UNIVERSITY OF Southampton

University of Southampton Research Repository
ePrints Soton

Copyright © and Moral Rights for this thesis are retained by the author and/or other copyright owners. A copy can be downloaded for personal non-commercial research or study, without prior permission or charge. This thesis cannot be reproduced or quoted extensively from without first obtaining permission in writing from the copyright holder/s. The content must not be changed in any way or sold commercially in any format or medium without the formal permission of the copyright holders.

When referring to this work, full bibliographic details including the author, title, awarding institution and date of the thesis must be given e.g.

AUTHOR (year of submission) "Full thesis title", University of Southampton, name of the University School or Department, PhD Thesis, pagination

http://eprints.soton.ac.uk

UNIVERSITY OF SOUTHAMPTON

FACULTY OF ENGINEERING AND THE ENVIRONMENT

Civil, Maritime and Environmental Engineering and Science

Quantification of new methods, behaviour and hydrodynamics for improving fish passage at anthropogenic barriers

by

James Robert Kerr

Thesis for the degree of Doctor of Philosophy

July 2015

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF ENGINEERING AND THE ENVIRONMENT
Civil, Maritime and Environmental Engineering and Science
Thesis for the degree of Doctor of Philosophy

QUANTIFICATION OF NEW METHODS, BEHAVIOUR AND HYDRODYNAMICS FOR IMPROVING FISH PASSAGE AT ANTHROPOGENIC BARRIERS

James Robert Kerr

Fish passes, which are designed to promote the free passage of fish past riverine obstructions, generally perform poorly for the entire community and even target species are not able to pass as well as previously thought. This is often because: 1) Fundamental knowledge of how fish interact with the complex hydrodynamic conditions within passes is lacking, 2) passage technology is less well developed for weaker swimming non-salmonid species, and 3) fish display complex behaviours, such as rejecting accelerating velocity gradients associated with downstream bypass intakes. This thesis addresses these issues.

Current understanding on how fish interact with complex flows is discussed, and limitations and knowledge gaps highlighted. Previous studies in this field have generally focussed on identifying correlative links between one of any number of hydrodynamic metrics. However, often the causal reason behind these links is obscure. This issue was addressed by returning to first principles and experimentally investigating the behaviour of brown trout, *Salmo trutta*, under the simple assumption that space use should be governed by energy conservation strategies. The results indicate that fish use space as predicted; through either the selection of low drag regions or where they could express specialised energy reducing behaviours (e.g. the Kármán gait). A simple, robust and biologically relevant hydrodynamic descriptor of drag that can be used as a proxy for the energetic cost of holding station in a turbulent flow is described and tested and two new specialised behaviours identified (wall holding and tail holding).

European eel, *Anguilla anguilla*, and river lamprey, *Lampetra fluviatilis*, are both weaker swimming non-salmonid fish, which are in decline, and for which conventional fish passes perform poorly. Experimental trials were undertaken to quantify the efficiency of a new method for improving the upstream passage of eel and lamprey at a model crump weir. Side-mounted and vertically oriented bristle passes improved the upstream passage of both species although there was interspecific differences in their efficacy, with the passes being more effective for eel than lamprey. Behavioural observations of both species as they used the bristle passes will aid in optimisation of this and similar pass types.

According to Signal Detection Theory (SDT), the ability to detect a signal (discriminability) decreases with increasing levels of internal and/or external noise. Brown trout were used to test whether hydrodynamic noise would mask the detection of an accelerating velocity gradient as fish moved downstream. The experimental results were inconclusive but they represent the first attempt to use SDT as a tool to manipulate animal behaviour and aid in the conservation of vulnerable species. As such they provide a useful platform for future research.

Experimental research presented within this thesis has advanced scientific knowledge that will aid in the development of methods to improve fish passage at migration barriers. The changes brought about as a result of this research will help conserve vulnerable fish species, something that should, in turn, help promote productive and resilient ecosystems that benefit society.

Table of Contents

ABSTRACT i

Table of Contents iii

List of Tables vii

List of Figures ix

Declaration of Authorship xv

Acknowledgements xvii

Notation and Glossary xix

1 Introduction 1

1.1 Research aim and objectives 4

1.2 Thesis overview 4

2 Literature review 7

2.1 Fish passes: history, design and function 7

2.2 Fish pass effectiveness/efficiency 10

2.3 Factors limiting passage 13

2.3.1 Factors limiting the efficiency of upstream passage infrastructure 14

2.3.2 Factors limiting the efficiency of downstream passage infrastructure 18

2.4 Additional considerations 19

2.5 Summary 21

3 Research methodology 25

3.1 Flume facility 25

3.2 Fish husbandry 27

3.3 Fish capture and handling 28

3.3.1 Tagging 29

3.4 Hydrodynamic measurements and spatial interpolation 30
    3.4.1 Hydrodynamic measurement 30
    3.4.2 Hydrodynamic metrics 31
    3.4.3 Spatial interpolation 32
3.5 Study Species 33
    3.5.1 European eel (*Anguilla anguilla*) 33
    3.5.2 River lamprey (*Lampetra fluviatilis*) 34
    3.5.3 Brown trout (*Salmo trutta*) 36
3.6 Analysis of fish behaviour 37

4 Quantification of fish behaviour in a hydrodynamically complex experimental flow field: What governs space use by fish and why? 39

4.1 Summary 39
4.2 Introduction 40
4.3 Methodology 43
    4.3.1 Experimental setup 43
    4.3.2 Experimental procedure 54
    4.3.3 Fish behaviour 55
4.4 Results 60
4.5 Discussion 70

5 Efficiency of a side-mounted vertically oriented bristle pass for improving upstream passage of European eel (*Anguilla anguilla*) and river lamprey (*Lampetra fluviatilis*) at an experimental Crump weir. 75

5.1 Summary 75
5.2 Introduction 77
5.3 Methodology 79
    5.3.1 Experimental setup 79

5.3.2 Experimental procedure 82

5.3.3 Fish behaviour 85

5.4 Results 89

5.5 Discussion 94

6 Masking an accelerating velocity gradient with turbulence: Application to improving the downstream migration of fish through bypass systems at anthropogenic barriers. 97

6.1 Summary 97

6.2 Introduction 99

6.3 Methodology 102

6.3.1 Experimental setup 102

6.3.2 Experimental procedure 107

6.3.3 Fish behaviour 107

6.4 Results 113

6.5 Discussion 118

7 Thesis discussion 121

7.1 Future research 132

7.2 Conclusion 134

7.3 Research impact, management application, and societal importance 137

References 143

List of Tables

Table 3.1 Hydrodynamic metrics, notations, equations and units. u, v and w are the instantaneous velocity variables corresponding to the x, y and z spatial coordinates, n is number of samples, overbar denotes time-average, prime denotes the fluctuating component, σ is the standard deviation of its subscript, ρ is water density (kg m^{-3}) (taken as 1000 kg m^{-3} in this report), t is time, and τ is time lag. 32

Table 4.1 Hydrodynamic metrics, equations and units. Uf is the cross-section mean velocity measured 500 mm downstream of the flow straightener (*ca.* 0.41 m s^{-1}), d is cylinder diameter (m), St is the Strouhal number (0.2, appropriate for the range of Reynolds numbers in the experiment - Sumer and Fredsøe, 1997), W is the width of the flume (m), d is the sum of the cylinder diameters, u, v and w are the instantaneous velocity variables corresponding to the x, y and z spatial coordinates, overbar denotes time-averaging, prime denotes the fluctuating component, σ is the standard deviation of its subscript, ρ is density (1000 kg m^{-3}), kv is kinematic viscosity (m^2 s^{-1}), t is time, and τ is time lag (1/50 second intervals). 47

Table 4.2 Reynolds number (Re), estimated vortex shedding frequency (f), and wake wavelength (λ) downstream of each cylinder (d) used in an experimental study to investigate space use of brown trout, *Salmo trutta*, in a hydrodynamically complex environment. 48

Table 4.3 Group statistics for brown trout, *Salmo trutta*, used during experiments conducted to assess hydrodynamic space use in a recirculating flume at the ICER facility (University of Southampton). Source, size class, fork length (FL), mass, number of fish (*N*), and mean and total duration of data acquired for each group and treatment per group. *DNLRC* is the percentage of fish that did not leave the release chamber. 55

Table 5.1 Conditions encountered by European eel, *Anguilla anguilla*, and river lamprey, *Lampetra fluviatilis*, during passage over a model Crump weir installed in a recirculating flume under a high (HV), medium (MV) or low (LV) velocity hydrodynamic regime with (treatment) or without (control) bristle passes installed during 2011 (eel) and 2013 (lamprey). *N* is the number of fish used per trial. 84

Table 5.2 Definition of the passage events and metrics obtained for the small eel, large eel (*LE*), and/or lamprey (*L*) as they passed over an experimental Crump weir, and the statistical tests used. 87

Table 6.1 Conditions encountered by brown trout, *Salmo trutta*, in experimental trials undertaken to assess their behavioural response to a velocity gradient (Factor A) under different levels of hydrodynamic noise (Factor B). *TKE* is the mean Turbulent Kinetic Energy recorded within the observation zone and *U* is the mean across channel velocity measured 1 metre upstream of the constriction point (150 mm depth). 105

Table 6.2 Definition of passage metrics obtained for brown trout, *Salmo trutta*, as they passed downstream through the experimental area and the statistical tests used. 108

Table 6.3 Proportion (%) of trout that were oriented positively as they *approached* and *passed* and exhibited an orientation switch or rejection at least once whilst within the observation zone for each treatment. 114

List of Figures

Figure 2.1 Example of a *lift* (a), *lock* (b), *pool and weir* (c), *pool and orifice* (d), *vertical slot* (e), *Denil* (f), *eel ladder* (g), and *nature-like* (h) fish pass.......9

Figure 2.2 Example of a typical small-scale guidance facility for downstream moving fish, consisting of an angled physical screen to deflect fish away from a detrimental route (in this case an irrigation canal) towards a bypass channel (surface entrance). Solid arrow indicates direction of bulk flow.......10

Figure 3.1 Twenty one metre long indoor flume facility at the International Centre for Ecohydraulics Research (ICER) facility, University of Southampton, UK.......26

Figure 3.2 External holding tanks (4 x 3000 litre) at the International Centre for Ecohydraulics Research (ICER) facility, University of Southampton, UK.......28

Figure 4.1 Plan (A) and profile (B) of the experimental area in a large recirculating flume at the ICER facility (University of Southampton) in which hydrodynamic space use of brown trout, *Salmo trutta*, was assessed. I) flow straightening device, II) cylinder array, III) mesh screen, IV) release chamber, V) release chamber orifice. Thick arrow indicates direction of bulk flow.......43

Figure 4.2 Cylinder arrays used to create 3 alternative hydrodynamic flow fields in a flume (treatments A, B, and control [no cylinders]). Numbers indicate the diameters of the cylinders (mm). Dashed lines delineate groups of cylinders of equivalent size.......45

Figure 4.3 Single point velocity sampling locations under the control (A) and Treatment A and B (B) and two-point cross-correlation velocity sampling locations measured under the incremental treatment (C). Each 'x' denotes an ADV sampling location.......46

Figure 4.4 Diagram of the directional forces on a sphere and drag (D) acting parallel to the mean flow (U) as a result of an instantaneous lateral velocity component (v).......50

Figure 4.5 Colour intensity plots of mean velocity (U) (m s^{-1}), turbulence intensity (TI) (m s^{-1}), relative turbulence intensity (k), turbulent kinetic energy (TKE) (J m^{-3}), horizontal Reynolds shear stress (τuv) (N m^{-2}), eddy diameter (Ed) (m) and drag (Dt) for treatment A in which the behaviour of brown trout, *Salmo trutta*, was assessed.......51

Figure 4.6 Colour intensity plots of mean velocity (U) (m s^{-1}), turbulence intensity (TI) (m s^{-1}), relative turbulence intensity (k), turbulent kinetic energy (TKE) (J m^{-3}), horizontal Reynolds shear stress (τuv) (N m^{-2}), eddy diameter (Ed) (m) and drag (Dt) for treatment B in which the behaviour of brown trout, *Salmo trutta*, was assessed.......52

Figure 4.7 Colour intensity plots of mean velocity (U) (m s^{-1}), turbulence intensity (TI) (m s^{-1}), relative turbulence intensity (k), turbulent kinetic energy (TKE) (J m^{-3}), horizontal Reynolds shear stress (τuv) (N m^{-2}), eddy diameter (Ed) (m) and drag (Dt) for the control in which the behaviour of brown trout, *Salmo trutta*, was assessed.......53

Figure 4.8 The mechanosensory field of detection (MFoD) allocated to each fish and used to assess the area it sampled during hydrodynamic space use experiments in a large open channel flume. 56

Figure 4.9 Schematic representation of how preference was calculated. Example using data for a wild trout (FL: 223 mm) under treatment A (Trial 54, duration: 3600 seconds) for turbulent drag (Dt). Schematic shows plots of the total available hydrodynamic habitat (Dt) (top middle), the area the fish sampled (grey area) (top left) and space used (blue dots – representing snout position each second) (top right) along with associated frequency distributions (Ht, Ss, and Su, respectively). Hydrodynamic preference, where $\mathrm{Hp} = \mathrm{Su}/\mathrm{Ss}$ (calculated for each bin of the Su and Ss data), is shown in the bottom plot as a solid blue line. Red dashed line in the bottom plot is for reference purposes and represents an even distribution (i.e. preference = 1)........ 59

Figure 4.10 Schematic representation of how excessive use of behavioural zones was accounted for in the data. Example using data for a large hatchery trout (FL: 323 mm) under treatment A (Trial 4, duration: 3600 seconds) with a specific focuses on the wall holding behavioural zone adjacent to the 90mm cylinder (dashed blue rectangle). A) Raw space use data – 272 instances of the trout being present in the wall holding zone. B) Modified space use data – If distribution had been even then the trout would have only used the zone 12 times. Hence 260 points (272 – 12) from within the zone were randomly removed. This was repeated for each behavioural zone. Hence the influence of fish preference for behavioural zones was removed from the final preference curves. 59

Figure 4.11 A) Plot of space use by a wild trout (FL: 223 mm) under treatment B (Trial 72, duration: 3507 seconds); and B) example of habitat sampled (H_s) (grey area) by a small hatchery fish (FL: 154 mm) under the control (Trial 120, duration: 856 seconds). Blue dots represent snout positions........ 60

Figure 4.12 A) Predicted drafting zones (red), entraining zones (green), bow wake zones (magenta), wall holding zones (blue) and tail holding zones (black) for a 285 mm long (FL) trout under treatment B; and B) space use by a hatchery trout (FL: 260 mm) under treatment A (Trial 13, duration: 3356 seconds) with hydrodynamic zones overlaid to emphasize the heavy use of entraining and wall holding zones and moderate use of tail holding and drafting zones............ 62

Figure 4.13 Box plot of percentage of the trial that wild and small, medium, and large hatchery brown trout, *Salmo trutta* (*N* = 8, 22, 16, 20, respectively), spent within the tail holding, entraining, wall holding, drafting and bow riding zones (data pooled from treatment A and B). Boxes represent interquartile range (IQR) and median. Whiskers represent the total range excluding standard (circles) and extreme (squares) outliers (greater than the upper quartile + 1.5 or 3 times the IQR, respectively). Dashed lines represent the proportion expected if distribution had been even. Asterisks represent incidences where the proportion of time spent within a region by individuals was consistently greater than that expected if distribution had been even (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). Y-axis scale is log base 2 to aid in interpretation... 63

Figure 4.14 Relationship between percentage of a trial that hatchery (crosses) and wild (triangles) trout spent in the tail holding (A), drafting (B) and bow riding (C) zones and fork length

(FL) (mm). Dashed line represents the linear correlation. Text is the Pearson's correlation coefficient (r_s) and significance level (p) and the bootstrapped (n = 2000) bias corrected and accelerated (BCa) 95% confidence intervals (CI) of r_s. 64

Figure 4.15 The relationship between trout fork length (mm) and the cylinder diameter (mm) of the entraining zone that trout preferentially choose to utilise (for all cases where peak time in a particular zone exceeded 10 seconds). Dashed line represents the linear correlation. Text is the Pearson's correlation coefficient (r_s) and significance level (p) and the bootstrapped (n = 2000) bias corrected and accelerated (BCa) 95% confidence intervals (CI) of r_s. 64

Figure 4.16 Relative drag (Dt) group hydrodynamic preference (GH_p) curves constructed using unmodified (A) and modified (B) space use (S_u) data for wild and small, medium and large hatchery brown trout, *Salmo trutta*, in treatment A. Left axis is group preference curve series scale and right axis is total available hydrodynamic space histogram (H_t) scale (grey bars). Solid grey line is for reference purposes and represents an even distribution (i.e. preference = 1). 65

Figure 4.17 Group preference curves for wild and small, medium and large hatchery brown trout *(salmo trutta)* under treatment A, B, and the control for mean velocity (U) (m s^{-1}), turbulence intensity (TI) (m s^{-1}), relative turbulence intensity (k), turbulent kinetic energy (TKE) (J m^{-3}), horizontal Reynolds shear stress (τuv) (N m^{-2}), drag (Dt), and eddy diameter (Ed) (m). Left axis is preference curve scale and right axis is total available hydrodynamic space histogram (H_t) scale (grey bars). Solid grey line is for reference purposes and represents an even distribution (i.e. preference = 1). Note: Axis scales differ between graphs to aid in interpretation........ 69

Figure 5.1 The Crump weir under control (A) and treatment (B) setups during which a bristled substrate (C) was vertically positioned against the channel walls to aid upstream movement of European eel and river lamprey under various hydrodynamic conditions. In A and B dashed lines indicate the position of half-duplex Passive Integrated Transponder (PIT) antennae coils and the dashed arrows indicates direction of flow. 80

Figure 5.2 Velocity (m s^{-1}) profiles for a Crump weir under high (HV), medium (MV) and low (LV) velocity regimes. Small and large black arrows indicate mean and bulk flow direction, respectively. Grey arrows indicate position of a hydraulic jump. Crosses denote electromagnetic flowmeter sample locations. 81

Figure 5.3 Mean *number of upstream passes* per fish for small eel (A), large eel (B), and lamprey (C) without (control: clear bars) and with (treatment: grey bars) bristle passes installed under the low (LV), medium (MV), and high (HV) velocity hydrodynamic regimes. Hatched sections of the grey bars indicate the proportion of upstream passes that occurred via the bristle passes. Error bars represent ± 1 S.E.. 89

Figure 5.4 Mean p*assage efficiency* (%) for small eel (A), large eel (B), and lamprey (C) without (control: clear bars) and with (treatment: grey bars) bristle passes installed under the low (LV), medium (MV), and high (HV) velocity hydrodynamic regimes. Error bars represent ± 1 S.E.. 90

Figure 5.5 *Passage success* (%) for large eel (A) and lamprey (B) without (control: clear bars) and with (treatment: grey bars) bristle passes installed under the low (LV), medium (MV), and high

(HV) velocity hydrodynamic regimes. Error bars are 95% confidence intervals calculated using the Clopper-Pearson exact method. 91

Figure 5.6 Cumulative Probability of Passage (CPP) upstream with number of attempts for large eel (A) and lamprey (B) with (treatment: grey lines) and without (control: black lines) bristle passes installed under the low (LV), medium (MV), and high (HV) velocity regimes. Crosses represent right censored data. 92

Figure 5.7 Cumulative Probability of Passage (CPP) upstream against time for large eel (A) and lamprey (B) with (treatment: grey lines) and without (control: black lines) bristle passes installed under the low (LV), medium (MV), and high (HV) velocity hydrodynamic regimes. Crosses represent right censored data. 92

Figure 5.8 Two examples of striated marks on the flanks of lamprey caused by bristle pass use. Scale is in mm.. 93

Figure 6.1 Schematic representation of the experimental area with velocity gradient present under low levels of hydrodynamic noise (TKE) (PL treatment). Thick grey arrows indicate the entrance and exit of the release chamber. Thick black arrow indicates bulk flow direction. Grey dashed lines indicate the flow modification location, the start of the observation zone, and the constriction point.. 103

Figure 6.2 A) The grid utilised to increase turbulence intensities in the high turbulence treatments: constructed of equally spaced (*M* = 122m) wooden batons (33 mm x 18 mm). B) The flow straightening device used to reduce turbulence intensities in the low turbulence treatments: 100 mm thick polycarbonate screen with elongated tubular porosity – 7 mm diameter.. 104

Figure 6.3 Colour intensity plots of velocity (m s^{-1}) under the four treatments (AL, AH, PL, and PH) created by manipulating *velocity gradient* (present or absent) and *hydrodynamic noise* (low or high *TKE*), for which the behavioural response of brown trout, *salmo trutta*, was assessed. Red dashed line delineates the extent of the accelerating velocity gradient (zone where velocity was at least 10% greater than background levels). 106

Figure 6.4 The four potential signal-response outcomes that may occur in the presence or absence of a specific environmental stimulus. In this study, the signal is the presence or absence of the velocity gradient and the response is the choice not to pass downstream during a trial (course scale assessment) or displaying a behavioural response (fine scale assessment). 109

Figure 6.5 Gaussian probability distributions illustrating internal response probability density functions for noise-alone (I) and for signal-plus-noise (II) under low noise (A) and high noise (B) conditions. The dashed vertical lines illustrate the position of the *response criterion* if the response was completely unbiased (c_b) (equal probability of a False Alarm or a Miss) or if there was a negative bias (c_a) (tendency to respond *yes* – higher probability of False Alarm than a Miss). The value *c* is the distance of the *response criterion* from being unbiased (illustrated by criterion c_b). *Discriminability*, *d′*, is the distance between the means of the distributions for noise-alone (I) and signal-plus-noise (II). 110

Figure 6.6 Example Receiver Operating Characteristic (ROC) curve. The diagonal, *d′* = 0, represents chance response. The diagonal, *c* = 0, represents unbiased response. The point illustrates a hypothetical response for which *d′* is between 1.0 and 2.0 and *c* is between 0 and 0.5 (a slightly conservative response bias). Movements in the A direction (increasing *c* value) represent an increasingly conservative response bias (i.e. increased tendency to respond *no*). Movements in the B direction (increasing d′ value) represent an increasing discriminability of the signal either through higher signal intensity or reduced background internal or external noise. 111

Figure 6.7 Proportion of brown trout, *Salmo trutta*, that passed downstream when velocity gradient was absent and present under low (light grey bars) and high (dark grey bars) levels of hydrodynamic noise (*TKE*). *N* = 22, 21, 21 and 21 for AL, AH, PL, and PH, respectively. Error bars are 95% confidence intervals. 113

Figure 6.8 A) Cumulative probability of passing downstream against time (minutes) for brown trout, *Salmo trutta*, when the velocity gradient was absent (solid lines) and present (dashed lines) under low (grey) and high (black) levels of hydrodynamic noise. B) Cumulative probability of passing downstream against time (minutes) for brown trout that entered the observational zone facing upstream (positive approach rheotaxis - black line) and downstream (negative approach rheotaxis - grey line) (aggregated data for constricted and unconstricted treatments). Crosses denote instances of right censored data. 115

Figure 6.9 Response distance (R_d) (mm) (A) and response velocity (R_v) (m s^{-1}) (B) at which brown trout, *salmo trutta*, responded (rejection or orientation switch) when the velocity gradient was present under low (light grey bars) and high (dark grey bars) levels of hydrodynamic noise (*TKE*). 116

Figure 6.10 Location of initial orientation switch (A) and rejection (B) when the velocity gradient was present under low (grey arrows) and high (black arrows) levels of hydrodynamic noise (*TKE*) superimposed onto colour intensity plots of flow velocity (m s^{-1}). Arrow head indicates head position of trout. 116

Figure 6.11 Receiver-Operating Characteristics (ROC) plot of Hit Rate (HR) against False Alarm Rate (FAR) for coarse (triangles) and fine (circles) scale assessment of the behavioural responses of brown trout, *Salmo trutta*, to a velocity gradient under low (black data points) and high (red data points) levels of hydrodynamic noise (*TKE*). Reference discriminability (*d′* = 0, 1, 2, 3) and response criterion (*c* = -1, -0.5, 0, 0.5, 1) lines are shown (solid and dashed grey lines, respectively). Increases in *d′* represent greater signal discriminability and increases in *c* represent greater bias towards responding. 117

Figure 7.1 Small Crump weir on the River Isbourne (4.5 m wide, 0.5 m high channel walls implying head differences of < 500 mm). Copyright David Stowell and licensed for reuse under the Creative Commons Licence 124

Figure 7.2 Commercially available multi-density eel tile available from Berry & Escott Engineering Ltd. (photo from www.berryescott.co.uk). 126

Declaration of Authorship

I, James Robert Kerr declare that this thesis and the work presented in it is my own and has been generated by me as the result of my own original research.

QUANTIFICATION OF NEW TECHNIQUES, BEHAVIOUR AND HYDRODYNAMICS FOR IMPROVING FISH PASSAGE AT ANTHROPOGENIC BARRIERS

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;

2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;

3. Where I have consulted the published work of others, this is always clearly attributed;

4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;

5. I have acknowledged all main sources of help;

6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;

7. Parts of this work have been published as:

Vowles, A.S., Eakins, L.R., Piper, A.T., Kerr, J.R. and Kemp, P.S. **2013**. Developing realistic fish passage criteria: An integrated approach. *In:* Maddock, I., Harby, A., Kemp, P. and Wood, P (eds.), Ecohydraulics: An Integrated Approach, John Wiley & Sons Ltd., pp. 464.

Kerr, J.R., Karageorgopoulos, P. and Kemp, P.S. **2015**. Efficacy of a side-mounted vertically oriented bristle pass for improving upstream passage of European eel (*Anguilla anguilla*) and river lamprey (*Lampetra fluviatilis*) at an experimental Crump weir. *Ecological Engineering (accepted pending minor revisions).*

Signed:...

Date:..

Acknowledgements

I wish to thank the many people who have helped me during the course of completing this thesis. Firstly I would like to thank my supervisor Paul Kemp for the countless hours he has put into reading my work and guiding me through this adventure. I will forever treasure the memory of the first occasion I won an argument with Paul. It didn’t happen often during the course of my studies and I believe he may still be in denial. I’m hoping I get the opportunity to win many more in years to come. I must also express my gratitude to my second supervisor, Costantino Manes, who always had a positive comment to spur me on, and who somehow didn’t throttle me despite my many attempts to hold my own during meetings to hash out complicated maths problems.

I am also deeply grateful to the members of ‘Team Fish’ (our appropriately nicknamed research group), who have supported me with comradery, technical advice, and help during long nights at our unheated research facility. You made the hard work bearable and often enjoyable and I definitely would not have completed this without you all. Andy, Tom, Laura, Adam, Lyn, Gill, Jasper, Maty and Matt, thank you. Particular thanks go to Andy Vowles who frequently helped me with technical advice, physical help, and proof reading, and who has had the questionable pleasure of not only working but living with me for much of my PhD candidature. You are also, and probably always will be, the main culprit in regards to many late night ‘fishy’ conversations in the pub! May they long continue! To Laura, I will always remember the ‘Funnel of Tun’! You had a remarkable ability to make the most mundane chores enjoyable. However, I will also remember the time you drugged me with chocolate covered espresso beans!! To Lyn and Gill, thank you for all the support over the years. Your friendship and expertise have helped me in so many ways.

I feel that recognition should also be given to my friends and family who have only vaguely been aware of what I have dedicated the last few years of my life to. I would like to thank you all for putting up with me through strange work commitments, long and unsociable working hours, and that ‘fishy’ talk in the pub late in the evening after one too many orange juices.

I also wish to thank Peri Karageorgopoulos and Dave Hunter, who provided technical advice during the early stages of the bristle pass experiments. Dave, particular thanks go to you for taking the time to source and return the eels for me during that experiment.

Two people who have my heartfelt gratitude are my Mum and Dad. I’m hugely grateful to you both for believing in me over the years and nudging me in the right direction on countless occasions. I would never even have got to the point where I could contemplate starting a PhD, let alone finishing it, if it hadn’t been for your ongoing support.

Finally to Steph, you have always had the remarkable ability to bring a smile to my face even after the most taxing of days. The list of ways you have supported me during the last few years would fill too many pages. Thank you for being there at the end of every day and always believing in me.

Funding for this research came from an EPSRC Doctoral Training Centre Grant. Additional financial support for technical expenditures during the bristle pass experiment was provided by the Environment Agency.

Notation and Glossary

A. Organisms referred to in this research:

A.1. Order

Acipenseriformes: An order of rather primitive fish characterised by a cartilaginous skeleton, a heterocercal tail fin, and a head with a pointed, protruding rostrum and ventrally located mouth. Extant groups in the order are the sturgeon and paddlefish.

Anguilliformes: The order containing the eels - Elongate fishes with pelvic fins and girdle absent or reduced.

Pleuronectiformes: An order containing flatfish species. Adults not bilaterally symmetrical, with one eye migrating to the other side of the cranium; dorsal and anal fins with long bases, dorsal fin base nearly always overlapping at least the neurocranium; body highly compressed, somewhat rounded on eyed side and flat on blind side; eyes can protrude above body surface allowing fish to see when buried in the substrate.

A.2. Family

Clupeidae: The family of the herrings, shads, sardines, hilsa, and menhadens.

Cyprinidae: Includes the carps, the true minnows, and their relatives (for example, the barbs and barbels).

Salmonidae: A family of ray-finned fish. It includes salmon, trout, chars, freshwater whitefishes, and graylings.

A.3. Genus

Anguilla: A genus of fish in the family Anguillidae; it contains the eels that complete part or all of their lifecycle in freshwater.

***Lampetra*:** A genus of fish in the family Petromyzontidae; it contains several species of lamprey.

***Oncorhynchus*:** A genus of fish in the family Salmonidae; it contains the Pacific salmon and Pacific trout. The name of the genus is derived from the Greek *onkos* ("hook") and *rynchos* ("nose"), in reference to the hooked jaws of males in the mating season.

