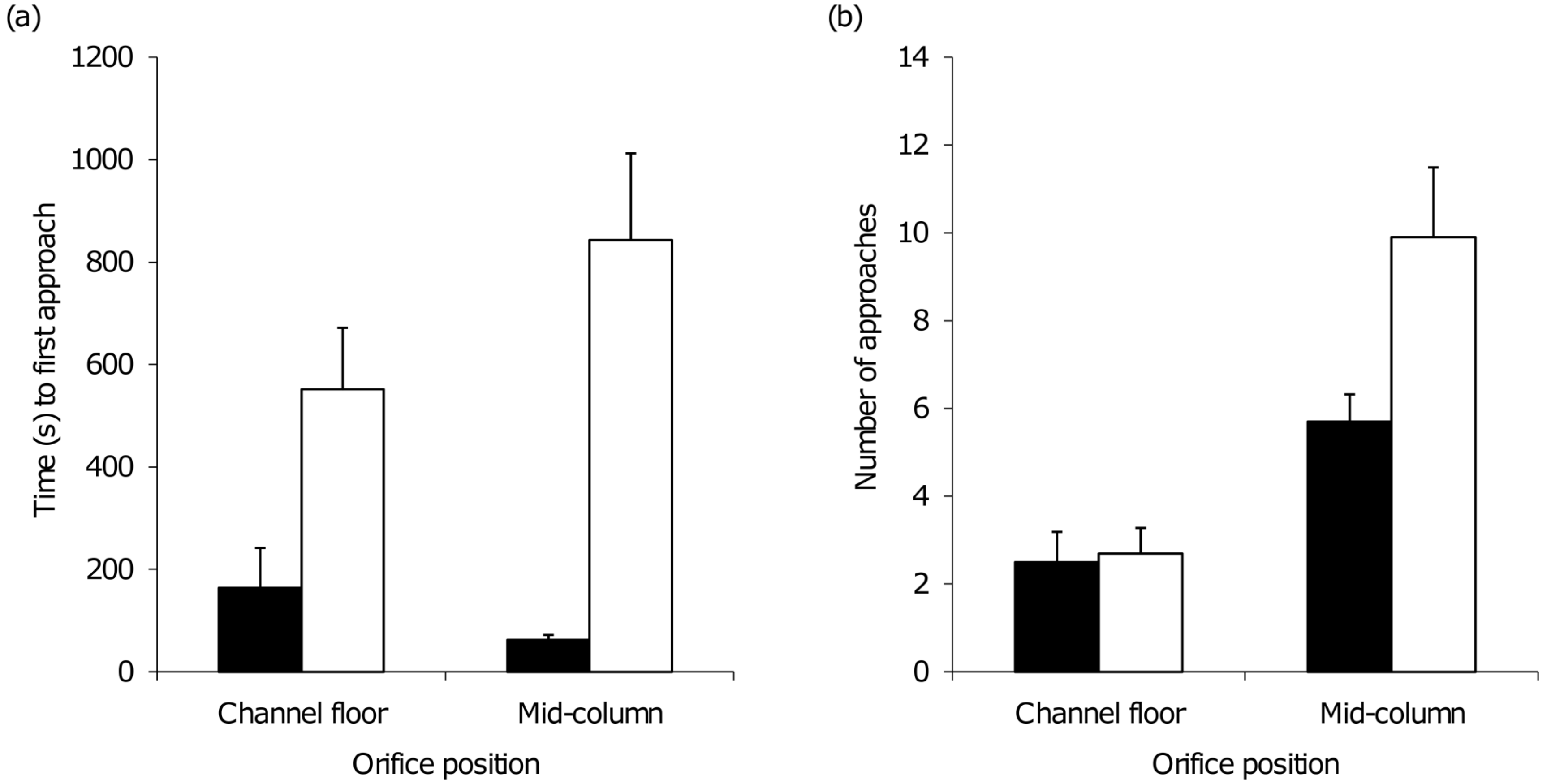

Fig. 7.3 Mean (a) time taken to first approach the weir after release and (b) number of approaches prior to trial termination by eel (solid bars) and trout (clear bars). Error bars represent standard error from the mean.

Interactions indicated respectively lesser and greater total time within the observation zone and that spent stationary for eel than trout at the channel-floor and mid-column orifice treatments (Fig. 7.4). Species and treatment had no influence on either dependent variable (Table 7.1). When stationary, eels tended to maintain contact with the channel-floor and regularly with the weir. Trout usually held position actively swimming against the flow a few centimetres above the channel floor and without making contact with the weir. Eels contacted the weir more frequently than trout (median [range] contact per approach: eel = 1.0 [1.6]; trout = 0.02 [5.0]; $H_1 = 41.33$, $P < 0.001$). Orifice treatment had no effect ($H_1 = 1.62$, $P > 0.05$). The majority (95% versus 7.5% for trout) of approaching eels demonstrated no response to the weir until making physical contact.

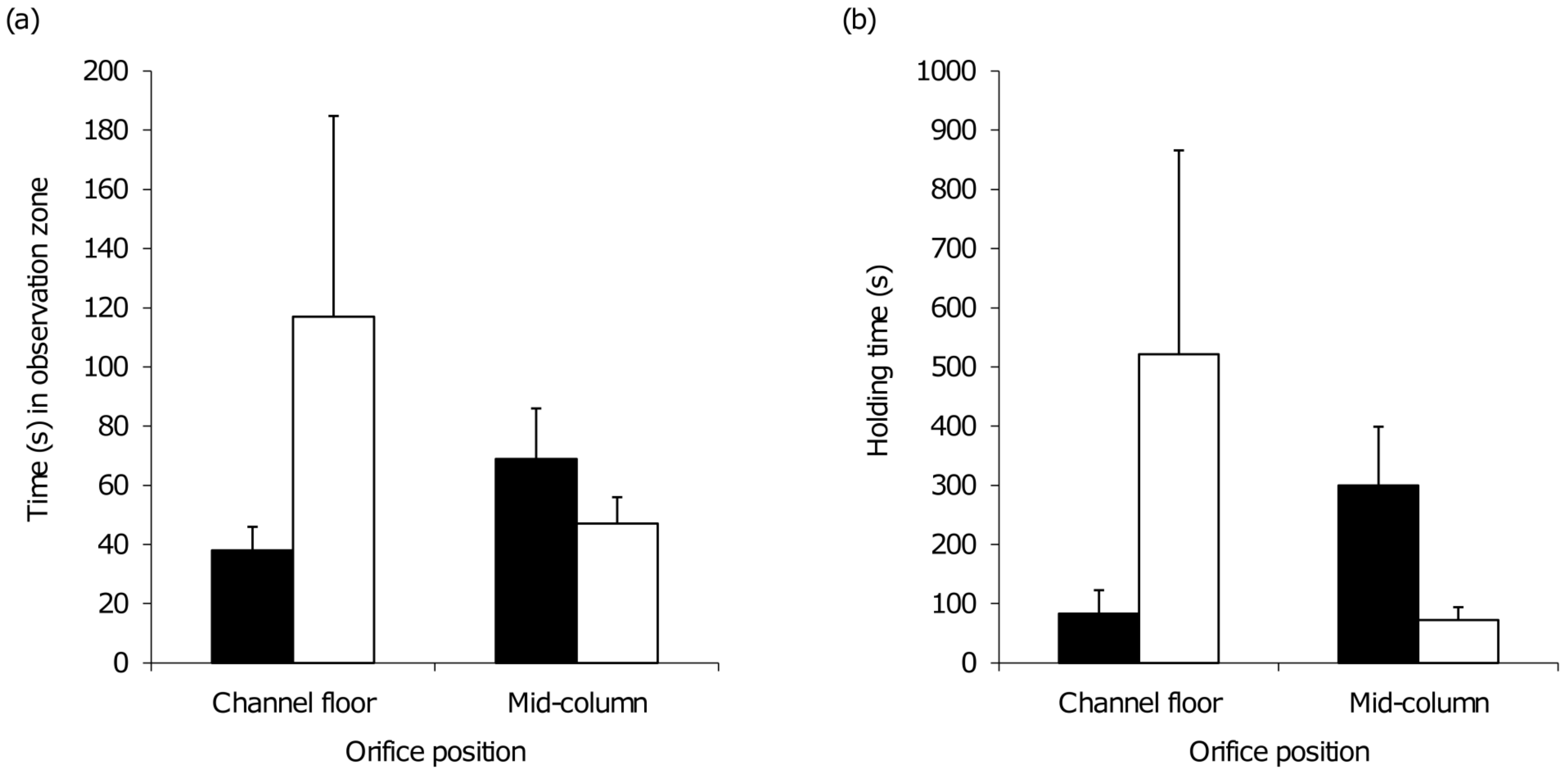

Fig. 7.4 Mean time (a) spent in and (b) holding station in the observation zone for eel (solid bars) and trout (clear bars) per approach. Error bars represent standard error from the mean.

In total, five fish failed to pass the weir (4 eels under mid-column and 1 trout under channel-floor treatment). Trout took significantly longer to pass the weir than eels (Fig. 7.5; Table 7.1). Both species took longer to pass a mid-column than a channel-floor orifice. There was no interaction between species and treatment (Table 7.1). The majority of eels (97.2%) that passed did so head first, in contrast to the trout that tended to pass maintaining a positive rheotactic orientation (92.3%).

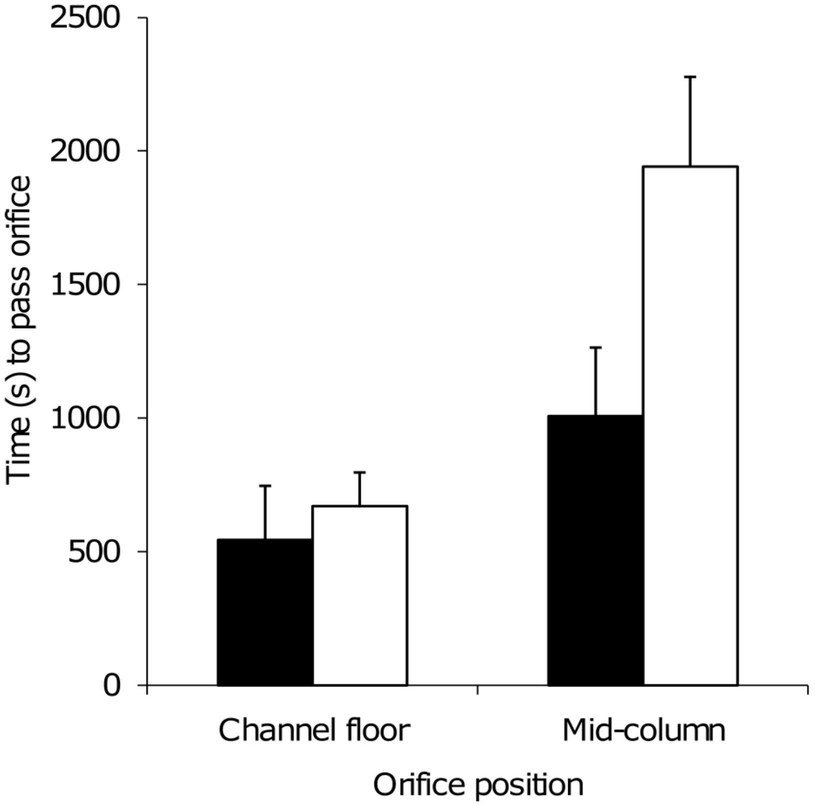

Fig. 7.5 Mean time taken by eel (solid bars) and trout (clear bars) from release to passing the orifice. Error bars represent standard error from the mean.

On approaching the channel floor and mid-column orifice treatments, respectively 2 (3.7%) and 1 (0.5%) trout maintained a positive rheotactic orientation. The mean distance from the orifice at the position of response during initial approach ($H_1 = 5.31$, $P < 0.05$; Fig. 7.6a), and the closest point reached ($H_1 = 5.82$, $P < 0.05$; Fig. 7.6b), was lower for the channel floor than the mid-column treatment. There was no effect of treatment on the corresponding *uG* for position of response (0.11 ± 0.03 cm s^{-1} per cm, $H_1 = 0.16$, $P > 0.05$) or closest point reached (0.79 ± 0.26 cm s^{-1} per cm, $H_1 = 0.01$, $P > 0.05$).

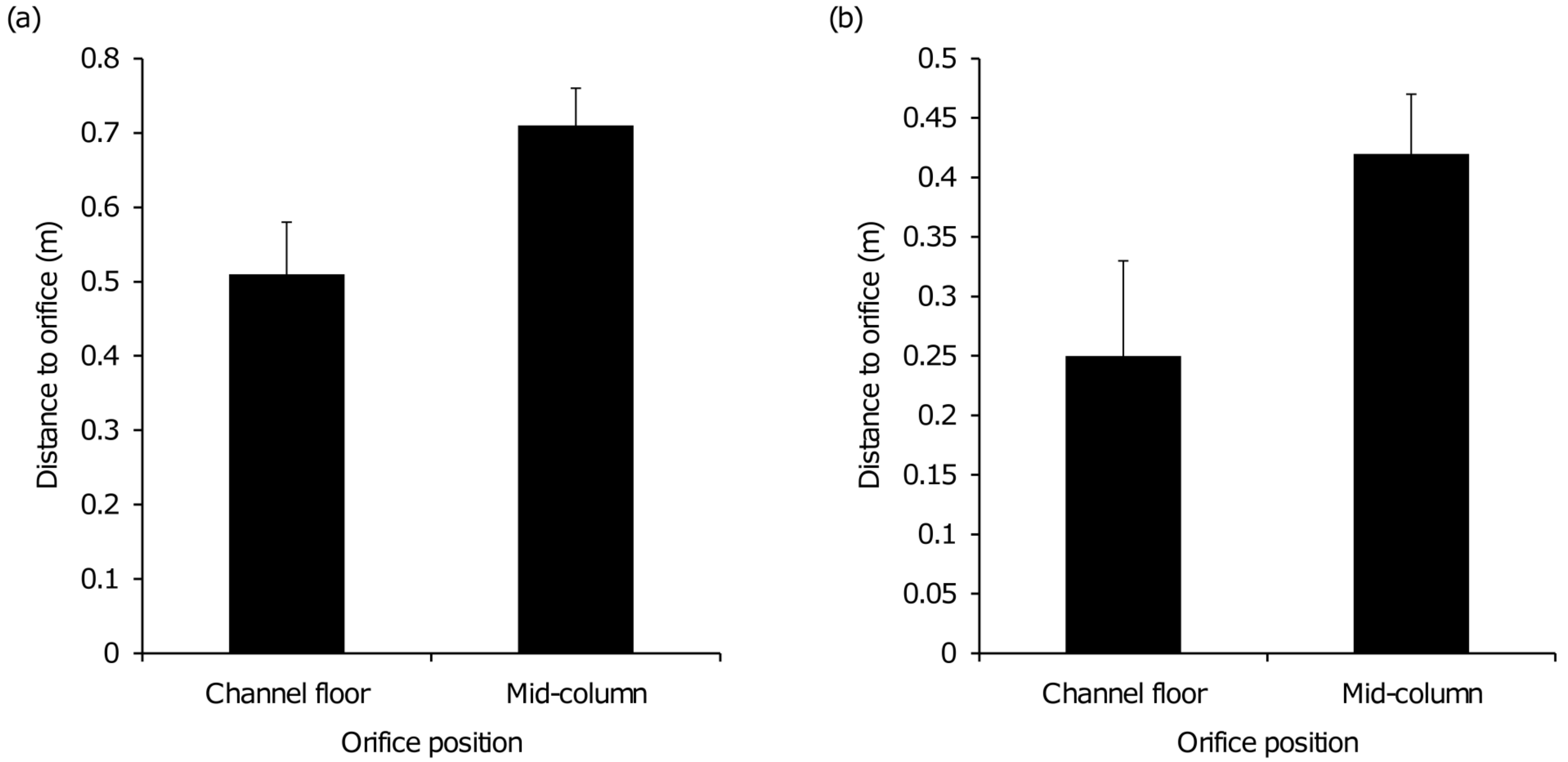

Fig. 7.6 Mean distance of trout from the orifice (a) immediately prior to turning to positive rheotaxis and (b) when closest, during the first approach of a trial. Error bars represent standard error from the mean.

Treatment influenced the slopes of the regression of approach number against distance to the orifice at position of response ($F_{1,\,23}$ = 12.99, P = 0.001) and closest point reached ($F_{1,\,27}$ = 16.83, $P < 0.001$), thus linear regressions were performed for treatments separately. For *uG* at position of response and closest point reached treatment had no significant effect and thus the data from the two treatments was pooled prior to conducting the linear regressions. The results of the regressions indicated no significant relationship between predictor and dependent variables (Table 7.2).