A.4. Species

Common name	*Latin name*
American shad	*Alosa sapidissima*
Amur sturgeon	*Acipenser schrenckii*

Atlantic salmon	*Salmo salar*
Australian smelt	*Retropinna semoni*
Bony herring	*Nematalosa erebi*
Brook lamprey	*Lampetra planeri*
Brown trout	*Salmo trutta*
Bullhead	*Cottus gobio*
Chinese paddlefish	*Psephurus gladius*
European eel	*Anguilla anguilla*
Golden perch	*Macquaria ambigua*
Guppy	*Poecilia reticulata*
Iberian Barbell	*Luciobarbus bocagei*
Pacific lamprey	*Lampetra tridentata*
Pallid sturgeon	*Scaphirhynchus albus*
Rainbow trout	*Oncorhynchus mykiss*
River lamprey	*Lampetra fluiviatilis*
Reeves shad	*Tenualosa reevesii*
Sea lamprey	*Petromyzon Marinus*
Sockeye salmon	*Oncorhynchus nerka*

A.5. Non-fish species

Common name	*Latin name*
European robin	*Erithacus rubecula*
Loggerhead turtle	*Caretta caretta*
Tree hopper	*Tylopelta gibbera*

B. Acronyms

AH	Absent High
AL	Absent How
ADV	Acoustic Doppler Velocimeter
ANOVA	Analysis of Variance
BCa	Bias Corrected and accelerated
BST	British Summer Time
CI	Confidence Interval
CITES	Convention on International Trade in Endangered Species

CPP	Cumulative Probability of Passage
DNLRC	Did Not Leave Release Chamber
EM	Electromagnetic
EMP	Eel Management Plan
FAR	False Alarm Rate
FET	Fisher's Exact Test
FL	Fork Length
HDX	Half Duplex
HR	Hit Rate
HV	High Velocity
ICER	International Centre for Ecohydraulics Research
IUCN	International Union for Conservation of Nature
IQR	Interquartile Range
LV	Low Velocity
TLS	Turbulent Length Scale
TKE	Turbulent Kinetic Energy
TI	Turbulence Intensity
MFoD	Mechanosensory Field of Detection
MV	Medium Velocity
PIT	Passive Integrated Transponder
PH	Present High
PL	Present Low
RLTS	Red List of Threatened Species
ROC	Receiver Operating Characteristics
SDT	Signal Detection Theory
TL	Total Length
VG	Velocity Gradient
WFD	Water Framework Directive

C. Notation

C.1 General notation

Notation	*Unit*	*Description*
u	m s^{-1}	longitudinal velocity component
v	m s^{-1}	Lateral velocity component

w	m s^{-1}	Vertical velocity component
U	m s^{-1}	Mean velocity – usually calculated as three dimensional velocity magnitude
σ		Standard deviation – often in reference to the standard deviation of velocity (i.e. σ_v lateral velocity standard deviation in m s^{-1})
TI	m s^{-1}	Turbulence intensity
k	N/A	Relative turbulence intensity
TKE	J m^{-3}	Turbulent kinetic energy
τ_{uw}	N m^{-2}	Horizontal Reynolds shear stress
D_t	N/A	Drag (including the influence of turbulent fluctuations)
N	Count	Number of fish
n	Count	Total number of samples
ρ	kg m^{-3}	Density
k_v	m^2 s^{-1}	Kinematic viscosity
t	s	Time
τ	s	Time lag
d_c	mm	Cylinder diameter
g_c	mm	Cylinder spacing – predominantly axis-to-axis spacing.
U_f	m s^{-1}	Free stream velocity – usually an across channel average taken away from obstructions.
St	N/A	Strouhal number
W	m	Channel width
R_e	N/A	Reynolds number
f	Hz	Vortex shedding frequency
λ	m	Wake wavelength
E_s	m s^{-1}	Convection speed of the dominant energy containing eddies
E_t	s	Turnover time of the dominant energy containing eddies
E_d	m	Characteristic size of the dominant energy containing eddies
C_d	N/A	Dimensionless drag coefficient
S	m^2	Form area
H_p	N/A	Hydrodynamic preference
S_u	N/A	Space used
S_s	N/A	Space sampled

GH_p	N/A	Group hydrodynamic preference
H_t	N/a	Total available hydrodynamic space
TD	s	Trial duration
r_s	N/A	Pearson's correlation coefficient
M	mm	Mesh size
R_d	mm	Distance from the constriction of initial response
R_v	m s^{-1}	Velocity at initial response
d'	*Z score*	Discriminability (in standard deviation units, Z score)
c	*Z score*	Response criterion (in standard deviation units, Z score)
Z_H	*Z score*	Probability of a Hit in standard deviation units (Z scores of the unit normal Gaussian distribution)
Z_{FA}	*Z score*	Probability of a False Alarm in standard deviation units (Z scores of the unit normal Gaussian distribution)

C.2 Scripts and accents

Subscripts	*Use*
$\square_u$	Of or relating to longitudinal velocity
$\square_v$	Of or relating to lateral velocity
$\square_w$	Of or relating to vertical velocity
$\square_c$	Of or relating to a cylinder i.e. d_c – cylinder diameter
$\square_i$	Index of summation
Superscripts	*Use*
$\square'$	The fluctuating component of velocity, i.e. u' (where $u' = u - \bar{u}$)
Bars	*Use*
$\bar{\square}$	Time averaged

C.3. Axis definitions as used in the laboratory

Axis	*Position*
x	Longitudinal axis
y	Lateral axis
z	Vertical axis

D. Glossary

Abiotic: Non-living aspects of the environment, used in reference to physical or chemical features.

Acclimation: The physiological adjustment of an organism to environmental conditions (e.g. osmotic balance).

Aliasing: In signal processing and related disciplines, aliasing is an effect that causes different signals to become indistinguishable (or aliases of one another) when sampled.

Anadromous: Diadromous fish for which the majority of feeding and growth is undertaken in marine environments before the adults migrate to freshwater to spawn.

Anguilliform: Shaped like or resembling an eel. Also a swimming mode (see anguilliform locomotion).

Anguilliform locomotion: A swimming mode where the whole body participates in large amplitude undulations. Since at least one complete wavelength of the propulsive wave is present along the body, lateral forces are adequately cancelled out, minimizing any tendencies for the body to recoil.

Anthropogenic: Relates to an effect or object resulting from or induced by human activity.

Baffle: A device used to restrain the flow of a fluid.

Bypass: An alternative route for downstream moving fish, allowing them to bypass anthropogenic river barriers. Designed to be a safer and more benign route that that of the bulk flow of the river (e.g. where the majority of the water may pass through a hydropower turbine).

Catadromous: Diadromous fish for which the majority of feeding and growth takes place within freshwater prior to adults migrating to the sea to spawn.

Conservation: The principles and practice of the science of preventing species extinctions.

Contiguous: Sharing a common border; touching.

Crump Weir: A triangular-profile submerged gauging structure which typically has an upstream slope of 1:2 and downstream slope of 1:5 (Crump, 1952).

Demersal: An organism that lives and feeds on or near the bottom of seas or lakes (i.e. inhabits the demersal zone).

Demersal zone: The demersal zone is the part of the sea or ocean or lake comprising the water column that is near to (and is significantly affected by) the seabed/lakebed and the benthos.

Diadromous: Fish that migrate between freshwater and marine environments.

Ecosystem services: The benefits humankind derives from the workings of the natural world.

Ecotypes: A distinct form or race of a plant or animal species occupying a particular habitat.

Effectiveness (in relation to fish passage): Effectiveness is a qualitative concept and concerns whether a structure is capable of passing its target species within the range of environmental conditions observed during the migration period (Larinier and Marmulla, 2004).

Efficiency (in relation to fish passage): The efficiency of a fish pass is a quantitative description of its performance. It may be defined as the proportion of stock present at an obstruction which then enters and successfully moves through the fish pass in an acceptable period of time (Larinier and Marmulla, 2004).

Elver: The juvenile lifestage of an eel between glass and yellow eel. Individuals are larger than glass eel and pigmented.

Entrain: To pull or draw along after itself.

Extirpation: Is the condition of a species (or other taxon) that ceases to exist in the chosen geographic area of study, though it still exists elsewhere.

Fatigue: The state, following a period of mental or physical activity, characterised by a lessened capacity for work and reduced efficiency of accomplishment.

Fish pass: A water passage around or through an obstruction, designed to dissipate the energy in the water in such a manner as to enable fish to ascend or descend without undue stress (Clay, 1995). Fish pass is synonymous with ‘fishway’, which is the more commonly used term in North America.

Fish passage facility: A fish pass plus any additional device/structure that aids in fish passage.

Fishway: See fish pass.

Fitness: The contribution an individual makes to the gene pool of the next generation, relative to the contribution made by others in its present population.

Freshwater fish: Fish that live all or a critical part of their life history in fresh, inland or brackish waters, including estuaries and mangrove swamps.

Glass eel: The lifestage of an eel between the leptocephali larvae and elver stage. Individuals conform to the elongated eel morphology but are unpigmented.

Habitat: An area that provides the resources (e.g. food, space) necessary for the existence of an organism or particular life-stage.

Habitat connectivity: The size and distribution of suitable habitat patches and the ease with which a species can move through the space between patches.

Habitat fragmentation: The subdivision of a specific habitat into smaller and more isolated fragments or patches, through either natural or anthropogenic activities, resulting in changes to the space composition, structure and function.

High-head barrier: Any riverine barrier > 5 m in height.

Hydraulic: Used synonymously with 'hydrodynamic' - Pertaining to forces in or motions of liquids.

Hydrodynamic: Pertaining to forces in or motions of liquids.

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

Interspecific: In reference to between different species.

Intraspecific: In reference to within the same species.

Kármán Vortex Street: In fluid dynamics, a Kármán vortex street is a repeating pattern of swirling vortices caused by the unsteady separation of the flow of a fluid around blunt bodies. It is named after the engineer and fluid dynamicist Theodore von Kármán and is responsible for such phenomena as the "singing" of suspended telephone or power lines, and the vibration of a car antenna at certain speeds.

Kinematics: Describes changes in body shape relative to the fish frame of reference (i.e. motions or rates of deformation). For example, a fish encountering faster flow velocities will, with respect to its own frame of reference, alter its swimming kinematics (e.g. increase lateral tail-beat amplitude) to swim faster (see Liao, 2007).

Lacustrine: Relating to or associated with lakes.

Leptocephali: A colourless, transparent, flattened larva, especially of certain eels and ocean fishes.

Linear interpolation: A method of curve fitting using linear polynomials.

Lotic: Meaning, or in reference to, flowing water environments.

Low-head barrier: Any riverine barrier < 5 m in height.

Louvers: A louver system consists of an array of evenly spaced, vertical slats aligned across a channel at a specified angle and leading to a bypass. Louver slats are typically oriented 90 degrees to the flow.

Lucifugous: Avoiding light.

Masking (in relation to signals): A change in the likelihood of perception of one signal in the presence of a second (Gelfand, 2010).

Mechanosensory: Pertaining to sensory activation in response to mechanical pressures or distortions.

Mitigation: The action intended to reduce the adverse impact of a specific project, development, or activity.

Motile: In biology, motility is the ability to move spontaneously and actively, consuming energy in the process.

Ontogenetic: The development of an individual organism from embryo to adult. Also called ontogenesis.

Parr: A young salmonid between the stages of fry and smolt, distinguished by dark rounded patches evenly spaced along its sides.

Potamodromous: Fish which undertake migrations that occur entirely within freshwater.

Riblets: A series of microscopic grooves set into a material to reduce drag.

Rheotaxis: Movement of an organism in relation to a current of water. Positive rheotaxis describes fish that are oriented facing into the current. Negative rheotaxis describes fish that are oriented facing with the current.

Rheotactic: Of or relating to Rheotaxis.

Silver eel: Eels at the end of the growth phase which have undergone reproductive and osmoregulatory changes in preparation for migration to spawning grounds. During these changes individual take on a silver hue.

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

Interpolation: The estimation of a value between two known values.

Speciation: The formation of new and distinct species in the course of evolution.

Spline interpolation: A form of interpolation where the interpolant is a special type of piecewise polynomial called a spline. Spline interpolation is often preferred over polynomial interpolation because the interpolation error can be made small even when using low degree polynomials for the spline. Spline interpolation avoids the problem of Runge's phenomenon, in which oscillation can occur between points when interpolating using high degree polynomials.

Striated: Striped or streaked.

Subcarangiform locomotion: Intermediate locomotory mode between anguilliform and carangiform locomotion. Swimming mode is similar to anguilliform locomotion but the amplitude of the undulations is limited anteriorly, and increases only in the posterior half of the body (e.g. trout).

Technical fish pass: Any fish pass that incorporates artificial flow reduction elements such as baffles (e.g. Denil) or steps (e.g. pool-and-weir, vertical-slot) (Bunt *et al.,* 2012).

Telemetry: A highly automated communications process by which measurements are made and other data collected at remote or inaccessible points and transmitted to receiving equipment for monitoring. Greek origins: *tele* = remote, *metron* =measure. In relation to fisheries science telemetry encompasses any situation where fish movements are recorded remotely. Typically fish positions are ascertained via communication between a transmitter surgically attached to /

implanted within a fish and either a fixed or static receiver/antennae. Common types include radio, acoustic, or passive integrated transponder (PIT) telemetry.

Thigmotactic: Moving in close proximity to the substrate and structured walls.

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

Turbulence: Chaotic vortical flow of multiple strengths and sizes superimposed onto a mean flow velocity (as per: Liao, 2007).

Very low-head barrier: Any riverine barrier < 2 m in height.

Velocity gradient: The difference in velocity (u) over a distance (x), i.e. $\delta u/\delta x$.

Yellow eel: Growth stage of catadromous eels. Individuals are usually dark in colour with yellow hues.

CHAPTER 1

1 Introduction

Freshwater ecosystems (wetlands, lakes and rivers) constitute only 1.1% of the planet's surface area but contribute an estimated US$1.7 trillion in ecosystem services per year, 22 and 32 times more per unit area than marine or terrestrial habitats, respectively (Costanza *et al.,* 1997). Fish are a hugely important part of freshwater ecosystems, constituting an essential part of food webs (Dodds and Whiles, 2010), providing nutrient inputs and cycling (Janetski *et al.,* 2009), and even altering the physical landscape (Moore, 2006). They are also an important subsistence food source for many non-aquatic species (Cederholm *et al.,* 1999), including humans (Loring and Gerlach, 2010). In the Mekong River basin alone, some 55.3 million people depend on freshwater fish for nutrition and livelihoods, with an estimated average consumption of 56.6 kg person^{-1} year^{-1} (Baran *et al.,* 2007). Fish also have significant cultural importance for many populations worldwide (Reeves, 2003). For example, Pacific lamprey, *Lampetra tridentata*, are used in traditional ceremonies and celebrations by the indigenous peoples in the mid-Columbia River Plateau, being one of many species considered to have a shukwat (spirit) (Close *et al.,* 2002).

Many freshwater fish species undertake lifecycle essential migrations, seasonally or on an ontogenetic basis, for spawning, feeding, or refuge (Lucas and Baras, 2001). Iconic fish migrations include those of diadromous salmonids, of which millions of adults return to their native rivers to spawn annually (Gresh *et al.,* 2000), and the European eel, *anguilla anguilla*, of which adults and juveniles undertake a *ca.* 6000km journey to/from spawning grounds (thought to be in the Sargasso Sea) to freshwater rearing habitat in Europe, northern Africa and Mediterranean Asia (van Ginneken and Maes, 2005). Fish migrate, laterally, vertically and longitudinally within rivers systems, entering flood plains during the wet season for feeding, using deep water during the winter for thermal refuge, and along rivers to access unique habitat for spawning (Lucas and Baras, 2001). Even so called 'resident' species that are considered non-migratory and have very small home ranges (< 100 m) undertake short distance migrations and fish movements sporadically over time that are critically important components of meta-population dynamics, resource management, evolution, and speciation (Fausch *et al.,* 2002).

However, humans have been modifying river systems for millennia, with the earliest recorded impounding of a water course occurring some 5000 years ago (Goudie, 2013). Reasons for modification include flood prevention, irrigation, power generation, navigation, gauging and to provide a reliable source of water (Goudie, 2013). Modification usually takes the form of damming (including weirs and barrages), channelization, or water abstraction (often in vast quantities for power plant cooling) (Goudie, 2013). The rate of modification has increased dramatically in recent years and it is now estimated that over half of the world's large river systems are fragmented (Nilsson *et al.,* 2005). This includes over 45,000 dams greater than 15 m high (World Commission on Dams, 2000) and likely orders of magnitude more smaller obstructions. The impact of such barriers on fish movement depends on factors such as: obstruction type and size, river hydrology, and species-specific features such as swimming capacities, behaviour, and timing of migration (Northcote, 1998). However, even very low head barriers (< 2 m high) can restrict (Lucas and Frear, 1997) or completely block (Russon *et al.,* 2011) fish movement, effect assemblages by reducing diversity (Porto *et al.,* 1999), and limit gene flow between populations (Junker *et al.,* 2012). High head barriers (> 5 m high) are usually completely impermeable to upstream fish movements (Xie, 2003) and dramatically reduce the availability of essential habitat (Hall *et al.,* 2011). In addition, at hydropower facilities, high levels of mortality can occur during the downstream movement of fish through hazardous routes (e.g. through turbines and overspills) (Coutant and Whitney, 2000; Larinier, 2008).

Worldwide, many populations of freshwater fish are in decline (Kruk, 2004; Nelson *et al.,* 2002; Dekker, 2007; Gustafson *et al.,* 2007; Burkhead, 2012). Significant declines are frequently associated with human modification/development of rivers (Moser *et al.,* 2002; Winter and Van Densen, 2001). For example, diadromous species such as the European eel, Amur sturgeon, *Acipenser schrenckii*, and Chinese paddlefish, *Psephurus gladius*, are critically endangered (Ruban and Qiwei, 2010; Qiwei, 2010; Jacoby and Gollock, 2014) and heavily in decline, with barriers to migrant life-stages considered to be a key limiting factor to a self-sustaining population of each (Qiwei *et al.,* 1997; Feunteun, 2002; Dekker, 2007). In addition, species such as the river lamprey, *Lampetra fluviatilis*, although not endangered (Freyhof, 2013a) have declined dramatically since the 1970's (Kelly and King, 2001), with barriers to migrant life stages severely limiting their access to essential spawning habitat (Igoe *et al*., 2004; Lucas *et al.,* 2009). In extreme cases populations have already become extinct. For example, in the Western United States, habitat degradation has been linked with the extinction of 29% of historic Pacific salmon populations (Gustafson *et al.,* 2007); in China, the construction of the Gezhouba dam resulted in the extinction of the reeves shad, *Tenualosa reevesii*, in the Qiantang River; and in France, obstructions have caused the extinction of entire stocks of salmon in the Rhine, Seine and Garonne rivers (Larinier, 2001). If present trends continue, further losses are expected with 78% of the native salmonids in California (Katz *et al.,* 2013) and 30 more freshwater species in North America as a whole (Burkhead, 2012) predicted to be extinct within the next century.

Many species now receive specific protection under legislation. For example, the Salmon and Freshwater Fisheries Act (1975) (England and Wales), the Eels Regulations (2009) (England and Wales), the Bern Convention (1982) (EU), the Habitats Directive (1992) (EU), the Convention on International Trade in Endangered Species of Wild Fauna and Flora (1975) (International), and the Endangered Species act (1973) (US). In addition, freshwater fish receive protection in more general terms, in Europe, under the Water Framework Directive (WFD) (2000/60/EC), which considers free passage and undisturbed migration of fish as a key component to restoring and managing watersheds (Weyand *et al.,* 2005), in the United States, under hydropower licensing, which requires that fish are provided with a safe and timely passage option past dams (Odeh, 1999), and in Canada, where the ultimate goal for habitat compensation programmes is No Net Loss (NNL), where restoration efforts legally must result in no decrease in fish producing capacity (Quigley and Harper, 2006).

In an effort to re-establish fluvial connectivity, reverse population declines, and conform to legislative requirements, a range of mitigation strategies have been developed, including the installation of fish passes at structural barriers to migration (Beach, 1984; Larinier and Marmulla, 2004; Solomon and Beach, 2004). Unfortunately, fish passes generally perform poorly for the entire fish community (Thiem *et al.,* 2013) with even target species not being able to pass as well as previously thought (Naughton *et al.,* 2005). To maintain a sustainable population, fish passes should facilitate the passage of a high proportion of individuals (Lucas and Baras, 2001). The majority of fish passes do not come close to achieving this (Bunt *et al.,* 2012). This is often because fundamental knowledge of how fish interact with the complex hydrodynamic conditions within fish passes is lacking (Castro-Santos *et al.,* 2009) or because fish display complex behaviours, such as rejecting accelerating velocity gradients associated with downstream bypass intakes (Kynard and Buerkett, 1997) (factors particularly relevant to this body of research). Even when passage is satisfactory, other negative effects of barriers, including delay and high energetic expenditure during migration, can have detrimental effects on fitness (see Noonan *et al.,* 2012). For a passage facility to function properly fish must not only be able to find the fish pass but have the ability and inclination to successfully ascend/descend it (Larinier, 2001; Aarestrup *et al.*, 2003). As such, both behaviour and swimming performance are critically important for successful passage (Castro-Santos *et al.*, 2009). This makes fish passage a complex phenomenon, especially considering the diversity in behaviours, morphology, and swimming ability of the different species attempting to use passes (Thiem *et al.,* 2013). Fish passage research is a growing area of fisheries science (Roscoe and Hinch, 2010) but there are many challenges still to overcome if vulnerable freshwater species are to be conserved.

1.1 Research aim and objectives

The broad aim of this study is to:

1) Advance scientific knowledge to aid in the development of methods to improve fish passage at migration barriers.

To meet this aim the following objectives were formulated:

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

2) Assess how fish utilise complex hydrodynamic conditions in a highly controlled and well measured experimental environment.

3) Assess a new method to improve the upstream passage of weaker swimming species at a commonly occurring low-head barrier.

4) Assess a novel method to reduce the rejection rate of a representative salmonid during downstream passage through an accelerating velocity gradient.

1.2 Thesis overview

The literature review undertaken to meet Objective 1 is presented in Chapter 2. Objectives 2, 3, and 4 were met by undertaking experiments in a large indoor recirculating flume, the results of which are presented in Chapters 4, 5, and 6, respectively. The results chapters are presented as stand-alone sections of research that independently introduce, report, and discuss the experiments undertaken to meet the aforementioned objectives. Chapter 3 outlines the general methodologies used during the experimental research and discusses the rationale behind their selection. In addition, Chapter 3 gives an overview on the ecology, distribution and conservation status of each fish species used during this research. Chapter 7 discusses all the results obtained in relation to the thesis aim, highlighting how the knowledge gained may be applied to improving practices concerning fish passage. Areas for future research and conclusions are highlighted including how the results provide a novel contribution to scientific understanding, their research impact and societal importance.

CHAPTER 2

2 Literature review

2.1 Fish passes: history, design and function

Fish passes have been used to facilitate the migration of fish past obstructions for almost 300 years (Clay, 1995). They can be broadly categorised into those that are designed to facilitate either the upstream or the downstream passage of fish, although many have dual functionality. There are many different types of fish pass but they are essentially:

> '…a water passage around or through an obstruction, designed to dissipate the energy in the water in such a manner as to enable fish to ascend… *or descend*… without undue stress' (Clay, 1995).

For upstream migrating fish, the primary impact of riverine obstructions is that they prevent individuals reaching lifecycle essential habitat (Lucas and Baras, 2001). Common types of upstream passes include *lifts, locks, pool and weir*, *pool and orifice*, *vertical slot*, *Denil*, *eel ladders,* and *nature-like* (Clay, 1995, Odeh, 1999) (Figure 2.1). All types except *lifts and locks* rely on a fish volitionally ascending the pass. Fish *lifts* consist of a mechanical system that first trap the migrating fish in a vessel located at the base of an obstruction, and then raises and empties them upstream (Travade and Larinier, 2002) (Figure 2.1a). Fish *locks* operate much like navigation locks. Fish enter into a large chamber downstream of the obstruction and the water level is gradually raised to that of the upstream reservoir to permit passage (Figure 1b). *Pool and weir*, *pool and orifice*, and *vertical slot* passes all rely on a series of pools in steps leading from above to below an obstruction (Figure 2.1c-e). The primary difference between each type stems from how the water flows between pools. In *pool and weir* passes the water flows over the top of the baffles dividing each pool (Figure 2.1c). In *pool and orifice* passes the water flows through submerged orifices in each baffle (Figure 2.1d). In *vertical slot* passes the water flows through an opening that spans the height of each baffle (Figure 2.1e). Fish pass upstream by jumping over or passing through each baffle to the next pool. In *pool-type* passes energy is dissipated through turbulent processes in each pool. Although it eludes simple description, turbulence is characterised by vortical flow of a wide range of temporal and spatial length scales (Pope, 2000). Within each pool, energy is absorbed, redistributed, and dissipated, via turbulent processes, as heat due to viscous friction forces. Ideally pool-type passes are designed so that the residence time of water in each pool is large enough to allow a significant proportion of the mean kinetic energy to be dissipated before the water flows past the next baffle (Clay, 1995). As such, mean flow velocity is reduced. Denil fish passes consist of a sloped channel with vanes on the side and bottom that cause part of the flow to turn back in on itself. The water turned by the vanes interacts with the main flow creating a reduced overall velocity through the pass (Clay, 1995). The pass is named after its designer, G. Denil, who was one of the first people to undertake systematic scientific studies on the hydrodynamics of fish passes (Denil, 1909; 1938). *Eel ladders* are species specific and rely on an eel's ability to crawl through/over rough substrates (Legault, 1988). A typical eel ladder consists of a sloped channel, lined with a roughness element, which surmounts an obstruction (often multiple tiers with resting pools). Water is pumped through the ladder and eels ascend by climbing through the wetted substrate (Solomon and Beach, 2004). In recent years there has been a trend towards providing more natural conditions for fish to pass obstructions (Aarestrup *et al.,* 2003; Santos *et al.,* 2005; Wang *et al.,* 2011). Such *nature-like* passes (Figure 2.1h) in theory provide a diverse range of hydrodynamic conditions that mimic the surrounding environment and enable all native fauna including invertebrates to pass, or even occupy it as habitat (Castro-Santos *et al.,* 2009). A huge amount of variation exists among and within each pass type, governed by physical factors such as head-difference, site size, and available discharge (Clay, 1995).

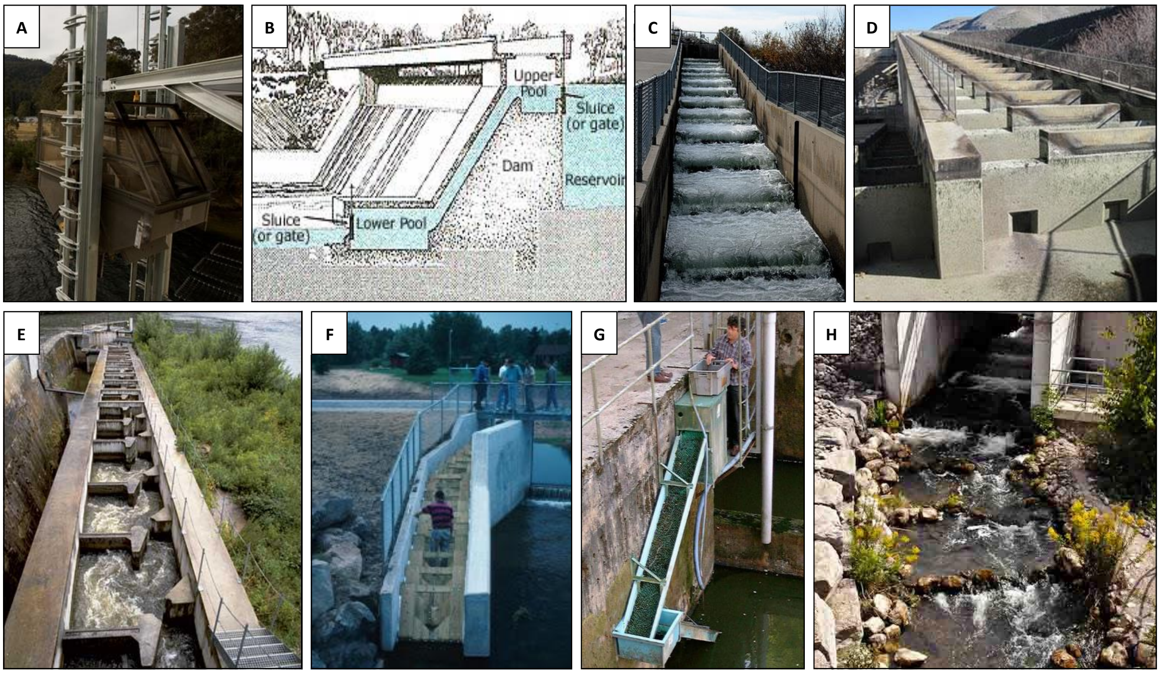


Figure 2.1 Example of a *lift* (a), *lock* (b), *pool and weir* (c), *pool and orifice* (d), *vertical slot* (e), *Denil* (f), *eel ladder* (g), and *nature-like* (h) fish pass.

For downstream migrating fish, anthropogenic infrastructure can delay or prevent the movement of individuals (Raymond, 1979; Bentley and Raymond, 1979; Venditti *et al.,* 2000), but the primary impact is the high level of injury/mortality that can occur due to passage through hazardous routes (e.g. through hydropower turbines, abstraction points, and overspills) (Taylor and Kynard, 1985; Stokesbury and Dadswell, 1991; Heisey *et al.,* 1992; Navarro *et al.,* 1996; Winter *et al*., 2006, Calles *et al.,* 2010). Sources of injury/mortality include: blade strike, pressure change, gas supersaturation, and vertical drops, and, indirectly: stress, disorientation, and increased susceptibility to predation and disease (see Cada *et al.,* 1990; Coutant and Whitney, 2000; Abernethy *et al.,* 2001; Budy *et al.,* 2002; Larinier, 2008). Historically, fisheries research focussed primarily on facilitating upstream passage (Katopodis and Williams, 2012; Larinier, 2008). Technologies that allow the safe downstream movement of fish are less well developed (Larinier, 2008). Typically, mitigating for the impact of obstructions on downstream migrating species involves the screening of hazardous routes, using either physical or behavioural devices to guide fish towards a favourable bypass channel. The most common type is geared towards salmonids and involves the use of physical screens to guide fish towards a bypass entrance located at the surface (Larinier, 2008; Greenberg *et al.,* 2012) (Figure 2.2). However, a diverse range of behavioural guidance systems are also used, including louvers (Kynard and Buerkett, 1997), light (Larinier and Boyer-Bernard, 1991; Croze and Larinier, 1999; Gosset & Travade, 1999), shade created by overhead cover (Greenberg *et al.,* 2012), sound

(Gosset & Travade, 1999; Maes *et al.,* 2004), infrasound (Sand *et al.,* 2001), electricity (Gosset & Travade, 1999), bubble screens (Welton *et al.,* 2002), or combinations of these (e.g. Kynard and O'Leary, 1993). In cases where conventional systems are not feasible more unique methods of facilitating both up and downstream passage do exist, such as trap and transfer schemes (e.g. Muir *et al.,* 2006).

Figure 2.2 Example of a typical small-scale guidance facility for downstream moving fish, consisting of an angled physical screen to deflect fish away from a detrimental route (in this case an irrigation canal) towards a bypass channel (surface entrance). Solid arrow indicates direction of bulk flow.

2.2 Fish pass effectiveness/efficiency

How well a fish pass functions can be assessed at two levels; its effectiveness or efficiency. Effectiveness is a qualitative concept and concerns whether a structure is capable of passing its target species (Larinier and Marmulla, 2004). A limitation of measuring effectiveness alone is that although a fish pass may facilitate the passage of a large number of individuals and a variety of species, this may represent only a small fraction of those trying to negotiate the structure. For example, Mallen-Cooper and Brand (2007) highlight that although a *pool and orifice* pass located in Australia passed 25,000 fish over a 5 year period, that this likely represented < 1% of those that wished to ascend. Common methods to assess passage effectiveness include trapping (e.g. Briand *et al.,* 2002), automated fish counters (e.g. Gowans *et al.,* 1999), or, at a coarser scale, via assessment of fish assemblages above and below a barrier (e.g. electric fishing - Santos *et al.,* 2006). Efficiency is a quantitative measure of a fish passes performance. It is the proportion of fish present at an obstruction which then enter and successfully move through the pass in an acceptable period of time (Larinier and Marmulla, 2004). Measures of passage efficiency are much more ecologically informative as they give an indication of the proportion of fish that wish to pass an obstruction that are able to. Common methods to assess passage efficiency include telemetry (e.g. Bunt *et al.,* 1999; Aarestrup *et al.,* 2003) or mark and recapture studies (e.g. Bunt, 2001).

Roscoe and Hinch (2010) reviewed 96 articles between 1960 and 2008 to ascertain how the effectiveness/efficiency of fish passes has been investigated. They found that research in the tropics had broader taxonomic scope than that from temperate locations; salmonids were the most studied family (58%); the majority of studies focused on adults and included exogenous (e.g. environmental, structural, and behavioural) but not endogenous (e.g. physiological) factors that influenced passage; and that few studies monitored migration after passage. They also highlighted that the number of studies undertaken has increased with time, with 66% of the articles published in the last ten years of the review period. More than half of the studies (52%) originated in North America, 30% from Europe, and 18% from South America and Australia. Increasing frequency and global distribution of studies in recent years highlights that fish passage is a growing area of research. However, the authors found that few studies dealt with passage efficiency and that most only recorded the abundance and species composition of fish using a facility (measures of effectiveness).

Bunt *et al.* (2012) reviewed the attraction and passage efficiency of different types of upstream fish pass. Attraction efficiency was defined as the proportion of a known quantity of fish that found the pass entrance. Passage efficiency was defined as the proportion of fish that found the fish pass entrance which then successfully ascended and exited upstream. Attraction efficiency was highly variable for *pool and weir* (mean = 77%, range = 29 - 100%), *vertical-slot* (mean = 63%, range = 0 - 100%), *Denil* (mean = 61%, range = 21 - 100%), and *nature-like* (mean = 48%, range = 0 - 100%) passes and inversely proportional to passage efficiency. The highest passage efficiency was for *nature-like* (mean = 70%, range = 0 - 100%), followed by *Denil* (mean = 51%, range = 0 - 97%), *vertical-slot* (mean = 45%, range = 0 - 100%), and then *pool-and-weir* (mean = 40%, range = 0 - 100%) passes. The authors found that variation in attraction was driven by biological characteristics whereas variation in passage was related to pass type, slope and elevation change.

Noonan *et al.,* (2012) reviewed 65 articles from between 1960 to 2011 and assessed the influence of fish size, species, and pass characteristics on passage efficiency. The authors found that, on average, downstream passage efficiency (68.5%) was higher than upstream (41.7%) and that salmonids were more successful than non-salmonids in passing both upstream (61.7 vs. 21.1%, respectively) and downstream (74.6 vs. 39.6%, respectively). Mean upstream passage efficiencies for salmonids and non-salmonids were *ca.* 71 and 42% for *pool and weir*, 53 and 31% for *pool and slot*, 63 and 22% for *nature-like*, 21 and 14% for *Denil*, and 33 and 11% for *lock/lift* type passes. The authors also found that mean passage time was longer for non-salmonids (5.52 days, S.E. = 1.61, n = 3) than for salmonids (0.87 days, S.E. = 0.10, n = 14). The best predictors of fish passage efficiency were order of fish (i.e. salmonids vs. non-salmonids), type of pass, and length of pass. Data on the range of efficiencies for each pass type were not presented in Noonan *et al.* (2012) but the authors highlighted that although numerous articles reported passage efficiency within the desired range to maintain a stable population (90 - 100%: Lucas and Baras, 2001), many more reported much lower efficiencies, including several facilities with 0% (e.g. Laine *et al.,* 1998; Bunt *et al.,* 2000; Knaepkens *et al.,* 2006; Mallen-Cooper and Brand, 2007).

Pompeu *et al.* (2012) reviewed fish passage at 16 facilities in South America and found that typically > 60% (range: 29 - 97%) of species found downstream of a dam were observed using the corresponding pass at some point, but that a few species (3 - 5) dominated in terms of abundance (> 80%). Once in the pass the proportion of species that successfully ascended ranged from 0.5 - 98%. When passage efficiency was evaluated, which was infrequently, it was generally low (< 14%). As such, in South America, despite recent high investment and effort, most fish passage facilities are considered ineffective for conservation purposes (Pompeu *et al.,* 2012). In some cases they are even considered to be promoting regional fisheries collapse by acting as ecological traps (see Lopes *et al.,* 2007; Pelicice and Agostinho, 2008).

It should be noted that although passage efficiency provides a very useful metric to assess fish passage facilities, direct comparisons between different pass types should be undertaken with caution. For example, although *nature-like* passes seem to function well and do so for a range of species (including weaker swimming species - Calles and Greenberg, 2007), it is important to consider that they tend to be built at sites with very low slope. It is possible that the superior passage performance of this pass type is largely attributable to slope rather than to any other intrinsic benefit of their design (Bunt *et al.,* 2012). Therefore, physical biases (e.g. head difference, slope, discharge etc.) should be considered when comparing efficiencies across pass types.

Another important consideration is the sheer range of fish species that reside in freshwater systems. Species diversity plays an important role in ecosystem productivity, decomposition, nutrient cycling, resistance/resilience to environmental perturbations, and the provision of ecosystem services (Loreau *et al.,* 2001; Balvanera *et al.,* 2006). Increased recognition of the need to promote ecosystem restoration as a whole (Poudevigne *et al.,* 2002) has led to growing support for the provision of passage past barriers for all fish species that reside within a watershed (Agostinho *et al.,* 2002; Thiem *et al.,* 2013; Williams *et al.,* 2012). However, only 4 and 38% of studies evaluating fish passage in America and Europe, respectively, assessed the whole community (Roscoe and Hinch, 2010), and in general fish passes are much less effective for non-salmonids than they are for salmonids (Noonan *et al.,* 2012).

It is clear that fish passes are not performing as well as they need to be to sufficiently mitigate habitat fragmentation for the complete fish community across a range of environmental conditions (Noonan *et al.,* 2012; Bunt *et al.,* 2012), with a large number preventing or delaying passage of both target (e.g. Aarestrup *et al.,* 2003; Caudill *et al.,* 2007; Naughton *et al.,* 2005; Bunt *et al.,* 2000) and non-target species (e.g. Mallen-Cooper and Brand 2007; Haro and Kynard 1997; Parsley *et al.,* 2007). If vulnerable species/ecosystems are to be conserved there is a need to better understand the factors that limit the efficiency of fish passes.

2.3 Factors limiting passage

Castro-Santos *et al.* (2009) defines the ideal fish pass from a biological perspective as one that:

> '…makes the dammed reach transparent to the movement of native species, allowing unfettered access to free-flowing reaches above and below the obstacle.'

The authors highlight that in order for this to be achieved the ideal fish pass should have the following characteristics:

1) any individual of any native species wishing to move upstream or downstream must be able to enter the fish pass without experiencing any delay,
2) entry is immediately followed by successful passage, with
3) no temporal or energetic costs, and
4) no stress, disease, injury, predation, or other fitness-relevant costs associated with passage.

Although an idealistic concept, it is clear that most fish passes around the world are failing to even come close to enabling the 'transparent' movement of fish past barriers (Bunt *et al.*, 2012; Noonan *et al.,* 2012; Pompeu *et al.*, 2012). But why is this? Temporarily ignoring secondary fitness costs, the fundamental application of a fish pass is to promote the passage of fish past an obstruction. To do this a fish must be able to 1) find, 2) enter, and 3) pass through the structure. Despite seeming relatively simple to facilitate, many fish passes fail on one or more of these fundamental principles.

2.3.1 Factors limiting the efficiency of upstream passage infrastructure

For upstream migrating fish both swimming performance and behaviour play a critical role in passage (Williams *et al.,* 2012). In general fish are attracted to areas of high flow as they migrate upstream (Larinier, 2008). The most frequent causes of fish failing to find/enter an upstream passage facility include poorly located entrances (e.g. located too far downstream or at an inappropriate depth) (Bunt, 2001; Moser *et al.,* 2002) or flows that are insufficient to attract fish away from other areas with higher distracting discharge (Bunt *et al.,* 1999; Gowans *et al.,* 1999; Bunt, 2001; Oldani and Baigun, 2002; Sprankle, 2005; Foulds and Lucas, 2013). In cases where fish have failed to find/enter a fish pass significant improvements have been made by increasing attraction flow (Larinier *et al.,* 2005); screening off competing attraction sources (e.g. dam tail race) (Gowans *et al.,* 1999); enlarging and relocating the fish pass entrance (Bunt, 2001); providing olfactory cues (e.g. conspecifics - Briand *et al.,* 2002); and altering attraction flow hydrodynamics (Piper *et al.,* 2012) or temperature (Solomon and Beach, 2004). However, interspecific differences in migratory behaviour also heavily influences the ability of a fish to find/enter a fish pass. For example, fish pass entrances located at different depths promote the passage of species depending on the height in the water column at which they predominantly migrate (Moser *et al.,* 2002).

Historically, most upstream fish passage facilities were designed for commercially important species, such as highly mobile salmonids (Katopodis and Williams, 2012), which have high burst and endurance swim speeds (Beamish, 1978), and can leap remarkably high (Mueller *et al.,* 2008). Such salmonid passes (e.g. *Denil* and *pool-type* passes) typically perform poorly for juvenile and weaker-swimming non-salmonid species as vertical drops and high velocities inhibit their ability to ascend (e.g. Slatick and Basham 1985; Jungwith, 1996; Bunt *et al*., 1999, 2000, 2001; Cooke *et al*., 2005, Knaepkens *et al.,* 2006; Mallen-Cooper and Brand, 2007; Noonan *et al*., 2012). For example, catadromous eel (*Anguilla* spp*.*) and anadromous lamprey (*Petromyzon* and *Lampetra* spp.), are both weaker swimming fish, for which conventional upstream salmonid passes are often ineffective (e.g. Laine *et al.,* 1998, Foulds and Lucas, 2013). In addition, poor passage efficiency has been specifically linked to high flow velocities for a number of other weaker swimming species (e.g. American shad, *Alosa sapidissima* - Haro and Kynard, 1997; bullhead, *Cottus gobio* - Knaepkens *et al.,* 2006; Australian smelt, *Retropinna semoni*, golden perch, *Macquaria ambigua*, and bony herring, *Nematalosa erebi*, - Mallen cooper and Brand, 2007), typically because conditions within the pass exceed their swimming performance.

Turbulence has also been linked with poor passage efficiency (e.g. Barry and Kynard, 1986; Haro and Kynard, 1997; Lucas *et al.,* 1999; Bunt *et al.,* 2000; Mallen-Cooper and Brand, 2007; Foulds and Lucas, 2013). However, finding a direct causal influence of turbulence on passage is difficult because fish behaviour and swimming performance in turbulent flows is complex (Liao, 2007) and biologically relevant turbulence-processes are difficult to describe (Lacey *et al.,* 2012). As such, the causal influence of turbulence on poor passage efficiency is often only alluded to. For example, Haro and Kynard (1997) found that: ‘High water velocity, air entrainment, and turbulence of a modified Ice Harbour fishway design appeared to inhibit American shad and sea lamprey, *Petromyzon marinus*, passage by disrupting upstream migratory motivation and visual and rheotactic orientation’; Lucas *et al.* (1999) report that: ‘It is conceivable that certain cues associated with baffle fish passes, such as high levels of turbulence, and a complex spatial environment may deter cyprinids from proceeding…’; Bunt *et al.* (2000) report that: ‘Behaviour modifying hydraulic conditions including turbulence, entrained air, backcurrents and whirlpools in fishway resting areas may delay or prevent successful upstream passage of walleyes’; Mallen-Cooper and Brand (2007) report that: ‘…poor passage of native fish is likely related to high turbulence, high water velocities or the baffle design not suiting fish behaviour'; and Foulds and Lucas (2013) report that: 'At the Denil fishway, the inherent turbulence behind the baffles, high water velocities, the high gradient slope and the length of the fishway are likely to act as behavioural and physical impediments to ascent'. As such, a better understanding of how turbulence affects swimming performance and behaviour in relation to fish passage is required (Mallen-Cooper and Brand, 2007; Castro-Santos *et al.,* 2009; Vowles *et al.,* 2013). Indeed, it has been speculated that it may be possible to enhance fish passage through the judicious control of turbulent structure (Castro-Santos *et al.,* 2009). Lacey *et al.* (2012) outline four separate characteristics of turbulence (Intensity, Periodicity, Orientation, and Scale - IPOS framework) which may be important for fish swimming performance and behaviour, but which are rarely all measured under controlled laboratory conditions (e.g. Smith *et al.,* 2005; 2006; Cotel *et al.,* 2006; Silva *et al.,* 2011) let alone in the field (e.g. Enders *et al.,* 2009a).

So far, laboratory studies have revealed that increases in the intensity of turbulence (magnitude of flow fluctuations about the mean) typically reduce swimming performance (Pavlov *et al.,* 1982; Shtaf *et al.,* 1983; Pavlov *et al*., 1994; Pavlov *et al.,* 2000; Lupandin, 2005) and increase energetic expenditure (Enders *et al.,* 2003; 2004; 2005a). When turbulent length scales are proportional to body length, fish can become destabilized as the rotational forces push the head and tail in opposite directions (Webb and Cotel, 2010). If the momentum of the rotational forces is large enough to overwhelm a fish's control mechanisms this can lead to a sudden change in posture and a breakdown in swimming trajectory (Webb and Cotel, 2010). In these circumstances a significant reduction in swimming performance is observed (Pavlov *et al.,* 2000; Lupandin, 2005; Tritico and Cotel, 2010), with eddies rotating about a horizontal axis having a greater effect on fish stability than eddies rotating about a vertical axis because most fish have reduced flexibility in this plane (Tritico and Cotel, 2010). However, further studies have highlighted the ability of fish to exploit specific predictable or stable flow structures to their advantage (Webb, 1998; Liao, 2003a; b; Przybilla *et al.,* 2010). For example, by slaloming between the alternately shed vortices generated in a Kármán street (von Kármán, 1937) fish can not only benefit from the reduced velocities in the wake of an immersed bluff body but capture energy from the vortices and maintain position with reduced muscle activity (termed the Kármán Gait) (Liao *et al.,* 2003b).

In fish passes, turbulence is typically quantified as Energy Dissipation Factor (EDF) in Watts per cubic metre (W m^{-3}) (Rodriguez *et al.,* 2006; Mallen-Cooper and Brand, 2007). The maximum recommended value of EDF for a fish pass varies considerably: from 192 W m^{-3}, for highly mobile diadromous salmonids (Bell, 1991), to 92 W m^{-3}, for weaker swimming small (10-25 cm) potamodromous non-salmonids (Mallen-Cooper, 1999), with even lower values, *ca.* 40 W m^{-3}, being linked with the successful passage of very small fish (< 10 cm) (Stuart and Mallen-Cooper, 1999). However, EDF is a very simplistic metric to surmise a complex three-dimensional flow phenomenon like turbulence (see Lacey *et al.,* 2012). Recent work shows that turbulent parameters such as relative Turbulence Intensity (TI - the standard deviation of the local flow velocity divided by its mean - dimensionless) (Smith *et al.,* 2005; Cotel *et al.,* 2006; Russon *et al.,* 2011), Turbulent Kinetic Energy (TKE - the kinetic energy associated with turbulent fluctuations - J m^{-3}) (Smith *et al.,* 2006; Silva *et al.,* 2011), Reynolds Shear Stress (τ - the momentum flux due to turbulent fluctuations - N m^{-2}) (Silva *et al.,* 2011; 2012a; b), and eddy size and orientation (Tritico and Cotel, 2010), can affect fish behaviour and swimming performance and may be important determinants of the efficiency of fish passage facilities. To complicate matters, fish response to turbulence can also be interspecific (Pavlov and Lupandin, 1994) and intraspecific (Skorobogatov *et al.,* 1996) and dependent on habituation (Skorobogatov *et al.,* 1996) and physiological condition (Lupandin and Pavlov, 1996).

Importantly, there is a tendency for scientists to attempt to find statistical links between patterns of fish distribution/movement and one or more of any number of turbulent flow characteristics, such as TI, relative TI (k), TKE, turbulent length scale (TLS), or τ (e.g. Smith *et al*., 2005; 2006; Russon *et al*., 2011; Silva *et al*., 2011; 2012a; 2012b; Duarte *et al*., 2012) without considering the causal links of these relationships (see Johnson and Rice, 2014). Hence, the biophysical interpretation of these statistical links is often obscure. In addition, there is a lack of research that has investigated the behaviour of fish in relation to turbulent flows that adequately control and describe hydrodynamic conditions in the absence of confounding variables. For example, attempts to quantify habitat use by fish in the field typically produce mixed results (e.g. Heggenes *et al*., 1991; Facey and Grossman, 1992; Jowett and Richardson, 1995; Mäki-Petäys *et al*., 1997; Cotel *et al*., 2006; Enders *et al*., 2009a) because space use is influenced by multiple confounding variables impossible to control in situ (e.g. food, predators, competitors, and mates). In general, there is still a lack of information on how turbulent flow conditions effect fish swimming performance and behaviour. For example, the composition of the turbulent flows (e.g. eddy characteristics) over the paths chosen by fish (Cotel and Webb, 2012) and the spatial and temporal scales of hydrodynamic flow features that are beneficial versus detrimental to station holding are largely unknown (but see Akanyeti and Liao, 2012).

Consequently although turbulence is likely to be affecting fish passage, definitive evidence is lacking because the impact it has on behaviour and ecology is still poorly understood. Williams *et al.* (2012) highlighted that the greatest improvements in fish passage facilities have resulted from research identifying how fish react to varying and well-defined hydrodynamic conditions (i.e. conditions they avoid or are attracted to). More research into how fish use turbulent flow fields would seem to be an important next step in improving upstream fish passage.

2.3.2 Factors limiting the efficiency of downstream passage infrastructure

The efficiency of downstream guidance systems, both physical and behavioural, has been found to vary dramatically due to interspecific differences in behaviour. For example, eel display a weaker 'behavioural' guidance effect upon encountering trashracks in comparison to salmonids (Larinier, 2008). This may be because eel tend to respond to physical screens upon contact rather than to associated changes in local hydrodynamics (Russon *et al.,* 2010). In addition, eel tend to be lucifugous (avoid light) (Hadderingh *et al.,* 1992; 1999) whereas light sources have been successfully used to attract other species (Larinier and Boyer-Bernard, 1991; Croze and Larinier, 1999; Gosset & Travade, 1999). Maes *et al.* (2004) found that sound (20 - 600 Hz) produced an avoidance response for *ca.* 60% of fish, but that it varied between species, with clupeids more effected than river lamprey and Pleuronectiformes (flat fish). To compound the problem, the efficacy of a particular guidance technique has been shown to vary between barriers for the same species/lifestage within the same river system (Greenberg *et al.,* 2012); indicating that additional site specific or temporal factors (e.g. time of day / illumination) may be influencing fish behaviour (e.g. Kynard and Buerkett, 1997). Animal behaviour is complex and is known to vary within individuals according to motivational status (e.g. Colgan, 1993), habituation (Knudsen *et al*., 1992, 1997; Mueller *et al*., 1998), prior experience (Kieffer and Colgan, 1992), context (Jelbert *et al.,* 2014), selective attention (Paulk *et al.,* 2014), emotion (Giske *et al.,* 2014), and may even be irrational (McNamara *et al.,* 2014). Such factors make generalising the behavioural response of a species difficult. In general behavioural screens tend to be less effective and more variable between species than physical screens although both can perform poorly (see Turnpenny and O'Keefe, 2005). However, it is not always feasible to install physical screens and in their absence behavioural devices are required (Turnpenny and O'Keefe, 2005). At present no clear behavioural solution exists that works effectively for the whole community (Williams *et al.,* 2012).

Fish have also been observed to actively avoid bypass entrances (Kynard and Buerkett, 1997; Larinier and Travade, 2002), thus reducing the efficiency of downstream passage infrastructure (Kynard and Buerkett, 1997). Experimental research suggests that juvenile Atlantic salmon, *Salmo salar*, and American shad are reluctant to enter the unnatural transitional conditions of accelerating water velocity at bypass entrances (Haro *et al.,* 1998). Further research supports this assumption, as Pacific salmon smolts, *Oncorhynchus spp.* (Kemp *et al.,* 2005; 2006; Enders *et al.,* 2009b; Vowles *et al.,* 2014), brown trout (Russon and Kemp, 2011a), and European eel (Piper *et al.,* 2015; Newbold *et al.,* 2015) also avoid areas of rapid flow acceleration. Presumably fish have evolved to reject an accelerating velocity gradient to avoid detrimental migration pathways (Enders *et al.,* 2012). However, such rejection behaviour at anthropogenic barriers can result in fish using alternative hazardous routes (Scruton *et al.,* 2007) and has been linked with increased delay and distance travelled prior to passage (Vowles *et al.,* 2014). Haro *et al.* (1998) successfully reduced the rejection rate of Atlantic salmon smolts by reducing the intensity of the velocity gradient at an experimental bypass intake (intake design modification). However, physical limitations (e.g. maximum bypass channel width / available discharge) may restrict the extent to which existing intakes can be modified. Vowles and Kemp (2012) hypothesised that illumination would reduce the rejection rate of fish at a velocity gradient, but found that responsiveness (avoidance) and delay of brown trout increased rather than decreased when multimodal stimuli were present. There appears to be a knowledge gap in regards to effective methods to stop fish rejecting bypass entrances, partly due to lack of research but also due to lack of sufficient knowledge on fish behaviour to effectively meet this requirement. Further research on the diversity of behaviours fish display in response to environmental stimuli and methods to reduce rejection rates at bypass entrances is warranted.

2.4 Additional considerations

From an operational perspective, fish passes should be designed, built, and operated as cheaply as possible (Castro-Santos *et al.,* 2009). An ideal fish pass in these terms would cost nothing to construct, would require no maintenance, use no water, power, or other resources to operate and would be free of licensing restrictions, whilst making the dammed reach completely transparent to fish movement (Castro-Santos *et al.,* 2009). Obviously it is not possible to create an ideal fish pass from both a biological and operational perspective but an appropriate compromise should be reached and it is important to remember that fish passes have to be built with socioeconomic restrictions in mind. A freestanding, concrete-reinforced, pool-type fish pass that takes no advantage of natural contours costs about US$2,600 per vertical metre, with annual expenses of about 1 - 2% of the capital cost (Clay, 1995). A *Denil* fish pass, costs about US$124,000 per vertical metre (Erkan, 2002) but has minimal maintenance and operation costs (Clay, 1995). Fish *locks* and *lifts* cost roughly US$2.6 million to install, with annual maintenance charges of 5% of the capital cost (Clay, 1995). In the UK a Larinier fish pass (a baffle type pass that functions on a similar principle to a Denil) costs between £19,000 - £250,000 depending on the scale of the installation, and a 28 m long nature-like pass *ca.* £70,000 (Environment Agency, 2011). Often funding to ease habitat fragmentation is limited and mitigation can only be undertaken at a select few barriers (Kemp and O'Hanley, 2010). As such, implementing cost-effective solutions is a primary concern when undertaking mitigation (Kemp and O'Hanley, 2010). Future fish passage research must, to some extent, focus on developing cost-effective technologies that are easily implementable at new infrastructure but also at the numerous and diverse range of barriers already in existence.

A lot of research is still required to improve the efficiency of fish passage technologies. Historically research took a trial-and-error approach and was not always effective (Katopodis and Williams, 2012). The successful development of efficient fish passage facilities occurs when engineers and biologists work together systematically to design structures based on the ability and willingness of fish to seek and accept the hydrodynamic conditions presented to them (Katopodis and Williams, 2012). However, such fundamental scientific research takes time whilst fish populations continue to decline (Allibone *et al.,* 2010; Moyle *et al.,* 2011). In the absence of fundamental knowledge, fisheries managers must continue to implement the most appropriate mitigation technologies available. As such, there is still a place for trial and error improvements in current technology as long as empirical observations are well documented and accessible to the wider community. Indeed, historic empirical documentation of fish passage systems has led to more comprehensive scientific research (Katopodis and Williams, 2012). As such, to advance the development of effective fish passage technologies, both fundamental and trial-and-error research, are appropriate.

Behaviour plays a key role in both upstream and downstream fish passage (Williams *et al.,* 2012; Katopodis and Williams, 2012; Kemp *et al.,* 2012). For fish passage to improve animal behaviour must be appropriately described (Vowles *et al.,* 2013). However animal behaviour is complex and can be influenced by complicated phenomenon (e.g. habituation - Goodwin *et al.,* 2014; context - Jelbert *et al.,* 2014; selective attention - Paulk *et al.,* 2014; emotion - Giske *et al.,* 2014). A key problem in analysing behaviour is that there is often a difference between what animals perceive and what they react to (response bias) (Green and Swets, 1966). Typically an animal's ability to perceive a stimulus is ascertained using invasive electrophysiological methods (Fay and Popper, 1974), by measuring the brainstem response of immobilized individuals (Kenyon *et al.,* 1998), or by behavioural means based on the principles of classical (Fay, 1988) or operant (Yan and Popper, 1992) conditioning which requires the training of the subject. These methods provide useful information on thresholds of discrimination, but are of limited use for defining the response of actively migrating wild fish that may or may not be inclined to respond to a stimulus when they detect it (Kemp *et al.,* 2012). Kemp *et al.* (2012) outlined the applicability of using Signal Detection Theory (SDT) (Tanner and Swets, 1954; Green and Swets, 1966) to understanding, quantifying and potentially manipulating the behaviour of actively migrating fish. SDT considers the relationship between magnitude and perceived intensity of a stimulus (signal) and the ability to discern between the signal and noise (discriminability). Discriminability is primarily influenced by the magnitude of the signal and the amount of external and internal noise. Importantly, SDT also accounts for internal bias; the probability of eliciting a response on detecting the signal. Psychophysical concepts such as SDT provide a useful framework to analyse fish behaviour (Kemp *et al.,* 2012) and may be useful in developing fish passage technology in the future.

2.5 Summary

For freshwater fish, a diverse range of passage technologies have been developed to reduce habitat fragmentation caused by anthropogenic infrastructure (Clay, 1995, Odeh, 1999; Travade and Larinier, 2002; Armstrong *et al.,* 2010). Historically fish passage design was driven by the need to facilitate the upstream passage of commercially important species, such as highly-mobile salmonids (Katopodis and Williams, 2012). Increased understanding of freshwater ecology and the importance of species diversity has highlighted the need to facilitate the unimpeded movement of all species/lifestages both up and downstream past barriers (Agostinho *et al.,* 2002; Thiem *et al.,* 2013; Williams *et al.,* 2012). However, much of the historic fish passage technology is poorly designed to promote the movement of weaker swimming non-salmonid species which often exhibit distinctly different behaviour and life history characteristics (e.g. eel, *Anguilla* spp.: Tesch, 2003 and lamprey, *Petromyzon* and *Lampetra* spp.*:* Kelly and King, 2001; Keefer *et al.,* 2011). For such species even very low head barriers can impede upstream movement (Russon *et al.,* 2011). Currently, although some fish passes are effective for their target species (e.g. Gowans *et al*., 1999), many are not (e.g. Naughton *et al.,* 2005), and very few, if any, provide passage opportunities for the whole community (Noonan *et al.,* 2012; Bunt *et al.,* 2012). The failure of fish passes to be effective for the whole community can be attributed to the diversity in behaviours, morphology, physiological capacity and swimming ability of the different species/lifestages that move within rivers (Thiem *et al.,* 2013).

The successful upstream passage of the whole community through a fish pass requires that velocities be sufficiently low to pass the species/lifestage with the weakest swimming ability (e.g. Mallen-Cooper and Brand, 2007). Within fish passes, water velocities are kept low through the dissipation of energy via turbulent processes (Clay, 1995). However, turbulence can reduce swimming performance (e.g. Lupandin, 2005; Enders *et al*., 2005a; Tritico and Cotel, 2010) and influence fish behaviour (Smith *et al.,* 2005; 2006; Cotel *et al.,* 2006; Silva *et al*., 2011; 2012a; b) and has been linked with poor passage efficiency in numerous cases (Barry and Kynard, 1986; Haro and Kynard, 1997; Lucas *et al.,* 1999; Bunt *et al.,* 2000; Mallen-Cooper and Brand, 2007; Foulds and Lucas, 2013). This creates contradictory pressures for those designing fish pass structures (Vowles *et al.,* 2013). In simplistic terms, it has been observed that fish can exploit turbulent flow regions characterized by coherent vortices to hold position and minimise energy expenditure (i.e. Liao *et al.,* 2003b; Taguchi and Liao, 2011). In contrast, fish tend to avoid flows that are less organized (i.e. more chaotic) and exhibit spatial and temporal scales that challenge their stability mechanisms (Liao*,* 2007). Ultimately, successful passage depends on fish finding hydrodynamic conditions they consider acceptable (Williams *et al.,* 2012). What is clear is that upstream fish passage research will benefit from a better understanding of the fundamental principles of how fish utilise complex flows (Castro-Santos *et al.,* 2009), and the hydrodynamic metrics that are most appropriate from a biological perspective to describe those flows (Lacey *et al.,* 2012; Vowles *et al.,* 2013).

Downstream passage is predominantly influenced by fish behaviour (Williams *et al.,* 2012). The diversity of behaviour between species heavily impacts the effectiveness of both physical (e.g. Russon *et al.,* 2010) and behavioural (e.g. Maes *et al.,* 2004) guidance systems. Currently, although physical screens are generally more consistently effective than behavioural (see Turnpenny and O'Keefe, 2005), there is no single solution that effectively guides all downstream moving species/lifestages (Williams *et al.,* 2012). In addition, at bypass entrances, fish tend to reject accelerating velocity gradients (Larinier and Travade, 2002), reducing the effectiveness of downstream passage facilities (Kynard and Buerkett, 1997). Some success in reducing the rejection rate of fish at bypass entrances has been achieved by modifying local hydrodynamic conditions (Haro *et al.,* 1998). However, fish behaviour is complex and influenced by a multitude of factors (e.g. time of day / illumination - Kynard and Buerkett, 1997; habituation- Goodwin *et al.,* 2014; context - Jelbert *et al.,* 2014; selective attention - Paulk *et al.,* 2014; emotion - Giske *et al.,* 2014). Further research on the diversity of fish behaviour in response to environmental stimuli and methods to reduce rejection rates at bypass entrances is warranted. Future fish passage research should not only be based on advances in novel technology that enable the complexity of the fluid environment to be determined at ever-finer resolution, but must also strive to improve methods by which animal behaviour is appropriately described (Vowles *et al.,* 2013)

CHAPTER 3

3 Research methodology

The following chapter provides details on the facilities, equipment, software, and fish species used during the research presented in this thesis, and rationale as to why specific techniques were employed. More detailed methodologies are provided in each research chapter (Chapters 4 - 6).

3.1 Flume facility

All practical experimentation was undertaken in a re-circulatory indoor open channel flume (Figure 3.1) located at the International Centre for Ecohydraulics Research (ICER) facility, University of Southampton, UK (50° 57’42.6”N, 1°25’26.9”W). The flume has a working length of 21.40 m, width of 1.38 m, and depth of 0.60 m. It has glass sided walls and a steel base (painted white), and is driven by three centrifugal pumps providing a maximum flow capacity of 0.47 $m^3 s^{-1}$ (individual capacities 0.09, 0.15, and 0.23 $m^3 s^{-1}$). The pumps can be used individually or in combination, with discharge further controlled by adjusting valves associated with each pump. The flume is fed via a sump filled with municipal tap water (pH: 7.8, Ammonia: 0ppm, Nitrite: 0ppm, Nitrate *ca.* 20ppm). Water depth within the flume is controlled using an overshot weir located at the downstream end of the channel. A standard double section of Item (profile 8, 80 x 40 mm - Item Industrietechnik, Germany) runs longitudinally along the top most edge of each wall, allowing structures associated with an experiment to be inserted into an otherwise uniform rectangular channel. The level of illumination was controlled by fully enclosing the flume with black sheeting (< 0.1 lux) or by undertaking trials during the hours of darkness. Overhead or side-mounted closed circuit video cameras were used to non-obtrusively monitor all experiments. Flume water temperature was continuously monitored using submersible temperature loggers (accuracy: ± 0.53°C) (HOBO Pendent temp/light logger, UA-002_08 - Onset Computer Corporation, USA).

Figure 3.1 Twenty one metre long indoor flume facility at the International Centre for Ecohydraulics Research (ICER) facility, University of Southampton, UK.

Undertaking flume rather than field experiments has advantages and disadvantages; both of which should be fully understood before work is undertaken (see Rice *et al.,* 2010). Flume work allows for the better control of dependent and confounding variables such as, but not limited to, discharge (Russen *et al.,* 2011), velocity (Tudorache *et al.,* 2007), illumination (Vowles and Kemp, 2012), and temperature (Lee *et al.,* 2003). In addition, flume studies allow data to be obtained at very fine-scale spatial resolution. For example, CCTV cameras in combination with appropriate video analysis software can be used to obtain sub-centimetre scale assessment of fish movement and kinematics at high frequencies (e.g. Liao, 2003) alongside hydrodynamic measurements at a similar resolution (e.g. Przybilla *et al.,* 2010). Despite recent technological developments, the most advanced field based telemetry systems (i.e. 3D acoustic telemetry) can only resolve fish positions down to *ca.* 0.5 m accuracy (e.g. Piper *et al.,* 2015). As such, although field studies provide valuable insights into large scale fish movements under realistic conditions, they can suffer from the subjective interpretation of behaviours in response to important environmental factors as a result of poor spatial resolution. To meet objectives 2 - 4 fine scale assessment of fish behaviour in response to hydrodynamic conditions and physical structures was required. As such, flume experiments provided the best option in each case. However, there is an argument that flume conditions are too different from natural conditions (e.g. olfactory cues and light and temperature regimes) to allow for direct relevance of the results, i.e. the idea of ‘realism’ (Rice *et al.,* 2010). As such, when undertaking flume experiments the upmost care should be taken to maintain an environment as near to representative of natural conditions as possible. During this research, this was achieved by undertaking work at or near representative river temperatures (see specific methodologies) and under a fixed illumination (< 0.1 lux). Differences in water chemistry, which it was impracticable to manipulate, were accounted for by slowly acclimating and habituating fish to local conditions (see section 3.2) (a common protocol to account for minor water chemistry/temperature differences between flume and holding tanks - Silva *et al.,* 2009; Russon and Kemp, 2011a).