Table 7.2. Results of linear regressions to determine trout acclimate to the various dependent variables over successive approaches (predictor variable) to an orifice weir.

Dependent variable	d.f.	F	R^2	P
1) Position of response at channel floor orifice	1, 34	0.06	0.002	> 0.05
2) Position of response at mid-column orifice	1, 187	2.43	0.013	> 0.05
3) Closest point reached at channel floor orifice	1, 42	1.05	0.024	> 0.05
4) Closest point reached at mid-column orifice	1, 198	1.26	0.080	> 0.05
5) uG at position of response with pooled orifice data	1, 223	0.99	0.004	> 0.05
6) uG at closest point reached with pooled orifice data	1, 205	1.81	0.038	> 0.05

7.5 DISCUSSION

In an era of increasingly stringent international environmental legislation, there is a need to advance more holistic multi-species fish passage solutions that recognise the importance of behaviour (Kemp and O’Hanley, 2010; Winter and van Densen, 2001). This study demonstrated significant differences in behaviour presented by two species with distinctly different body morphologies and life-history characteristics on encountering velocity gradients, conditions common to fish passes and screening structures, when moving downstream. The results have important implications for progressing mitigation technology to ameliorate for environmental impacts of river and estuary infrastructure development.

Eels are thigmotactic, i.e. they tend to be structure oriented (Adam *et al.*, 1999; Russon *et al.*, 2010) when compared to salmonids (Figs. 7.1 and 7.2). Trout responded primarily to the hydraulic conditions encountered at the orifices, switching to a positive rheotactic orientation (probably providing an element of control during downstream movement; see Kemp *et al.*, 2006 for juvenile Pacific salmon [*Oncorhynchus* spp.]) on encountering a velocity gradient, rarely contacting the structure itself (previously observed by Enders *et al.*, 2009; Kemp *et al.*, 2005a). Successful fish passage requires attraction towards the entrance and then the fish must choose to enter (Bunt, 2001; Castro-Santos *et al.*, 2009). The mid-channel orientation (both vertically and laterally) of trout may be due to a general attraction towards the increased water velocity at the orifice (Peake & McKinley, 1998; Svendsen *et al.*, 2007) and/or utilisation of the faster mid-channel flows to enhance downstream movement (Kemp *et al.*, 2005b) prior to demonstrating a sudden switch to a positive rheotaxis when the velocity gradient reached a threshold level. This attraction towards the higher water velocities at the orifice is further supported by the observed change in trout behaviour to approaching higher in the water column with a raised orifice (Fig. 7.2).

In this study, independent of treatment, the trout approached more often (Fig. 7.3) and passed the weir later than eels (Fig. 7.5). Trout also initially approached later than eels probably because they held station upstream of the observation zone (although this can not be verified in this study). However, speculatively the longer time taken for the trout to pass could be due to differences in their motivations to move (e.g. the eels were in their migratory phase and trout farmed), but farmed Atlantic salmon tend to be bolder and take greater risks than wild individuals (Huntingford & Adams, 2005) and would thus be expected to approach and pass sooner than they did (taking *ca*. 30 minutes to pass a mid-column orifice compared to *ca*. 15 minutes for eel). This suggests that the conditions associated with the orifice weirs may have had a repellent effect on the hydraulic oriented responding trout, particularly for the mid-column orifice at which trout spent less time in the immediate vicinity (Fig. 7.4) and took longest to pass (Fig. 7.5). Contrary to trout that passed the orifice tail-first after flow testing, eels passed head-first on their first encounter without responding to the hydraulic conditions, thus passing sooner and approaching fewer times before successful passage. This combined with their thigmotactic nature also accounts for the increased number of approaches and longer time taken by eels to locate and pass a mid-column than channel floor oriented orifice.

Although predicted that fish (trout in this case as eels did not undertake a hydraulic response) would initially respond on their first approach further away and take longer to pass if the stimuli that induces avoidance (e.g. uG) is stronger, the opposite was actually observed, initially responding and taking longer to pass a mid-column orifice. It is not clear why this is the case but speculatively suggests a reduced general attraction flow due to the lower water acceleration (Larinier, 2008). However, at the channel floor orifice, the total time spent in and holding station within the observation zone was lowest for eel compared to trout, but these parameters switched at the mid-column orifice, further suggesting the thigmotactic behaviour of eels means they locate a channel floor orifice sooner. However, the change in time spent in and holding station with orifice position could also denote the conditions associated with the mid-column orifice had some repellent effect on trout with alternative hydraulic parameters (e.g. turbulence intensity or shear stresses) being of more importance than velocity gradient. However, the mid-channel orifice had the lowest variation in water acceleration, yet flows with chaotic and wide fluctuations tend to repel fish (Liao, 2007). Liao (2007) also states that dependent upon the study conditions parameters such as turbulence intensity can both repel and attract fish, thus the wider variation in acceleration of flow at the channel floor orifice may be too low to have a repellent effect and other associated hydraulic conditions are more attractive than for the mid-column.

Although the trout were closer to a channel floor than mid-column orifice when initially responding and when closest during their first approach (Fig. 7.6), the corresponding *uG* at these points remained constant. This supports the findings of Enders *et al.* (2009), with both studies finding similar *uG* (*ca.* 0.8 cm s^{-1} per cm) when they are either closest to the orifice prior to "escaping" during an approach (present study) or demonstrating an initial escape response (Enders *et al.*, 2009). Wild Pacific salmonids during their downstream migration were used by Enders *et al.* (2009), and the finding that the farmed brown trout respond to similar hydraulic parameters (i.e. *uG*) would suggest that these values will also apply to wild brown trout. Although further research utilising wild brown trout is required to fully assess whether farmed fish are a good indicator for downstream migrant wild populations. This finding suggests that there may be a generic range of *uG* likely to induce a behavioural response for a particular species or group. The avoidance of specific hydraulic thresholds such as *uG* could be utilised to prevent fish entering e.g. hydropower turbines, and preferentially selecting a safe route of passage.

Despite expectations (e.g. see Goodwin *et al.*, 2006), the trout did not appear to acclimate to any of the treatments presented in this study (Table 7.2). It is possible that the velocity gradients presented were not high enough for acclimation to be necessary for successful passage to occur. Alternatively, it may take days to acclimate to a condition (e.g. Nordgreen *et al.*, 2010, allowed 8 days for fish to learn a conditioned response). Under the conditions provided fish may have passed before acclimating, thus responding to constant threshold levels of varying flow. At larger structures fish may spend several days milling in the forebays (e.g. Venditti *et al.*, 2000), during which time acclimation to the associated conditions may occur prior to successful passage.

The need for greater understanding of the requirements of multiple species of downstream migrating fish in the development of fish passage and screening facilities is recognized (Schilt, 2007). Attaining information of how fish respond to hydrodynamics, such as velocity gradients, is a key constituent of this research agenda. This study has described the response of representatives of the *Anguillidae* and *Salmonidae*, two families that substantially differ in terms of behaviour and morphology. The management implications of these findings relate to the development of screening devices, and understanding of the mechanisms that underpin avoidance induced delay at river infrastructure (including fish passes).

Passage of eels through hydropower turbines is associated with high levels of mortality (Winter *et al.*, 2006, 2007; Calles *et al.*, 2010) due to blade strike and sudden changes in water velocity and pressure (Larinier, 2008). To reduce entrainment through turbines screening systems are used to divert fish to safe routes of passage. The thigmotactic nature and lack of response to hydraulic gradients of eels, with their relatively poor swimming ability (Calles *et al.*, 2010; Russon *et al.*, 2010), could result in increased impingement at screening facilities designed primarily for salmonids, as it will be too late to escape once a response is initiated (Russon *et al.*, 2010). Based on these findings, the development of mechanical devices such as angled bar racks (Adam *et al.*, 1999; Russon *et al.*, 2010), which will direct the fish to a bypass entrance without causing damage (due to the flow along the face of the structure being greater than the through flow), along with suitable positioning of bypass entrances (i.e. at the channel floor and wall) could greatly reduce mortality due to impingement at screening facilities.

Delay caused by anthropogenic barriers to fish migration can lead to increased predation pressure (Peake *et al.*, 1997), an increase in energy expenditure (Osborne, 1961), and for fish on their spawning run a reduction in reproductive success (Geen, 1975). To reduce delay it is necessary to identify and understand the underlying mechanisms causing it. In this study trout demonstrated a higher delay and avoidance behaviour compared with the eels to the hydraulics associated with the orifice. Quantification of uG at which the trout responded provided valuable information necessary for the advancement of fish passage criteria, e.g. in an effort to manipulate hydraulic conditions to minimise occurrence of rejection. However, further study is required to determine specific thresholds for response to a variety of hydraulic parameters (that act as either attractants or deterrents) for multiple species to improve passage facilities. Although trout did not appear to acclimate to the conditions presented in the way predicted, it does not necessarily mean that acclimation did not take place, only that the behaviour exhibited did not suggest repeated sampling of increasingly higher velocities. Further research is required to better understand the role of acclimation in delayed migration, and whether techniques might be employed to manipulate this to improve fish passage efficiency. Ultimately, it is envisaged that the techniques employed and the findings of this study will help improve the process of fish passage design and provision based on accurate behavioural information, increasing survival for multiple species and life-stages.

Chapter 8: Disadvantages of group membership for those that are left behind: diminishing shoal integrity in the brown trout, *Salmo trutta*.

8.1 SUMMARY

Benefits of group membership have been widely described in ecology, while the mechanisms of how group cohesion is lost and the consequent impacts on behaviour of former members has received comparatively limited attention. In fish, group integrity can be disrupted when movement is partially impeded. For example, velocity gradients can induce behavioural avoidance in some species and form partial barriers to movement. In this study, the impact of encountering an acceleration of flow at a weir and orifice on the downstream movement, shoal integrity, and behaviour of individual and groups (n = 5) of brown trout, *Salmo trutta*, was experimentally assessed under conditions of low light intensity. Fish in groups were more active than isolated individuals (controls), as indicated by more rapid first approach and more frequent repeat encounters with the structure. Although there was no relationship between treatment (group versus control) and mean time to pass, the standard deviation was higher for group fish. The first 4 fish per group on average passed the weir as, or more, rapidly than the control, while the remaining individual tended to be reluctant. This study suggests that fish are more active and more likely to pass a hydraulic barrier when conspecifics are present, but as group integrity diminishes the remaining fish exhibits higher levels of

avoidance and is likely to suffer a disproportionate disadvantage of delayed migration.

8.2 INTRODUCTION

Multiple ecological benefits of gregarious behaviour conferred to individuals have been widely reported. Being part of a group can reduce the probability of prey animals being caught and eaten if vigilance (i.e. the “more eyes” paradigm; Powell, 1974; Pulliam, 1973), chance of escape due to a confusion effect (Jeschke & Tollrian, 2007; Krause & Ruxton, 2002), or potential to overwhelm and subdue an attacker (e.g. Carbyn & Trottier, 1988), is improved. “More eyes” allows individuals within groups to devote more time to feeding (Elgar, 1989; Lima, 1990, 1995), while gregarious animals can acquire information (e.g. of food resources; Krebs *et al.*, 1972) quickly and efficiently from more knowledgeable group members through social learning, without incurring the costs of exploration (Brown *et al.*, 2006). Other benefits include increased communal care (e.g. Doolan & Macdonald, 1999), and reduced energetic expense due to hydro-/aero-dynamic advantages gained from others during movement (e.g. Gould & Heppner, 1974). However, being gregarious can also be disadvantageous, particularly as group size increases, due to increased competition for localized resources and associated costs of aggressive interactions (e.g. food and mates; Chapman & Reiss, 1999), and efficient ectoparasite and disease transmission (e.g. Hoogland, 1979, 1981).

Due to the propensity of many species to shoal, at least during one phase of their life-cycle (Shaw, 1978), fish have been widely used as models to investigate the ecology of group membership (see Pitcher & Parrish, 1993, for a review of the advantages of shoaling). Social assemblies of fish are not easy to define due to their broad diversity from densely formed schools of pelagic species to highly dynamic groups in shallow water ecosystems (Hoare & Krause, 2003), but are frequently described as schools, shoals, or aggregations. Schools are social assemblies of fish demonstrating polarised and synchronised behaviour, whereas shoals encompass broader associations, without implications of structure or function but is a social rather than exogenously-determined assembly (Pitcher, 1979, 1983; Pitcher & Parrish, 1993). While schools break down in the absence of visual cues when dark (e.g., Glass *et al.*, 1986; Higgs & Fuiman, 1996; Kemp & Williams, 2009), shoals are maintained at low light intensities. Grouping can also occur due to exogenous factors e.g. at anthropogenic impediments to migration. At these locations fish can form loose aggregations of individuals, which may influence one another's behaviour, even though they are not a social assembly of fish, as are schools and shoals.

Benefits of group membership in fish have been demonstrated in relation to foraging (Pitcher, 1986; Pitcher & Parrish, 1993). Information transfer between individuals within the group is a key component of this process. For example, naïve golden shiner, *Notemigonus crysoleucas*, were observed to follow a minority of informed individuals to an experimental feeding area, learning the location and time of food release quicker than if all were inexperienced (Reebs, 2000). Group membership may be advantageous from the perspective of reducing (or sharing) costs of anti-predator defence, e.g. in terms of vigilance. The development of shoaling in the Atlantic herring, *Clupea harengus*, during metamorphosis from the larvae to juvenile stage, is suggested to be in response to more intense predation pressure at this stage (Gallego & Heath, 1994), while larger groups of bluntnose minnow, *Pimephales notatus*, received fewer predatory attacks from smallmouth bass, *Micropterus* *dolomieu* (Morgan & Colgan, 1987). Shoaling and schooling fish may also benefit from exploiting vortices produced by leaders to attain more efficient swimming (Liao, 2007; Weihs, 1973). Conversely, disadvantages of shoaling have been demonstrated, e.g. in relation to enhanced transmission of disease (e.g., in Australian pilchards, *Sardinops sagax*, Murray *et al.*, 2001).

Shoal integrity is temporally dynamic and can be lost and reformed. Fish in the wild encounter and negotiate multiple natural and anthropogenic impediments to movement which can compromise group cohesion (Kemp *et al.*, 2006). This can cause delay, stress and injury to both downstream and upstream migrating life-stages (Larinier, 2002b) and hinder access to suitable habitat (Amoros & Bornette, 2002; Cote *et al.*, 2009). For example, shoals of upstream migrating American, *Alosa sapidissima*, and Allis, *A. alosa*, shad can be impeded at vertical slot fish passes (Larinier & Travade, 2002b), while successful migrants may rapidly return to rejoin the group left behind. In some cases shad may hold position in the resting pools of fish ladders for weeks, resulting in high levels of mortality (Castro-Santos *et al.*, 2009). For downstream migrants, such as juvenile salmonids, partial barriers that induce behavioural avoidance, e.g. in response to velocity gradients, can disrupt group cohesion as some individuals pass and others remain upstream (e.g. Kemp & Williams, 2009). Structures which reduce shoal integrity may impact survival as associated benefits are lost, potentially increasing stress and risk of predation (Haro *et al.*, 1998). However, when presented with a novel environment, fish as individuals could experience greater uncertainty than shoals as they have no access to social information (Ward *et al.*, 2011), which can also lead to delay. Where delay occurs there is often an accumulation of fish, which form loose aggregations of mixed and non-shoaling species, potentially influencing the behaviour of other individuals present. These aggregations provide increased opportunity for predation, as the length of time prey are available is increased at sites where predators learn their prey may be available at high densities (Peake *et al.*, 1997).

Loss of group cohesion at barriers to migration, with consequent impacts on fish behaviour and performance, and ultimately the interaction between benefits and costs have not been widely investigated. This study assessed the behaviour of individuals and groups of brown trout, *Salmo trutta*, as they encountered a partial behavioural impediment to downstream movement created by a hydraulic gradient at an experimental weir and orifice. Brown trout have variable life-history strategies (Hindar *et al.*, 1991) that range from distinct anadromy (where the species is commonly termed sea trout) to potamodromy during which fish may still embark on considerable freshwater migrations, e.g. of 40 km or more (e.g. Schulz & Berg, 1992). During migrations the fish generally become less aggressive and more likely to form loose aggregations (Saltveit *et al.*, 2001), particularly at barriers to movement. Thus, brown trout provide an ideal subject to investigate the influence of group cohesion on the ability to negotiate impediments to migration. Whether the presence of conspecifics could enhance the ability of individuals within the group to negotiate the impediment, and whether these benefits would persist as group size diminished, was tested.

8.3 MATERIALS AND METHODS

Experiments were conducted in a 21.4 m long, 1.4 m wide and 0.6 m deep, glass-walled recirculatory flume at the International Centre for Ecohydraulics Research's (ICER) experimental facility (University of Southampton). Discharge and depth were controlled by manipulation of the volume of water passing through the centrifugal pumps and the height of an adjustable weir at the downstream end of the flume. Screens erected along the channel walls prevented lateral illumination and disturbance to the fish by the observer. A weir (1.8 cm thick and 50.0 cm high) spanning the channel width, with a 20 x 20 cm square orifice positioned midway and 15 cm above the channel floor was placed in the flume. Approach (from the perspective of a downstream migrating fish) velocities (± SE) measured 2 m upstream of the weir (60% depth along a lateral transect of 5 equidistant points) averaged 0.10 ± 0.01 m s^{-1}. Water depth along the transect was 0.45 m. The maximum velocity at the centre of the orifice was 1.50 m s^{-1}. Assuming constant one dimensional motion for simplicity acceleration of water was 0.56 m s^{-2} over 2 m. Mean discharge (± SE) was 63.37 ± 2.60 L s^{-1}.

Two low-light cameras placed above the weir (at 2.1 m above the channel floor) provided a field of view (termed the observation zone) that extended 1 m upstream of the structure. Two side mounted cameras (one on each wall) were placed 0.5 m upstream of the weir to provide further coverage of the observation zone. Four 15 W infrared units emitting light at 850 nm wavelength illuminated the observation zone and allowed fish behaviour to be recorded under low light intensities (mean ± SE = 0.42 ± 0.02 lux). Brown trout were assumed capable of discriminating by visual means presence of other members of the group at these levels of illumination, as salmonids are able to detect prey at light intensities as low as 0.03-0.1 lux (Giroux *et al.*, 2000). Twenty-two months old brown trout (mean total length (L_t) ± SE = 254 ± 2 mm; mean wet mass (M) ± SE = 188 ± 4 g) were obtained from a local trout farm and transported to the facility on 11 December 2008 in aerated transportation tanks. Fish were maintained in a 3000 L holding tank at a maximum stocking density of 7.41 kg m^{-3}, and mean temperature (± SE) of 12.2 ± 0.4°C for between 4 and 8 days prior to use in experimental trials. Although, the trout were of farmed origin their behavioural responses to a velocity gradient are similar to observations of wild Pacific salmonid smolts during downstream movement (see chapter 7).

Thirty trials (n = 15 per treatment, alternated between trials) using individuals (controls) or groups of 5 fish, were undertaken between 15 and 19 December 2008 during the nocturnal period (17:00-05:15) when brown trout are thought to be most active during the winter (Giroux *et al.*, 2000; Heggenes *et al.*, 1993), and lasted a maximum of 2-hours or until the last fish passed through the orifice. Groups of 5 fish were chosen to represent a similar shoal size as occurring in small streams where shoals of 2-10 fish are most common for anadromous salmonid smolts (see Davidsen *et al.*, 2005; for Atlantic salmon, *Salmo salar*) and similar densities to those in nature for brown trout (Sloman *et al.*, 2000), which will allow up-scaling of the observations made to larger systems. Fish were acclimated for a minimum of 1.5 hours at the upstream end of the flume in porous black plastic containers prior to release 10 m upstream of the weir. Territoriality and dominance hierarchies were unlikely to of formed during this time as these can take days rather than hours to establish in brown trout when in the wild (e.g. Sloman *et al.*, 2000), and farmed fish (as used in this study) are less aggressive, reducing the chance of dominance being displayed (Weir *et al.*, 2004). Mean flume water temperature (± SE) at the start of experimental trials was 13.7 ± 1.0°C.

The behaviour exhibited by fish as they entered the observation zone was digitally recorded for later analysis. An approach occurred when the entire body length of the fish entered the observation zone. Rejection, or behavioural avoidance, of the area of accelerating flow at the orifice was deemed to occur when the downstream moving fish exhibited positive rheotaxis and started to swim upstream. The time to first approach (from point of release to first entry to the observation zone) and the total number of approaches and rejections per trial (used to calculate the mean approaches or rejections per fish, respectively, to provide a measure of activity) were recorded. For group trials, the number of approaches where 2 or more fish entered the observation zone within an arbitrarily defined period of 2 seconds of each other was recorded to provide an arbitrary measure of grouping. This is similar to the method used by Haro *et al.* (1998) with Atlantic salmon smolts and juvenile American Shad, where a 1.5 second interval was used to determine grouping as fish were usually no greater than 1 m apart during this time. A pass was deemed to occur when the entire length of the fish had passed the orifice. Time to pass was recorded as the period between release and passage through the orifice. The total number of passes per trial were recorded and used to calculate the proportion of passes per approach. For the group treatment, the “position” (e.g. 1st, 2nd, 3rd etc.) of fish to pass was recorded for each individual.

Tests of normality and homogeneity of variance were performed using Shapiro-Wilk and Levene’s tests respectively. Where necessary, non-parametric data were normalized using natural log (L_n) transformation. A one-way ANOVA was used to assess the influence of treatment (fixed factor) on the dependent variables: 1) L_n transformed time to first approach, 2) number of approaches per fish, 3) mean time to pass per trial (based on pass times of all fish in a group), and 4) mean time to pass per position. Where attempts to normalize data failed, a non-parametric Mann-Whitney *U* test was performed to assess the influence of the same fixed factor on the dependent variables: 5) number of orifice rejections per fish, and 6) number of passes per approach.

8.4 RESULTS

Nearly one-fifth of approaches during group trials involved fish entering the observation zone in close proximity to at least one other individual, indicating loose shoaling behaviour, rather than well defined polarized and cohesive schooling, or random distribution of individuals acting independently of others.

On average, individuals took longer to approach the weir than the first fish in groups (ANOVA: $F_{1,\,28} = 11.83$, $P = 0.002$; Fig. 8.1) and approached (ANOVA: $F_{1,\,28} = 8.35$, $P = 0.007$; Fig. 8.2) and rejected (Mann-Whitney: $U = 25.00$, $z = -3.72$, $P < 0.001$, $r = -0.68$; Fig. 8.3) less often than group fish. There was no difference between treatments in the passes per approach (Mann-Whitney: $U = 101.00$, $z = -0.48$, $P = 0.630$, $r = -0.09$; individuals median = 0.05, range = 1.00; groups median = 0.09, range = 0.23), and mean time taken to pass (ANOVA: $F_{1,\,79} = 1.26$, $P = 0.266$; Fig. 8.4), although the standard deviation in time to pass was greater for groups (1268 s) compared to control individuals (776 s). During group trials, 1 fish failed to pass the orifice in 3 (20%) cases, whereas 6 (40%) control trials ended with no successful passage.

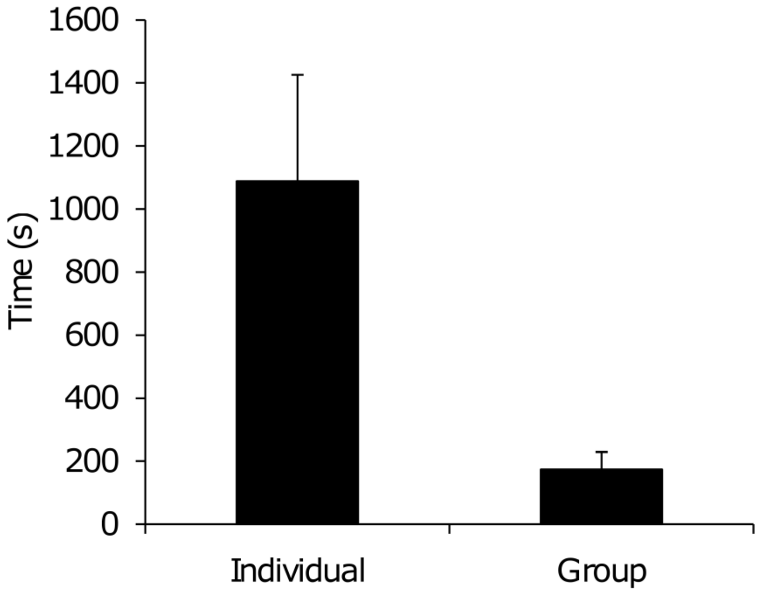

Fig. 8.1. Mean time of first approach to an acceleration of flow associated with an experimental weir and orifice by downstream moving brown trout, *Salmo trutta*, during individual and group trials. Error bars represent the standard error of the mean.

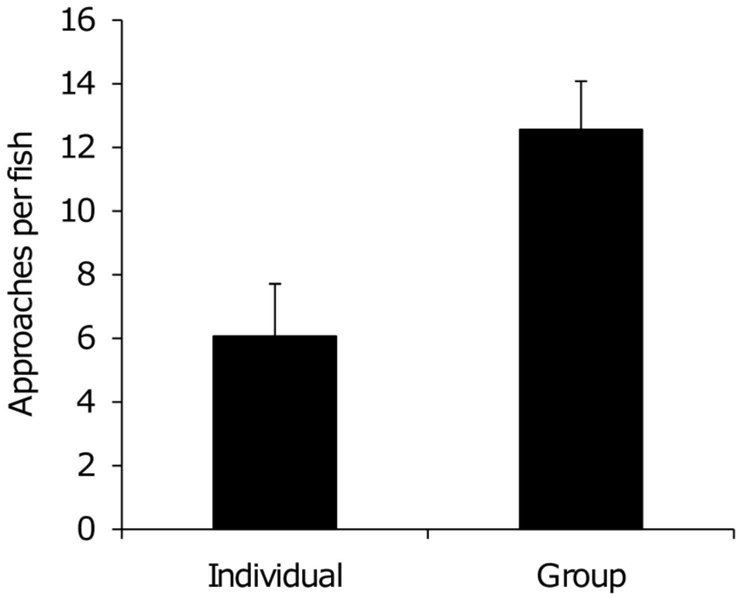

Fig. 8.2. Mean number of downstream approaches to an experimental weir and orifice by brown trout during individual and group trials. Error bars represent the standard error of the mean.

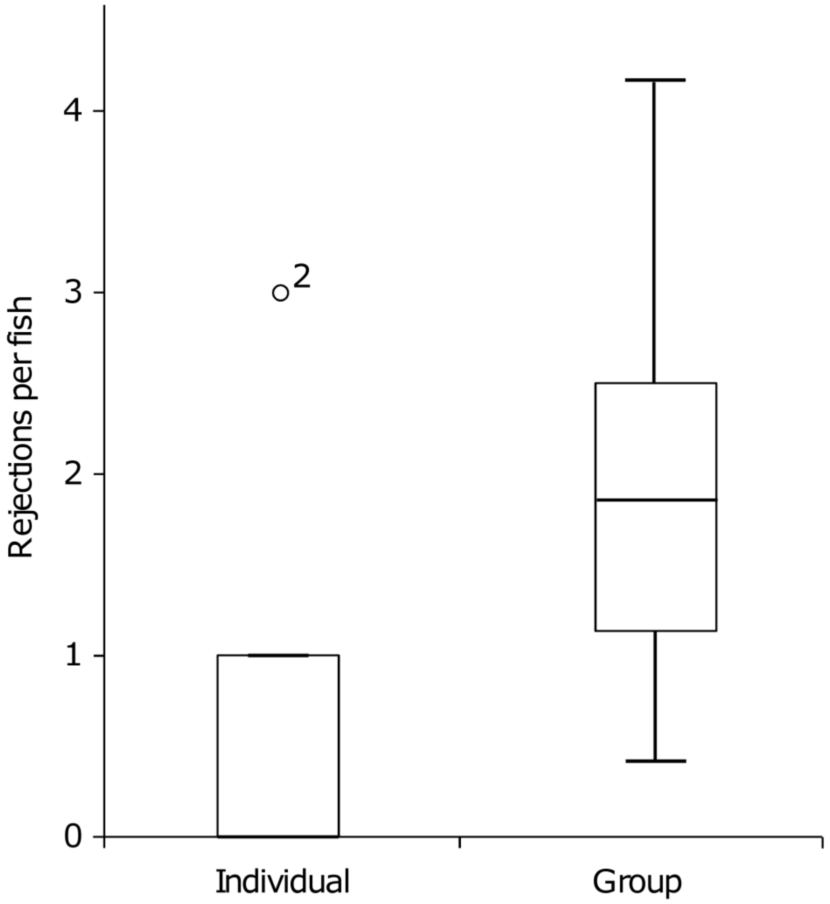

Fig. 8.3. Median number of rejections of an acceleration of flow associated with an experimental weir and orifice by brown trout during individual and group trials. Box bottom and top represent the 1st and 3rd quartiles respectively. Whiskers represent the minimum and maximum values.

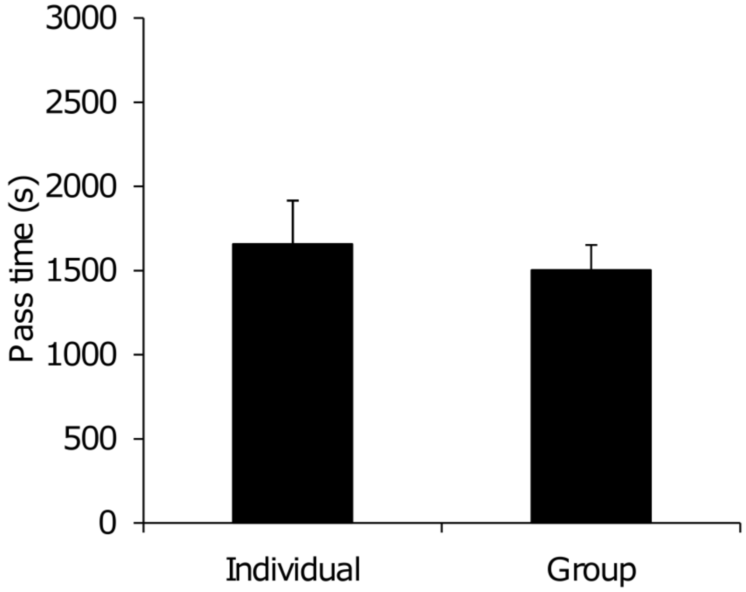

Fig. 8.4. Mean time taken for downstream moving brown trout to pass the orifice weir during individual and group trials. Error bars represent the standard error of the mean.

The mean time to pass for the 1st (ANOVA: $F_{1,\,22} = 21.83$, $P < 0.001$) and 2nd (ANOVA: $F_{1,\,22} = 10.75$, $P = 0.003$) fish was less than for control trials, with the 5th fish passing significantly later (ANOVA: $F_{1,\,19} = 8.12$, $P = 0.010$) (Fig. 8.5). There was no difference in mean time to pass for the 3rd (ANOVA: $F_{1,\,22} = 3.53$, $P = 0.074$) and 4th (ANOVA: $F_{1,\,22} = 0.13$, $P = 0.727$) fish, compared to the control.

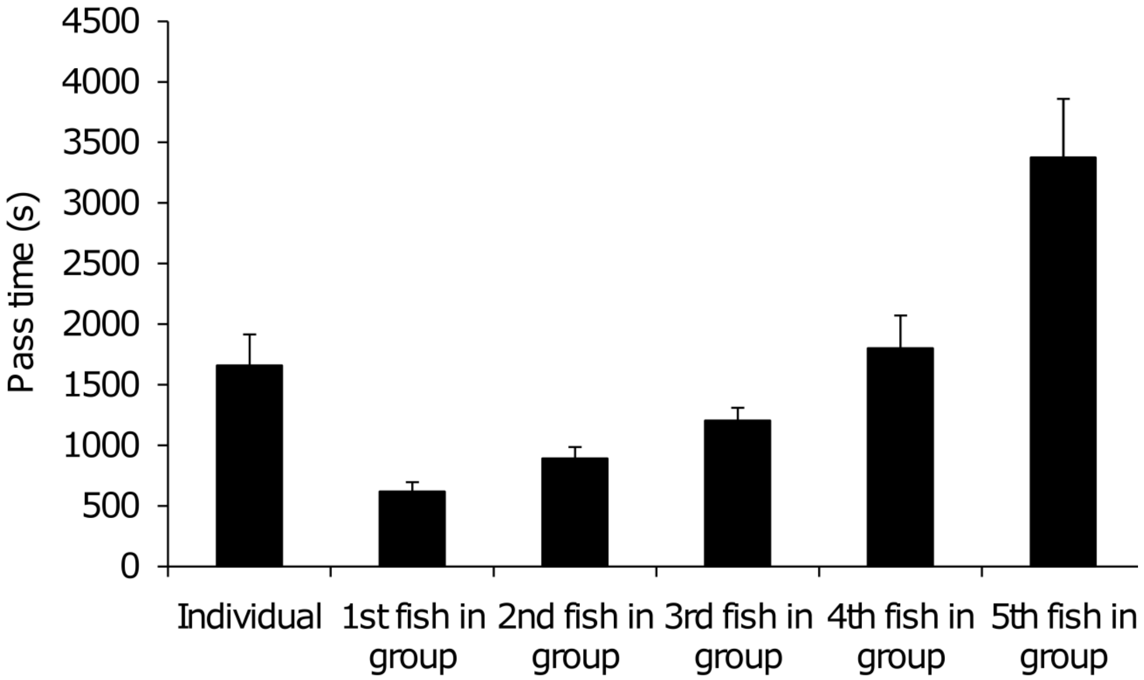

Fig. 8.5. Mean time taken for downstream moving brown trout individuals (control) and individual group members (dependent on “position of passage” e.g. 1st, 2nd, 3rd etc.) to pass the orifice weir. Error bars represent the standard error of the mean.