3.2 Fish husbandry

Fish husbandry was undertaken in the four external holding tanks at the ICER facility (Figure 3.2). Each tank is 3000 litre with an individual gravity fed biological and mechanical filtration system and inline ultraviolet filter. Water is continuously aerated using a Venturi valve fitted on the return pipe of each filtration system and through a separate air pump. Water conditions were maintained through frequent water changes with dechlorinated municipal tap water (pH: 7.8, Ammonia: 0ppm, Nitrite: 0ppm, Nitrate: < 40ppm). Tank temperatures were continuously logged using submersible temperature loggers (accuracy: ± 0.53°C) (HOBO Pendent temp/light logger, UA-002_08 - Onset Computer Corporation, USA). Experimental trials were not undertaken if the temperature of the holding tanks differed by more than 4°C compared to that of the flume.

Figure 3.2 External holding tanks (4 x 3000 litre) at the International Centre for Ecohydraulics Research (ICER) facility, University of Southampton, UK.

3.3 Fish capture and handling

Fish were sourced from the wild whenever possible to increase the applicability of the results. When it was not possible to source fish from the wild in sufficient quantities to provide statitistical power hatchery individuals were used. The use of hatchery fish in experimental research is common practice (e.g. in kinematic - Liao *et al.,* 2003b, habitat use - Smith *et al.,* 2005, physiological - Schill and Elle, 2000, behavioural - Vowles and Kemp, 2012, and passage - Russon and Kemp, 2011a experiments), often as they are easily accessible and represent the most ecologically sensitive option (i.e. not removing fish from the wild). However, hatchery bred and reared fish can be morphologically different (Fleming *et al.,* 1994) and have a reduced swimming performance (Enders *et al.,* 2004; Pederson *et al.,* 2008), and display different behaviour (e.g. foraging behaviour - Bachman, 1984; antipredator responses - Jackson and Brown, 2011) in comparison to wild individuals. In contrast, they also often display behaviours typical of wild populations (e.g. switches in orientation when approaching a velocity gradient - Russon and Kemp, 2011a; Vowles and Kemp, 2012). In this body of research, if hatchery fish were used, a small number of wild individuals were used to validate results where possible (e.g.

Chapter 4). When it was not possible to source wild individuals (e.g. Chapter 6) the limitations of using hatchery fish should be considered when drawing conclusions from the results.

Wild fish were electric fished either by the Environment Agency or by The Game and Wildlife Conservation Trust by qualified and experienced personnel. Hatchery fish were obtained from reputable local farms after holding conditions and individual specimens had been vetted for common health issues (e.g. fin erosion due to overstocking). All fish were transported in aerated 250 litre transportation tanks or sealed polyurethane bags (with the addition of pure oxygen) filled with locally sourced water. On arrival at the holding facility fish were acclimatised to local conditions through gradual water exchange over the course of at least one hour. All fish were allowed at least 48 hours to acclimatise to holding tank conditions before experimental trials took place. Fish handling before and after each experiment was kept to a minimum to reduce stress.

Fish morphometrics (e.g. weight, body length, fin length) were taken under anaesthetic (2-Phenoxy-1-ethanol) to reduce the risk of handling stress. Exact aneasthetic concentrations are outlined in each experimental methodology as they vary between species. Depending on species, body length was taken as either:

- Total length (TL): Measured form the tip of the snout to the tip of the longer probe of the caudal fin.
- Fork length (FL): Measured from the tip of the snout to the end of the middle caudal fin rays.

The method of length measurment is noted in each results chapter.

3.3.1 Tagging

Half-duplex (HDX) Passive Integrated Transponder (PIT) tags in combination with HDX PIT antenna were utilised in one experiment to identify individual fish during group trials (Chapter 5). HDX PIT antennas consist of two or more coils of insulated stranded copper wire. The antenna radiates an alternating magnetic field created by voltage from an interrogator or ‘reader’ (Wyre Micro Design, UK). When a PIT tag, containing a ferrite cored copper wire coil and integrated circuit (encased in a bio-stable glass capsule), enters this magnetic field, it becomes energised and transmits a unique signal via its own alternating magnetic field, through the antenna, back to the interrogator. Each HDX PIT tag has a unique code and as such the identification of individual tags is possible as they pass through the antenna. Due to the absence of an integrated battery, HDX PIT tags are small (length 12.0 - 23.0 mm, width 2.1 - 3.6 mm, weight 0.3 - 0.6 g - range used in this research) which allows for a less invasive implantation technique (in comparison to larger radio or acoustic tags) and survival and retention rates are generally high (Gries and Letcher, 2002; Ficke *et al.,* 2012: Hirt-Chabbert and Young, 2012).

The fish to be tagged were anaesthetised (2-Phenoxy-1-ethanol) and had HDX PIT tags inserted through a small mid-ventral incision made in the posterior quarter of their peritoneal cavity. The incision was sealed with medical cyanoacrylate glue which suppresses the inflammatory response and grants higher survival rates (Baras and Jeandrain, 1998). Home Office procedures were adhered to and surgery undertaken by qualified and experienced personnel. Post-surgery fish were held in small aerated holding tanks for observation before being released back into the external holding tanks. Studies have shown that PIT tagging does not affect behaviour, growth rates or swimming performance of fish (Ficke *et al.,* 2012; Hirt-Chabbert and Young, 2012; Newby *et al.,* 2007).

3.4 Hydrodynamic measurements and spatial interpolation

3.4.1 Hydrodynamic measurement

Velocities were preferentially measured using an Acoustic Doppler Velocimeter (ADV) (Vectrino+, Nortek). ADV’s work by measuring the frequency shift of emitted sound reflected from entrained particles in a flow. An ADV probe consists of a transmitter, which emits short pairs of sound pulses, and three to four receivers (depending on model), that enable measurement of the instantaneous longitudinal (u), transverse (v), and vertical (z) velocity component. ADV’s provide a weakly intrusive flow measurement (the sample volume is *ca.* 5 cm away from the sensing element) of a small sample volume (approximately 0.25 cm^3) at high frequency (25 - 200Hz) (Nikora and Goring, 1998). The main sources of ADV error are Doppler noise, aliasing of the signal, and erroneous measurements incorporated into the data in highly turbulent conditions and in the presence of entrained air (Cea *et al.,* 2007). To reduce the effects of erroneous data, raw ADV velocities were filtered using a 3 dimensional cross-correlation filter in Matlab version 7.10.0.499 (as per Cea *et al.*, 2007). The filter works by comparing the fluctuating part of the three orthogonal velocity components (u’, v’, w’) against each other (i.e. u’-v’, u’-w’, v’-w’). Where $u' = u - \bar{u}$ (overbar denotes time average). Each measurement is considered as a single event independent of the contiguous data. The filter assumes that ‘good’ data cluster inside an ellipsoid with axis extents based on a theoretical result which claims that the expected maximum of n independent, normal distributed, random variables, with zero mean and standard deviation σ, is equal to λσ, with $\lambda = \sqrt{2\ln(n)}$ (Donoho and Johnstone, 1994). The centre of the ellipsoid which separates the valid data from the corrupted data and the rotation angle of its principal axes are computed using a linear regression analysis of the data. All points that fall outside of the ellipsoid are considered spikes and replaced by linear interpolation of contiguous data (see Cea *et al.,* 1997).

When it was not possible to use an ADV, due to limited water depth or exceptionally high levels of air entrainment, an Electromagnetic (EM) flowmeter was used to measure velocity (Model 801, Flat, Valeport). EM flowmeters work based on Faraday's Law, which states that the voltage induced across any conductor as it moves at right angles through a magnetic field is proportional to its relative velocity. Unlike ADVs, EM flowmeters are intrusive and their slow response speed make them unsuitable for fine-scale hydrodynamic analysis (Voulgaris and Trowbridge, 1998). However, they allow for the evaluation of mean unidirectional velocity and standard deviation of velocity in areas where more advanced flowmeters cannot function.

3.4.2 Hydrodynamic metrics

Numerous hydrodynamic metrics were calculated from the ADV data.
Table 3.1 outlines the metrics used during experimentation and the relevant equations and units. The hydrodynamic metrics utilised in this report conform to recent suggestions to enable comparability between studies (Lacey *et al.*, 2012). For example, metrics were not made dimensionless (or if they were they are presented alongside non-dimensionless equivalents) so that comparisons can be made with natural rivers and streams. In addition the four characteristics of turbulence outlined by Lacey *et al.* (2012), intensity, periodicity, orientation and scale (IPOS framework), were controlled and reported where appropriate.

Table 3.1 Hydrodynamic metrics, notations, equations and units. $\boldsymbol{u}$, $\boldsymbol{v}$ and $\boldsymbol{w}$ are the instantaneous velocity variables corresponding to the $\boldsymbol{x}$, $\boldsymbol{y}$ and $\boldsymbol{z}$ spatial coordinates, $\boldsymbol{n}$ is number of samples, overbar denotes time-average, prime denotes the fluctuating component, $\boldsymbol{\sigma}$ is the standard deviation of its subscript, $\boldsymbol{\rho}$ is water density (kg m^{-3}) (taken as 1000 kg m^{-3} in this report), $\boldsymbol{t}$ is time, and $\boldsymbol{\tau}$ is time lag.

Metric	Notation	Equation	Units
Longitudinal velocity	$\bar{u}$	$\frac{1}{n}\sum_{1}^{n} u$	m s^{-1}
Lateral velocity	$\bar{v}$	$\frac{1}{n}\sum_{1}^{n} v$	m s^{-1}
Vertical velocity	$\bar{w}$	$\frac{1}{n}\sum_{1}^{n} w$	m s^{-1}
Longitudinal standard deviation of velocity	σ_u	$\sqrt{\frac{1}{n}\sum_{1}^{n}(u')^2}$	m s^{-1}
Lateral standard deviation of velocity	σ_v	$\sqrt{\frac{1}{n}\sum_{1}^{n}(v')^2}$	m s^{-1}
Vertical standard deviation of velocity	σ_w	$\sqrt{\frac{1}{n}\sum_{1}^{n}(w')^2}$	m s^{-1}
Three dimensional velocity magnitude	U	$(\bar{u}^2+\bar{v}^2+\bar{w}^2)^{0.5}$	m s^{-1}
Three dimensional magnitude of standard deviation / Turbulence Intensity	TI	$({\sigma_u}^2+{\sigma_v}^2+{\sigma_w}^2)^{0.5}$	m s^{-1}
Relative Turbulence Intensity	k	TI/U	N/A (dimensionless)
Turbulent Kinetic Energy	TKE	$0.5\rho\left(\overline{u'^2}+\overline{v'^2}+\overline{w'^2}\right)$	J m^{-3}
Horizontal Reynolds Shear Stress	τ_{uv}	$-\rho\overline{u'v'}$	N m^{-2}
Drag (including the influence of velocity variation)	D	$\sqrt{U^2+{\sigma_v}^2+{\sigma_w}^2}\cdot U$	N/A (relative)
Autocorrelation function of the lateral velocity component	/	$\overline{v'(t)v'(t-\tau)}\Big/\overline{v'^2}$	N/A (dimensionless)
Cross-correlation function of the lateral velocity component	/	$\overline{v_1'(t)v_2'(t-\tau)}\Big/\overline{v_1'v_2'}$	N/A (dimensionless)

3.4.3 Spatial interpolation

Depending on the complexity of the hydrodynamic conditions and metrics analysed, either Matlab v7.10.0.499 (The MathsWorks Inc., USA) or ArcMAP v10 (Esri, USA) was used to spatially map hydrodynamic conditions. Whenever possible the simplest interpolation function was used to map the results (linear interpolation in Matlab or spline interpolation in ArcMAP). Further information is provided in each results chapter.

3.5 Study Species

3.5.1 European eel (*Anguilla anguilla*)

The European eel, *Anguilla anguilla* (Linnaeus, 1758), has a wide geographic distribution covering a range of habitats in Europe, northern Africa and Mediterranean Asia (Dekker, 2003a). It is a catadromous species that matures in estuaries and rivers before migrating to oceanic spawning grounds thought to be located *ca.* 6000 km away in the Sargasso Sea (van Ginneken and Maes, 2005). The transparent willow leaf shaped larvae (leptocephali) use oceanic currents to facilitate their migration back to the continental shelf (Bonhommeau *et al.,* 2009) at which point they metamorphose into the more familiar eel shape. As this life stage still lacks pigmentation they are termed glass eels. Using Selective Tidal Stream Transport (STST), a method of drifting with the incoming tide and holding position during the outgoing tide, glass eels are transported into estuaries until they reach the tidal limit or a significant salinity barrier. At this stage they start to pigment and are referred to as elvers. The elvers actively swim upstream to colonise river systems where they grow until partially mature around 6 - 20 years later. During this later growth and maturation period eels are generally more sedentary and are referred to as yellow eels. As such, the colonisation of eels into freshwater can be loosely classified into three stages (combination of stages outlined by Gascuel [1986] and Ibbotson [2002]): 1) the estuarine migration of glass eels by STST towards freshwater, 2) a rapid, active, dispersion upstream driven by density at the point source by elvers, and 3) the continued expansion upstream by yellow eels, equivalent to a random diffusion of particles. Once of a sufficient size, usually > 6 years and > 10 years old for males and females, respectively, yellow eels begin to metamorphose into silver eels (a process that physiologically prepares them for marine conditions - termed silvering) and start to migrate downstream in preparation for their transatlantic journey back to spawning grounds in the Sargasso Sea.

Glass, yellow and silver phase European eel are all fished within Europe and North Africa for consumption (Jacoby and Gollock, 2014). Glass eel are also fished for farming (Jacoby and Gollock, 2014). However, since the early 1980s, a steady and almost continent wide decline of *ca.* 90% has been observed in the recruitment of glass eels to the European continent (Dekker, 2003a; Dekker *et al,* 2007; Moriarty and Tesch, 1996). The decline in recruitment was preceded by a reduction in fisheries landings two or more decades earlier (Dekker, 2003b). The decline in landings is thought to reflect a reduction in the continental stock (Dekker, 2003a) although accurate population data is limited (Jacoby and Gollock, 2014). Several hypotheses have been proposed as to why recruitment and continental stocks have declined, including: climate change, changes in oceanic conditions, overfishing, migration barriers, pollution, habitat loss, loss of body condition, predation, parasitism (specifically by the invasive species *Anguillicola crassus*) and disease (reviewed in: Feunteun, 2002; Jacoby and Gollock, 2014).

European eel are ‘critically endangered’ (International Union for the Conservation of Nature’s [IUCN] Red List of Threatened Species [RLTS] - Jacoby and Gollock, 2014) and are listed under Appendix II of the Convention on Trade in Endangered Species of Wild Fauna and Flora (CITES, 3 March, 1973). In addition, they receive protection under ‘The Eels (England and Wales) Regulations 2009’ (UK Statutory Instrument No. 3344) which dictates measures for the conservation of European eel in England and Wales through implementation of EU Council Regulation 1100/2007 (‘Establishing measures for the recovery of the stock of European eel’, 18 Sept, 2007). Eel Management Plans (EMPs) have been developed in European countries since 2007 as a stipulation of the regulation. The objective of each EMP is to reduce anthropogenic mortalities so as to permit, with high probability, the escapement to sea of at least 40% of the silver eel biomass relative to the best estimate of escapement that would have existed if no anthropogenic influences had impacted the stock (Jacoby and Gollock, 2014). In 2008, *A. anguilla* was also added to the OSPAR List of threatened and/or declining species in the northeast Atlantic (Reference Number: 2008 - 6) which is used as a guide for setting priorities for further work on the conservation and protection of marine biodiversity.

European eel used in this study were collected by electric fishing from the Rivers Itchen (50° 57’ 19.2” N, 1° 20’ 15.8” W), Wallington (50° 51’ 45.4” N, 1° 09’ 54.5” W) and Meon (50° 53’ 53.2” N, 1° 11’ 14.3” W), UK, by the Environment Agency (EA). The fish were returned to their native rivers by the EA after experimentation.

3.5.2 River lamprey (*Lampetra fluviatilis*)

River Lamprey, *Lampetra fluviatilis* (Linnaeus, 1758) are found in European watersheds, where their range extends from southern Norway to the western Mediterranean (Freyhof, 2013a; Kelly and King, 2001). It is an anadromous species that matures in marine environments and spawns in freshwater (Kelly and King, 2001). Spawning occurs in crude nests or depressions (redds) formed in areas with gravel, pebble or stony substrata and swift-running water (Jang and Lucas, 2005), of which the majority is usually located in the upper reaches of the catchment (Lucas *et al.,* 2009). After hatching, larvae are carried downstream by the current to areas of slow-flow and fine sediment where they burrow and feed on detritus for 3 - 8 years (Kelly and King, 2001). Metamorphosis from larva to adult takes place over several months, followed by migration downstream to sea. Adults stay at sea for 2 - 3 years during which time they are parasitic, feeding, via continuous attachment using their oral disc, on the blood, body fluids and tissue of marine fish (Kelly and King, 2001). In August, fully mature adults *ca.* 350 mm in length, migrate into rivers, residing in freshwater for several months before spawning in spring/early summer (Jang and Lucas, 2005). Lampreys cease active feeding before spawning (Gibson, 1953) and the spent adults die soon after (Larsen, 1980; Maitland and Campbell, 1992).

Lampreys have long been considered a gastronomic delicacy in Europe and they are an important source of income for many fishermen in Sweden and Finland (Kelly and King, 2001). However, throughout Europe populations of anadromous lampreys have declined dramatically over the last 30 years (Kelly and King, 2001). Multiple factors are highlighted as being responsible for this decline including pollution, human disturbance of redds, siltation of spawning gravels or de-siltation of nursery areas due to habitat modification or land management practices, and migration barriers (Igoe *et al.,* 2004; Kelly and King, 2001; Renaud, 1997). Migration barriers have specifically been highlighted as a major limiting factor in lamprey distribution (Igoe *et al.,* 2004). For example, in the River Derwent, North East England, telemetry studies have revealed that the cumulative effect of anthropogenic barriers has led to the majority (98.2%) of lamprey spawners being restricted to using only 2% of the potential spawning habitat within the river system (Lucas *et al.,* 2009).

Despite declines, river lamprey are currently listed as of 'least concern' in the IUCN RLTS (Freyhof, 2013a) although many consider that they should be regarded as endangered (e.g. Renaud, 1997). They receive conservation protection under Annex III of the Bern Convention (Convention on the Conservation of European Wildlife and Natural Habitats, 19 Sept, 1979) and under Annex II and V of the European Habitats Directive (Directive - 92/43/EEC, 21 May, 1992), through which their protection requires special areas of conservation (SACs) to be designated and their exploitation and taking in the wild may be subject to management measures.

L. fluviatilis used in this study were trapped in the River Ouse (53° 53′ 26.2″N, 1° 5′ 36.8″W), UK, by a licenced commercial fisherman. The lamprey made up part of a yearly catch quota and were euthanised in accordance with Home Office procedures after experimentation.

3.5.3 Brown trout (*Salmo trutta*)

Brown trout, *Salmo trutta* (Linnaeus, 1758), are indigenous to Europe, North Africa and western Asia, but have been introduced into at least 24 additional countries and now have a world-wide distribution (Klemetsen *et al.,* 2003). They have a plastic life history, having anadromous, lacustrine and resident ecotypes (*reviewed in*: Klemetsen *et al.,* 2003). Spawning occurs in rivers in autumn and winter months (Armstrong *et al.,* 2003) in redds preferentially dug in areas with substrate diameter, depth and water velocity of 16 - 64 mm, 15 - 45 cm, and 0.20 - 0.55 m s^{-1}, respectively (Louhi *et al.*, 2008). After hatching, the fry and then juvenile trout (parr) feed and grow in rivers or lakes for 2 - 3 years (Klemetsen *et al.,* 2003). Around the 2 - 3 year point (although this age varies dramatically depending on environmental factors), a proportion of juvenile trout undergo physiological and biochemical changes in preparation for a life at sea (smoltification) (Freyhof, 2013b). All juveniles seem to have the ability to smoltify and migrate but the factors that control this divergence are not well understood, although environmental and genetic factors likely play a key role (Nielsen *et al.,* 2003). In most rivers, a greater proportion of females than males migrate, probably due to a greater need for reproductive energy (Freyhof, 2013b). Smolts start to migrate downstream in April or May when temperatures increase above 5 - 11°C (Freyhof, 2013b). The marine phase may be for the summer only or for 2 or more years before returning to rivers to spawn (Klemetsen *et al.,* 2003). A part of the spawning population survives and spawns again (30 - 60%), depending on environmental factors, but many die as a consequence of the reproduction process (Klemetsen *et al.,* 2003). Those that do not smoltify, the resident ecotypes, do not undergo a marine phase and mature sexually between 1 and 10 years (Klemetsen *et al.,* 2003), at which point they undergo seasonal migrations to and from spawning and feeding grounds within the freshwater system (Klemetsen *et al.,* 2003).

Brown trout are widespread and are currently listed in the IUCN RLTS as of ‘least concern’ (Freyhof, 2013b). In this study, although the anadromous ecotype of brown trout is of conservation concern (Marine Scotland, 2013), especially in relation to anthropogenic habitat fragmentation (Jutila *et al.,* 2006), the species is primarily used as a model salmonid. Worldwide, salmonids have huge economic and cultural importance (Liu *et al.,* 2011; Montgomery, 2003), but many populations, which typically have a less adaptive life history than *S. trutta*, have suffered dramatic declines, with some having become locally extirpated (Brown *et al.,* 1994; Friedland *et al.,* 2003; 2009; Gustafson *et al.,* 2007; Katz *et al.,* 2013). Key causes for salmonid decline include poor land-use practices, breakdown of genetic integrity of native stocks (i.e. through hatchery introductions), introduced parasitism and diseases, overfishing, climate change, blockage and degradation of streams, and reduction of critical habitat and flow by dams and water diversions (Brown *et al.,* 1994; Costello, 2009; Hansen *et al.,* 2009; Yoshiyama *et al.,* 1998). Salmonids receive protection under legislation such as the Endangered Species Act (U.S.) 1973, Salmon and Freshwater Fisheries Act (UK) 1975, and European Habitats Directive 1992.

Hatchery *S. trutta* were obtained from either Allenbrook Trout Farm, Wimbourne, UK (50° 53’ 43.9” N, 1° 58’ 27.4” W) or Bibury Trout Farm, Bibury, UK (51° 45’ 37.5” N, 1° 50’ 08.9” W). A small number of wild *S. trutta* (*N* = 14) were obtained by electric fishing from Tadnoll Brook, a tributary of the River Frome, Dorset, UK (50° 41’ 02.5” N, 2° 17’ 28.4” W), by experienced members of the Game and Wildlife Trust. All trout were euthanised in accordance with Home Office procedures after experimentation.

3.6 Analysis of fish behaviour

Fish behaviour within the flume was predominantly assessed using overhead camera footage. Experiments were conducted in the dark and filmed under near-infrared illumination (wavelength: *ca.* 840 nm). Although comprehensive physiological data on the spectral sensitivity of fish is often sparse (Parkyn and Hawryshyn, 2000) the species used in this research have similar spectral sensitivity as humans (*A. anguilla*: Peak absorption [k_{max}] = 482 nm, Archer *et al.* 1995; Hope *et al.* 1998; absorption range [k_{range}] = *ca.* 300 - 600 nm, Andjus *et al.* 1998; *L. fluviatilis*: k_{max} = 515 - 520 nm; k_{range} = *ca.* 400 - 640 nm, Govardovskii and Lychakov, 1984; Salmonidae: k_{max} = 503 - 527 nm, Kusmic and Gualtieri, 2000; k_{range} = 391 - 669 nm although some salmonids also have vision in the near ultraviolet range, Mazur and Beauchamp, 2006) and are considered not to be able to see light in the near-infrared spectrum (700 - 1400 nm).

Behaviour was quantified from the videos by categorising and counting discrete events (e.g. an attempt to pass a structure or switch in rheotaxis), through tracking of fish spatial positions (x and y spatial coordinates) using video analysis software (Logger Pro v3.8.2 – Vernier Software and Technology, USA), or a combination of both. During tracking fish spatial positions were assessed in relation to a fixed location within the flume and head and/or tail x and y offsets recorded for individual video frames or at 1Hz. PIT telemetry was used in one experiment (Chapter 5) to aid video analysis by pinpointing passage events and identifying individuals during group trials. Specific details are outlined within each results chapter.

CHAPTER 4

4 Quantification of fish behaviour in a hydrodynamically complex experimental flow field: What governs space use by fish and why?

4.1 Summary

The selection of appropriate hydrodynamic metrics that predict space use by fish is the subject of recent debate and a cause of controversy. This is for three reasons: 1) flow characteristics are often oversimplified, 2) confounding variables are not always controlled, and 3) there is limited understanding of the explanatory mechanisms that underpin the biophysical interactions between fish and their hydrodynamic environment. Returning to first principles, it is hypothesised that, regardless of flow complexity and in the absence of confounding variables, fish should select hydrodynamic conditions where they can reduce energetic costs and enhance fitness. This study tested this hypothesis by investigating the space use of brown trout, *Salmo trutta*, in a complex hydrodynamic flow field created using an array of different sized vertically oriented cylinders in a large open-channel flume. A hydrodynamic drag function based on a single-point time-averaged velocity statistic that incorporates the influence of turbulent fluctuations (D_t) was used to infer the energetic cost of steady swimming. Hydrodynamic preference curves were formulated and used to assess the appropriateness of D_t as a descriptor of space use compared to other commonly used metrics. Unique swimming behaviours (e.g. Kármán gaiting, entraining, and bow riding) that enable fish to hold position whilst reducing energetic costs (termed 'specialised behaviours') were indirectly accounted for by analysing and removing space use in key zones. Results indicate that, as predicted, hydrodynamic space use by trout was governed by the selection of areas where they could reduce energetic expenditure, through either exhibiting specialised behaviours or by selecting low drag regions.

4.2 Introduction

Understanding how the physical environment influences the distribution and movement of animals is a fundamental theme in ecology (Moorcroft, 2012). To maximise fitness, individuals must utilise space in ways that efficiently facilitates energy intake, through the acquisition of food, while minimising energetic expenditure (Krebs, 1978; Maynard Smith, 1978). Those that most effectively do so can allocate a greater proportion of available resources (time and energy) to other activities, such as the detection and evasion of predators, growth, and reproduction (Parker and Maynard Smith, 1990). For stream dwelling fish adapted to the challenges imposed by a spatially and temporally complex hydrodynamic environment, energetic costs include those associated with maintaining stability (Tritico and Cotel, 2010; Webb and Cotel, 2011), swimming (Enders *et al.,* 2003; Liao, 2004) and capturing food (Chesney, 1989). The use of space that enables fish to minimise energy expenditure under complex flows is of interest to evolutionary biologists, ecologists, and fisheries managers and conservationists, and is the focus of this study.

The selection of appropriate hydrodynamic metrics that predict space use by fish has been the subject of recent debate (Lacey *et al*. 2012) and a cause of controversy. This is for three reasons. First, traditional methods tend to heavily rely on the correlation between single-point time-averaged velocity statistics with space use by fish (e.g. Bovee, 1986; DeGraaf & Bain, 1986; Facey and Grossman, 1992; Mäki-Petäys *et al*., 1997; Jenkins and Keeley, 2010). Such measures fail to capture important flow-fish interaction mechanisms that rely on turbulent flow properties that vary both in time and space. For example, fish can slalom between the alternately rotating wake vortices shed from a bluff body to capture fluid momentum and minimise swimming costs (Kármán gait - Liao, 2003a; 2004). Second, attempts to quantify habitat use by fish in the field typically produce mixed results (e.g. Heggenes *et al*., 1991; Facey and Grossman, 1992; Jowett and Richardson, 1995; Mäki-Petäys *et al*., 1997; Cotel *et al*., 2006; Enders *et al*., 2009a) because space use is influenced by multiple confounding variables impossible to control *in situ* (e.g. food, predators, competitors, and mates). Third, laboratory studies continue to attempt to find statistical links between patterns of fish distribution/movement and one or more of any number of turbulent flow characteristics, such as turbulence intensity (TI), relative turbulence intensity (k), turbulent kinetic energy (TKE), turbulent length scale (TLS), or Reynolds shear stresses (τ) (e.g. Smith *et al*., 2005; 2006; Russon *et al*., 2011; Silva *et al*., 2011; 2012a; 2012b; Duarte *et al*., 2012). However, often the biophysical interpretation of these statistical links is obscure. This results in the failure to understand the explanatory mechanisms that underpin interactions between fish and their hydrodynamic environment. There is a need to return to first principles and quantify space use by fish in response to complex flows under controlled laboratory conditions. Furthermore, experimental data must be interpreted in-line with the general principle that space use is dictated by energy conservation, or more specifically, strategies to minimise the costs of swimming.

The energetic cost of locomotion for motile organisms is intrinsically linked to drag and mass-related gravitational forces (Biewener *et al*., 2003). For fish, which are typically of a similar density to the surrounding medium, hydrodynamic drag imposes the largest influence on locomotion because mass-related gravitational forces are negligible (Biewener *et al*., 2003). As such, the reduction of hydrodynamic drag plays an important role in improving swimming performance. Fish have evolved numerous passive and active mechanisms to reduce drag and hence energetic costs during locomotion. For example, the streamlined morphology of a fish reduces flow separation and minimises form drag (Vogel, 1996), while epidermal mucus (Daniel, 1981) and riblets (Dean and Bhushan, 2010) reduce skin friction (passive mechanisms). In addition, swimming kinematics are optimised to prevent flow separation during undulation (Anderson *et al*., 2001), fish can take advantage of reduced drag during non-undulatory phases of intermittent burst-glide locomotion (Weihs, 1974), and, as already mentioned, they can use stable or predictable flow characteristics around bluff bodies to hold position whilst reducing energetic expenditure (Taguchi and Liao, 2011) (active mechanisms). As such, energy conservation strategies play a fundamental role in fish ecology and hence are likely to be an important driver in space use.

The aim of this study is to present and evaluate new methods for assessing how fish behave in complex hydrodynamic environments and to test the hypothesis that in a complex hydrodynamic environment, in the absence of confounding variables, space use is governed by energy minimising strategies. To achieve this a reductionist approach was adopted and hydrodynamic space use by brown trout, *Salmo trutta*, investigated under a controlled experimental setting in which key confounding variables (e.g. visual cues, food, predators and conspecifics) were absent. The position of individual fish was recorded at high spatial resolution in a complex flow field created using an array of different sized vertically oriented cylinders in a large open-channel flume. The flow field offered a highly heterogeneous hydrodynamic environment and consequently a wide range of potential positions from which the fish could choose A hydrodynamic drag function (D_t) based on single-point time-averaged velocity statistics that incorporates the influence of turbulent fluctuations was used to infer the energetic cost of steady swimming. The influence of unique swimming behaviours (e.g. Kármán gaiting, entraining, and bow riding) that rely on spatial and/or temporal flow features and enable fish to hold position with reduced energetic cost (termed 'specialised behaviours') were indirectly accounted for and assessed separately by analysing and removing space use in key zones. Preference curves were constructed to assess the appropriateness of D_t as a descriptor of space use in comparison to other common hydrodynamic metrics: mean velocity (U), TI, k, TKE, horizontal Reynolds shear stress (τ_{uv}), and TLS. A fundamental assumption and potential source of error of conventional methods of calculating preference (use-versus-availability) is that an organism has access to and knowledge of all space available to them (Beyer *et al*., 2010). In this study preference calculations were refined by assessing space use of individual fish in relation to area sampled rather than total available. The results of this study have important implications for the understanding of the ecology of fluvial fish that live in hydrodynamically complex environments, and for fisheries management and conservation.