8.5 DISCUSSION

Although costs and benefits of being part of a group (e.g. Magurran, 1990; Pitcher & Parrish, 1993) and factors that influence cohesion (e.g. familiarity: Chivers *et al.*, 1995; Griffiths & Magurran, 1997; and association preferences: Olsen *et al.*, 2003; Ward *et al.*, 2005) have been widely discussed for fish, the mechanisms describing loss of shoal integrity and implications of such have been less so (examples of exceptions include Day *et al.*, 2001; Croft *et al.*, 2003; Webster *et al.*, 2007). In this study, group integrity of downstream moving brown trout was lost as individuals either passed or avoided conditions created by a weir and orifice, a finding similar to those reported elsewhere for other species (e.g. Kemp & Williams, 2009, for juvenile Pacific salmonids, *Oncorhynchus* spp). Group size was reduced as a result of differential behavioural response to an abiotic factor, rather than an active decision to split away from conspecifics, and thus reflects a passive mechanism of shoal fission (Croft *et al.*, 2003). Of particular interest, however, was that the avoidance behaviour exhibited by the remaining individual left behind was greater than for fish that had not previously been part of a group (Fig. 8.5), and for which the consequential disadvantages of delay in downstream movement are likely to be disproportionately high.

When part of a group, trout generally approached the weir in relatively close proximity to other members, not necessarily exhibiting polarized schooling behaviour, but clear aggregations which may be referred to as shoals (Pitcher & Parish, 1993) rather than random distribution. Based on frequency of approach and rejection (Figs. 8.2 and 8.3), group fish were more active than controls, and the first two to pass the hydraulic barrier did so more rapidly. It is not immediately obvious why fish in groups exhibited greater levels of exploratory activity, and why all but the fish left behind should have passed as, or more, quickly than controls (Fig. 8.5). It is unlikely that competition and site attachment would explain the observed results as territoriality and dominance hierarchies can take days, rather than hours as provided in this study, to establish in brown trout (e.g. Sloman *et al.*, 2000). However, there are at least 3 speculative hypotheses that might be proposed.

First, being part of a group may provide some form of hydrodynamic advantage that improves the efficiency with which fish moved up and downstream through the flume as they repeatedly approached and rejected the structure. Despite debate for (Abrahams & Colgan, 1987; Weihs, 1973) and against (Partridge & Pitcher, 1979) hydrodynamic advantages of schooling, it is at least theoretically possible for some fish within a well defined school to benefit from reversed Karman vortex streets shed from upstream fish (Deng & Shao, 2006). However, it is unlikely that this provides the most plausible explanation for the scenario reported here as fish formed loosely aggregated haphazard shoals rather than maintained close contact within polarized schools which would have been expected if hydrodynamic advantages were to be gained.

Alternatively, the presence of others may have enhanced the “confidence” of individual participants through social facilitation (where the presence of at least one other individual has either a positive or negative effect on an animals ability to undertake a task; Guerin, 1993), resulting in increased boldness and thus greater exploration and passage. The “shy-bold continuum” (Sneddon, 2003; Wilson & Stevens, 2005; Wilson *et al.*, 1994) suggests that some animals within a group are characteristically bold and assertive, and others shy and timid (Huntingford *et al.*, 2010). Shy fish are likely to follow bold individuals when in a shoal, and this added motivation to move is likely to be absent in shy isolated individuals. In fact, it is suggested that through selection for fast growth and fish that flourish in intensive aquaculture, farmed Atlantic salmon tend to be bolder and take greater risks when foraging than their wild counterparts (Huntingford & Adams, 2005). Thus, the associated delays for wild fish that are left behind may be even greater and involve higher numbers than those found during this study using farmed trout. However, farmed fish are kept in larger concentrations than normally encountered in nature (although wild trout smolts are also more likely to shoal when moving downstream; Saltveit *et al.*, 2001), which may increase the negative impact of loss of group cohesion for individuals left behind.

Finally, socially acquired information may have enhanced efficiency of exploration resulting in more active movement and approach/rejection of the barrier. By acting on the information provided by others, acquisition costs and sampling bias associated with that gained by the individual is reduced (Dall *et al.*, 2005). Thus the time needed to acquire sufficient information on which to base decisions may have been reduced for fish in groups, and was expected to result in higher rates of downstream passage. However, avoidance presumable induced by the velocity gradient associated with the weir and orifice could have been reinforced by others exhibiting similar behaviours, ultimately resulting in the high degree of reluctance of the fish left behind to pass the orifice. Day *et al.* (2001) demonstrated laboratory populations of guppy, *Poecilia reticulata*, would forage more efficiently in larger than smaller groups when unimpeded by copying the behaviour of others. On the introduction of an opaque partition with a hole through which fish must pass to feed smaller groups learned the task fastest as fish preferred to remain in a larger group (which they could see) than leave the shoal to locate food. However, when an identical transparent partition was used, larger groups of fish once again learned the task sooner than smaller ones. In the case of this study, such avoidance may be considered to represent maladaptive social transmission of information (see Laland & Williams, 1998) due to the higher delay realized by the remaining individual compared to a fish moving downstream alone. This study is unusual in that it provides evidence for transmission of social information being maladaptive only for one component of the population, i.e. those that are reluctant. Reluctance may have also represented a period of adjustment during which a switch from reliance on socially acquired information shifted to independent sampling.

As always, it is apparent there is a need for further bespoke experimental research to move beyond the realms of speculation currently presented here. Nevertheless, the results of this study provide an interesting observation of how costs and benefits of group membership may be temporally dynamic, and that isolation of the fish left behind may be disproportionately disadvantageous. However, it should also be noted that for the first fish to pass, additional disadvantages likely exist in terms of elevated predation risk "on-the-other-side" for a potentially disoriented "pioneer" (discussed by Kemp *et al.*, 2006).

Implicit in this study is the assumption that delayed migration carries costs, e.g. increased energy expenditure, elevated predation risk, prolonged stress, mechanical abrasion when attempts are continuously made to pass a physical impediment and associated probability of infection, and late arrival at the final destination and subsequent loss of opportunity (e.g. spawning, sheltering, or feeding) due to earlier arrival of competitors. The findings have implications for fisheries management in light of efforts made to improve the passage of fish, e.g. at dams and other anthropogenic river infrastructure. To reduce delay and energy expenditure at barriers to migration engineering solutions to safely divert and pass the majority of migrants, may now require consideration of the influence of maladaptive behaviours that reinforce delay for the minority e.g. the use of transparent materials around bypass entrances (see Day et al. 2001). Thus there is a need to better integrate understanding of animal behaviour in application to environmental engineering.

Chapter 9: Conclusions and recommendations

The research reported in this dissertation primarily aimed at contributing towards a generic rule base of fish passage criteria for the under researched diadromous anguilliform fish (European eel, *Anguilla anguilla*, and river lamprey, *Lampetra fluviatilis*) and downstream migrant life-stages (European eel and Brown trout, *Salmo trutta*). To meet the primary aim a number of sub-aims were investigated (Fig. 2.1) involving 5 experimental studies (chapters 4-8). In this chapter, the key findings are summarised and recommendations for the application of the results and future work explored.

9.1 SUMMARY OF KEY FINDINGS

This section provides an overview of the key findings from this research project.

i) By permitting volitional movement and natural compensatory behaviours (chapter 4), the maximum burst swimming speeds of European eel and river lamprey were found to be higher (1.75-2.12 m s^{-1}) than previously reported (*ca*. 1.35 m s^{-1} for eel [Solomon & Beach, 2004]; *ca*. 1.66 m s^{-1} for lamprey [Kemp *et al*., 2011]). This information contributes to sub-aims 1 and 3 (Fig. 2.1).

ii) Small gauging weirs may severely impede upstream movement of spawning run river lamprey under low discharge conditions, with no passage of a model Crump and only limited passage of a flat-v weir occurring (chapter 5). Shallow water depth (<2.1 cm no passage occurred) and high water velocity (between 1.50 and 2.08 m s^{-1}, when depth was >2.1 cm) on the weir face are likely the limiting factors. This information contributes to sub-aims 1 and 3 (Fig. 2.1).

iii) Throughout all of the research chapter's eels and/or lamprey were observed to be highly thigmotactic (structure oriented), being in regular contact with the flume channel floor and walls, and only demonstrating a response after contact with structure. In comparison, salmonids (brown trout in this research programme) respond primarily to hydraulic parameters, rarely contacting the flume or model barriers. This finding contributes to sub-aims 1, 3 and 4 (Fig. 2.1).

iv) European eels in chapter 6 were found to potentially be attracted to areas of increased levels of turbulence intensity (*K*) during downstream movement, by switching the side of the flume channel they approached to associate with areas of higher *K*. This finding contributes to sub-aim 2 (Fig. 2.1).

v) Brown trout respond to specific velocity gradients (*uG*) along their body length (see chapter 7) during downstream movement (0.11 ± 0.03 cm s^{-1} per cm when initially turning to positive rheotaxis, and 0.79 ± 0.26 cm s^{-1} per cm at the closest point to a velocity barrier source reached before returning upstream), which do not differ with increasing velocities and discharge. These findings and gradients are similar to those reported by Enders *et al.* (2009) for Pacific salmonids, suggesting there may be a generic range of *uG* that will induce a behavioural response for a particular group or species. This finding contributes to sub-aims 1, 2 and 4 (Fig. 2.1).

vi) The findings of chapter 8 suggest that fish are more active and likely to pass a hydraulic barrier in the presence of conspecifics. However, as group integrity diminished due to a differential behavioural response to an abiotic factor, the remaining fish exhibits higher and disproportionate levels of avoidance and delay than if they were simply individuals to start with. This finding contributes to sub-aims 1 and 4 (Fig. 2.1).

9.2 GENERAL COMMENTS AND RECOMMENDATIONS

This section discusses the application of the key findings of this research programme (see section 9.1) to improving and potentially changing practices concerning fish passage in the future. Key recommendations and the application of flume based research to nature are discussed.

9.2.1 KEY RECOMMENDATIONS

A number of key recommendations necessary to improve multiple species fish passage were identified during this thesis, and are presented and discussed below.

9.2.1.1 *Recommendation 1: Swimming speeds should be attained under conditions where natural compensatory swimming behaviours can be undertaken.*

Swimming speeds of fish are one of the main biological components used in fish passage (Tudorache *et al.*, 2008). Thus it is important to attain accurate swimming speed information for multiple fish species under conditions that they will encounter in nature. This thesis has demonstrated that faster maximum burst speeds of fish are attained when they are allowed to undertake natural compensatory behaviours (e.g. "burst-and-glide") within a flume environment, compared to the confined conditions of a swim chamber, supporting the findings reported by Peake (2004) and Peake & Farrell (2004) for Smallmouth bass, *Micropterus dolomieu*, and Tudorache *et al.* (2007) for common carp, *Cyprinus carpio*. Indeed, European eel and river lamprey passed a velocity barrier attaining maximum burst swimming velocities in the range of 1.75–2.12 m s^{-1}. Previously, maximum reported swimming speeds of river lamprey and European eel were only 1.66 m s^{-1} (Kemp *et al.*, 2011) and 1.35 m s^{-1} (Solomon & Beach, 2004) respectively. These findings support the recommendation that swimming estimates obtained using large open channel flumes are more appropriate for developing fish passage design criteria than those based on traditional swim chamber tests (Haro *et al.*, 2004; Kemp *et al.*, 2008; Mallen-Cooper, 1992; Peake & Farrell, 2004). In the future, similar methods should be employed to attain realistic swimming performance information, which can be applied to multiple species fish pass development, e.g. by manipulation of water velocity to accommodate passage of all target species.

However, the fish used in chapter 4 had only to pass a single short velocity barrier, providing information applicable to e.g. a single undershot sluice or a small bypass system. It would be interesting in the future to assess the fishes ability to pass multiple brief velocity barriers (e.g. by using the same fish for repeated trials), simulating conditions that occur at fish ladders, where multiple pools/velocity barriers must be negotiated. This will provide additional information concerning the effect of fatigue when the species of interest have to repeatedly undertake maximum burst swimming to fully negotiate a barrier.

9.2.1.2 *Recommendation 2: Small low-head structures should only be installed when absolutely necessary*.

Small model structures within the flume at Chilworth have been demonstrated to cause significant impediments to non-salmonids throughout the work presented in this thesis, with the cumulative effect of multiple small-scale structures in a catchment potentially having a greater negative impact than a single larger impediment (Jungworth *et al.*, 1998). Structures such as gauging weirs should only be installed where absolutely necessary, but where they are needed those providing adequate water depth at low enough water velocities to allow free swimming of fish, e.g. the centre of a flat-v weir under low discharge conditions in chapter 5, should be preferentially installed. Further research concerning adaptations of such structures, e.g. baffle systems or bottlebrush material on a gauging weir face (Servais, 2006), to accommodate relatively weak swimmers is necessary to provide effective multiple species fish passage facilities.

9.2.1.3 *Recommendation 3: Multiple fish pass entrances are necessary to accommodate multiple species*.

Different species and groups demonstrate a variety of swimming abilities and behaviour. A key finding of this thesis, as highlighted in section 9.1, was the thigmotactic nature of downstream moving European eels (see chapters 4, 6 and 7), being channel floor and wall oriented and only demonstrating a response after contact with the structure, similar to previous findings of Adam *et al.* (1999) and Calles *et al.* (2010) when researching the response of downstream migrating European eels to screens in a flume and the field, respectively. However, salmonids (for which fish passes are most commonly provided [Calles & Greenberg, 2005; Clay, 1995; Enders *et al.*, 2009; Kemp & O'Hanley, 2010; Laine *et al.*, 1998; Larinier, 2008; Larinier & Travade, 2002a]) are located higher in the water column (Arnekleiv *et al.*, 2007) and respond to hydraulic conditions, rarely contacting the structure itself, during downstream movement (as previously observed by Enders *et al.*, 2009; Kemp *et al.*, 2005a; but also see chapter 7). This behaviour meant that even a small barrier of 15 cm in height caused a significantly greater delay to passage for downstream moving eels than a channel floor opening (see chapter 7). In fact, field studies using telemetry have shown that downstream moving European eel do not approach and use surface oriented bypass entrances designed for salmonid smolts (Brown *et al.*, 2009).These significantly different behaviours between just two downstream migrant species/groups mean that it may be necessary to provide multiple bypass entrances, e.g. at the surface and channel floor, and the channel edges (to accommodate the channel wall oriented nature of eels), to accommodate multiple species at migratory barriers, rather than attempt to create an all encompassing bypass entrance.

9.2.1.4 *Recommendation 4: Screens/bar racks angled relative to the flow should be used to direct thigmotactic species of fish to bypass entrances*.

Similar to field observations of Calles & Bergdahl (2009), the research presented in this thesis (see chapter 6) identified that angled screening facilities should be employed to divert downstream migrants away from turbine intakes to a bypass, reducing impingement and entrainment and improving location of the bypass entrance by the fish. The angles should not exceed 45° on the vertical or horizontal planes so that through do not exceed sweeping velocities, which would lead to impingement and associated mortalities (Calles *et al.*, 2010). Surface oriented bypasses are regularly used to accommodate the downstream migration of salmonid smolts, which move in the upper reaches of the water column (Arnekleiv *et al.*, 2007). The installation of screens angled on the horizontal plane relative to the channel floor (Plate

1.3 and Fig. 6.2) may be the best option to divert downstream moving fish over hydropower turbines, towards a surface oriented bypass. If these screens span the entire depth of the water column, channel floor oriented species such as European eels will follow the screen to the surface and into the bypass entrance, while still catering for surface (and indeed mid-column) oriented species such as Atlantic salmon. However, the installed screens must be constructed of material that will not cause damage to the fish, i.e. European eels, as due to their thigmotactic nature they will contact the screen while moving up in the water column.

9.2.1.5 *Recommendation 5: Manipulation of hydraulic conditions should be undertaken to accommodate fish response to hydraulics to improve fish pass efficiency*.

A successful fish pass requires fish to detect and choose to enter and then physically swim through the structure, both of which are determined by the associated hydraulic conditions and fish behaviour (Bunt, 2001; Castro-Santos *et al.*, 2009). Incorporating the maximum swimming speed data and the response to hydraulic conditions demonstrated by fish during the research undertaken in this thesis will help improve fish pass entry for both up- and downstream migrants. Maximum swim speeds are important to determine the maximum permitted water velocities which will pass the target species for upstream fish passes. For passage of multiple species the weakest swimmers should be accommodated for (e.g. Peake *et al.*, 1997; Schwalme *et al.*, 1985), but attraction flows must still attract the faster swimmers. For those species that do demonstrate a response to flow, the hydraulic conditions at fish passes should be manipulated to improve attraction and reduce rejection of the bypass entrance. For example, by widening a Denil fish pass entrance and increasing the attraction flow, Bunt (2001) observed increased attraction efficiency of pumpkinseed, *Lepomis gibbosus*, to the entrance when moving upstream.

The results of chapter 7 found there to be specific velocity gradients to which a downstream moving brown trout responds, e.g. *ca*. 0.1 cm s^{-1} per cm when initially responding and *ca.* 0.8 cm s^{-1} per cm before returning upstream of a velocity barrier, supporting the findings of Enders *et al*. (2009). There is also a suggestion that downstream migrant adult European eels may be attracted to increased levels of *K*, however, further research is needed to determine the exact response of eels to this parameter and to attain the range of *K* in which a response is elicited. It is probable that there is a threshold level of *K* (and indeed other hydraulic parameters) where instead an avoidance response is elicited, as seen for brown trout rejecting a velocity gradient. Manipulation of the hydraulic conditions at downstream bypass entrances to account for these responses would reduce the delay experienced before successful entry into the bypass; thus, reducing the risk of predation (Peake *et al*., 1997) and increasing the fishes overall fitness and reproductive success (Geen, 1975; Osbourne, 1961). This information could potentially also be applied too manipulate conditions to cause rejection of the associated hydraulics at e.g. turbine forebays and water offtakes, causing less fish to be entrained and reducing mortalities.

Further research is needed concerning the response of multiple fish species to a variety of hydraulic conditions to attain specific thresholds and parameters to which the target species respond. The hydraulic cues to which fish respond are likely to differ widely between species, life-history stage and groups, but knowledge of these will allow optimisation of the flow conditions at fish passes to successfully pass the majority of migrants.

9.2.2 APPLICATION OF FINDINGS TO NATURE

9.2.2.1 *Up-scaling of observations*

Larger flumes, such as the one used throughout this research programme, provide a semi-natural environment that permits natural compensatory swimming behaviours to be undertaken by the fish (Peake, 2004; Tudorache *et al.*, 2007), whilst providing conditions where the motivational state and the stimuli encountered are controlled for. Obviously, many of the model structures used in this research programme are smaller than often encountered in nature, however, by determining fish responses to specific hydraulic conditions (e.g. *uG* at which brown trout respond to a velocity gradient, and maximum swimming speeds of fish), the information attained can be applied to manipulating these conditions at any situation and scale. There are however, significantly more small low-head impediments to fish migration than larger ones (Lucas *et al.*, 2009). Many of which are a similar size to those used in this research (Servais, 2006), for example gauging weirs are often used in small streams (Plate. 9.1). Thus, the results obtained in this study are directly applicable to certain small low-head barriers that are used in nature.

Plate 9.1 Flat-v weir under low discharge conditions at Kingsclere, UK (photo taken January 2008).

The group sizes selected for when concerned with the influence of conspecifics on behaviour (chapters 5 and 8) represented that which occurs in nature, permitting application of the observations made to larger systems. For brown trout groups of 5 (as used in chapter 8) are similar to shoal sizes occurring in small streams which are typically 2-10 salmonid smolts (see Davidsen *et al.*, 2005 for Atlantic salmon) and at similar densities to those in nature for brown trout (Sloman *et al.*, 2000). River lamprey during their spawning runs will regularly congregate at migratory bottlenecks (e.g. see Plate. 1.1), thus using groups of 30 fish in chapter 5 represents similar densities (Dr Martyn Lucas, pers. comm.).

As already discussed in the recommendations, the results obtained during this flume-based research should be combined with the broader scale information attained through field studies (usually utilising telemetry techniques). By combining the information from fine-scale observations in the flume and broad-scale measurements in the field, it will be possible to fully optimise fish passes for the target species.

9.2.2.2 *Use of farmed brown trout*

During the research presented in this thesis the eels and lamprey used were wild fish caught during their spawning migration, guaranteeing their motivation to move. Unfortunately, this was not possible for brown trout therefore farmed fish were used as a substitute to wild ones. Thus, future studies comparing the observed results for farmed fish should be compared to wild brown trout to fully ascertain their applicability to the wild populations. However, the use of the farmed fish data for application to situations in nature should not be ruled out. Indeed, the velocity gradients that the farmed brown trout responded to in chapter 7 were similar to those observed for downstream migrating wild Pacific salmonid (*Oncorhynchus* spp.) smolts, even though they were not in a migratory life-stage. It is also possible that the large delay observed in farmed brown trout passing a velocity barrier (chapters 7 & 8), particular for those left behind when group integrity breaks down, is conservative when compared to wild fish. This is because farmed fish tend to be bolder and take greater risks than wild individuals (see Huntingford & Adams, 2005 for Atlantic salmon), and the potentially conservative nature of the results should be taken into account when assessing the risk posed by barriers to migration.

9.3 CLOSING REMARKS

As highlighted in this thesis, in river infrastructure can have major negative impacts on migratory fish species, in particular for the non-salmonids and downstream migrants where mitigation has less often been considered (Kemp & O'Hanley, 2010; Lucas *et al.*, 2000) when compared to the commercially viable salmonids (Laine *et al.*, 1998; Roscoe & Hinch 2010). Information of fish behaviour and swimming capabilities in relation to fish passage is often lacking or not applicable to many anthropogenic barriers to migration for all species, including the salmonids, leading to often less efficient than expected passage facilities (Haro & Kynard, 1997; Winter & van Densen, 2001). This problem must be addressed and requires interdisciplinary cooperation between aquatic biologists and hydraulic engineers to attain realistic and applicable fish pass criteria.

There is a need to collate information of fish swimming capability and behaviour, such as that obtained in this thesis, with information attained from past, present and future research into a centrally controlled and constantly updated database (as previously suggested by Kemp & O'Hanley, 2010) for multiple fish species and life history stages. This will provide fish pass engineers in collaboration with aquatic biologists and ecologists, with the information necessary to construct and design efficient multi-species fish passes for new, or to retrofit old, in river installations, and will also aid adaptation of already installed fish passes for multiple species. If information concerning habitat quality, with the number and current passage efficiency of already installed structures are further incorporated into this database, it may be possible to prioritise which barriers to mitigate for, and the best method to employ, to attain maximum gain in passage efficiency on an entire catchment when on a limited budget.

The research presented in this thesis provides a basis by which to obtain accurate and realistic swimming performance and behaviour of fish during volitional movement under the controlled conditions of a large open-channel flume. The use of a large flume allowed for fine-scale observations of fish behaviour to be attained, which is difficult in the field (Rice *et al.*, 2010), whilst they are still able to undertake more natural behaviours. A combination of fine-scale flume based studies, and broad-scale field based telemetry studies will complement one another and is necessary to fully assess fish swimming behaviour and capabilities applicable to fish passage. As per the primary aim of this thesis (Fig. 2.1) the results obtained have improved the understanding and knowledge base of diadromous fish species during up- and down-stream movement, providing fish passage criteria that can be applied to design, improve and successfully implement passage facilities for multiple species and life-stages at anthropogenic impediments to migration; improving fish passage, limiting construction costs, and ultimately contributing to the conservation of the biodiversity of our rivers.

References

Aarestrup, K., Økland, F., Hansen, M.M., Righton, D., Gargan, P., Castonguay, M., Bernatchez, L., Howey, P., Sparholt, H., Pedersen, M.I. & McKinley, R.S. (2009). Oceanic spawning migration of the European Eel (*Anguilla anguilla*). *Science* **325,** pp. 1660.

Abrahams, M.V. & Colgan, P.W. (1987). Fish schools and their hydrodynamic function: a reanalysis. *Environmental Biology of Fishes* **20,** 79–80.

Adam, B., Schwevers, U. & Dumont, U. (1999). Beitrage zum schutz abwandernder fische, verhaltensbeobachungen in einem modellgerinne. *Bibliothek Natur & Wissenschaft Band* **16,** 1-63, ISBN: 978-3-927889-32-3. [Translated from German by EPRI (Electric Power Research Institute), 2001. *Review and Documentation of Research Technologies on Passage and Protection of Downstream Migrating Catadromous Eels at Hydroelectric Facilities*. Prepared by Versar, Inc., EPRI Report TR-1000730, Palo Alto, California.]

Aieta, A.E. & Oliveira, K. (2009). Distribution, prevalence, and intensity of the swim bladder parasite *Anguillicola crassus* in New England and eastern Canada. *Diseases of Aquatic Organisms* **84,** 229–235.

Allan, J.D. (1995). *Stream Ecology: Structure & Function of running waters*. London: Chapman & Hall, 436 pp.

Amaral, S.V., Winchell, F.C., McMahon, B.J. & Dixon, D.A. (2003). Evaluation of angled bar racks and louvers for guiding silver phase American eels. In: Dixon, D.A. (ed.) *Biology, management and protection of catadromous eels*. American Fisheries Society, Symposium 33, Bethesda, Maryland, pp 367–376.

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

Anderson, J.J. (1988). Diverting migrating fish past turbines. *The Northwest Environmental Journal* **4,** 109-128.

Andjus, R.K., Damjanović, I., Gačić, Z., Konjević, D.J. & Andjus, P.R. (1998). Electroretinographic evaluation of spectral sensitivity in yellow and silver eels (*Anguilla anguilla*). *Visual Neuroscience* **15,** 923-930.

Anon (1995). *Fish Passage Technologies: Protection at Hydropower Facilities, OTA-ENV-641*. Washington DC: U.S. Government Printing Office, 173 pp.

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

Armstrong G., Aprahamian M., Fewings A., Gough P., Reader N. & Varallo P. (2004). *Guidance notes on the legislation, selection and approval of fish passes in England and Wales*. Environment Agency: National Fish Pass Manual, Version 1.1, cd edition.

Arnekleiv, J.V., Kraabøl, M. & Museth, J. (2007). Efforts to aid downstream migrating brown trout (*Salmo trutta* L.) kelts and smolts passing a hydroelectric dam and a spillway. *Hydrobiologia* **582,** 5-15.

ASMFC (Atlantic States Marine Fisheries Commission) (2000). *Interstate fishery management plan for American eel (Anguilla rostrata)*. Fishery Management Report No. 36, 79 pp.

Bakshtansky, E.L., Nesterov, V.D. & Haro, A. (1993). Some aspects of juvenile anadromous salmonid behaviour and behavioural studies, and their application to development of fish passage systems. In: Bates, K. (ed.) *Fish Passage Policy and Technology*. American Fisheries Society, Bioengineering Section, Bethesda, Maryland, pp. 205-209.

Bark, A., Williams, B. & Knights, B. (2007). Current status and temporal trends in stocks of European eel in England and Wales. *ICES Journal of Marine Science* **64,** 1368-1378.

Baumgartner, L. (2005). *Fish in Irrigation Supply Offtakes: A Literature Review.* NSW Department of Primary Industries - Fisheries Research Report Series: No 11. Cronulla, New South Wales, Australia.

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

Beach M.H. (1984). *Fish pass design - criteria for the design and approval of fish passes and other structures to facilitate the passage of migratory fish in rivers*. Fisheries Research Technical Report No. 78. Lowestoft: MAFF Directorate of Fisheries Research, 46 pp.

Beamish, F.W.H. (1980). Biology of the North American anadromous sea lamprey, *Petromyzon marinus*. *Canadian Journal of Fisheries and Aquatic Science* **37,** 1924-1943.

Beamish, F.W.H. (1978). Swimming capacity. In: Hoar, W.S. & Randall, D.J. (eds.), *Fish Physiology, Volume VII*. Academic Press, New York, pp. 101-187.

Beamish R.J. & Northcote T.G. (1989). Extinction of a population of anadromous Pacific lamprey, *Lampetra tridentata*, upstream of an impassable dam. *Canadian Journal of Fisheries and Aquatic Sciences* **46,** 420-425.

Behrmann-Godel, J. & Eckmann, R. (2003). A preliminary telemetry study of the migration of silver European eel (*Anguilla anguilla* L.) in the River Mosel, Germany. *Ecology of Freshwater Fish* **12,** 196-202.

Bell, M.C. (1986). Fisheries Handbook of Engineering Requirements and Biological Criteria: Useful factors in life history of most common species. US 116 Army Corps of Engineers, Portland, Oregon. Contract number DACW57-68-C- 0086, 290 pp.

Bell, S. & McGillivray, D. (2006). *Environmental Law 6th Edition*. Oxford University Press, 910 pp.

Boiten W. (2002). Flow measurement structures. *Flow Measurement and Instrumentation* **13,** 203-207.

Bowmaker, J.K. & Dartnall, H.J.A. (1980). Visual pigments of rods and cones in a human retina. *The Journal of Physiology* **298,** 501-511.

Bracewell, P., Cowx, I.G. & Uglow, R.F. (2004). Effects of handling and electrofishing on plasma glucose and whole blood lactate of *Leuciscus cephalus*. *Journal of Fish Biology* **64,** 65-71.

Brett, J.R. (1964). The respiratory metabolism and swimming performance of young sockeye salmon. *Journal of the Fisheries Research Board of Canada* **21,** 1183-1226.

British Hydropower Association (2009). *Re: Consultation on modernisation of Salmon and Freshwater Fisheries legislation: New order to address fish passage*.

Brown, L., Haro, A. & Castro-Santos, T. (2009). Three-dimensional movement of silver-phase American eels in the forebay of a small hydroelectric facility. In: Casselman, J.M. & Cairns, D.K. (eds.) *Eels at the edge: science, status and conservation concerns*. American Fisheries Society, Symposium 58, Bethesda, Maryland, pp. 277-291.

Brown, C., Laland, K. & Krause, J. (2006). *Fish Cognition and Behavior*. Oxford, UK: Blackwell publishing, 352 pp.

Brown, L.R., Moyle, P.B. & Yoshiyama, R.M. (1994). Historical decline and current status of Coho salmon in California. *North American Journal of Fisheries Management* **14,** 237-261.

BS ISO 4377 (2002). *Hydrometric determinations - Flow measurement in open channels using structures - Flat-vee weirs*. London: British Standards Institution, 42 pp.

BS 3680-4B (1986). *Measurement of liquid flow in open channels - Part 4: Weirs and flumes - Part 4B: Triangular Profile Weirs*. London: British Standards Institution, 22 pp.

Bunt, C.M. (2001). Fishway entrance modifications enhance fish attraction. *Fisheries Management and Ecology* **8,** 95-105.

Butterworth J.A., Hewitt E.J. & McCartney M.P. (2000). Discharge measurement using portable dilution gauging flowmeters. *Water and Environment Journal* **14,** 436-441.

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

Calles, O. & Bergdahl, D. (2009). *Ålens nedströmspassage av vattenkraftverk. Forskningsrapport 2009:19*. Karlstads Universitet, Sweden, ISBN 978-91-7063-242-6. In Swedish. (Translated title: *The downstream passage of eels past hydropower plants.*), 44 pp.

Calles, O. & Greenberg, L. (2009). Connectivity is a two-way street - The need for a holistic approach to fish passage problems in regulated rivers. *River Research and Applications* **25,** 1205-1338. Doi: 10.1002/rra.1228.

Calles, E.O. & Greenberg, L.A. (2007). The use of two nature-like fishways by some fish species in the Swedish River Emån. *Ecology of Freshwater Fish* **16,** 183-190.

Calles, E.O. & Greenberg, L.A. (2005). Evaluation of nature-like fishways for re-establishing connectivity in fragmented salmonid populations in the River EMÅN. *River Research and Applications* **21,** 951-960.