4.3 Methodology

4.3.1 Experimental setup

The study was conducted in a large indoor recirculating flume (21.4 m long, 1.4 m wide, and 0.6 m deep) at the International Centre for Ecohydraulics Research (ICER) facility, University of Southampton, UK (50° 57’42.6”N, 1°25’26.9”W). The experimental area consisted of a centrally located 2.94 m long section of the flume (Figure 4.1), screened at the upstream end by a 100 mm thick polycarbonate flow straightener (elongated tubular porosity - 7 mm diameter) to minimise incoming turbulent fluctuations, and downstream by a 10 mm diameter wire mesh, both of which prevented fish leaving. A wire mesh release chamber (0.7 m long, 0.4 m wide, and 0.5 m deep) in which the subject fish were held immediately prior to the start of each trial was connected to the experimental area by a centrally located rectangular orifice (0.2 m wide and 0.15 m high) in the downstream screen (Figure 4.1). Polyurethane sheeting was used to prevent light entering the experimental area and thus eliminate visual cues. Light intensities were below the visual threshold at which a human observer could see. Fish behaviour was recorded using low light cameras under infrared illumination.

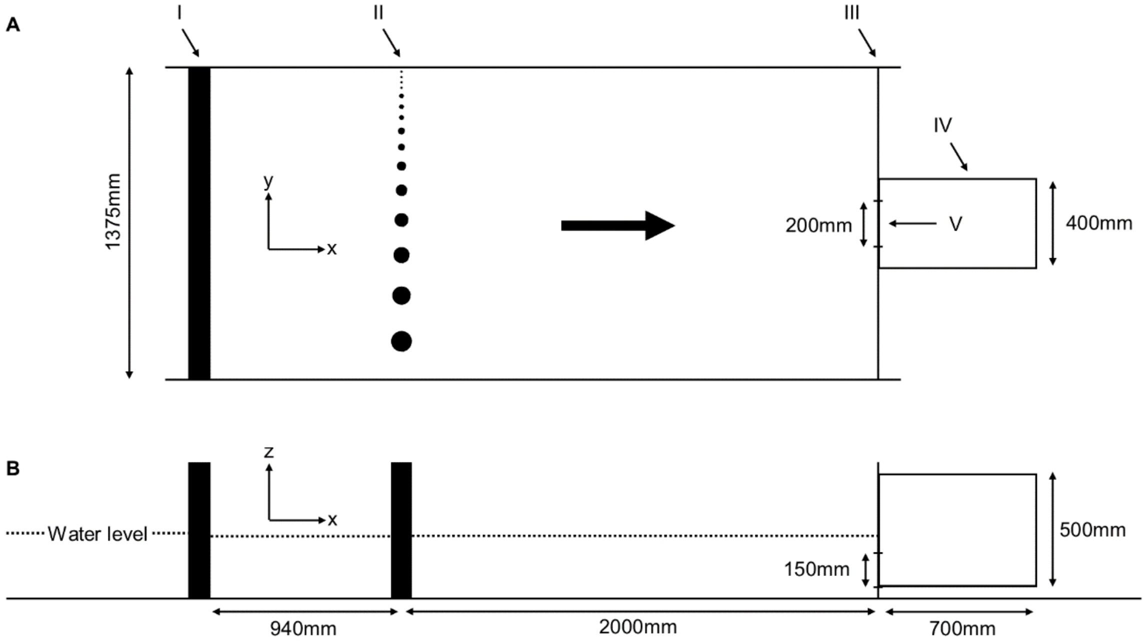


Figure 4.1 Plan (A) and profile (B) of the experimental area in a large recirculating flume at the ICER facility (University of Southampton) in which hydrodynamic space use of brown trout, *Salmo trutta*, was assessed. I) flow straightening device, II) cylinder array, III) mesh screen, IV) release chamber, V) release chamber orifice. Thick arrow indicates direction of bulk flow.

An array of 15 vertically oriented cylinders (10 - 90 mm diameter) positioned across the flume 0.94 m downstream from the flow straightener (Figure 4.1) created a complex hydrodynamic flow field with distinct regions of differing turbulent intensities and length scales. Hydrodynamic variation was greater in the x - y than in the x - z plane. The cylinders were spaced at a sufficient distance apart to avoid wake interference in the near-wake region (see Zhang and Zhou, 2001; Akilli *et al.,* 2004; Gao *et al.,* 2010) and to minimise areas of laminar gap flow. This was achieved by ensuring that axis-to-axis (or axis-to-channel boundary for the cylinder immediately adjacent to the flume wall) cylinder spacing (g_c mm) was set at a constant ratio to cylinder diameter (d_c mm) (Eq. 1).

$$g_c \Big/ \left(\frac{d_{c1}+d_{c2}}{2}\right) = 2.375 \qquad \text{Eq. 4.1}$$

Fish experienced flow fields created by one of two treatments (A or B) or a control (no cylinders present) during the study. In treatment A, cylinder diameter increased incrementally across the flume width so that the smallest and largest cylinders were located adjacent to the channel walls (Figure 4.2) and turbulence intensity and scale increased incrementally from one side of the flume to the other. In treatment B the combination of cylinders was switched so that the largest and smallest occupied locations close to the channel centre (Figure 4.2) and an abrupt turbulence transition from low to high intensity and small to large scales occurred mid-channel. Treatments were arranged as such to enable comprehensive assessment of space use by fish in response to a varied selection of turbulence scales and intensities and associated gradients. The orientation of the cylinder array in each treatment was randomised (by rotating the array 180° about the central vertical axis) among trials to control for any hydrodynamic variation associated with the flume. Data collected under the randomised cylinder array orientations were aggregated for each treatment. Discharge remained constant (0.15 $m^3 s^{-1}$) during each trial independent of treatment. Water depth was constant (270 mm) throughout the experimental area under the control. Under both treatments depth was greater upstream (275 mm) than downstream (265 mm) of the array due to head losses generated by the cylinders.

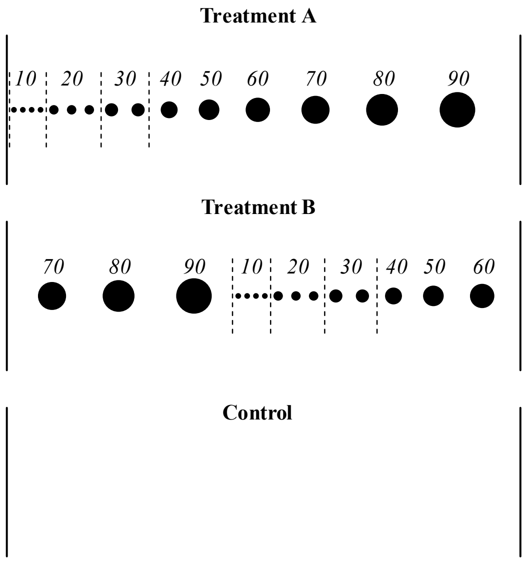


Figure 4.2 Cylinder arrays used to create 3 alternative hydrodynamic flow fields in a flume (treatments A, B, and control [no cylinders]). Numbers indicate the diameters of the cylinders (mm). Dashed lines delineate groups of cylinders of equivalent size.

Instantaneous velocity in the longitudinal (u), transverse (v) and vertical direction (w) were measured (n = 671, 678 and 84 for treatments A, B, and control, respectively) using an Acoustic Doppler Velocimeter (ADV) (Vectrino, Nortek-AS, Norway - frequency 50 Hz, sampling volume 0.05 cm^3, record duration 3 min, height above bed 90 mm) (Figure 4.3). Raw ADV data was filtered using a 3D velocity cross-correlation algorithm (Cea *et al.,* 2007) and the time-averaged (overbar) and fluctuating parts (prime) (e.g. $u' = u - \bar{u}$) of each instantaneous velocity component calculated, along with *U, TI, k, TKE* and τ_{uv} (see Table 4.1).

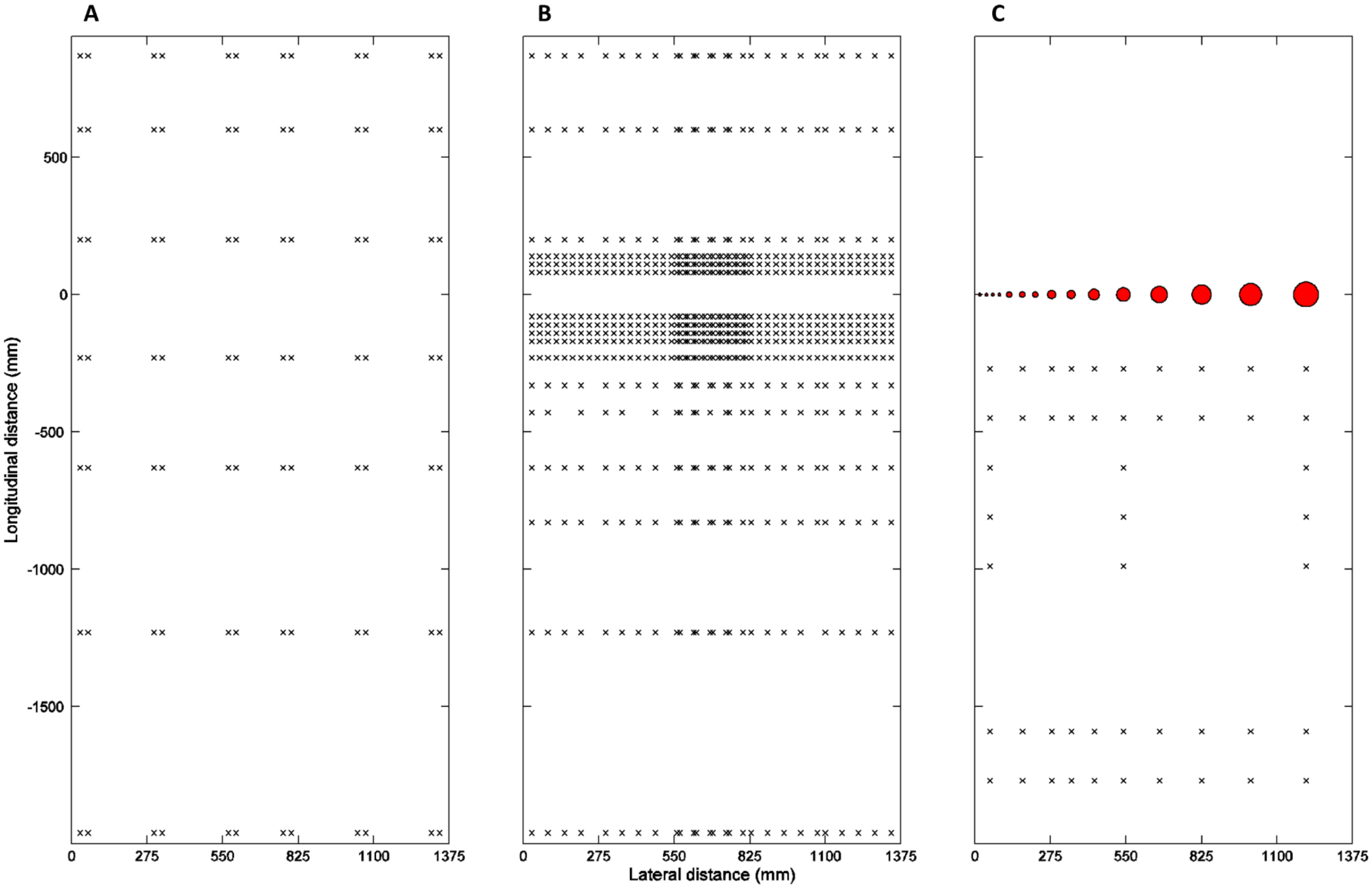


Figure 4.3 Single point velocity sampling locations under the control (A) and Treatment A and B (B) and two-point cross-correlation velocity sampling locations measured under the incremental treatment (C). Each 'x' denotes an ADV sampling location.

Table 4.1 Hydrodynamic metrics, equations and units. $\boldsymbol{U_f}$ is the cross-section mean velocity measured 500 mm downstream of the flow straightener (*ca.* 0.41 m s^{-1}), $\boldsymbol{d}$ is cylinder diameter (m), $\boldsymbol{St}$ is the Strouhal number (0.2, appropriate for the range of Reynolds numbers in the experiment - Sumer and Fredsøe, 1997), $\boldsymbol{W}$ is the width of the flume (m), $\sum \boldsymbol{d}$ is the sum of the cylinder diameters, $\boldsymbol{u}$, $\boldsymbol{v}$ and $\boldsymbol{w}$ are the instantaneous velocity variables corresponding to the $\boldsymbol{x}$, $\boldsymbol{y}$ and $\boldsymbol{z}$ spatial coordinates, overbar denotes time-averaging, prime denotes the fluctuating component, $\boldsymbol{\sigma}$ is the standard deviation of its subscript, $\boldsymbol{\rho}$ is density (1000 kg m^{-3}), $\boldsymbol{k_v}$ is kinematic viscosity (m^{2} s^{-1}), $\boldsymbol{t}$ is time, and $\boldsymbol{\tau}$ is time lag (1/50 second intervals).

Metric	Notation	Equation	Units
Reynolds Number	R_e	$U_f d / k_v$	N/A (dimensionless)
Vortex shedding frequency	f	StU_r/d	Hz
Wake wavelength	λ	U_f/f	mm
Estimated velocity of the restricted flow past each cylinder	U_r	$U_f \left({}^{W}/_{(W - \sum d)} \right)$	m s^{-1}
Mean velocity	U	$(\bar{u}^2 + \bar{v}^2 + \bar{w}^2)^{0.5}$	m s^{-1}
Turbulence intensity	TI	$({\sigma_u}^2 + {\sigma_v}^2 + {\sigma_w}^2)^{0.5}$	m s^{-1}
Relative turbulence intensity	k	TI/U	N/A (dimensionless)
Turbulent kinetic energy	TKE	$0.5\rho\left(\overline{u'^2} + \overline{v'^2} + \overline{w'^2}\right)$	J m^{-3}
Horizontal Reynolds shear stress	τ_{uv}	$-\rho\overline{u'v'}$	N m^{-2}
Autocorrelation function of the lateral velocity component	/	$\overline{v'(t)v'(t-\tau)} \Big/ \overline{v'^2}$	N/A (dimensionless)
Cross-correlation function of the lateral velocity component	/	$\overline{v_1'(t)v_2'(t-\tau)} \Big/ \overline{v_1'v_2'}$	N/A (dimensionless)

Based on the Reynolds numbers (Table 4.2), each cylinder wake was expected to be completely turbulent with both sides of the cylinder experiencing boundary layer separation (subcritical wake regime - Sumer and Fredsøe, 1997).

Table 4.2 Reynolds number ($\boldsymbol{R_e}$), estimated vortex shedding frequency ($\boldsymbol{f}$), and wake wavelength ($\boldsymbol{\lambda}$) downstream of each cylinder ($\boldsymbol{d}$) used in an experimental study to investigate space use of brown trout, *Salmo trutta*, in a hydrodynamically complex environment.

$\boldsymbol{d}$ (mm)	$\boldsymbol{R_e}$	$\boldsymbol{f}$ (Hz)	$\boldsymbol{\lambda}$ (m)
10	2699	13.67	0.03
20	5398	6.83	0.06
30	9097	4.56	0.09
40	10797	3.42	0.12
50	13496	2.73	0.15
60	16195	2.28	0.18
70	18894	1.95	0.21
80	21593	1.71	0.24
90	24292	1.52	0.27

The Taylors Hypothesis of frozen turbulence (i.e. the hypothesis that turbulent-eddies are advected at or near mean flow velocity - Taylor, 1938), is notoriously violated in the near-wake region of bluff bodies (see Pope, 2000). As such, two-point simultaneous ADV measurements were used to accurately assess the convection speed of the dominant energy containing eddies (E_S) and infer TLSs. Two to 5 simultaneous measurements (*n* = 28, sample length 5 mins) were taken downstream of the central axis of each cylinder in treatment A using two longitudinally aligned (spacing 180 mm) and synchronised ADVs (Figure 4.3c). E_S was calculated as the quotient of the distance between ADVs and the time lag (τ) corresponding to the first peak appearing in the cross-correlation function of the synchronised lateral velocity data (Table 4.1). Well defined cross-correlation peaks were observed directly downstream of the cylinders for the majority of simultaneous measurements, except downstream of the smallest cylinders (10 mm diameter) where eddy coherence was lost. E_S was found to be linearly related (r^2 = 0.687) and similar to the mean velocity (U) between the two probes ($E_S = 0.77U + 0.12$) (i.e. convection velocity was similar to flow velocity behind all cylinders). As such, it was deemed valid to use U_f as a proxy for convection velocity in all treatments to calculate TLSs from the single point measurements as $E_d = U_f E_t/2$, where E_d is the characteristic size (m) and E_t is the turnover time (s) of the dominant energy containing eddies. E_t was calculated as the time between first and second positive peak in the autocorrelated lateral velocity data. E_d downstream of each cylinder (11 – 123 mm for the 10 - 90 mm diameter cylinders, respectively) was similar (linear trend: y = 0.98x + 0) and highly correlated (r^2 = 0.975) to the estimated values (λ/2 in Table 4.2).

The drag force (D) acting on a fish holding its position is normally calculated as $D = 0.5\rho S U^2 C_d$ (kg m s^{-2}), where ρ is fluid density (kg m^{-3}), S is the frontal area of the fish (i.e. its maximum projection on to a plane normal to the direction of flow) (m^2), U is the mean longitudinal flow velocity (m s^{-1}), and C_d is the dimensionless drag coefficient (Webb, 1975). As sources of thrust and drag are not separable in axial undulating self-propulsion, the empirical calculation of C_d for a swimming fish is difficult (Schultz and Webb, 2002). To simplify matters, at first approximation S and C_d can be assumed to be constant (Vogel, 1996), hence $D \propto U^2$. However, this definition applies strictly only to steady flows, which are rare in natural lotic habitats. It is generally accepted that, turbulence contributes to destabilise fish and hence to increase energetic costs of swimming. This is generally true unless turbulence displays a high level of coherence and eddies can be exploited using specialised swimming kinematics (e.g. Kármán gait, Liao, 2003a). Turbulence can affect swimming performance in many ways. In particular, abrupt lateral and vertical velocity fluctuations prevent a fish from aligning with the instantaneous flow direction and utilising its streamlined shape to reduce form drag. This means that, instantaneously, the frontal area exposed to the incoming flow increases and drag with it. Furthermore, even in the unlikely event a fish is able to align instantaneously with the flow, vertical and lateral turbulent fluctuations will increase drag forces, because of the non-linear dependence of D on velocity. This can be easily explained by the following example: Assuming, for simplicity, a fish behaves like a sphere whose drag is insensitive to flow direction. If it holds position against a steady flow with velocity U, then the drag force it is subjected to can be computed as $D \propto U^2$. If a lateral velocity component which fluctuates between $\pm v$ is added, this has the effect of instantaneously changing the flow direction and magnitude, while keeping average lift forces (i.e. forces perpendicular to the mean flow direction) close to zero (see Figure 4.4). The drag force that the fluid exerts on the sphere-fish can now be computed as $D \propto (U^2 + v^2)\cos\theta$, where $\cos\theta = U/\sqrt{U^2 + v^2}$ and hence $D \propto U\sqrt{U^2 + v^2}$, which is greater than $D \propto U^2$. It is difficult to quantify the effects of turbulence to accurately compute drag forces (and hence energetic costs of swimming) acting on real fish as a response to the mechanisms described above. However, it is proposed that a metric defined as $D \propto U\sqrt{U^2 + {\sigma_v}^2 + {\sigma_z}^2}$ (which also includes the influence of a vertical velocity component) does take into account such effects and represents a good approximation of drag. Standard deviations of the lateral and vertical velocity components (σ_v and σ_z, respectively) are used as the metric will be used to infer drag from time-averaged velocity data and σ_v and σ_z provide a good representation of the magnitude of the instantaneous v and z fluctuations over time. Theoretically (Vogel, 1996) and experimentally (Feldkamp, 1987; Basolo and Alcaraz, 2003) drag forces are known to be intrinsically linked with the energetic cost of locomotion. In this research the drag metric outlined above is used as a proxy for the energetic costs of a fish swimming in turbulent flows and is hereafter referred to as turbulent drag (D_t). Although this approximation of drag is new to the field of Ecohydraulics similar approximations are used elsewhere (e.g. canopy drag - Dupont *et al.,* 2008; sedimentology - Nalpanis *et al.,* 1993).

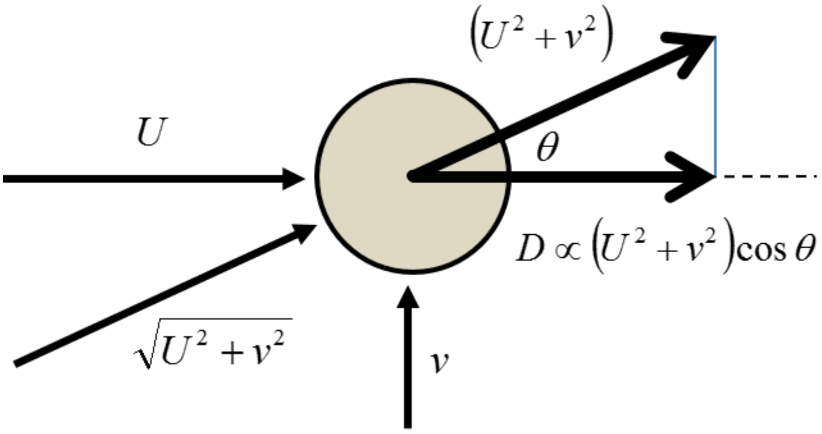


Figure 4.4 Diagram of the directional forces on a sphere and drag ($\boldsymbol{D}$) acting parallel to the mean flow ($\boldsymbol{U}$) as a result of an instantaneous lateral velocity component ($\boldsymbol{v}$)

U, TI, k, TKE, τ_{uv}, E_d and D_t were linearly interpolated at 1 mm resolution to create hydrodynamic maps of the experimental area (Figure 4.5, Figure 4.6 and Figure 4.7 for treatment A, B and control, respectively). As ADV measurements were not possible within 30 mm of the flume walls, a fitted logarithmic function, based on measurements taken at the walls under the control, was used to estimate boundary conditions. Sensitivity analysis revealed that boundary layer estimation method (several were trialled) had little effect on overall trends. The fitted logarithmic function was used as it was thought to better represent actual conditions.

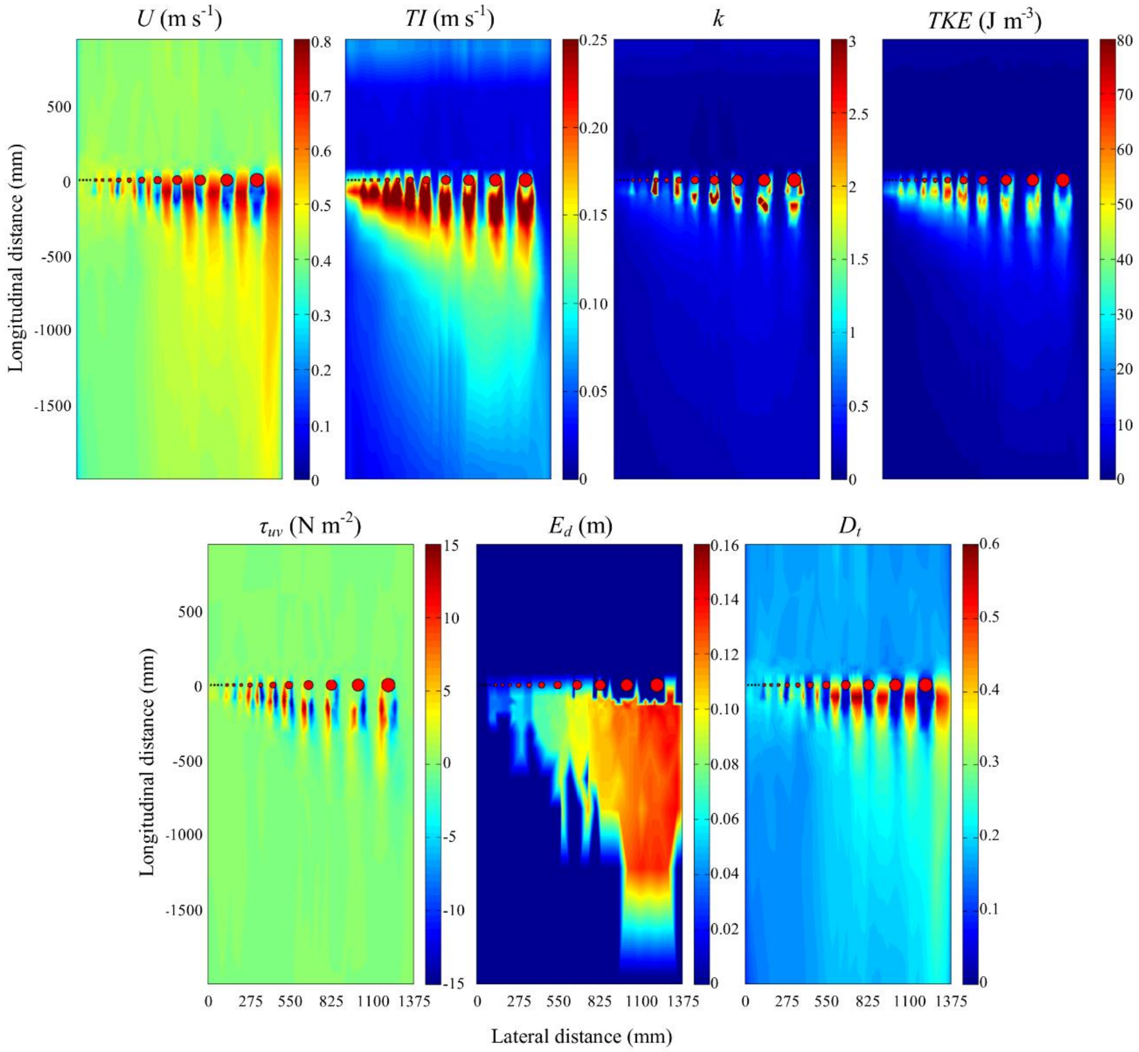


Figure 4.5 Colour intensity plots of mean velocity ($\boldsymbol{U}$) (m s^{-1}), turbulence intensity ($\boldsymbol{TI}$) (m s^{-1}), relative turbulence intensity ($\boldsymbol{k}$), turbulent kinetic energy ($\boldsymbol{TKE}$) (J m^{-3}), horizontal Reynolds shear stress ($\boldsymbol{\tau_{uv}}$) (N m^{-2}), eddy diameter ($\boldsymbol{E_d}$) (m) and drag ($\boldsymbol{D_t}$) for treatment A in which the behaviour of brown trout, *Salmo trutta*, was assessed.

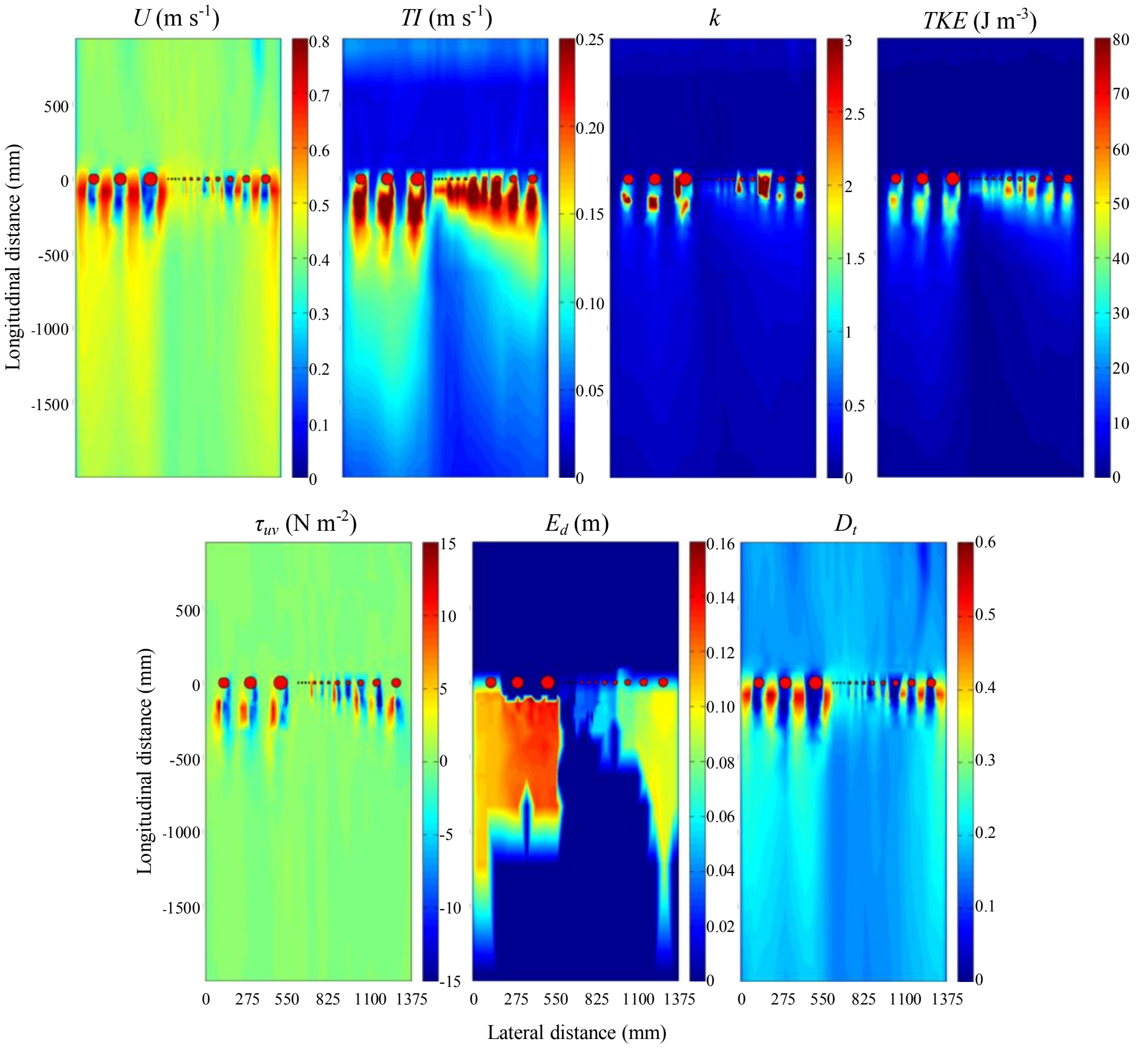


Figure 4.6 Colour intensity plots of mean velocity ($\boldsymbol{U}$) (m s^{-1}), turbulence intensity ($\boldsymbol{TI}$) (m s^{-1}), relative turbulence intensity ($\boldsymbol{k}$), turbulent kinetic energy ($\boldsymbol{TKE}$) (J m^{-3}), horizontal Reynolds shear stress ($\boldsymbol{\tau_{uv}}$) (N m^{-2}), eddy diameter ($\boldsymbol{E_d}$) (m) and drag ($\boldsymbol{D_t}$) for treatment B in which the behaviour of brown trout, *Salmo trutta*, was assessed.

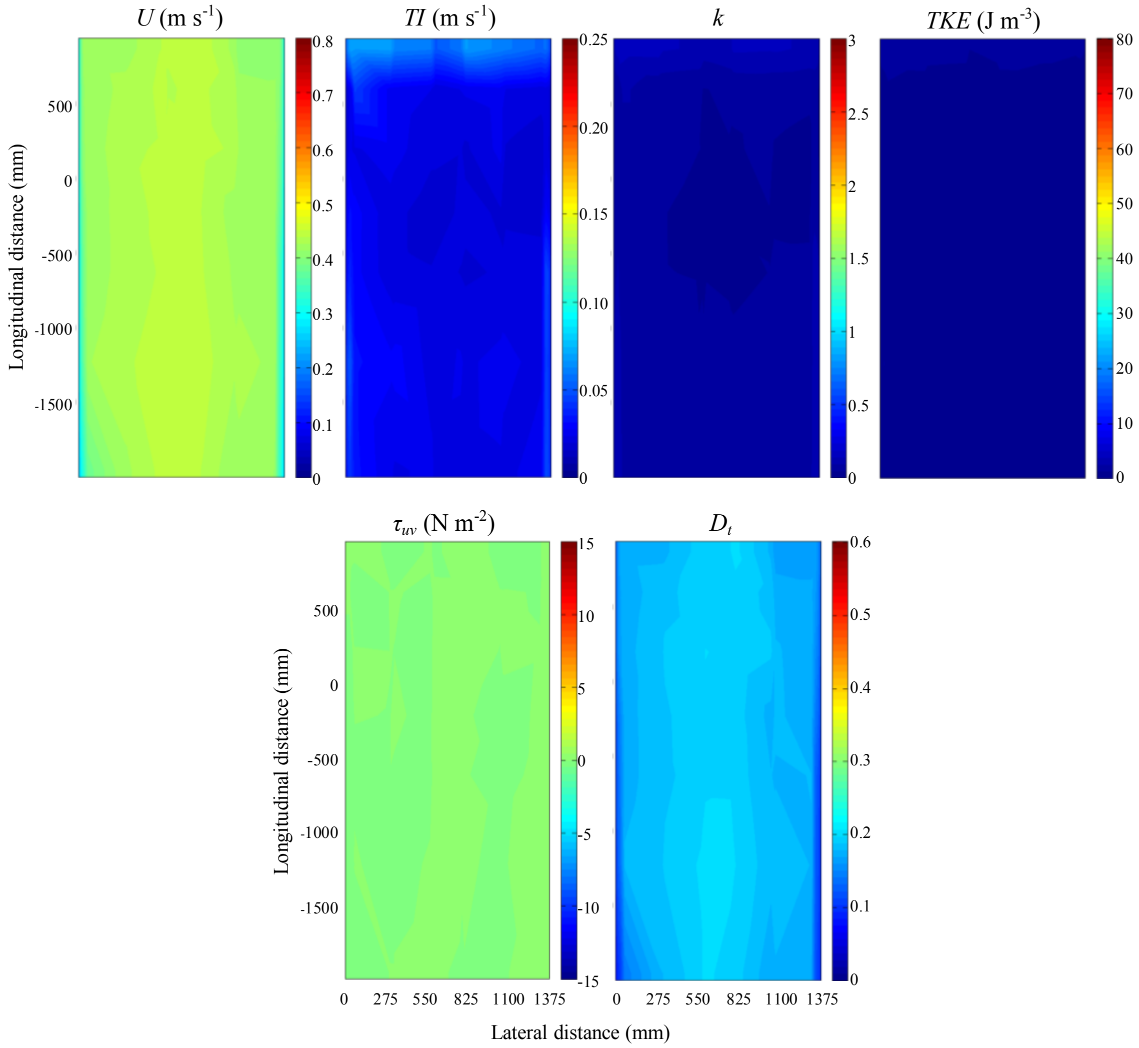


Figure 4.7 Colour intensity plots of mean velocity ($\boldsymbol{U}$) (m s^{-1}), turbulence intensity ($\boldsymbol{TI}$) (m s^{-1}), relative turbulence intensity ($\boldsymbol{k}$), turbulent kinetic energy ($\boldsymbol{TKE}$) (J m^{-3}), horizontal Reynolds shear stress ($\boldsymbol{\tau_{uv}}$) (N m^{-2}), eddy diameter ($\boldsymbol{E_d}$) (m) and drag ($\boldsymbol{D_t}$) for the control in which the behaviour of brown trout, *Salmo trutta*, was assessed.

4.3.2 Experimental procedure

Three size classes (age cohorts) of hatchery raised brown trout were obtained to assess the effect of fish length and absolute swimming capacity on space use: medium and large fish from Allenbrook Trout Farm (Wimbourne, 50° 53′ 43.9″ N, 1° 58′ 27.4″ W) and small fish from Bibury Trout Farm (Bibury, 51° 45′ 37.5″ N, 1° 50′ 08.9″ W) on 15th March 2011 and 12th March 2012, respectively (Table 4.3). Wild trout, caught by electric fishing at Tadnoll Brook, a tributary of the River Frome (Dorset, 50° 41′ 02.5″ N, 2° 17′ 28.4″ W) on 14th March 2012 (Table 4.3), were used to validate the results obtained from the more readily available hatchery fish. The wild trout group was not divided into size classes due to the low number and small size range caught. Instead comparisons were made against an equivalent size range of hatchery fish where possible. Trout were transported to the ICER facility in aerated water and held in filtered 3000 litre holding tanks (pH: 7.5-7.8, Ammonia: 0, Nitrite: 0, Nitrate: < 40, 50% weekly water change) at ambient temperature (2011: μ = 14.07˚C, σ = 3.63˚C; 2012: μ = 10.23˚C, σ = 0.80˚C). Fish were fed once daily with commercial trout pellets.

A total of 118 one-hour trials were conducted; 51 between 29th March and 7th April 2011 (medium and large hatchery trout; flume temp: μ = 14.80˚C, σ = 3.02˚C), and 67 between 21st and 30th March 2012 (small hatchery and wild trout; flume temp: μ = 10.37˚C, σ = 0.79˚C) (Table 4.3). Individual trout were allowed to acclimatise for a minimum of 1 hour in a porous container positioned within the flume before being placed into the release chamber from which they could volitionally enter the experimental area. A trial commenced once a trout entered the experimental area; fish that failed to enter within 20 minutes, or did so but became impinged on the downstream screen for more than 10 seconds, were removed and the trial terminated. Each trial lasted a maximum of 1 hour during which each trout was allowed to freely explore and utilise the experimental area. Trout were used once only and at the end of each trial weighed (g) and measured (Fork Length [FL] - mm) under anaesthetic (2-Phenoxy-1-ethanol, 0.2 ml l^{-1}). All trials were conducted between 08:00 and 18:00 (BST).

Table 4.3 Group statistics for brown trout, *Salmo trutta*, used during experiments conducted to assess hydrodynamic space use in a recirculating flume at the ICER facility (University of Southampton). Source, size class, fork length (FL), mass, number of fish (*N*), and mean and total duration of data acquired for each group and treatment per group. *DNLRC* is the percentage of fish that did not leave the release chamber.

								Treatment Statistics		
Source	***Size class***	***FL μ ± σ (Range) (mm)***	***Mass μ ± σ (Range) (g)***	***N***	***DNLRC (%)***	***Mean duration of trial (MM:SS) (μ ± σ)***	***Total duration of data available (hr: min: sec)***	***Treat-ment***	***N***	***Total duration of data available (hr: min: sec)***
Hatchery	*Small*	*144.5 ± 12.5, (110-174)*	*46.8 ± 10.7, (19-70)*	*53*	*43.4*	*21:07 ± 16:31*	*10:33:26*	*Control*	*12*	*02:36:18*
								A	*19*	*04:24:08*
								B	*22*	*03:33:00*
Hatchery	*Medium*	*224.0 ± 10.0 (202-245)*	*163.5 ± 25.7, (120-200)*	*25*	*32.0*	*57:58 ± 16:04*	*16:25:26*	*Control*	*3*	*03:00:00*
								A	*14*	*10:06:59*
								B	*8*	*03:18:27*
Hatchery	*Large*	*280.7 ± 10.24 (259-294)*	*355.3 ± 31.4, (266-396)*	*26*	*3.8*	*49:46 ± 18:30*	*20:44:20*	*Control*	*4*	*03:04:04*
								A	*15*	*10:40:16*
								B	*7*	*07:00:00*
Wild	*N/A*	*195.2 ± 36.1 (138-247)*	*110.5 ± 54.1, (36-202)*	*14*	*21.4*	*51:49 ± 14:14*	*09:29:59*	*Control*	*5*	*01:57:21*
								A	*4*	*03:00:00*
								B	*5*	*04:32:38*

4.3.3 Fish behaviour

For each trial, fish snout position (x and y spatial coordinates) was obtained every second from the overhead video footage (maximum of 3600 data points per trial) using Logger Pro v3.8.2 (Vernier, US) and plots of space use and space sampled were created. Space sampled was deemed to be that which fell within a fish's mechanosensory field of detection (MFoD) during a trial. The threshold distance for fish to detect hydrodynamic signals using the lateral line (primary mechanosensory organ), varies depending on a number of factors (e.g. signal type, orientation, and magnitude) but is approximately 1.5 FLs (Coombs, 1999), with signal discriminability being considerable higher at closer distances. In this study, a conservative estimate of the spatial extents of a fish's MFoD, deemed to be an area within which it can fully interpret the surrounding flow field, was set as a rectangle extending 0.5FL upstream, 1.5FL downstream and 0.5FL either side of the fish snout position (Figure 4.8).

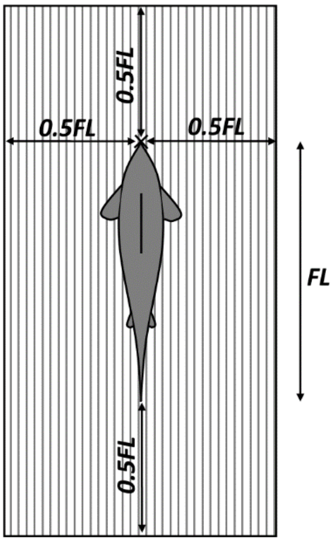


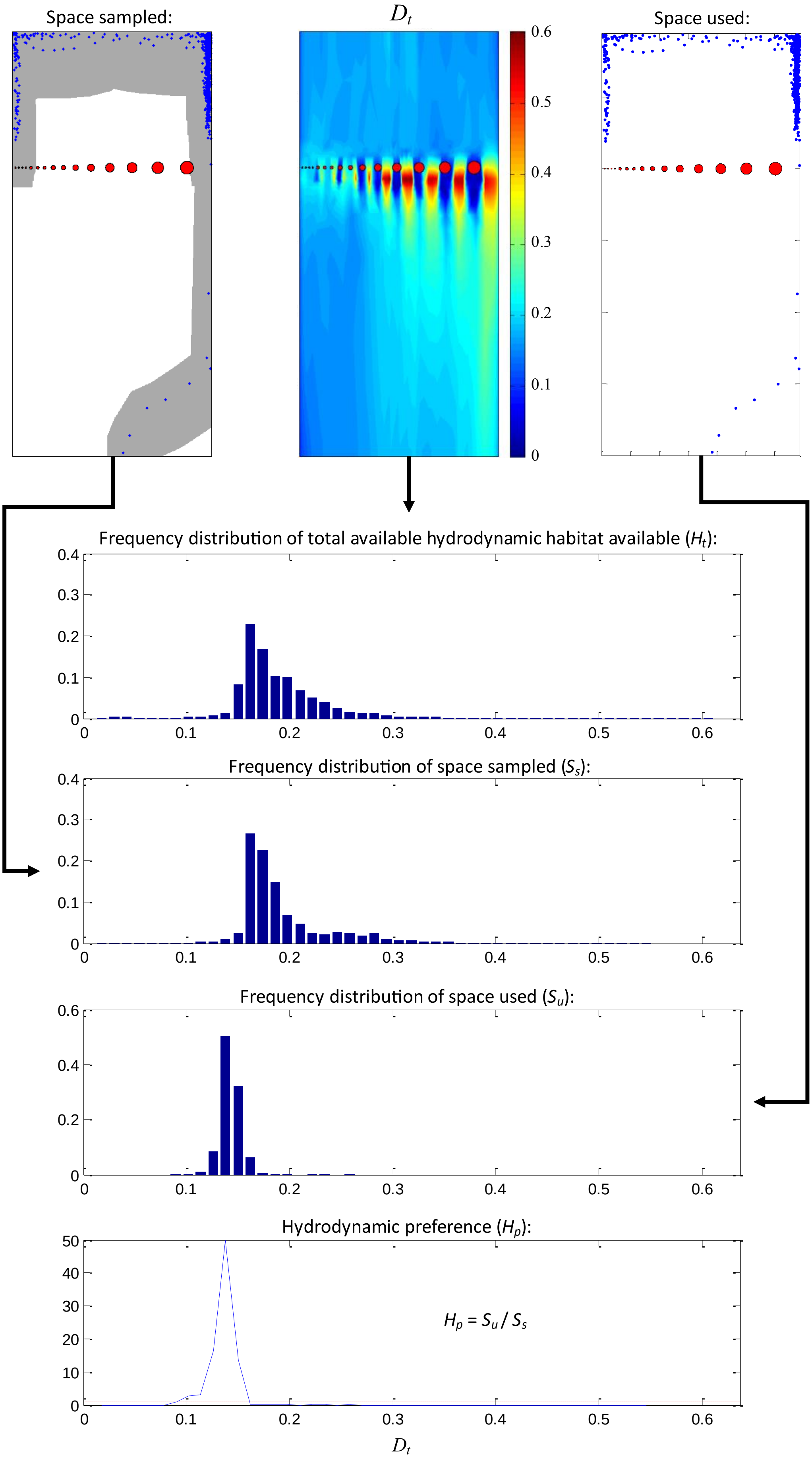
Figure 4.8 The mechanosensory field of detection (MFoD) allocated to each fish and used to assess the area it sampled during hydrodynamic space use experiments in a large open channel flume.

Zones expected to provide opportunities for fish to reduce the energetic costs of station holding through the expression of specialised behaviours (behavioural zones - e.g. Kármán gaiting, entraining, bow riding) were identified based on information obtained from the literature (e.g. Liao *et al.* 2003a; b; Liao, 2006; Przybilla *et al.,* 2010), observation of trout during the trials and clustering evident in the plots of space use. Using data aggregated from both treatments the proportion of time individual trout spent in each behavioural zone was calculated and comparisons made between: 1) observed and expected if fish had been evenly distributed throughout the experimental area (all trout: Wilcoxon signed-rank tests), and 2) wild and hatchery trout, using a sample (N = 30) of hatchery fish of equivalent size to those obtained from the wild (Mann-Whitney tests). In addition, the relationship between FL and 3) the proportion of time spent in each behavioural zone (all trout) and 4) the diameter of the cylinder that fish spent the highest proportion of time associated with (for all cases where peak time in a particular zone exceeded 10 seconds) were assessed (Pearson's correlation with bootstrapped and bias corrected confidence interval - Efron and Tibshirani, 1993).

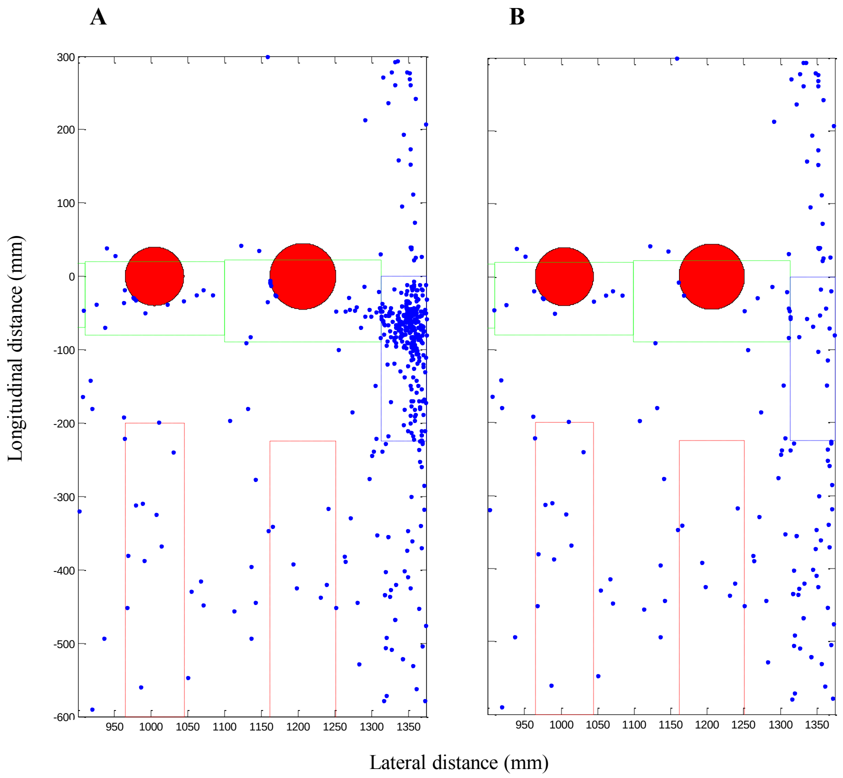
To quantify hydrodynamic space use, preference curves were constructed for each measured metric. Hydrodynamic preference (H_p) for individual trout was calculated as $H_p = S_u/S_s$, where S_u and S_s are frequency distributions (50 bins) of space used and space sampled, respectively (see ← Figure 4.9). S_u and S_s distributions were extrapolated from the interpolated hydrodynamic data based on the snout positions and the area that fell within a fish's MFoD, respectively, during each trial. Average hydrodynamic preferences for trout in each group (wild and small, medium and large hatchery trout - GH_p) were calculated for each metric as a weighted average of H_p normalised by trial duration (TD) (Eq. 4.2).

$$GH_p = \frac{\sum_{i=1}^{N} H_{pi} TD_i}{\sum_{i=1}^{N} TD_i} \qquad \text{Eq. 4.2}$$

where i represents an individual trout and N is the total number of trout in each group. Trends in the GH_p curves were compared to frequency distributions of total available hydrodynamic space (H_t). Trout preference for hydrodynamic space that was rarely available (< 0.1% of total area) was disregarded by assessing GH_p curves only over the range of conditions where $H_t >$ 0.001. To assess the influence of specialised behaviours, GH_p curves were calculated using both unmodified and modified S_u data. The modified S_u data was constructed by identifying behavioural zones trout used more frequently than expected if their distribution had been even, and randomly removing the excess proportion of points that occurred within them (see ↑ Figure **4.10**). As such, the potential influence of specialised behaviours was removed from the modified preference curves. Differences in trends evident in the GH_p curves constructed using the modified and unmodified S_u data were assessed. Final conclusions in relation to hydrodynamic space use by brown trout were drawn from the GH_p curves constructed using the modified S_u data. Data analysis and visualisation was undertaken using Matlab v7.10.0.499 (MathWorks, US), SPSS v20.0.0 (IBM, US), and, SigmaPlot v12.5.038 (Systat Software Inc., US)


Space sampled:
D_t
Space used:
0.6
0.5
0.4
0.3
0.2
0.1
0
Frequency distribution of total available hydrodynamic habitat available (H_t):
0.4
0.3
0.2
0.1
0
0.1
0.2
0.3
0.4
0.5
0.6
Frequency distribution of space sampled (S_s):
0.4
0.3
0.2
0.1
0
0.1
0.2
0.3
0.4
0.5
0.6
Frequency distribution of space used (S_u):
0.6
0.4
0.2
0
0.1
0.2
0.3
0.4
0.5
0.6
Hydrodynamic preference (H_p):
50
40
30
20
10
0
$H_p = S_u / S_s$
0.1
0.2
0.3
0.4
0.5
0.6
D_t

← **Figure 4.9** Schematic representation of how preference was calculated. Example using data for a wild trout (FL: 223 mm) under treatment A (Trial 54, duration: 3600 seconds) for turbulent drag (D_t). Schematic shows plots of the total available hydrodynamic habitat (D_t) (top middle), the area the fish sampled (grey area) (top left) and space used (blue dots – representing snout position each second) (top right) along with associated frequency distributions (H_t, S_s, and S_u, respectively). Hydrodynamic preference, where $H_p = S_u/S_s$ (calculated for each bin of the S_u and S_s data), is shown in the bottom plot as a solid blue line. The red dashed line in the bottom plot is for reference purposes and represents an even distribution (i.e. preference = 1).



↑ **Figure 4.10** Schematic representation of how excessive use of behavioural zones was accounted for in the data. Example using data for a large hatchery trout (FL: 323 mm) under treatment A (Trial 4, duration: 3600 seconds) with a specific focus on the wall holding behavioural zone adjacent to the 90 mm cylinder (dashed blue rectangle). **A**) Raw space use data – 272 instances of the trout being present in the wall holding zone. **B**) Modified space use data – If distribution had been even then the trout would have only used the zone 12 times. Hence 260 points (272 – 12) from within the zone were randomly removed. This was repeated for each behavioural zone. Hence the influence of fish preference for behavioural zones was removed from the final preference curves.

4.4 Results

Space use varied dramatically among individuals and treatments with trout tending to be thigmotactic under the control and influenced by the cylinders under the treatments (Figure 4.11). Only 17.6% of trout sampled 100% of the experimental area (Mdn: 86.5%, Range: 7.0 – 100%). The extent of the experimental area sampled was not limited to the downstream section and did not follow a regular pattern (example: Figure 4.11b).

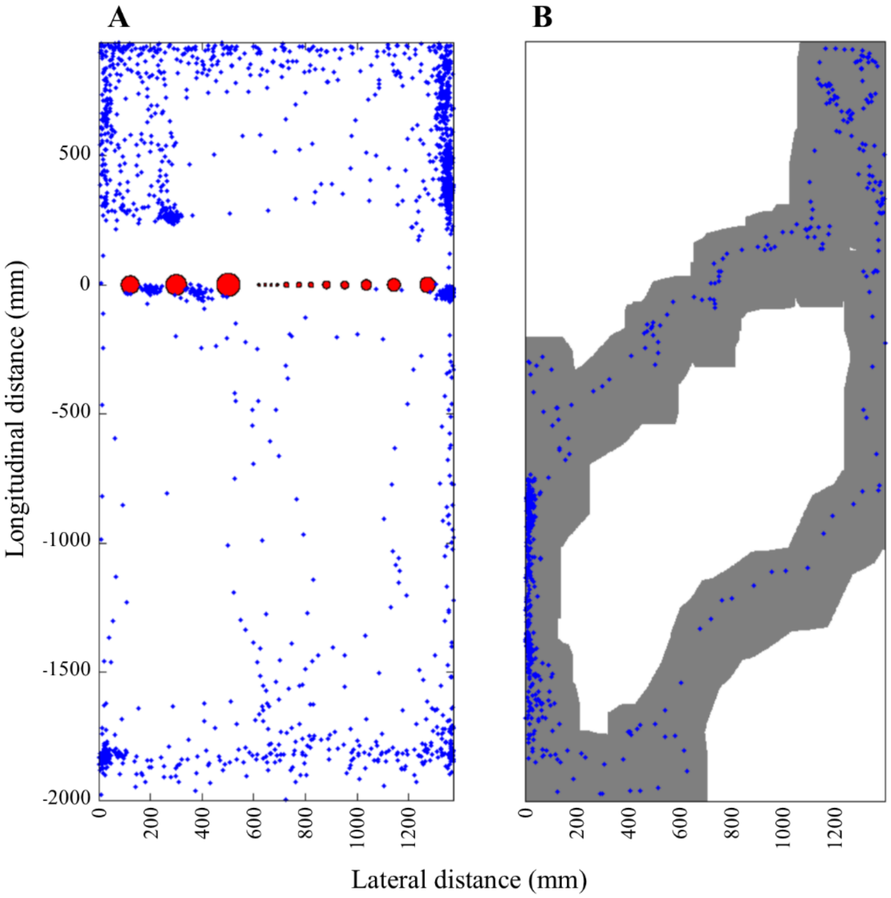


Figure 4.11 A) Plot of space use by a wild trout (FL: 223 mm) under treatment B (Trial 72, duration: 3507 seconds); and B) example of habitat sampled (H_s) (grey area) by a small hatchery fish (FL: 154 mm) under the control (Trial 120, duration: 856 seconds). Blue dots represent snout positions.

The following hydrodynamic zones where specialised behaviours were deemed possible were identified: a) *drafting zones* - the velocity deficit behind a bluff body where fish can alter their body kinematics to synchronise with the vortices shed (e.g. Kármán gait) (2.5d_c to 7.5d_c downstream of each cylinder, 1d_c wide); b) *entraining zones* - area in close proximity to the side of a bluff body where fish can hold position by tilting their body off parallel to the bulk flow to use the resulting lift and wake suction forces to mitigate for drag (e.g. Przybilla *et al.,* 2010) (-d_c/4 to 1.5d_c downstream of each cylinder, 2.375d_c wide); c) *bow riding zones* - the low-velocity high-pressure area in front of a bluff body where fish can hold position with a reduced trailing edge pressure deficit (Liao *et al.,* 2003a) (1FL to 1FL+d upstream of each cylinder, 1d_c wide); d) *tail holding zones* - where fish were able to hold position facing the flow by placing their tail against the downstream screen and their body along the channel wall (0.6FL to 1.2FL upstream of the downstream screen, flush with the flume wall, 0.25FL wide); and e) *wall holding zones* – where fish were able to hold position close to the flume wall and slightly downstream of the cylinder array with observed reduced body undulation (inline to 2.5d_c downstream of each cylinder, flush with flume wall, 2.375d_c/4 wide) (Figure 4.12). Although very similar to entraining as defined by Liao (2006) and Przybilla *et al.* (2010), wall holding was considered a separate behaviour because kinematics and focal position were clearly influenced by the proximity of the channel sides (Figure 4.12b).

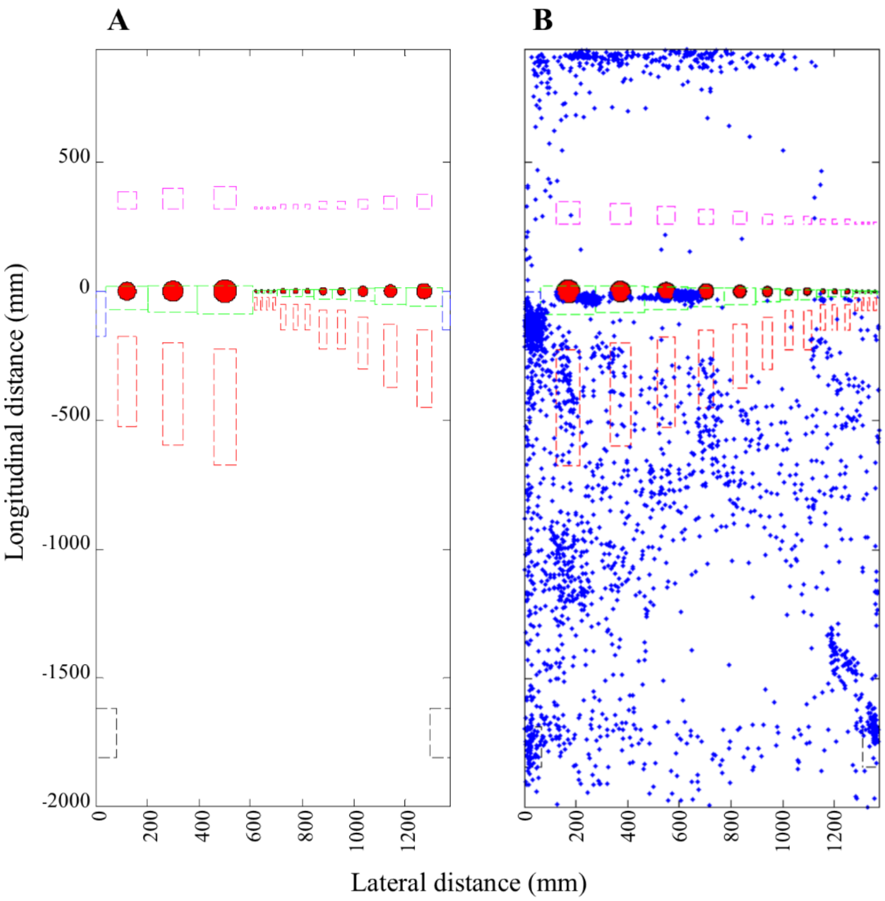


Figure 4.12 A) Predicted drafting zones (red), entraining zones (green), bow wake zones (magenta), wall holding zones (blue) and tail holding zones (black) for a 285 mm long (FL) trout under treatment B; and B) space use by a hatchery trout (FL: 260 mm) under treatment A (Trial 13, duration: 3356 seconds) with hydrodynamic zones overlaid to emphasize the heavy use of entraining and wall holding zones and moderate use of tail holding and drafting zones.

At a group level only tail holding regions, by small ($z = 4.107$, $p < 0.001$), medium ($z = 2.896$, $p < 0.01$), and large ($z = 3.173$, $p < 0.001$) hatchery trout, and wall holding regions, by large hatchery trout ($z = 3.363$, $p < 0.001$), were consistently used more frequently than expected if distribution had been even, although there was large amount of variability among individuals (Figure 4.13). There was no difference in the percentage of time wild trout spent in each zone compared to hatchery trout of equivalent size. Smaller hatchery fish spent a higher proportion of time in tail holding ($r_s = -0.428$, $p < 0.001$, 95% BCa CI: -0.571, -0.250) and a lower proportion in the drafting ($r_s = 0.5451$, $p < 0.001$, 95% BCa CI: 0.301, 0.588) and bow riding ($r_s = 0.242$, $p < 0.05$, 95% BCa CI: 0.072, 0.462) zones than larger trout (Figure 4.14). There was no correlation between FL and the proportion of time spent in the entraining or wall holding zones. Smaller trout were more likely to use entraining zones associated with smaller cylinders than larger trout ($r_s = 0.599$, $p < 0.01$, 95% BCa CI: 0.244, 0.835) (Figure 4.15). There was no correlation between FL and cylinder diameter in relation to the drafting or bow riding zones which trout used.

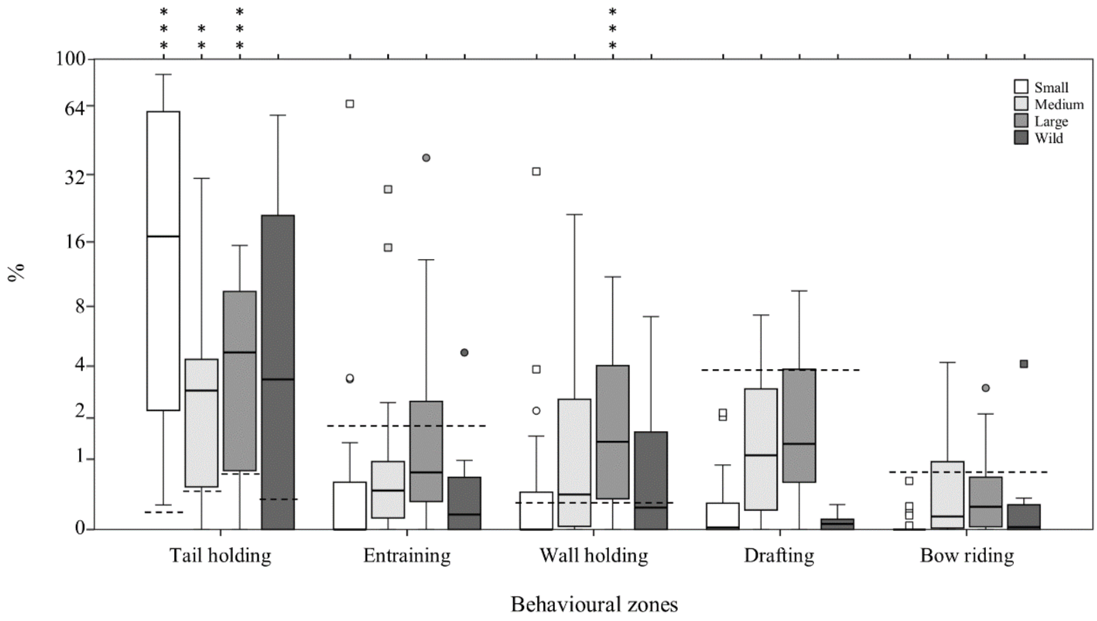


Figure 4.13 Box plot of percentage of the trial that wild and small, medium, and large hatchery brown trout, *Salmo trutta* (N = 8, 22, 16, 20, respectively), spent within the tail holding, entraining, wall holding, drafting and bow riding zones (data pooled from treatment A and B). Boxes represent interquartile range (IQR) and median. Whiskers represent the total range excluding standard (circles) and extreme (squares) outliers (greater than the upper quartile + 1.5 or 3 times the IQR, respectively). Dashed lines represent the proportion expected if distribution had been even. Asterisks represent incidences where the proportion of time spent within a region by individuals was consistently greater than that expected if distribution had been even (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). Y-axis scale is log base 2 to aid in interpretation.