Cantwell, Murkowski, Murray, Feinstein, Boxer, Wyden, Merkley & Begich (2009). *S.817, Pacific Salmon Stronghold Conservation Act of 2009: A Bill*. Introduced at the 111th Congress 1st Session. 28 pp.

Carbyn, L.N. & Trottier, T. (1988). Descriptions of wolf attacks on bison calves in Wood Buffalo national park. *Arctic* **41,** 297-302.

Castro-Santos, T. (2004). Quantifying the combined effects of attempt rate and swimming capacity on passage through velocity barriers. *Canadian Journal of Fisheries and Aquatic Sciences* **61,** 1602-1615.

Castro-Santos, T., Cotel, A. & Webb, P. (2009). Fishway evaluations for better bioengineering: An integrative approach. In: Haro, A.J., Smith, K.L., Rulifson, R.A., Moffitt, C.M., Klauda, R.J., Dadswell, M.J., Cunjak, R.A., Cooper, J.E., Beal K.L. & Avery T.S. (eds.). *Challenges for diadromous fishes in a dynamic global environment*. American Fisheries Society, Symposium 69, Bethesda, Maryland, pp. 557-575.

Cea, L., Puertas, J. & Pena, L. (2007). Velocity measurements on highly turbulent free surface flow using ADV. *Experiments in Fluids* **42,** 333-348.

CEWG (Canadian Eel Working Group) (2007). *American eel management plan, draft, January 15 2007*. Available from www.aquaticspeciesatrisk.gc.ca [accessed 2 September 2009].

Chapman, J.L. & Reiss, M.J. (1999). *Ecology: Principles and Applications*. Cambridge, UK: Cambridge University Press, 330 pp.

Cheong, T.S., Kavvas, M.L. & Anderson, E.K. (2006). Evaluation of adult white sturgeon swimming capabilities and applications to fishway design. *Environmental Biology of Fishes* **77,** 197-208.

Chivers, D.P., Brown, G.E. & Smith, R.J.F. (1995). Familiarity and shoal composition in fathead minnows (*Pimephales promelas*): implications for antipredator behaviour. *Canadian Journal of Zoology* **73,** 955-960.

Clay, C.H. (1995). *Design of fishways and other fish facilities, 2nd edition*. Lewis Publishers, Boca Raton, 256 pp.

Close, D.A., Fitzpatrick, M.S. & Li, H.W. (2002). The ecological and cultural importance of a species at risk of extinction, Pacific lamprey. *Fisheries* **27,** 19-25.

Close, D.A., Fitzpatrick, M., Li, H., Parker, B., Hatch, D. & James, G. (1995). *Status report of the Pacific lamprey (Lampetra tridentata) in the Columbia River basin*. Prepared for the U.S. Department of Energy, Bonneville Power Administration, Contract number 95BI39067, Project number 94-026, Portland, Oregon, 35 pp.

Colgate, J.E. & Lynch, K.M. (2004). Mechanics and control of swimming: A review. *IEEE Journal of Oceanic Engineering* **29,** 660-673.

Cote, D., Kehler, D.G., Bourne, C. & Wiersma, Y.F. (2009). A new measure of longitudinal connectivity for stream networks. *Landscape Ecology* **24,** 101–113.

Cotel, A.J., Webb, P.W. & Tritico, H. (2006). Do brown trout choose locations with reduced turbulence? *Transactions of the American Fisheries Society* **135,** 610–619.

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

Cowx, I.G. & Lamarque, P. (1990). *Fishing with electricity – applications in freshwater fisheries management*. Fishing News Books, Blackwell Scientific Publications, Oxford, UK, 248 pp.

Crisp, D.T. (1996). Environmental requirements of common riverine European salmonid fish species in fresh water with particular reference to physical and chemical aspects. *Hydrobiologia* **323,** 201–221.

Croft, D.P., Arrowsmith, B.J., Bielby, J., Skinner, K., White, E., Couzin, I.D., Magurran, A.E., Ramnarine, I. & Krause, J. (2003). Mechanisms underlying shoal composition in the Trinidadian guppy, *Poecilia reticulata*. *Oikos* **100,** 429–438.

Croze, O. & Larinier, M. (1999). A study of Atlantic salmon (*Salmo salar* L.) smolt behaviour at the Pointis hydroelectric powerhouse water intake on the Garonne River and an estimate of downstream migration over the Rodere dam. *Bulletin Francais de la Peche et de la Pisciculture* **353/354,** 141–156.

Dall, S.R.X., Giraldeau, L.A., Olsson, O., McNamara, J.M. & Stephens, D.W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology and Evolution* **20,** 187–193.

Dauble, D.D., Moursund, R.A., and Bleich, M.D. (2006). Swimming behaviour of juvenile Pacific lamprey, *Lampetra tridentata*. *Environmental Biology of Fishes* **75,** 167-171.

Davidsen, J., Svenning, M.-A., Orell, P., Yoccoz, N., Dempsen, J.B., Niemelä, E., Klemetsen, A., Lamberg, A. & Erkinaro, J. (2005). Spatial and temporal migration of wild Atlantic salmon smolts determined from a video camera array in the sub-Arctic River Tana. *Fisheries Research* **74,** 210-222.

Day, R.L., Macdonald, T., Brown, C., Laland, K.N. & Reader, S.M. (2001). Interactions between shoal size and conformity in guppy social foraging. *Animal Behaviour* **62,** 917-925.

DECC (Department of Energy & Climate Change) (2009). *The UK Renewable Energy Strategy, July 2009*. London: DECC. Available at www.decc.gov.uk [accessed 12 November 2010].

DEFRA (2006). *Report of the Review of Salmon and Freshwater Fisheries Legislative Project: 04 October 2006*. www.defra.gov.uk [accessed 8 March 2010].

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

Deng, J. & Shao, X. (2006). Hydrodynamics in a diamond-shaped fish school. *Journal of Hydrodynamics, Ser. B.* **18 (supplement 1),** 438-442.

Doolan, S.P. & Macdonald, D.W. (1999). Co-operative rearing by slender-tailed meerkats (*Suricata suricatta*) in the Southern Kalahari. *Ethology* **105,** 851-866.

EA (2009). *Good practice guidelines annex to the Environment Agency hydropower handbook on the environmental assessment of proposed low head hydro power developments: August 2009*. Available from www.environment-agency.go.uk [accessed 27 October 2009].

EC (2007). Council Regulation (EC) no 1100/2007 of 18 September 2007 establishing measures for the recovery of the stock of European eel. *Official Journal of the European Union* **L248,** 17-23.

EC (2000). Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for community action in the field of water policy. *Official Journal of the European Communities* **L327,** 1-72.

EC (1992). Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Official Journal of the European Communities* **L206,** 7-50.

Edel, R.K. (1975). The effect of shelter on the activity of male silver eels. *Helgoländer wiss. Meeresunters* **27,** 167-174.

Elgar, M.A. (1989). Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Review* **64,** 13-33.

Enders, E.C., Gessel, M.H. & Williams, J.G. (2009). Development of successful fish passage structures at dams for downstream migrants requires knowledge of their behavioural response to accelerating flow. *The Canadian Journal of Fisheries and Aquatic Sciences* **66,** 2109-2117.

Eriksson, T. & Eriksson, L.-O. (1993). The status of wild and hatchery propagated Swedish salmon stocks after 40 years of hatchery releases in the Baltic rivers. *Fisheries Research* **18,** 147-159.

Farlinger, S. & Beamish, F.W.H. (1978). Changes in blood chemistry and critical swimming speed of largemouth bass, *Micropterus salmonids*, with physiological conditioning. *Transactions of the American Fisheries Society* **107,** 523-527.

Farrell, A.P. (2007). Cardiorespiratory performance during prolonged swimming tests with salmonids: a perspective on temperature effects and potential analytical pitfalls. *Philosophical Transactions of the Royal Society B: Biological Sciences* **362,** 2017-2030.

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

Fisher, R. & Hogan, J.D. (2007). Morphological predictors of swimming speed: a case study of pre-settlement juvenile coral reef fishes. *The Journal of Experimental Biology* **210,** 2436-2443.

Freyhof, J. & Kottelat, M. (2008). *Anguilla anguilla*. In: *IUCN 2008. 2008 IUCN Red List of Threatened Species*. www.iucnredlist.org [accessed 3 November 2010].

Frost, W.E. & Brown, M.E. (1967). *The Trout*. Collins, London, UK, 320 pp.

Gallego, A. & Heath, M.R. (1994). The development of schooling behaviour in Atlantic herring *Clupea harengus*. *Journal of Fish Biology* **45,** 569-588.

Geen, G.H., (1975). Ecological consequences of the proposed Moran Dam on the Fraser River. *Journal of the Fisheries Research Board of Canada* **32,** 126-135.

Giroux, F., Ovidio, M., Philippart, J.-C. & Baras, E. (2000). Relationship between the drift of macroinvertebrates and the activity of brown trout in a small stream. *Journal of Fish Biology* **56,** 1248-1257.

Glass, C.W., Wardle, C.S. & Mojsiewicz, W.R. (1986). A light intensity threshold for schooling in the Atlantic mackerel, *Scomber scombrus*. *Journal of Fish Biology* **29 (supplement A),** 71-81.

Goodwin, R.A., Nestler, J.M., Anderson, J.J. & Weber, L.J. (2007). A new tool to forecast fish movement and passage. *Hydro Review* **26,** 1-8.

Goodwin, R.A., Nestler, J.M., Anderson, J.J., Weber, L.J. & Loucks, D.P. (2006). Forecasting 3-D fish movement behavior using a Eularian-Langrangian-agent method (ELAM). *Ecological Modelling* **192,** 197-223.

Gosset, C., Travade, F., Durif, F., Rives, J. & Elie, P. (2005). Tests of two types of bypass for downstream migration of eels at a small hydroelectric power plant. *River Research and Applications* **21,** 1095-1105.

Gould, L.L. & Heppner, F. (1974). The vee formation of Canada geese. *Auk* **91,** 494-506.

Gowans, A.R.D., Armstrong, J.D., Priede, I.G. & Mckelvey, S. (2003). Movements of Atlantic salmon migrating upstream through a fish-pass complex in Scotland. *Ecology of Freshwater Fish* **12,** 177-189.

Griffiths, S.W. & Magurran, A.E. (1997). Familiarity in schooling fish: how long does it take to acquire? *Animal Behaviour* **53,** 945-949.

Guerin, B. (1993). *Social Facilitation*. Cambridge University Press, Cambridge, UK, 252 pp.

Guiny, E., Armstrong, J.D. & Ervine, D.A. (2003). Preferences of mature male brown trout and Atlantic salmon parr for orifice and weir fish pass entrances matched for peak velocities and turbulence. *Ecology of Freshwater Fish* **12,** 190-195.

Haddering, R.H., Van Aerssen, G.H.F.M., De Beijer, R.F.L.J. & Van Der Velde, G. (1999). Reaction of silver eels to artificial light sources and water currents: An experimental deflection study. *Regulated Rivers: Research and Management* **15,** 365-371.

Hamill, L. (2001). *Understanding Hydraulics: Second Edition*. Palgrave Macmillan, Basingstoke, UK, 608 pp.

Han, Y.-S., Sun, Y.-L., Liao, Y.-F., Liao, I-C., Shen, K.-N. & Tzeng, W.-N. (2008). Temporal analysis of population genetic composition in the overexploited Japanese eel *Anguilla japonica*. *Marine Biology* **155,** 613-621.

Haro, A. (2003). Downstream migration of silver-phase anguillid eels. In Aida, K., Tsukamoto, K. & Yamauchi, K. (eds.), *Eel Biology*. Springer, Tokyo, pp. 215-222.

Haro, A. & Kynard, B. (1997). Video evaluation of passage efficiency of American Shad and Sea lamprey in a modified Ice Harbor fishway. *North American Journal of Fisheries Management* **17,** 981-987.

Haro, A., Castro-Santos, T., Noreika, J. & Odeh, M. (2004). Swimming performance of upstream migrant fishes in open-channel flow: a new approach to predicting passage through velocity barriers. *Canadian Journal of Fisheries and Aquatic Sciences* **61,** 1591-1601.

Haro, A., Castro-Santos, T. & Boubée, J. (2000a). Behaviour and passage of silver-phase eels, *Anguilla rostrata* (LeSueur), at a small hydroelectric facility. *Dana* **12,** 33-42.

Haro, A., Richkus, W., Whalen, K., Hoar, A., Busch, W-D., Lary, S., Brush, T. & Dixon, D. (2000b). Population decline of the American eel: implications for research and management. *Fisheries* **25,** 7-16.

Haro, A., Odeh, M., Noreika, J. & Castro-Santos, T. (1998). Effect of water acceleration on downstream migratory behaviour and passage of Atlantic salmon smolts and juvenile American shad at surface bypasses. *Transactions of the American Fisheries Society* **127,** 118-127.

Haselbauer, M.A. & Martinez, C.B. (2007). Proposal of a sluice-type fish pass. *Neotropical Ichthyology* **5,** 223-228.

Heggenes, J., Krog, O.M.W., Lindås, O.R., Dokk, J.G. & Bremnes, T. (1993). Homeostatic behavioural responses in a changing environment: brown trout (*Salmo trutta*) become nocturnal during winter. *Journal of Animal Ecology* **62,** 295-308.

Herskin, J. & Steffensen, J.F. (1998). Energy savings in sea bass swimming in a school: Measurements of tail beat frequency and oxygen consumption at different swimming speeds. *Journal of Fish Biology* **53,** 366-376.

Higgs, D.M. & Fuiman, L.A. (1996). Light intensity and schooling behaviour in larval gulf menhaden. *Journal of Fish Biology* **48,** 979-991.

Hinch S.G. & Rand P.S. (1998). Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): role of local environment and fish characteristics. *Canadian Journal of Fisheries and Aquatic Sciences* **55,** 1821-1831.

Hindar, K., Jonsson, B., Ryman, N. & Stáhl, G. (1991). Genetic relationships among landlocked, resident and anadromous brown trout *Salmo trutta* L. *Heredity* **66,** 83-91.

Hoare, D.J. & Krause, J. (2003). Social organisation, shoal structure and information transfer. *Fish and Fisheries* **4,** 269-279.

Hoogland, J.L. (1981). The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*). *Ecology* **62,** 252-272.

Hoogland, J.L. (1979). Aggression, ectoparasitism, and other possible costs of prairie dog (Sciuridae, *Cynomys* spp.) coloniality. *Behaviour* **69,** 1–35.

Hope, A.J., Partridge, J.C. & Hayes, .K. (1998). Switch in rod opsin gene expression in the European eel, *Anguilla anguilla* (L.). *Proceedings of the Royal Society of London B: Biological Sciences* **265,** 869–874.

Hudspeth, A.J. (1989). How the ear's works work. *Nature* **341,** 397–404.

Hulme M., Jenkins G.J., Lu X., Turnpenny J.R., Mitchell T.D., Jones R.J., Lowe J., Murphy J.M., Hassell D., Boorman P., McDonald R. & Hill S. (2002). *Climate change scenarios for the United Kingdom: The UKCIP02 scientific report*. Norwich: Tyndall Centre for Climate Change Research, 124 pp.

Huntingford, F. & Adams, C. (2005). Behavioural syndromes in farmed fish: implications for production and welfare. *Behaviour* **142,** 1207–1221.

Huntingford, F.A., Andrew, G., Mackenzie, S., Morera, D., Coyle, S.M., Pilarczyk, M. & Kadri, S. (2010). Coping strategies in a strongly schooling fish, the common carp *Cyprinus carpio*. *Journal of Fish Biology* **76,** 1576–1591.

ICES (2007). *Report of the joint EIFAC/ICES working group on eels, 3–7 September 2007*. Rome, Italy. ICES Document CM 2007/ACFM:23, 534 pp.

ICES (2006). *Report of the joint EIFAC/ICES working group on eels, 23–27 January 2006*. Rome, Italy. ICES Document CM 2006/ACFM: 16, 367 pp.

Jaeger, J.A.G., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B. & Tluk von Toschanowitz, K. (2005). Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. *Ecological Modelling* **185,** 329–348.

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

Jayne B.C. & Lauder G.V. (1996). New data on axial locomotion in fishes: How speed affects diversity of kinematics and motor patterns. *American Zoologist* **36,** 642-655.

Jellyman, D.J., Chisnall, B.L., Sykes, J.R.E. & Bonnett, M.L. (2002). Variability in spatial and temporal abundance of glass eels (*Anguilla* spp.) in New Zealand waterways. *New Zealand Journal of Marine and Freshwater Research* **36,** 511-517.

Jeschke, J.M. & Tollrian, R. (2007). Prey swarming: which predators become confused and why? *Animal Behaviour* **74,** 387-393.

Johnson, G.E. & Dauble, D.D. (2006). Surface flow outlets to protect juvenile salmonids passing through hydropower dams. *Reviews in Fisheries Science* **14,** 213-244.

Johnson, R.L. & Moursund, R.A. (2000). Evaluation of juvenile salmon behavior at Bonneville Dam, Columbia River, using a multibeam technique. *Aquatic Living Resources* **13,** 313-318.

Jungwirth, M., Schmutz, S. & Weiss, S. (1998). *Fish Migration and Fish Bypasses*. Cambridge: Fishing News Books, 448 pp.

Kearn, G.C. (2004). *Leeches, Lice and Lampreys: A Natural History of Skin and Gill Parasites of Fishes*. Springer, Dordrecht, The Netherlands, 432 pp.

Kelly F.L. & King J.J. (2001). A review of the ecology and distribution of three lamprey species, *Lampetra fluviatilis* (*L.*), *Lampetra planeri* (Bloch) and *Petromyzon marinus* (*L.*): A context for conservation and biodiversity considerations in Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy* **101B,** 165–185.

Kemp, P.S. & O'Hanley, J.R. (2010). Procedures for evaluating and prioritising the removal of fish passage barriers: a synthesis. *Fisheries Management and Ecology* **17,** 297–322.

Kemp, P.S. & Williams, J.G. (2009). Illumination influences the ability of migrating juvenile salmonids to pass a submerged experimental weir. *Ecology of Freshwater Fish* **18,** 297–304.

Kemp, P.S. & Williams, J.G. (2008). Response of migrating chinook salmon (*Oncorhynchus tshawytscha*) smolts to in-stream structure associated with culverts. *River Research and Applications* **24,** 571–579.

Kemp, P.S., Russon, I.J., Vowles, A. & Lucas, M.C. (2011). The influence of discharge and temperature on the ability of upstream migrant adult river lamprey (*Lampetra fluviatilis*) to pass experimental overshot and undershot weirs. *River Research and Applications* **27,** 488–498.

Kemp P.S., Tsuzaki T. & Moser M.L. (2009). Linking behaviour and performance: intermittent locomotion in a climbing fish. *Journal of Zoology* **277,** 171–178.

Kemp, P.S., Gessel, M.H. & Williams, J.G. (2008). Response of downstream migrant juvenile Pacific salmonids to accelerating flow and overhead cover. *Hydrobiologia* **609,** 205–217.

Kemp, P.S., Gessel, M.H., Sandford, B.P. & Williams, J.G. (2006). The behaviour of Pacific salmonid smolts during passage over two experimental weirs under light and dark conditions. *River Research and Applications* **22,** 429–440.

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

Kemp, P.S., Gessel, M.H. & Williams, J.G. (2005b). Seaward migrating subyearling Chinook salmon avoid overhead cover. *Journal of Fish Biology* **67,** 1381-1391.

King, A.J. & O'Connor, J.P. (2007). Native fish entrapment in irrigation systems: A step towards understanding the significance of the problem. *Ecological Management and Restoration* **8,** 32–37.

Knaepkens, G., Baekelandt, K. & Eens, M. (2006). Fish pass effectiveness for bullhead (*Cottus gobio*), perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) in a regulated lowland river. *Ecology of Freshwater Fish* **15,** 20–29.

Krause, J. & Ruxton, G.D. (2002). *Living in Groups*. Oxford, UK: Oxford University Press, 210 pp.

Kraus, N.C., Lohrmann, A. & Cabrera, R. (1994). New acoustic meter for measuring 3D laboratory flows. *Journal of hydraulic engineering* **120,** 406–412.

Krebs, J.R., MacRoberts, M.H. & Cullen, J.M. (1972). Flocking and feeding in the great tit, *Parus major* – an experimental study. *Ibis* **114,** 507–530.

Kynard, B. (1993). Fish behaviour important for fish passage. In Bates, K. (ed.) *Fish Passage Policy and Technology*. American Fisheries Society, Bioengineering Section, Bethesda, Maryland, pp. 129-134.

Kynard, B., Horgan, M., Pugh, D., Henyey, E. & Parker, T. (2008). Using Juvenile sturgeons as a substitute for adults: A new way to develop fish passage for large fish. In Amaral, S.V., Mathur, D. & Taft III, E.P. (eds.) *Advances in Fisheries Bioengineering*. American Fisheries Society, Symposium 61, Bethesda, Maryland, pp. 1-21.

Laine, A., Kamula, R. & Hooli, J. (1998). Fish and lamprey passage in a combined Denil and vertical slot fishway. *Fisheries Management and Ecology* **5**, 31-44.

Laland, K.N. & Williams, K. (1998). Social transmission of maladaptive information in the guppy. *Behavioral Ecology* **9**, 493-499.

Landa, J.T. (1998). Bioeconomics of schooling fishes: selfish fish, quasi-free riders, and other fishy tales. *Environmental Biology of Fishes* **53**, 353-364.

Larinier, M. (2008). Fish passage experience at small-scale hydro-electric power plants in France. *Hydrobiologia* **609**, 97-108.

Larinier, M. (2002). Fishways - General considerations. *Bulletin Français de la Pêche et de la Pisciculture* **364 supplement**, 21-27.

Larinier, M. (1998). Upstream and downstream fish passage experience in France. In Jungwirth, M., Schmutz, S. & Weiss, S. (eds.), *Migration and fish bypasses*. Cambridge: Fishing News Books, pp. 127-145.

Larinier, M. & Travade, F. (2002a). Downstream migration: Problems and facilities. *Bulletin Français de la Pêche et de la Pisciculture* **364 supplement**, 181-207.

Larinier, M. & Travade, F. (2002b). The design of fishways for shad. *Bulletin Français de la Pêche et de la Pisciculture* **364 supplement,** 135-146.

Leaniz, C.G. (2008). Weir removal in salmonid streams: implications, challenges and practicalities. *Hydrobiologia* **609,** 83-96.

Lehner B., Döll P., Alcamo J., Henrichs T. & Kaspar F. (2006). Estimating the impact of global change on flood and drought risks in Europe: A continental, integrated analysis. *Climatic Change* **75,** 273-299.

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

Liao, J.C., Beal, D.N., Lauder, G.V. & Triantafyllou, M.S. (2003). The Kármán gait: novel body kinematics of rainbow trout swimming in a vortex street. *The Journal of Experimental Biology* **206,** 1059-1073.

Lima, S.L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour* **49,** 11-20.

Lima, S.L. (1990). The influence of models on the interpretation of vigilance. In: Bekoff, M. & Jamieson, D. (eds.) *Interpretation and Explanation in the Study of Animal Behaviour. Volume II: Explanation, Evolution, and Adaptation*. Oxford, UK: Westview Press Inc., pp. 246-267.

Lohrmann, A., Cabrera, R. & Kraus, N.C. (1994). Acoustic Doppler Velocimeter (ADV) for laboratory use. *Proceedings of symposium on fundamentals and advancements on hydraulic measurements and Experimentation ASCE*, pp. 351-365.

Long, C. (1968). Diel movement and vertical distribution of juvenile anadromous fish in turbine intakes. *Fishery Bulletin* **66,** 599-609.

Lucas, M.C. & Baras, E. (2001). *Migration of Freshwater Fishes*. Blackwell Science, Oxford, UK, 440 pp.

Lucas, C.M. & Frear, P.A. (1997). Effects of a flow-gauging weir on the migratory behaviour of adult barbel, a riverine cyprinid. *Journal of Fish Biology* **50,** 382-396.

Lucas, M.C., Bubb, D.H., Jang, M.-H., Ha, K. & Masters, J.E.G. (2009). Availability of and access to critical habitats in regulated rivers: effects of low-head barriers on threatened lampreys. *Freshwater Biology* **54,** 621-634.

Lucas, M. C., Mercer, T., McGinty, S. & Armstrong, J. D. (2000). Development and evaluation of a flat-bed passive integrated transponder detection system for recording movement of lowland river fishes through a baffled pass. In Moore, A. & Russel, I. (eds.), Advances in Fish Telemetry. CEFAS, Suffolk, pp. 117-127.

Lundqvist, H., Rivinoja, P., Leonardson, K. & McKinnell, S. (2008). Upstream passage problems for wild Atlantic salmon (*Salmo salar* L.) in a regulated river and its effect on the population. *Hydrobiologia* **602,** 111-127.

Lundqvist, H., McKinnel, S., Jonsson, S. & Ostergren, J. (2006). Is stocking with Sea Trout compatible with the conservation of wild trout (Salmo trutta L.)? In *Sea Trout: Biology, Conservation and Management*. Blackwell Publishing Ltd: Oxford UK, pp. 356-371.

Magurran, A.E. (1990). The adaptive significance of schooling as an anti-predator defence in fish. *Annales Zoologici Fennici* **27,** 51-66.

Maitland, P.S. (2004). *Keys to the Freshwater Fish of Britain and Ireland*. Freshwater Biological Association, Ambleside, UK, 248 pp.

Maitland, P.S. & Campbell, R.N. (1992). *Freshwater Fishes of the British Isles*. Harper Collins, London, 368 pp.

Mallen-Cooper, M. (1992). Swimming ability of juvenile Australian bass, *Macquaria novemaculeata* (Steindachner), and juvenile barramundi, *Lates calcarifer* (Bloch), in an experimental fishway. *Australian Journal of Marine and Freshwater Research* **43,** 823-834.

Marks, W.B., Dobelle, W.H. & MacNichol, E.F. (1964). Visual pigments of single primate cones. *Science* **143,** 1181-1183.

Masters, J.E.G., Jang, M.H., Ha, K., Bird, P.D., Frear, P.A. & Lucas, M.C. (2006). The commercial exploitation of a protected anadromous species, the river lamprey (*Lampetra fluviatilis* (L.)), in the tidal River Ouse, north-east England. *Aquatic Conservation: Marine and Freshwater Ecosystems* **16,** 77-92.

McDowall, R.M. (1997). The Evolution of diadromy in fishes (revisited) and its place in phylogenetic analysis. *Reviews in Fish Biology and Fisheries* **7,** 443-462.

McDowall, R.M. (1992). Particular problems for the conservation of diadromous fish. *Aquatic Conservation: Marine and Freshwater Ecosystems* **2,** 351-355.

McLaughlin, R.L. & Noakes, D.L.G. (1998). Going against the flow: an examination of the propulsive movements made by young brook trout in streams. *Canadian Journal of Fisheries and Aquatic Sciences* **55,** 853-860.

Mesa, M.G., Bayer, J.M. & Seelye, J.G. (2003). Swimming performance and physiological responses to exhaustive exercise in radio-tagged and untagged Pacific lampreys. *Transactions of the American Fisheries Society* **132,** 483-492.

Meyer, J.L., Strayer, D.L., Wallace, J.B., Eggert, S.L., Helfman, G.S. & Leonard, N.E. (2007). The contribution of headwater streams to biodiversity in river networks. *Journal of the American Water Resources Association* **43,** 86-103.

Mitton, C.J.A. &McDonald, D.G. (1994). Effects of electroshock, air exposure, and forced exercise on swim performance in rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* **51,** 1799-1803.

Montén, E. (1985). *Fish and turbines: fish injuries during passage through power station turbines*. Vattenfall, Statens vattenfallsverk, Stockholm.

Moore, A., Ives, S., Mead, T.A. & Talks, L. (1998). The migratory behaviour of wild Atlantic salmon (*Salmo salar* L.) smolts in the River Test and Southampton Water, southern England. *Hydrobiologia* **371/372,** 295-304.

Morgan, M.J & Colgan, P.W. (1987). The effects of predator presence and shoal size on foraging in bluntnose minnows, *Pimephales notatus*. *Environmental Biology of Fishes* **20,** 105-111.

Moser, M.L. & Butzerin, J.M. (2007). Capture and collection of lampreys: the state of the science. *Reviews in Fish Biology and Fisheries* **17,** 45-56.

Moser, M.L., Ocker, P.A., Stuehrenburg, L.C. & Bjornn, T.C. (2002a). Passage efficiency of adult Pacific lampreys at hydropower dams on the lower Columbia River, USA. *Transactions of the American Fisheries Society* **131,** 956-965.

Moser, M.L., Matter, A.L., Stuehrenberg, L.C. & Bjornn, T.C. (2002b). Use of an extensive radio receiver network to document Pacific lamprey (*Lampetra tridentata*) entrance efficiency at fishways in the lower Columbia River. *Hydrobiologia* **483,** 45-53.

Moss, B. (1998). *Ecology of Fresh Waters: Man and Medium, Past to Future, 3rd Edition*. Oxford: Blackwell, 557 pp.

Moursund, R. A., Mueller, R.P., Degerman, T.M. & Dauble, D.D. (2001). *Effects of dam passage on juvenile Pacific lamprey (Lampetra tridentata)*. Report of Batelle Pacific Northwest National Laboratories to the U.S. Army Corps of Engineers, Contract number DE-AC06-76RL01830, Portland District, Portland, OR, 69 pp.

Muller, G. & Kauppert, K. (2004). Performance characteristics of water wheels. *Journal of Hydraulic Research* **42,** 451-460.

Murray, A.G., O'Callaghan, M. & Jones, B. (2001). A model of transmission of a viral epidemic among schools within a shoal of pilchards. *Ecological Modelling* **144,** 245-259.

Naughton, G.P., Caudill, C.C., Peery, C.A., Clabough, T.S., Jepson, M.A., Bjornn, T.C. & Stuehrenberg, L.C. (2007). Experimental evaluation of fishway modifications on the passage behaviour of adult chinook salmon and steelhead at Lower Granite Dam, Snake River, USA. *River Research and Applications* **23,** 99-111.

Naughton, G.P., Caudill, C.C., Keefer, M.L., Bjornn, T.C., Stuehrenberg, L.C. & Peery, C.A. (2005). Late-season mortality during migration of radio-tagged adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia River. *Canadian Journal of Fisheries and Aquatic Sciences* **62,** 30-47.

Nikora, V.I., Aberle, J., Biggs, B.J.F., Jowett, I.G. & Sykes, J.R.E. (2003). Effects of fish size, time-to-fatigue and turbulence on swimming performance: a case study of *Galaxias maculatus*. *Journal of Fish Biology* **63,** 1365-1382.

Noakes, D.J., Beamish, R.J. & Kent, M.L. (2000). On the decline of Pacific salmon and speculative links to salmon farming in British Columbia. *Aquaculture* **183,** 363-386.

Nordgreen, J., Janczak, A.M., Hovland, A.L., Ranheim, B. & Horsberg, T.E. (2010). Trace classical conditioning in rainbow trout (*Oncorhynchus mykiss*): what do they learn? *Animal Cognition* **13,** 303-309.

Nunn A.D., Harvey J.P., Noble R.A.A. & Cowx I.G. (2008). Condition assessment of lamprey populations in the Yorkshire Ouse catchment, north-east England, and the potential influence of physical migration barriers. *Aquatic Conservation: Marine and Freshwater Ecosystems* **18,** 175-189.

O'Brien T. (1999). Overcoming physical barriers to fish migration. In: D.A. Hancock, D.C. Smith & J. Koehn (eds.) *Proceedings of the Fish Movement and Migration Workshop 1999*. Bendigo, Victoria: Australian Society for Fish Biology, pp. 129-134.

Odeh, M. (ed.) (1999). *Innovations in Fish Passage Technology*. The American Fisheries Society, Bethesda, Maryland, 224 pp.

Odling-Smee, L. & Braithwaite, V.A. (2003). The role of learning in fish orientation. *Fish and Fisheries* **4,** 235-246.

Oliveira J.M., Ferreira M.T., Pinheiro A.N. & Bochechas J.H. (2004). A simple method for assessing minimum flows in regulated rivers: the case of sea lamprey reproduction. *Aquatic Conservation: Marine and Freshwater Ecosystems* **14,** 481-489.

Olsen, K.H., Grahn, M. & Lohm, J. (2003). The influence of dominance and diet on individual odours in MHC identical juvenile Arctic charr siblings. *Journal of Fish Biology* **63,** 855-862.

OPSI (1991). *Water Resources Act 1991*. Office of Public Sector Information www.opsi.gov.uk [accessed 19 October 2010].

OPSI (1963) *Water Resources Act 1963*. Office of Public Sector Information www.opsi.gov.uk [accessed 19 October 2010].

Osbourne, M.F.M. (1961). The hydrodynamical performance of migratory salmon. *Journal of Experimental Biology* **38,** 365-390.