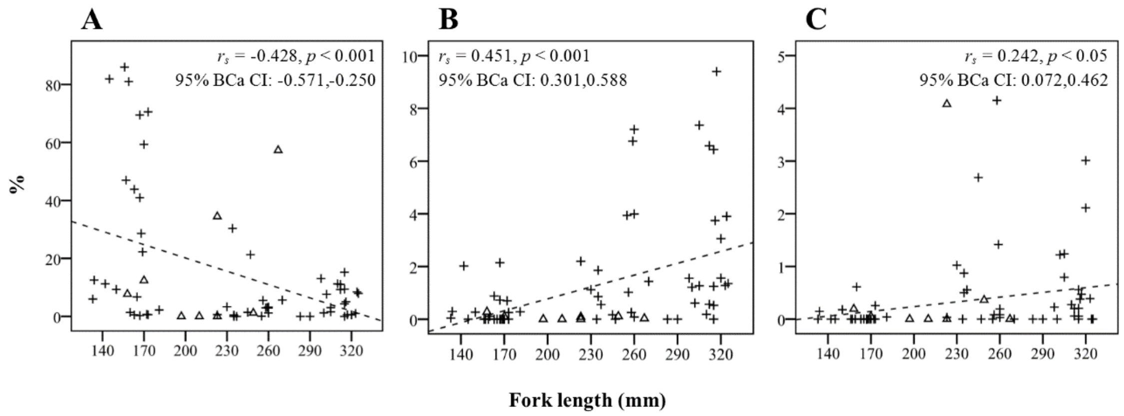


Figure 4.14 Relationship between percentage of a trial that hatchery (crosses) and wild (triangles) trout spent in the tail holding (A), drafting (B) and bow riding (C) zones and fork length (FL) (mm). Dashed line represents the linear correlation. Text is the Pearson's correlation coefficient (r_s) and significance level (p) and the bootstrapped (n = 2000) bias corrected and accelerated (BCa) 95% confidence intervals (CI) of r_s.

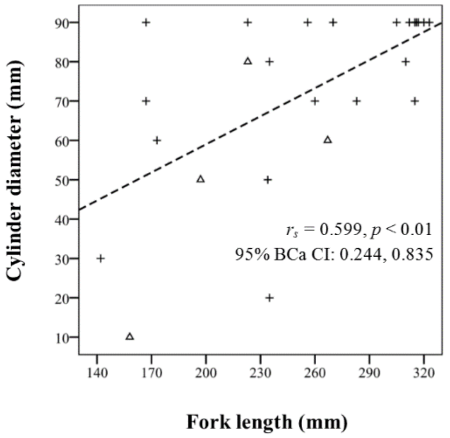


Figure 4.15 The relationship between trout fork length (mm) and the cylinder diameter (mm) of the entraining zone that trout preferentially choose to utilise (for all cases where peak time in a particular zone exceeded 10 seconds). Dashed line represents the linear correlation. Text is the Pearson's correlation coefficient (r_s) and significance level (p) and the bootstrapped (n = 2000) bias corrected and accelerated (BCa) 95% confidence intervals (CI) of r_s.

The key difference resulting from the two ways of calculating GH_p was the absence of an additional peak in the U and D_t preference curves constructed using the modified S_u data (*example:* Figure 4.16). The additional peaks in the GH_p curves constructed using the unmodified

S_u data represent the influence of occupying space where specialised behaviours could be exhibited.

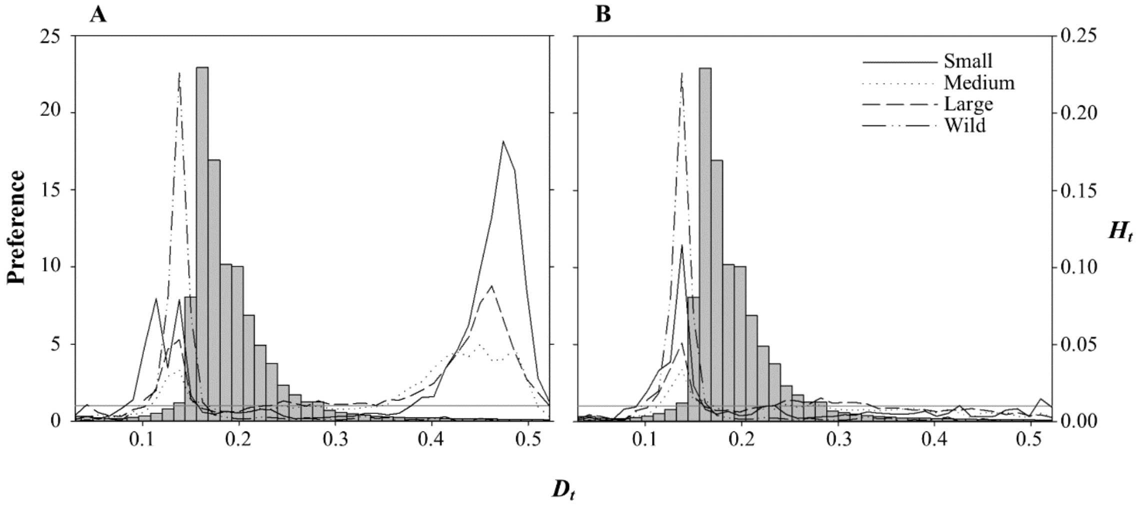


Figure 4.16 Relative drag ($\boldsymbol{D_t}$) group hydrodynamic preference (GH_p) curves constructed using unmodified (A) and modified (B) space use (S_u) data for wild and small, medium and large hatchery brown trout, *Salmo trutta*, in treatment A. Left axis is group preference curve series scale and right axis is total available hydrodynamic space histogram (H_t) scale (grey bars). Solid grey line is for reference purposes and represents an even distribution (i.e. preference = 1).

GH_p curves constructed using modified S_u data for each trout group, treatment, and hydrodynamic metric are presented in Figure 4.17. Preference for specific areas was highest (up to 25 times) for *U* and D_t, with all groups preferentially using areas with lower *U* and D_t than was most frequently available under each treatment and the control. Preference for low drag areas was generally higher for wild and small hatchery trout than medium or large fish. In treatment A and B, preference for *TI*, *k*, *TKE*, and τ_{uv} followed the H_t histograms, being higher for areas with low levels of each metric. There were a few exceptions, which included a slight preference exhibited by large fish for areas of high *TKE* (12.3 J m^{-2}: 1.1 times) and τ_{uv} (7.8 N m^{-3}: 1.6 times) in treatment A and B, respectively. Under the control all groups preferentially used areas with higher than most frequently available *TI*, *k*, *TKE*, and τ_{uv}. However, the range and magnitude of turbulence available was low. Trout preference for E_d differed for each group under each treatment. Under treatment A, peak preference of wild and small, medium and large hatchery trout was for areas where E_d = *ca.* 0, 10, 40, and 60 mm, respectively. Medium and large hatchery trout also exhibited an additional slight preference (*ca.* 1.3 times) for areas where E_d = *ca.* 125-140 mm. Under treatment B, peak preference of wild and small and medium hatchery trout was for areas with very small E_d (*ca.* 0 mm), but large hatchery trout showed no clear preference for E_d of any size.

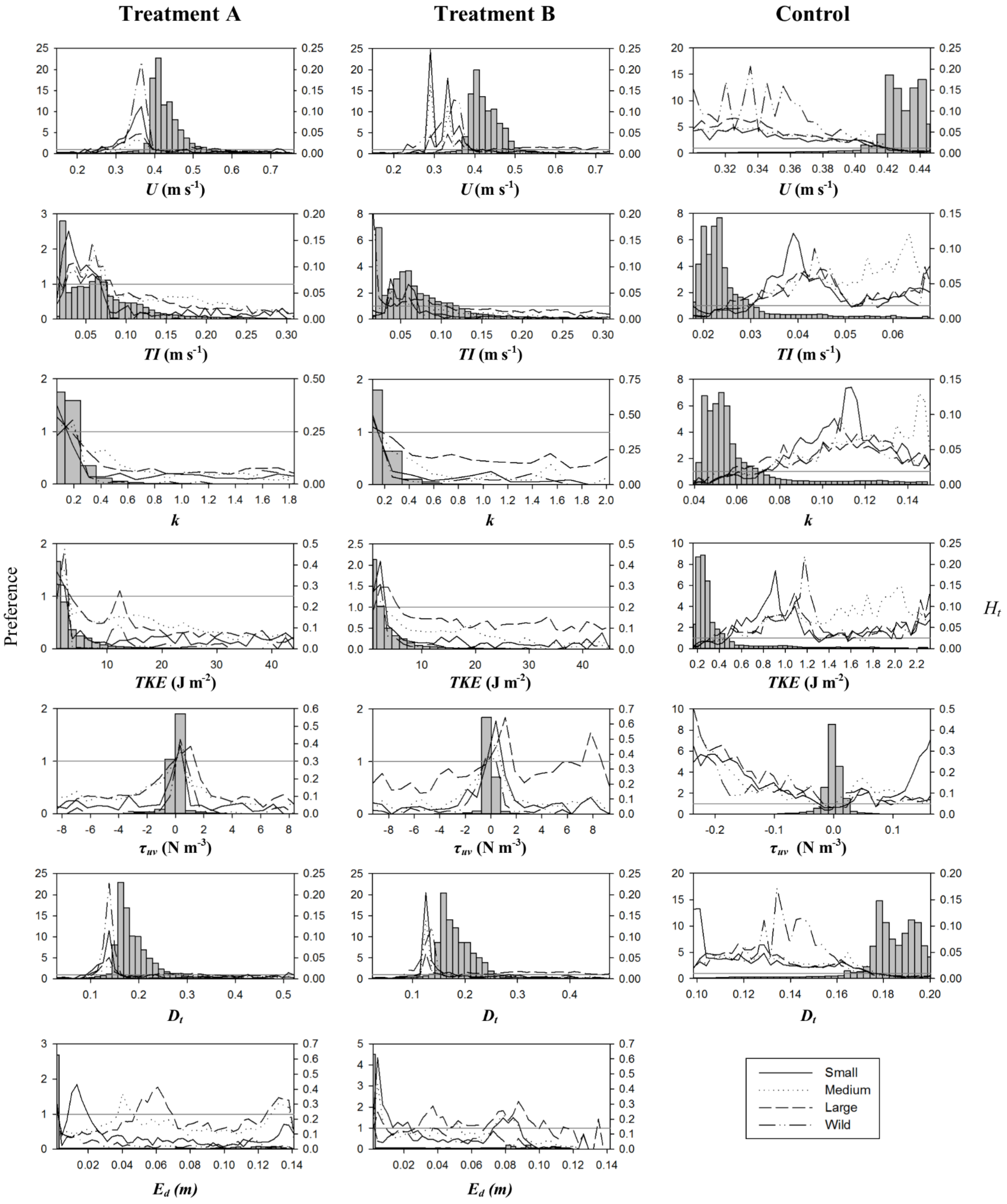

Treatment A
Treatment B
Control
Preference
H_t
U (m s^{-1})
TI (m s^{-1})
k
TKE (J m^{-2})
τ_{uv} (N m^{-3})
D_t
E_d (m)
0.2 0.3 0.4 0.5 0.6 0.7
0.32 0.34 0.36 0.38 0.40 0.42 0.44
0.05 0.10 0.15 0.20 0.25 0.30
0.02 0.03 0.04 0.05 0.06
0.2 0.4 0.6 0.8 1.0 1.2 1.4 1.6 1.8 2.0
0.04 0.06 0.08 0.10 0.12 0.14
10 20 30 40
0.2 0.4 0.6 0.8 1.0 1.2 1.4 1.6 1.8 2.0 2.2
-8 -6 -4 -2 0 2 4 6 8
-0.2 -0.1 0.0 0.1
0.1 0.2 0.3 0.4 0.5
0.10 0.12 0.14 0.16 0.18 0.20
0.02 0.04 0.06 0.08 0.10 0.12 0.14
Small
Medium
Large
Wild

Figure 4.17 Group preference curves for wild and small, medium and large hatchery brown trout *(salmo trutta)* under treatment A, B, and the control for mean velocity (U) (m s^{-1}), turbulence intensity (TI) (m s^{-1}), relative turbulence intensity (k), turbulent kinetic energy (TKE) (J m^{-3}), horizontal Reynolds shear stress (τ_{uv}) (N m^{-2}), drag (D_t), and eddy diameter (E_d) (m). Left axis is preference curve scale and right axis is total available hydrodynamic space histogram (H_t) scale (grey bars). Solid grey line is for reference purposes and represents an even distribution (i.e. preference = 1). Note: Axis scales differ between graphs to aid in interpretation.

4.5 Discussion

This study assessed space use by a stream dwelling fish, the brown trout, under complex turbulent flow conditions. A simple, robust and biologically relevant hydrodynamic descriptor of drag that incorporated both mean and fluctuating velocity components (D_t) provided a proxy for the energetic cost of holding station. Specialised behaviours (e.g. entraining and bow riding) that could not be described by this proxy were accounted for by controlling for excessive space use in key zones. As predicted, under controlled experimental conditions in which density dependent (conspecifics) and other confounding factors (e.g. visual cues, food, predators) were absent, fish adopted energy conservation strategies through the selection of areas with reduced drag or where they could exhibit specialised performance enhancing behaviours.

Peaks observed in the drag preference curves were also evident in the velocity data (U). This is expected because in the flow configurations tested U is generally higher than σ_v and σ_w and hence U is also a good proxy for drag and concurrently energetic expenditure. However, space use trends were clearer within the drag preference curves (i.e. a sharper peak) indicating that the incorporation of flow fluctuations within the metric refined its predictive power. Regardless, drag, simply derived or incorporating turbulent fluctuations (D_t), is a more meaningful metric to describe space use than mean velocity, as it has direct implications on energetic expenditure during swimming.

Previous studies that have focussed on turbulence rather than drag have identified correlative links between how fish use complex flow environments and individual turbulent metrics such as *TI*, *k*, *TKE*, or, τ_{uv} (Smith *et al.,* 2005; 2006, Cotel *et al.*, 2006; Silva *et al,* 2011; 2012a; 2012b: Duarte *et al.,* 2012). However, although individually valid, such statistical links are difficult to interpret form a bio-physical point of view. For example, why do fish select areas with low or high turbulent shear stress? What bio-physical principle would explain such a link? In this study, a reductionist approach of assessing habitat use in relation to potential energetic expenditure and the removal of the influence of specialised behaviours enabled clearer conclusions to be drawn.

Trout were observed to undertake two new types of specialised behaviour during the trials; wall holding and tail holding. Wall holding, although very similar to entraining as defined by Liao (2006) and Przybilla *et al.* (2010), was considered a separate specialised behaviour because focal position were clearly influenced by the proximity of the channel sides. It is likely under these conditions that the proximity of a boundary layer modified local flow conditions and altered the directionality of the resulting forces acting on the fish whilst entraining (e.g. lift and drag). Similar ‘wall holding’ clustering was depicted by Przybilla *et al.* (2010 - Fig. 2) but wasn’t included in their analysis or discussed. Fine scale assessment of the hydrodynamic processes involved in ‘wall holding’ is beyond the scope of this research but warrants further investigation.

Tail holding differed compared to the other specialised behaviours as fish held position against a physical object rather than using spatial and/or temporal variations in hydrodynamics. Out of the potential specialised behaviours identified (entraining, drafting, bow riding, wall holding, and tail holding), individual fish spent the highest proportion of time in tail holding, followed by entraining, and then wall holding zones. However at the group level only tail holding and wall holding zones were consistently used. Observations of tail holding during the trials indicated that trout could hold position using this behaviour for long periods with almost no corrective fin movement or body undulation. As the other specialised behaviours require some level of body undulation or corrective fin movement (e.g. Kármán gait - Liao *et al.,* 2003b; entraining - Przybilla *et al.,* 2010; bow riding - Taguchi and Liao, 2011; wall holding - experimental observation in this study) it is likely that tail holding is the least energetically costly station holding behaviour. From an energetics perspective, it is logical that tail holding was the most prevalent behaviour expressed. The only other consistently used behavioural zone was the wall holding zone (by large hatchery trout). Although the exact mechanisms that allow fish to maintain position with reduced body undulation in this location requires further analysis, the fact that this was the only other behavioural zone consistently utilised hints towards its energy saving potential.

During the trials smaller trout spent a higher proportion of time in tail holding regions than larger trout. As there is a causal relationship between fish length and absolute swimming performance (Beamish, 1978; Clough *et al*., 2004) smaller trout were likely more energetically taxed during each trial than larger individuals and were probably more inclined to tail hold due to their heightened need to conserve energy. This assumption is supported by the fact that on average smaller trout swam for a shorter duration before becoming impinged and exhibited a heightened preference for low drag regions in comparison to medium and large individuals. Hockley *et al.* (2014) identified similar links between fish size, energetics, and habitat use with larger guppies, *Poecilia reticulata*, displaying more frequent movement and swimming further than smaller individuals.

Analysis of the specialised behaviours indicated that fish chose to entrain on cylinders proportional in size to their body length; with small fish frequently entraining on the smaller cylinders whilst larger fish predominantly entrained on the largest cylinder. This is presumably because there is finite spatial size range of cylinder wakes that produce favourable hydrodynamic conditions for entraining and that this range is proportional to fish length. This finding has important implications for often ineffective habitat restoration schemes, where bluff bodies are used to increase habitat heterogeneity and fish densities within rivers (Palmer *et al.,* 2010). Although further data is required to refine the relationship between fish length and the size of object they preferentially choose to entrain on, the results of this study indicate that the use of instream objects of proportional size to target species / life stage might improve the effectiveness of such management techniques.

Fish maintain stability in a turbulent flow passively by self-correcting mechanisms or actively with powered movements (typically using the median and paired fins) (Webb *et al.,* 2006). However, if perturbations are sufficiently large or occur to quickly for a fish to react, postural control (stability) may be lost and the fish translated downstream, resulting in a reduction in swimming performance (Tritico and Cotel, 2010). The critical size of eddies required to destabilise a fish has been found to be those approximately equivalent to its body length (Pavlov *et al.,* 2000; Lupandin, 2005, Tritico and Cotel, 2010). Based on this relationship, a large proportion of the small trout used in this study may have been destabilised by eddies produced downstream of the larger cylinders. It is not possible to meaningful deduce avoidance from preference curves but whilst medium and large hatchery trout exhibited a preference for areas with large eddy diameters (125 - 140 mm) in treatment A, no preference for such areas was exhibited by the small hatchery trout in any treatment. In addition, smaller trout peak preference was for smaller eddy diameters compared to larger fish in treatment B. Although not direct evidence that fish avoid scales of turbulence that challenge their stability, these findings do not contradict this assumption.

This study provided insight into fish behaviour in a hydrodynamically complex flow environment and has important implications for management practises, such as assessing habitat quantity and quality. Results indicate that time-averaged single point hydrodynamic metrics do not accurately predict space use by fish in complex flow environments unless specialised behaviours that rely on spatial and temporal flow features are accounted for. When such behaviours are accounted for, space use of trout was predominantly governed by the selection of areas where they could reduce energetic expenditure, through the selection of areas with reduced drag or where they could exhibit specialised performance enhancing behaviours. The findings of this study represent a step forward in the understanding of fish behaviour in hydrodynamically complex environments and will help improve fisheries management and conservation.

CHAPTER 5

---

5 Efficiency of a side-mounted vertically oriented bristle pass for improving upstream passage of European eel (*Anguilla anguilla*) and river lamprey (*Lampetra fluviatilis*) at an experimental Crump weir.

5.1 Summary

Globally, populations of diadromous anguilliform morphotype fish, such as eel and lamprey, have experienced substantial declines, partly as a result of habitat fragmentation caused by river infrastructure. In the UK, a new configuration of hydrodynamically unobtrusive bristle pass (side-mounted and vertically oriented) has been developed to help upstream moving European eel (*Anguilla anguilla*) negotiate gauging weirs. The efficiency of vertically oriented bristle passes remains untested, despite their potential as a low-cost low-maintenance solution to improve habitat connectivity at low-head structural barriers worldwide. This study assessed the ability of small (82 – 320 mm) and large (322 – 660 mm) European eel and adult (291 – 401 mm) river lamprey (*Lampetra fluviatilis*) to pass upstream over an experimental Crump weir installed in a large open-channel flume with (treatment) and without (control) side-mounted vertically oriented bristle passes under three different hydrodynamic regimes. Both species were highly motivated to explore their surroundings and move upstream during the trials. Under flooded control conditions, passage efficiency (the total number of times fish passed the structure as a percentage of total attempts) and passage success (the number of fish that passed the structure as a percentage of those that attempted) were high, delay was short, and number of failed attempts before passage was low for both species. When difference in head was at its greatest (230 mm) and velocity and its variation downstream were high (maximum u and σ: 2.43 m s^{-1} and 0.66 m s^{-1}, respectively), the upstream movement of small eel and lamprey was blocked, and passage efficiency and success for large eel low (4.6% and 17.2%, respectively). For large eel that successfully passed, delay was long, and number of failed attempts before upstream passage was high. When bristle passes were installed, passage efficiency for small (91.5%) and large eel (56.7%), and passage success for large eel (76.5%) and lamprey (36.7%) was higher, while delay and the number of attempts before passage was lower for both species. Bristle passes helped

European eel and river lamprey pass a small experimental Crump weir, although interspecific variation in efficacy was evident.

5.2 Introduction

Impacts of infrastructure, such as dams, weirs and barrages, on the physical and chemical processes of rivers are well established (Petts, 1980). Impoundments alter flow and sediment regimes (Nilsson *et al.,* 2005; Xu and Milliman, 2009), channel morphology (Gordon and Meentemeyer, 2006), and nutrient and oxygen availability (Bellanger *et al.,* 2004; Gresh *et al.,* 2000). Ecological impacts include changes in invertebrate communities (Boon, 1988), and for fish the loss of, or reduced access to, critical habitat (Pess *et al.,* 2008), delayed migration (Caudill *et al.,* 2007), population isolation (Morita and Yamamoto, 2002), and reduced productivity and diversity (Agostinho *et al.,* 2008; Matzinger *et al*., 2007). As a consequence, populations of riverine fish have declined worldwide (Aparicio *et al.,* 2000; Dekker, 2007; Kruk, 2004; Nelson *et al.,* 2002). For diadromous species these declines are often due to impeded migration between essential habitats (Feunteun, 2002; Lucas and Baras, 2001; Ojutkangas *et al.,* 1995; Yoshiyama *et al.,* 1998).

In an effort to re-establish fluvial connectivity and reverse population declines a range of mitigation strategies have been developed, including the installation of fish passes at structural barriers to migration (Beach, 1984; Clay, 1995; Larinier and Marmulla, 2004). Unfortunately, fish passes, such as those developed for upstream migrating salmonids, often perform poorly for weaker-swimming non-salmonid species (Bunt *et al.,* 1999, 2000, 2001; Cooke *et al.,* 2005; Noonan *et al*., 2012; Slatick and Basham, 1985). For example, anguilliform morphotype fish, such as eel (*Anguilla* spp.) and lamprey (e.g. *Lampetra* spp. *and Petromyzon Marinus*), exhibit distinctly different forms of locomotion (Sfakiotakis *et al.,* 1999) and behaviour (Russon and Kemp, 2011a), compared to those with a subcarangiform morphology. Although anguilliform morphotypes have good acceleration and are highly manoeuvrable (Muller *et al.,* 2001; Sfakiotakis *et al.,* 1999), they do not leap at barriers and their burst swimming speeds are relatively low (Beamish, 1978; Clough *et al.,* 2004, Russon and Kemp, 2011b; Keefer *et al.,* 2012). Instead, if required, eel and lamprey adopt alternative strategies to ascend obstacles; juvenile eel climb wetted slopes using substrate surface irregularities (Legault, 1988; Tesch, 2003), while lamprey use their oral disk to attach to structures to rest between intermittent bouts of activity (Kemp *et al.,* 2009; Quintella *et al.,* 2004; Russon *et al.,* 2011). In recognition of these adaptations, and in response to environmental legislation (e.g. The Eels [England and Wales] Regulations 2009; CITES; European Habitats Directive [92/43/EEC]; EU Water Framework Directive [2000/60/EC]; Bern Convention [COE, 1979]) enacted in an attempt to reverse population declines (Dekker, 2003a; b; Dekker, 2007; ICES, 2012; Kelly and King, 2001; Moriarty and Tesch, 1996; Renaud, 1997), specialist fish passes have been developed and employed for several anguilliform morphotype fish (Moser *et al.,* 2011; Solomon and Beach, 2004).

For upstream migrating juvenile eel, specialist fish passes predominantly rely on their ability to climb (Legault, 1988; Tesch, 2003). A variety of substrates have been developed to facilitate climbing (Environment Agency, 2011; Porcher, 2002), including those that incorporate clusters of bristles (usually synthetic), set at regular intervals, protruding from a solid surface (see Environment Agency, 2011). This ‘bristled substrate’, when used in a traditional configuration (where the base is oriented horizontally, or slightly off horizontal, with water flowing through the bristles), has proved effective at facilitating the upstream passage of a large number (hundreds of thousands per year) (Briand, 2005; Jellyman and Ryan, 1983; Moriarty, 1986) and a broad size range (60 – 500 mm) (Moriarty, 1986, Robinet *et al.,* 2003) of eel worldwide. Further, there is some evidence that lamprey passage can also be enhanced by the judicial use of a bristled substrate (Laine *et al.,* 1998). Bristled substrate is now being used as a cost effective and hydrodynamically unobtrusive (Environment Agency, 2010a) addition to low-head gauging structures, such as Crump weirs (common in the UK), to facilitate the upstream passage of eel (Environment Agency, 2011) and possibly other anguilliform morphotype species. However, to minimise flow interference and negate the need for a separate water source (i.e. as required for ‘up and over’ installations - see Environment Agency, 2011), the bristled substrate is oriented vertically and attached with the bristles protruding perpendicularly towards the wing wall of a gauging structure. The efficiency of this configuration of bristle pass is currently untested, despite regional implementation and the recommendation of nationwide deployment in England and Wales (Environment Agency, 2011).

This study investigated the behaviour of European eel (*Anguilla anguilla*) and European river lamprey (*Lampetra fluviatilis*) as they attempted to pass an unmodified (control), or modified (treatment - with bristle passes installed) Crump weir, under experimental conditions. The experiment was repeated under three hydrodynamic regimes (low, medium and high velocity) that represent flow conditions similar to those encountered at Crump weirs in the field (comparable mean discharge scaled to width [m^3 s^{-1} m^{-1}] as many *in situ* crump weirs - data extracted from National River Flow Archive). Passage and delay were quantified and the influence of hydrodynamic regime and treatment assessed.

5.3 Methodology

5.3.1 Experimental setup

A model Crump weir (2.38 m long, 1.38 m wide and 0.34 m high) (Figure 5.1) was installed midway along an indoor recirculating flume (21.40 m long, 1.38 m wide, and 0.60 m deep) at the International Centre for Ecohydraulics Research (ICER) facility, University of Southampton, UK (50° 57’42.6”N, 1°25’26.9”W). A 14 m long experimental area, sectioned off from the rest of the channel by flow straightening devices (100 mm thick polycarbonate screens with elongated tubular porosity - 7 mm diameter), extended 7 m either side of the weir crest. Under treatment conditions, vertically oriented bristle passes (10 mm thick polypropylene board covered with 30 mm spaced orthogonally oriented clusters of *ca.* 24 synthetic fibres [70 mm long x 1.5 mm diameter]) were attached with bristles protruding towards the flume wall on each side of the channel (Figure 5.1b, c). The bristled substrate was installed in accordance with Environment Agency guidelines to maintain a 70 mm cavity (equal to bristle length) between the bristle board and flume wall (see Environment Agency, 2011).

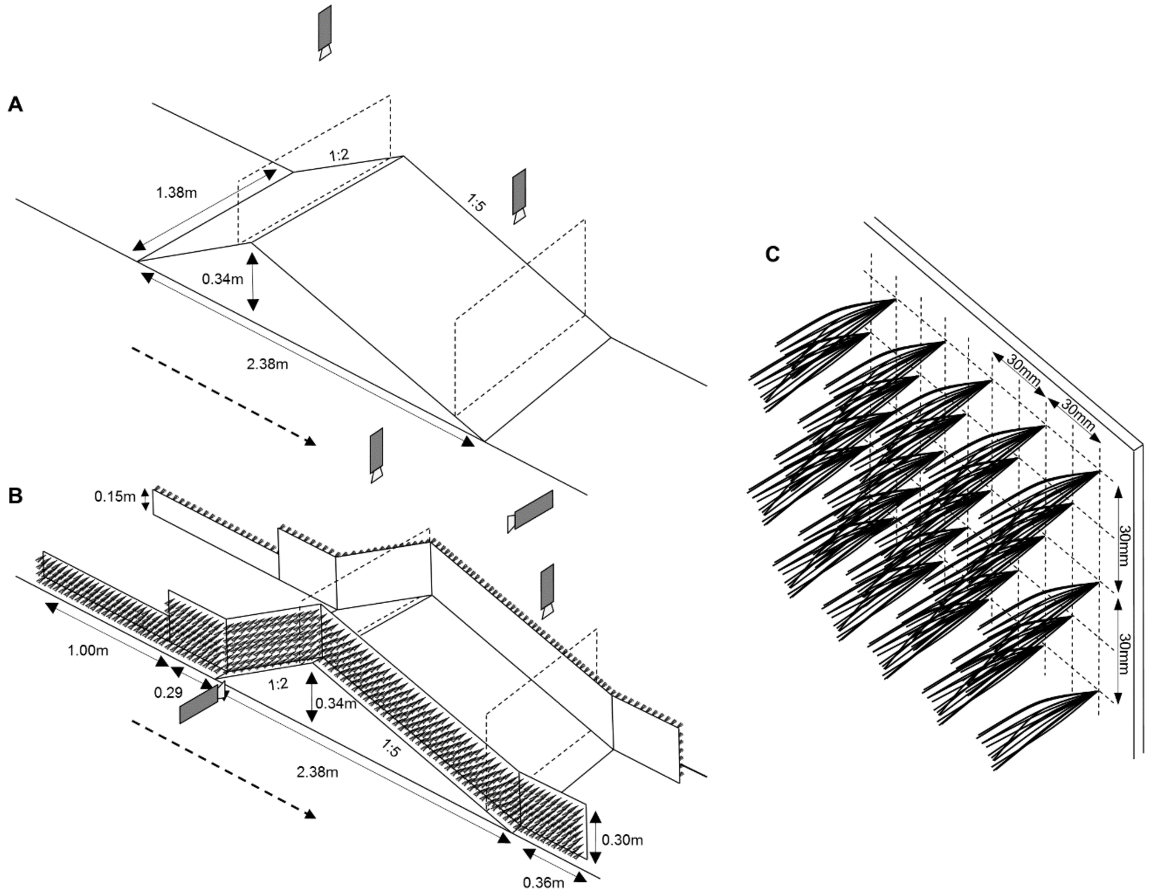


Figure 5.1 The Crump weir under control (A) and treatment (B) setups during which a bristled substrate (C) was vertically positioned against the channel walls to aid upstream movement of European eel and river lamprey under various hydrodynamic conditions. In A and B dashed lines indicate the position of half-duplex Passive Integrated Transponder (PIT) antennae coils and the dashed arrows indicates direction of flow.