Paragamian, V.L., Whitman, V., Hammond, J. & Andrusak, H. (2000). Collapse of the burbot fisheries in Kootenay Lake, British Columbia Canada, and the Kootenai River, Idaho, USA, post-Libby Dam. In Paragamian, V.L. & Willis, D.W. (eds.). *Burbot: Biology, Ecology, and Management*. American Fisheries Society, Bethesda, Maryland. Pp. 155-164.

Partridge, B.L. & Pitcher, T.J. (1979). Evidence against a hydrodynamic function for fish schools. *Nature* **279,** 418-419.

Peake, S. (2004). An evaluation of the use of critical swimming speed for determination of culvert water velocity criteria for smallmouth bass. *Transactions of the American Fisheries Society* **133,** 1472-1479.

Peake, S.J. & Farrell, A.P. (2004). Locomotory behaviour and post-exercise physiology in relation to swimming speed, gait transition and metabolism in free-swimming smallmouth bass (*Micropterus dolomieu*). *The Journal of Experimental Biology* **207,** 1563-1575.

Peake, S.J. & Farrell, A.P. (2005). Postexercise physiology and repeat performance behaviour of free-swimming smallmouth bass in an experimental raceway. *Physiological and Biochemical Zoology* **78,** 801-807.

Peake, S. & McKinley, R.S. (1998). A re-evaluation of swimming performance in juvenile salmonids relative to downstream migration. *Canadian Journal of Fisheries and Aquatic Sciences* **55,** 682-687.

Peake, S., McKinley, R.S. & Scruton, D.A. (1997). Swimming performance of various freshwater Newfoundland salmonids relative to habitat selection and fishway design. *Journal of Fish Biology* **51,** 710-723.

Pedersen, L.-F., Koed, A. & Malte, H. (2008). Swimming performance of wild and F1-hatchery-reared Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) smolts. *Ecology of Freshwater Fish* **17,** 425-431.

Pess, G.R., McHenry, M.L., Beechie, T.J. & Davies, J. (2008). Biological impacts of the Elwha River dams and potential salmonid responses to dam removal. *Northwest Science* **82 special issue,** 1-19.

Pitcher, T.J. (1979). Sensory information and the organisation of behaviour in a shoaling cyprinid fish. *Animal Behaviour* **27,** 126-149.

Pitcher, T.J. (1983). Heuristic definitions of fish shoaling behaviour. *Animal Behaviour* **31,** 611-613.

Pitcher, T.J. (1986). Functions of shoaling behaviour in teleosts. In: Pitcher, T.J. (ed.) *Behaviour of Teleost Fishes*. Chapman & Hall, London, UK, pp. 294-33.

Pitcher, T.J. & Parrish, J.K. (1993). Functions of shoaling behaviour in teleosts. In: Pitcher, T.J. (ed.) *The Behaviour of Teleost Fishes. 2nd edition*. London, UK: Chapman & Hall. pp. 363-439.

Porcher, J.P. & Travade, F. (2002). Fishways: Biological basis, limits and legal considerations. *Bulletin Français de la Pêche et de la Pisciculture* **364 supplement,** 9-20.

Powell, G.V.N. (1974). Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Animal Behaviour* **22,** 501-505.

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

Pulliam, H.R. (1973). On the advantages of flocking. *Journal of Theoretical Biology* **38,** 419–422.

Quintella B.R., Póvoa I. & Almeida P.R. (2009). Swimming behaviour of upriver migrating sea lamprey assessed by electromyogram telemetry. *Journal of Applied Ichthyology* **25,** 46–54.

Quintella, B.R., Andrade, N.O., Koed, A. & Almeida, P.R. (2004). Behavioural patterns of sea lampreys' spawning migration through difficult passage areas, studied by electromyogram telemetry. *Journal of Fish Biology* **65,** 961–972.

Reebs, S.G. (2000). Can a minority of informed leaders determine the foraging movements of a fish shoal? *Animal Behaviour* **59,** 403–409.

Reinhardt U.G., Eidietis L., Friedl S.E. & Moser M.L. (2008). Pacific lamprey climbing behavior. *Canadian Journal of Zoology* **86,** 1264–1272.

Renaud C.B. (1997). Conservation status of Northern hemisphere lampreys (Petromyzontidae). *Journal of Applied Ichthyology* **13,** 143–148.

Rhodes D.G. & Servais S.A. (2008). *Low-cost modifications of the Crump weir to improve fish passage*. Science report SC010027. Bristol: Environment Agency, 76 pp.

Rice, S.P., Lancaster, J. & Kemp, P. (2010). Experimentation at the interface of fluvial geomorphology, stream ecology and hydraulic engineering and the development of an effective, interdisciplinary river science. *Earth Surface Processes and Landforms* **35,** 64–77.

Rivinoja, P., McKinnell, S. & Lundqvist, H. (2001), Hindrances to upstream migration of Atlantic salmon (*Salmo salar*) in a northern Swedish river caused by a hydroelectric power-station. *Regulated Rivers: Research and Management* **17,** 101–115.

Roni, P., Beechie, T.J., Bilby, R.E., Leonetti, F.E., Pollock, M.M. & Pess, G.R. (2002). A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. *North American Journal of Fisheries Management* **22,** 1-20.

Roscoe, D.W. & Hinch, S.G. (2010). Effectiveness monitoring of fish passage facilities: historic trends, geographic patterns and future directions. *Fish and Fisheries* **11,** 12-23.

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

Saltveit, S.J., Halleraker, J.H., Arnekleiv, J.V. & Harby, A. (2001). Field experiments on stranding in juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) during rapid flow decreases caused by hydropeaking. *Regulated Rivers: Research & Management* **17,** 609-622.

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

Schulz, U. & Berg, R. (1992). Movements of ultrasonically tagged brown trout (*Salmo trutta* L.) in Lake Constance. *Journal of Fish Biology* **40,** 909-917.

Schwalme, K., Mackay, W.C. & Lindner, D. (1985). Suitability of vertical slot and Denil fishways for passing North-temperate, non-salmonid fish. *Canadian Journal of Fisheries and Aquatic Sciences* **42,** 1815-1822.

Scruton, D.A., Pennell, C.J., Bourgeois, C.E., Goosney, R.F., King, L., Booth, R.K., Eddy, W., Porter, T.R., Ollerhead, L.M.N. & Clarke, K.D. (2008). Hydroelectricity and fish: A synopsis of comprehensive studies of upstream and downstream passage of anadromous wild Atlantic salmon, *Salmo salar*, on the Exploits River, Canada. *Hydrobiologia* **609,** 225-239.

Scruton, D.A., Pennell, C.J., Robertson, M.J., Clarke, K.D., Eddy, W. & McKinley, R.S. (2005). Telemetry studies of the passage route and entrainment of downstream migrating wild Atlantic salmon (*Salmo salar*) smolts at two hydroelectric installations on the Exploits River, Newfoundland, Canada. In Spedicato, M.T., Lembo, G. & Marmulla, G. (eds.) *Aquatic Telemetry: Advances and Applications. Proceedings of the fifth conference on fish telemetry held in Europe. Ustica, Italy, 9-13 June 2003*. Rome, FAO/COISPA, pp. 91-101.

Scully, R.J., Leitzinger, E.J. & Petrosky, C.E. (1990). Idaho habitat evaluation for off-site mitigation record. 1998 Annual Report Bonneville Power Administration. Contract no. DE-A179-84BP13388, Portland, Oregon. 76 pp.

Sébert, P., Scaion, D. & Belhomme, M. (2009). High hydrostatic pressure improves the swimming efficiency of European migrating silver eel. *Respiratory Physiology & Neurobiology* **165,** 112-114.

Servais, S.A. (2006). *Physical modelling of low-cost modifications to the Crump weir in order to improve fish passage: Development of favourable swimming conditions and investigation of the hydrometric effect*. PhD thesis, Cranfield University, Engineering systems department, UK, 341 pp.

Shaw, E. (1978). Schooling fishes. *American Scientist* **66,**166-175.

Shepard, D.B., Kuhns, A.R., Dreslik, M.J. & Phillips, C.A. (2008). Roads as barriers to animal movement in fragmented landscapes. *Animal Conservation* **11,** 288-296.

Silva, A.T., Santos, J.M., Ferreira, M.T., Pinheiro, A.N. & Katopodis, C. (2010 early view). Effects of water velocity and turbulence on the behaviour of Iberian barbel (*Luciobarbus bocagei*, Steindacher 1864) in an experimental pool-type fishway. *River Research and Applications*. DOI: 10.1002/rra.1465.

Sloman, K.A., Gilmour, K.M., Taylor, A.C. & Metcalfe, N.B. (2000). Physiological effects of dominance hierarchies within groups of brown trout, *Salmo trutta*, held under simulated natural conditions. *Fish Physiology and Biochemistry* **22**, 11-20.

Smith, V.C. & Pokorny, J. (1972). Spectral sensitivity of color-blind observers and the cone photopigments. *Vision Research* **12**, 2059-2071.

Sneddon, L.U. (2003). The bold and the shy: individual differences in rainbow trout. *Journal of Fish Biology* **62**, 971-975.

Solomon, D.J. & Beach, M.H. (2004). *Fish pass design for eel and elver (Anguilla anguilla)*. R&D Technical Report W2-070/TR1. The Environment Agency, Bristol.

Sprankle, K. (2005). Interdam movements and passage attraction of American shad in the lower Merrimack River main stem. *North American Journal of Fisheries Management* **25**, 1456-1466.

Svendsen, J.C., Eskesen, A.O., Aarestrup, K., Koed, A. & Jordan, A.D. (2007). Evidence for non-random spatial positioning of migrating smolts (Salmonidae) in a small lowland stream. *Freshwater Biology* **52**, 1147-1158.

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

Taylor, K., Wippelhauser, G., Hazel, A. & Bell, H. (2008). *Review of the Atlantic States Marine Fisheries Commission fishery management plan for American eel (Anguilla rostrata)*. Atlantic States Marine Fisheries Commission, 15 pp.

Tesch. F.-W. (2003). *The Eel: 5th Edition*. Blackwell Publishing Company, Oxford, UK, 416 pp.

Thiel R., Winkler H.M., Riel P., Neumann R., Gröhsler T., Böttcher U., Spratte S. & Hartmann U. (2009). Endangered anadromous lampreys in the southern Baltic Sea: spatial distribution, long-term trend, population status. *Endangered Species Research* **8,** 233-247.

Thorpe, J.E., Ross, L.G., Struthers, G. & Watts, W. (1981). Tracking Atlantic salmon smolts, *Salmo salar* L., through Loch Voil, Scotland. *Journal of Fish Biology* **19,** 519-537.

Tudorache, C., Viaenen, P., Blust, R. & De Boeck, G. (2007). Longer flumes increase critical swimming speeds by increasing burst-glide swimming duration in carp *Cyprinus carpio*, L.. *Journal of Fish Biology* **71,** 1630-1638.

Tudorache, C., Viaene, P., Blust, R., Vereecken, H. & De Boeck, G. (2008). A comparison of swimming capacity and energy use in seven European freshwater fish species. *Ecology of Freshwater Fish* **17,** 284-291.

Turnpenny, A.W.H., Struthers, G. & Hanson, K.P. (1998). *A UK guide to intake fish-screening regulations, policy, and best practice*. Contractors report to the energy technology support unit. Harwell. ETSU H/00052/00/00.

Tuunainen P., Ikonen E. & Auvinen H. (1980). Lampreys and lamprey fisheries in Finland. *Canadian Journal of Fisheries and Aquatic Sciences* **37,** 1953-1959.

Tytler, P., Thorpe, J.E. & Shearer, W.M. (1978). Ultrasonic tracking of the movement of Atlantic salmon smolts (*Salmo salar* L) in the estuaries of two Scottish rivers. *Journal of Fish Biology* **12,** 575-586.

U.S. Fish and Wildlife Service (2010). www.fws.gov [accessed 12 November 2010].

Van den Thillart, G., Palstra, A. & Van Ginneken, V. (2007). Simulated migration of European silver eel; Swim capacity and cost of transport. *Journal of Marine Science and Technology* **Special Issue,** 1-16.

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

Venditti, D.A., Rondorf, D.W. & Kraut, J.M. (2000). Migratory behaviour and forebay delay of radio-tagged juvenile fall Chinook salmon at a lower Snake River impoundment. *North American Journal of Fisheries Management* **20,** 41-52.

Videler, J.J. (1993). *Fish Swimming*. London: Chapman & Hall, 260 pp.

Videler, J.J. & Wardle, C.S. (1991). Fish swimming stride by stride: speed limits and endurance. *Reviews in Fish Biology and Fisheries* **1,** 23-40.

Viscido, S.V., Parrish, J.K. & Grünbaum, D. (2005). The effect of population size and number of influential neighbours on the emergent properties of fish schools. *Ecological Modelling* **183,** 347-363.

Vøllestad, L.A., Jonsson, B., Hvidsten, N.A., Naesje, T.F., Haraldstad, O. & Ruud-Hansen, J. (1986). Environmental factors regulating the seaward migration of European silver eels, *Anguilla anguilla*. *Canadian Journal of Fisheries and Aquatic Sciences* **43,** 1909-1916.

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

Ward, A.J.W., Holbrook, R.I., Krause, J. & Hart, P.J.B. (2005). Social recognition in sticklebacks: the role of direct experience and habitat cues. *Behavioral Ecology and Sociobiology* **57,** 575-583.

Ward, A.J.W., Herbert-Read, J.E., Sumpter, D.J.T. & Krause, J. (2011). Fast and accurate decisions through collective vigilance in fish shoals. *Proceedings of the Natural Academy of Sciences of the United States of America* **108**, 2312-2315.

Wardle, C.S. (1980). Effects of temperature on the maximum swimming speeds of fish. In: Ali, M.A. (ed.), *Environmental Physiology of Fishes*. Plenum Press, New York, pp. 519-531.

WCD (World Commission on Dams) (2000). *Dams and development: a new framework for decision-making*. London: Earthscan Publications Ltd, 404 pp.

Weber, E.H. (1846). Der tastsinn und das gemeingefühl. In: Wagner, R. (ed.), *Handwörterbuch der Physiologie: Band 3, Abt. 2*. Braunschweig, Bieweg.

Webster, M.M., Goldsmith, J., Ward, A.J.W. & Hart, P.J.B. (2007). Habitat-specific chemical cues influence association preferences and shoal cohesion in fish. *Behavioral Ecology and Sociobiology* **62,** 273-280.

Weihs, D. (1973). Hydromechanics of fish schooling. *Nature* **241,** 290-291.

Wessels P. & Rooseboom A. (2009). Flow-gauging in South African rivers part 2: Calibration. *Water SA* **35,** 11-19.

Weyand, M., Redeker, M. & Nusch, E.A. (2005). Restoration of fish passage: development and results of a master plan established for the Ruhr River basin. *Water Science and Technology* **52,** 77-84.

White, W.R., Iredale, R. & Armstrong, G. (2006). Fishpasses at flow measurement structures. *Proceedings of the Institution of Civil Engineers: Water Management* **159,** 165-171.

Williams, I.V. & Brett, J.R. (1987). Critical swimming speed of Fraser and Thompson River pink salmon (*Oncorhynchus gorbuscha*). *Canadian Journal of Fisheries and Aquatic Sciences* **44,** 348-356.

Williams, A., Milner, N., O'Keefe, N., Clarke, A. & Webb, H. (2009). *River Tees Salmon Action Plan Review*. Environment Agency Report, February 2009. APEM reference EA 410441, 108 pp.

Wilson, A.D.M. & Stevens, E.D. (2005). Consistency in context-specific measures of shyness and boldness in rainbow trout, *Oncorhynchus mykiss*. *Ethology* **111,** 849-862.

Wilson, D.S., Clark, A.B., Coleman, K. & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology and Evolution* **9,** 442-446.

Winter, H.V. & van Densen, W.L.T. (2001). Assessing opportunities for upstream migration of non-salmonid fishes in the weir-regulated River Vecht. *Fisheries Management and Ecology* **8,** 513-532.

Winter, H.V., Jansen, H.M. & Breukelaar, A.W. (2007). Silver eel mortality during downstream migration in the River Meuse, from a population perspective. *ICES Journal of Marine Science* **64,** 1444-1449.

Winter, H.V., Jansen, H.M. & Bruijs, M.C.M. (2006). Assessing the impact of hydropower and fisheries on downstream migrating silver eel, *Anguilla anguilla*, by telemetry in the River Meuse. *Ecology of Freshwater Fish* **15**, 221–228.

Yoshiyama, R.M., Fisher, F.W. & Moyle, P.B. (1998). Historical abundance and decline of Chinook salmon in the central valley region of California. *North American Journal of Fisheries Management* **18**, 487–521.