Experiments were conducted under three hydrodynamic regimes: high (HV), medium (MV) and low velocity (LV), created by altering the downstream water level (depth: 220, 330 and 450 mm, respectively) by adjusting an overshot weir (located at the downstream end of the channel), under a constant discharge (0.09 $m^3 s^{-1}$). The HV and MV regimes were within the modular limits of the experimental weir with upstream water level (depth: 450 mm) independent of that downstream. The LV regime was outside the modular limits of the weir (flooded conditions - upstream water depth: 455 mm). As such, head difference under the HV, MV and LV regime was 230, 120, and 5 mm, respectively. Velocities were measured under control conditions for each hydrodynamic regime using an Acoustic Doppler Velocimeter (ADV) (Vectrino, Nortek-AS, Norway - frequency 50 Hz, sample volume 0.05 cm^3, record length 60 sec), and mean velocity ($U = \sqrt{\bar{u}^2 + \bar{v}^2 + \bar{w}^2}$) and Turbulence Intensity ($TI = \sqrt{{\sigma_u}^2 + {\sigma_v}^2 + {\sigma_w}^2}$) calculated. Where u,

v and w are the instantaneous velocity values corresponding to the x, y and z spatial coordinates, overbar denotes time-average, and σ is the standard deviation of its subscript. In conditions that precluded using the ADV, i.e. when depth was < 60 mm or air entrainment was high, an electromagnetic (EM) flow meter (Model 801 Flat, Valeport, UK - frequency 1 Hz, record length 30 sec) was used to measure *U* and estimate *TI* (taken as longitudinal standard deviation of velocity). ADV and EM velocity measurement locations in the vertical-longitudinal plane are depicted in Figure 5.2 (small black arrows and crosses, respectively). These measurement points were repeated at three distances laterally across the flume: 690 mm (mid channel – results shown in Figure 5.2), 100 mm and 30 mm away from the true right flume wall. Spatial maps of the hydrodynamics associated with the Crump weir were generated in ArcMap v10 (Esri, USA) using a spline interpolation.

Flow velocity at the crest of the weir was similar under each regime (*ca*. 0.83 m s^{-1}) (Figure 5.2). Maximum velocity (2.43, 1.91, and 0.80 m s^{-1} under the HV, MV, and LV regimes, respectively) was inversely related to head difference (Figure 5.2) and occurred at the weir crest under the LV regime and just upstream of the hydraulic jump under the MV and HV regime (Figure 5.2). The hydraulic jump consisted of a standing wave generated as the super-critical flow along the face of the weir rapidly decelerated on reaching the downstream water level. Despite flooded conditions under the LV regime, a small hydraulic jump occurred *ca.* 100 - 150 mm downstream of the weir crest (Figure 5.2). Downstream of the hydraulic jump, under all regimes, velocity gradually decreased as the channel deepened (Figure 5.2).

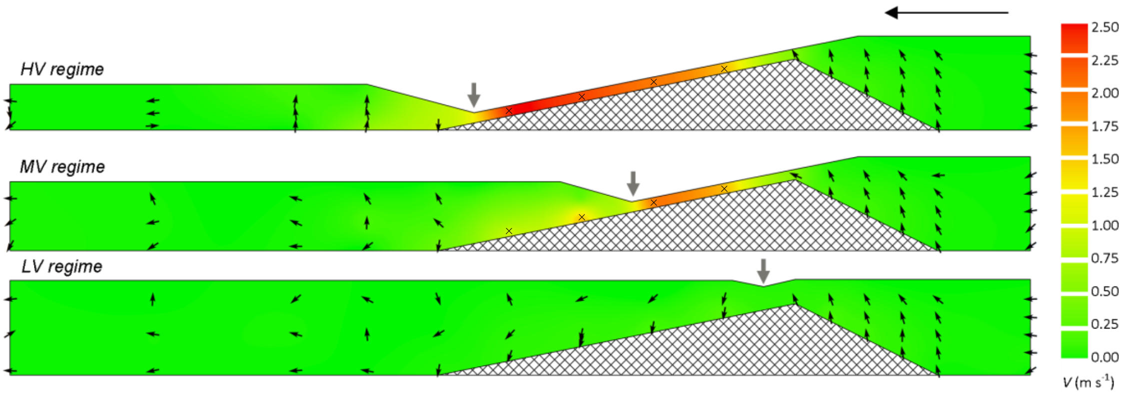


Figure 5.2 Velocity (m s^{-1}) profiles for a Crump weir under high (HV), medium (MV) and low (LV) velocity regimes. Small and large black arrows indicate mean and bulk flow direction, respectively. Grey arrows indicate position of a hydraulic jump. Crosses denote electromagnetic flowmeter sample locations.

Upstream of the weir the intensity of turbulence was low and similar under each regime (*TI = ca.* 0.05 m s^{-1}). High intensities of turbulence, relative to maximum velocity, were generated at the hydraulic jump (*TI* = 0.66, 0.27 and 0.17 m s^{-1} under the HV, MV and LV regime, respectively), and gradually dissipated with distance downstream. At the extent of the hydrodynamically mapped region (3.74 m downstream of the weir crest), turbulence had almost returned to background levels (*TI* = 0.10, 0.08 and 0.05 m s^{-1} under the HV, MV and LV regime, respectively).

5.3.2 Experimental procedure

Yellow phase European eel were collected by electric fishing from the Rivers Itchen (50° 57′ 19.2″ N, 1° 20′ 15.8″ W, *N* = 208, Total Length [TL]: μ = 397 mm, σ = 108 mm, Range = 149 – 660 mm), Wallington (50° 51′ 45.4″ N, 1° 09′ 54.5″ W, *N* = 31, TL: μ = 277 mm, σ = 58 mm, Range = 111 – 386 mm) and Meon (50° 53′ 53.2″ N, 1° 11′ 14.3″ W, *N* = 32, TL: μ = 178 mm, σ = 72 mm, Range = 82 – 333 mm) by the Environment Agency between 1st May and 12th July 2011. Actively migrating adult river lamprey were trapped in the River Ouse (53° 53′ 26.2″N, 1° 5′ 36.8″W) by a commercial fisherman on 4th December 2012 (*N* = 96, TL: μ = 358 mm, σ = 21 mm, Range = 291 – 401 mm). Fish were transported to the ICER facility in sealed polyurethane bags (river water and pure oxygen atmosphere - eels) or transportation tanks (aerated river water - lamprey) and held in separate 3000 litre outdoor holding tanks (aerated and filtered, 50% weekly water change) at ambient temperature (μ = 16.2 °C, σ = 1.9 and μ = 7.6 °C, σ = 3.1 for eel and lamprey, respectively). All fish were acclimated to holding tank conditions over 2 hours via gradual water exchange. Eel > 320 mm TL and all lamprey were tagged, under anaesthetic (2-Phenoxy-1-ethanol, 1 ml l^{-1}), with half-duplex Passive Integrated Transponder (PIT) tags (23 mm and 12 mm long, respectively) inserted through a small mid-ventral incision in the posterior quarter of the peritoneal cavity (mortality 0%, tag retention 99.6%,). Large eel and lamprey were weighed and measured during the tagging procedure and allowed at least 48 hours to recover from surgery before being used in experiments.

Treatment replicates were undertaken with multiple small (82 - 320 mm TL) or large (322 - 660 mm TL) eel between the 3rd May and 21st July 2011 (temperature: μ = 16.2°C, σ = 0.8) or lamprey (291 - 401 mm TL) between the 24th January and 7th February 2013 (temperature: μ = 8.8°C, σ = 1.5) (Table 5.1). Timings and temperatures were representative of peak migration periods for both species (lamprey: Jang and Lucas, 2005; eel: Moriarty, 1986). The duration between capture and experimentation ranged from 2 - 17 and 51 - 65 days for eels and lamprey, respectively. Each replicate lasted 5.5 hours and was undertaken at night (23:00 - 04:30) (< 0.1

lux) to coincide with peak eel and lamprey activity (eel: Haro and Kynard, 1997; Laffaille *et al*., 2007; Tesch, 2003, lamprey: Kelly and King, 2001; Moser *et al.,* 2002). Fish were acclimated to flume conditions in a porous container in the channel for 1 hour (22:00 - 23:00) before release into the experimental area 3 metres upstream of the downstream screen. Small eel were weighed and measured under anaesthetic (2-Phenoxy-1-ethanol, 1ml l^{-1}) after each replicate. Each fish was used only once during the study. Due to limited fish availability, passage experiments with lamprey were conducted only under the LV and HV regime. Temperature increase during experiments due to the pumps was small for both eel (μ = 0.4°C, σ = 0.5) and lamprey (μ = 0.6°C, σ = 0.5).

Table 5.1 Conditions encountered by European eel, *Anguilla anguilla*, and river lamprey, *Lampetra fluviatilis*, during passage over a model Crump weir installed in a recirculating flume under a high (HV), medium (MV) or low (LV) velocity hydrodynamic regime with (treatment) or without (control) bristle passes installed during 2011 (eel) and 2013 (lamprey). *N* is the number of fish used per trial.

Date	***Hydro-dynamic regime***	***Setup***	***Water depth (mm)*** [a]		***Maximum velocity ($m\ s^{-1}$)***	***Maximum Turbulence Intensity ($m\ s^{-1}$)***	***Mean water temp (°C)***	***N***	***Length range (mm)***	***PIT tagged***
			Upstream	***Downstream***						
Small European eel										
9 May	*HV*	*Control*	*450*	*220*	*2.43*	*0.66*	*16.5*	*10*	*195-290*	*No*
10 May	*MV*	*Control*	*450*	*330*	*1.91*	*0.27*	*16.8*	*10*	*215-317*	*No*
11 May	*LV*	*Control*	*455*	*450*	*0.81*	*0.17*	*16.6*	*10*	*149-314*	*No*
7 Jun	*LV*	*Control*	*455*	*450*	*0.81*	*0.17*	*15.4*	*10*	*220-302*	*No*
8 Jun	*MV*	*Control*	*450*	*330*	*1.91*	*0.27*	*15.8*	*10*	*149-290*	*No*
21 Jun	*HV*	*Treatment*	*450*	*220*	*2.43*	*0.66*	*16.0*	*8*	*222-297*	*No*
15 Jul	*HV*	*Control*	*450*	*220*	*2.43*	*0.66*	*17.5*	*10*	*113-290*	*No*
17 Jul	*HV*	*Treatment*	*450*	*220*	*2.43*	*0.66*	*17.5*	*12*	*82-315*	*No*
18 Jul	*MV*	*Treatment*	*450*	*330*	*1.91*	*0.27*	*17.2*	*10*	*98-320*	*No*
19 Jul	*LV*	*Treatment*	*455*	*450*	*0.81*	*0.17*	*17.1*	*10*	*111-315*	*No*
20 Jul	*MV*	*Treatment*	*450*	*330*	*1.91*	*0.27*	*17.2*	*10*	*211-317*	*No*
21 Jul	*LV*	*Treatment*	*455*	*450*	*0.81*	*0.17*	*17.2*	*10*	*205-320*	*No*
Large European eel										
3 May	*LV*	*Control*	*455*	*450*	*0.81*	*0.17*	*14.7*	*10*	*437-660*	*Yes*
4 May	*MV*	*Control*	*450*	*330*	*1.91*	*0.27*	*15.0*	*10*	*361-582*	*Yes*
8 May	*HV*	*Control*	*450*	*220*	*2.43*	*0.66*	*16.2*	*10*	*366-575*	*Yes*
12 May	*LV*	*Control*	*455*	*450*	*0.81*	*0.17*	*16.3*	*10*	*360-585*	*Yes*
16 May	*MV*	*Control*	*450*	*330*	*1.91*	*0.27*	*15.3*	*10*	*357-630*	*Yes*
17 May	*HV*	*Control*	*450*	*220*	*2.43*	*0.66*	*15.9*	*10*	*365-540*	*Yes*
18 May	*MV*	*Control*	*450*	*330*	*1.91*	*0.27*	*15.8*	*10*	*325-481*	*Yes*
19 May	*LV*	*Control*	*455*	*450*	*0.81*	*0.17*	*16.3*	*10*	*333-501*	*Yes*
9 Jun	*HV*	*Control*	*450*	*220*	*2.43*	*0.66*	*15.8*	*10*	*347-549*	*Yes*
13 Jun	*HV*	*Treatment*	*450*	*220*	*2.43*	*0.66*	*15.1*	*10*	*405-544*	*Yes*
14 Jun	*HV*	*Treatment*	*450*	*220*	*2.43*	*0.66*	*15.9*	*10*	*322-585*	*Yes*
15 Jun	*MV*	*Treatment*	*450*	*330*	*1.91*	*0.27*	*16.6*	*10*	*335-543*	*Yes*
16 Jun	*MV*	*Treatment*	*450*	*330*	*1.91*	*0.27*	*16.7*	*10*	*373-520*	*Yes*
19 Jun	*HV*	*Treatment*	*450*	*220*	*2.43*	*0.66*	*15.6*	*10*	*326-510*	*Yes*
22 Jun	*HV*	*Treatment*	*450*	*220*	*2.43*	*0.66*	*16.2*	*10*	*338-537*	*Yes*
River lamprey										
24 Jan	*HV*	*Treatment*	*450*	*220*	*2.43*	*0.66*	*5.5*	*8*	*329-384*	*Yes*
26 Jan	*HV*	*Control*	*450*	*220*	*2.43*	*0.66*	*6.8*	*8*	*320-395*	*Yes*
27 Jan	*LV*	*Control*	*455*	*450*	*0.81*	*0.17*	*7.7*	*8*	*320-379*	*Yes*
28 Jan	*LV*	*Treatment*	*455*	*450*	*0.81*	*0.17*	*8.7*	*8*	*320-373*	*Yes*
29 Jan	*HV*	*Treatment*	*450*	*220*	*2.43*	*0.66*	*10.2*	*8*	*338-401*	*Yes*
30 Jan	*HV*	*Control*	*450*	*220*	*2.43*	*0.66*	*10.6*	*8*	*340-388*	*Yes*
31 Jan	*HV*	*Control*	*450*	*220*	*2.43*	*0.66*	*10.6*	*8*	*339-395*	*Yes*
1 Feb	*LV*	*Control*	*455*	*450*	*0.81*	*0.17*	*10.2*	*8*	*291-388*	*Yes*
2 Feb	*LV*	*Treatment*	*455*	*450*	*0.81*	*0.17*	*9.2*	*8*	*322-379*	*Yes*
3 Feb	*HV*	*Treatment*	*450*	*220*	*2.43*	*0.66*	*9.0*	*8*	*314-391*	*Yes*
4 Feb	*LV*	*Treatment*	*455*	*450*	*0.81*	*0.17*	*9.3*	*8*	*324-371*	*Yes*
6 Feb	*LV*	*Control*	*455*	*450*	*0.81*	*0.17*	*7.6*	*8*	*327-388*	*Yes*

a: Measured 5 metres upstream or downstream of the weir crest.

Due to staggered eel availability, source location could not be randomised among treatments. For the purpose of this study it was assumed that there were no differences in behaviour / swimming ability among sources. Mean water temperature did not differ among treatments for any group. Mean TL did not differ among treatments for small and large eel. Despite random allocation, the mean TL of lamprey differed among treatments (one-way ANOVA: $F(3, 8) = 4.578$, $p < 0.05$), being higher under the HV control. Across treatment comparisons were considered acceptable as the difference was deemed small from a biological perspective (8.7 mm).

5.3.3 Fish behaviour

Fish behaviour was monitored using 2 - 4 low-light digital video cameras (AV-TECH Sony Effio 580TVL CCD) under infrared illumination, enabling visual assessment of movement and differentiation of route selection by individuals (Figure 5.1). The field of view of the two overhead cameras (control + treatment conditions) spanned the width of the flume at the crest and downstream extent of the weir (Figure 5.1). The two side cameras (treatment conditions only) monitored fish movement in the bristle passes at the crest of the weir through the glass walls (Figure 5.1). Video footage was recorded and reviewed using split-screen multi-channel acquisition and playback software (NUUO ltd., Taiwan). Individual large eel or lamprey were identified during movement over the weir using Half Duplex PIT telemetry (antennae installed at the trailing edge and crest of the weir, Figure 5.1a, b). Each antenna (3 coils of 2.5 mm^2 stranded 0.25 mm copper wire) was connected to a PIT detection system incorporating a single reader and two external dynamic tuning units (DEC-HDX-MUX-LOG 134.2 kHz, Wyre Micro Design Ltd., UK), powered using a 110Ah 12v leisure battery, and connected to an external data logger (AntiLog RS232, Anticyclone Systems Ltd., UK). The antenna wiring was attached directly to the face of the weir and had minimal impact on flow due to its low profile. The PIT system was tested by ensuring that tags (either size) held in a clenched fist were consistently detected when passed through each loop at any angle or location.

For each replicate the video footage and/or PIT data were interrogated and relevant passage events recorded (Table 5.2). As fish could move freely both up and downstream of the weir throughout the experimental period, multiple upstream passage events per fish were possible during each replicate. Based on the passage events the following metrics were calculated for all fish groups: 1) *number of failed attempts,* 2) *number of upstream passes,* 3) *bristle pass use*, and 4) *passage efficiency* (Table 5.2). For large eel and lamprey, to which passage events could be attributed to individual tagged fish, additional metrics were calculated: 5) *percentage attempts*,

6) *passage success*, 7) *number of attempts before upstream passage*, and 8) *delay* (Table 2). Tagged fish not detected at the downstream PIT antenna during the experiments (3 lamprey: 2 LV treatment, 1 LV control), were considered not to have explored their surroundings or sampled treatment conditions, and were not included in these metrics. For lamprey, which have the ability to attach to surfaces using their oral disc (Kemp *et al.,* 2009), specific attachment metrics were also calculated: 9) *percentage attachment*, 10) *number of attachments*, and 11) *mean duration of attachment* (Table 5.2).

Table 5.2 Definition of the passage events and metrics obtained for the small eel, large eel (*LE*), and/or lamprey (*L*) as they passed over an experimental Crump weir, and the statistical tests used.

Event/metric	**Definition**	**Group**	**Statistical test for variable:**	
			Hydrodynamic regime	Treatment
Events				
Attempt	*Progression upstream, of any part of the body onto the downstream face of the weir upstream of the hydraulic jump.*	All	N/A	
Upstream pass over the weir	*Passage of whole body upstream beyond the weir crest.*	All	N/A	
Upstream pass via a bristle pass	*Passage of whole body upstream beyond the weir crest via a bristle pass.*	All	N/A	
Attachment	*Attachment using oral disk on the downstream face of the weir upstream of the hydraulic jump.*	L	N/A	
Metrics				
1. Number of failed attempts	*Total number of attempts not resulting in upstream passage normalised by the number of fish per replicate.*	ALL	*One-way ANOVA*[a]	*Student t tests*
2. Number of upstream passes	*Total number of upstream passes normalised by the number of fish per replicate.*	ALL	*One-way ANOVA*[a]	*Student t tests*
3. Bristle pass use	*Quotient of the number of upstream passes via a bristle pass and total number of upstream passes per replicate.*	ALL	*Not assessed*	*Not assessed*
4.Passage efficiency	*Total number of times fish passed the weir as a percentage of total attempts per replicate.*	ALL	*One-way ANOVA*[a]	*Student t tests*
5. Percentage attempts	*Number of fish that attempted as a percentage of the total per treatment.*	LE, L	*Pearson's Chi-square (X^2) tests.*[b]	
6. Passage success	*Number of fish that passed the weir as a percentage of those that attempted per treatment.*	LE, L	*Pearson's Chi-square (X^2) tests.*[b]	
7. Number of attempts before upstream passage	*Number of attempts before first upstream passage event for each fish.*	LE, L	*Discrete-time hazard model (Logit function) and the Wald statistic (W).*[c]	
8. Delay	*Time between the first detection at the downstream PIT antennae and first upstream passage for each fish.*	LE, L	*Kaplan-Meier product-limit estimator and the Log Rank (Mantel-Cox) statistic (X^2_{mc}).*[c]	
9. Percentage attachments	*Total number of fish that attached as a percentage of the total that attempted per treatment.*	L	*Pearson's Chi-square (X^2) tests.*[b]	
10. Number of attachments	*Number of attachments normalised by the number of fish per replicate.*	L	*Two-way ANOVA*	
11. Mean duration of attachment	*Quotient of total duration and number of attachments per replicate.*	L	*Two-way ANOVA*	

a: Brown and Forsyth F ratio used in cases that violated homogeneity of variance.
b: Fisher's exact tests (FET) used if expected frequencies were < 5.
c: Event time analysis (Singer and Willet, 2003).

Discrete attempts (see Table 5.2) were delineated by a fish drifting back downstream of the hydraulic jump for > 1 second or by an attachment (see Table 5.2) on the downstream face of the weir (lamprey only). Any further upstream progression observed on the downstream face of the weir was considered a separate attempt as it involved an observable increase in swimming speed to counter the high velocity flow. All statistical analysis was undertaken in SPSS v20 (IBM, USA). Due to low replicate numbers it was not possible to assess interaction effects. Hence, the influence of hydrodynamic regime was assessed under control conditions only and the influence of treatment was assessed separately under each hydrodynamic regime. Percentage data were arcsine square root transformed prior to statistical analysis (see Sokal and Rohlf, 1995). *Delay* and *number of attempts before upstream passage* were assessed using time to event analysis (Singer and Willet, 2003) (Table 5.2). This method provides unbiased estimates by including fish that fail to pass the weir (right-censored individuals) in a probability function (Cumulative Probability of Passage [CPP]) at any given time or number of attempts (see Castro-Santos and Haro, 2003).

5.4 Results

A high percentage of the observed passage events were detected by the PIT system (Large eel: 97.2%, Lamprey: 93.0%) allowing identification of the majority of individuals. Passage events with no directly associated PIT data were assigned to individuals with a high degree of confidence by assessing historic and future detections combined with visual tracking of the fish over time.

Number of failed attempts was not influenced by hydrodynamic regime or treatment for any group (μ ± S.E.: small eel = 1.87 ± 0.64, large eel = 3.74 ± 1.10, and lamprey = 5.24 ± 1.47).

Number of upstream passes was negatively related to maximum velocity for all groups (small eel: $F(1, 3) = 157.984$, $p < 0.01$, large eel: $F(1, 6) = 19.020$, $p < 0.01$, and lamprey $F(1, 4) = 91.240$, $p < 0.01$), but was not influenced by treatment (Figure 5.3).

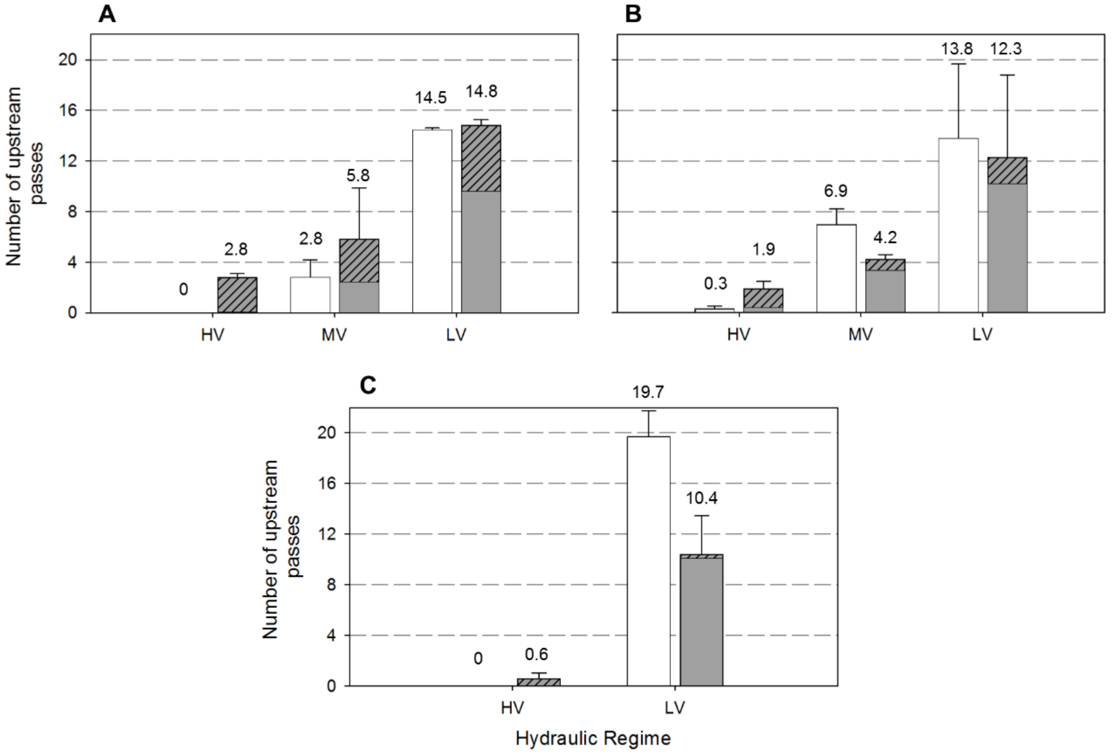


Figure 5.3 Mean *number of upstream passes* per fish for small eel (A), large eel (B), and lamprey (C) without (control: clear bars) and with (treatment: grey bars) bristle passes installed under the low (LV), medium (MV), and high (HV) velocity hydrodynamic regimes. Hatched sections of the grey bars indicate the proportion of upstream passes that occurred via the bristle passes. Error bars represent ± 1 S.E..

Bristle pass use (μ ± S.E.) was highest under the HV, and lowest under the LV regime for small eel (100 ± 0.0%; 35.1 ± 6.0%), large eel (78.3 ± 6.3%; 16.7 ± 6.1%), and lamprey (100 ± 0.0%; 2.6 ± 1.1%) (Figure 5.3).

Passage efficiency was negatively related to maximum velocity for small eel (*F*(1, 3) = 43.841, $p < 0.01$), large eel (*F*(1, 5) = 24.961, $p < 0.01$) and lamprey (*F*(1, 4) = 145.462, $p < 0.001$) (Figure 5.4). Under the HV regime, passage efficiency was higher for small (91.5%; t(1) = -31.658, $p < 0.05$) and large eel (56.7%; t(3) = -5.057, $p < 0.05$) when the bristle passes were installed (Figure 5.4). Treatment did not significantly influence *passage efficiency* for lamprey under the HV regime, or for any group under the MV or LV regime.

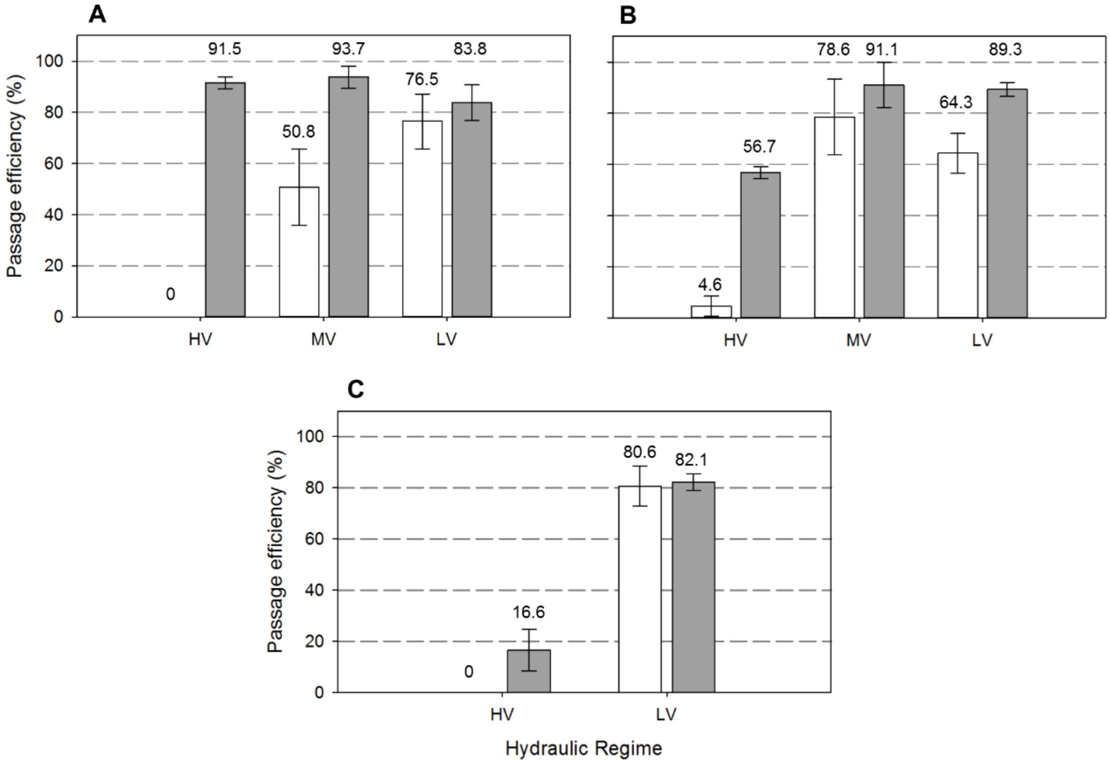


Figure 5.4 Mean p*assage efficiency* (%) for small eel (A), large eel (B), and lamprey (C) without (control: clear bars) and with (treatment: grey bars) bristle passes installed under the low (LV), medium (MV), and high (HV) velocity hydrodynamic regimes. Error bars represent ± 1 S.E..

Percentage attempts for large eel was not influenced by hydrodynamic regime or treatment, and was consistently high (> 85%). For lamprey, *percentage attempts* was not influenced by treatment but was lower under the HV (62.5%) compared to the LV (95.6%) regime ($X^2(1) = 15.034$, $p < 0.001$).

For large eel, *passage success* was lower under HV (17.2%) than the MV (92.3%) ($X^2(1) = 41.85$, $p < 0.001$) and LV control (100%) ($X^2(1) = 30.99$, $p < 0.001$), but not different between the MV and LV control (Figure 5.5a). For lamprey, *passage success* was lower under the HV (0%) than LV control (100%) ($X^2(1) = 37$, $p < 0.001$) (Figure 5.5b). *Passage success* was higher under the HV treatment than control for both large eel (76.5%; $X^2(1) = 5.785$, $p < 0.001$) and lamprey (35.7%; *FET*: $p < 0.05$) (Figure 5.5). There was no influence of treatment under the MV or LV regime (Figure 5.5).

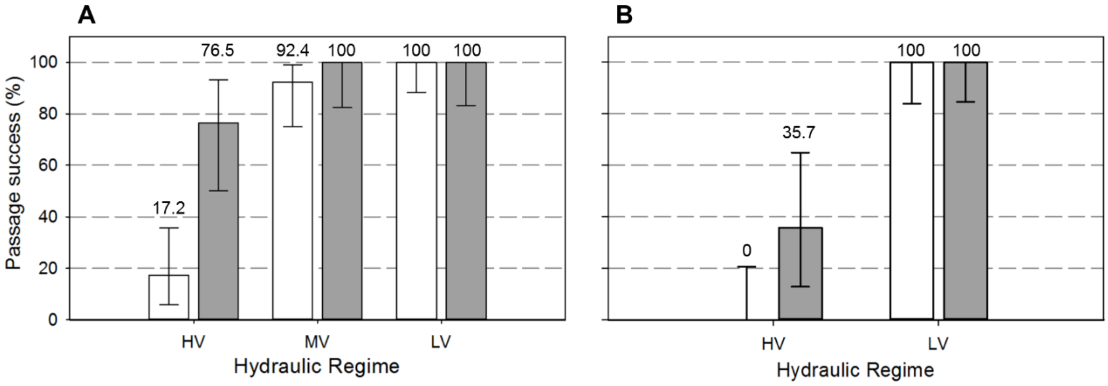


Figure 5.5 *Passage success* (%) for large eel (A) and lamprey (B) without (control: clear bars) and with (treatment: grey bars) bristle passes installed under the low (LV), medium (MV), and high (HV) velocity hydrodynamic regimes. Error bars are 95% confidence intervals calculated using the Clopper-Pearson exact method.

For large eel, *number of attempts before upstream passage* was higher under HV control (20.5% CPP after 3 attempts) than the MV (> 50% CPP after the 1st attempt) ($W_s(1) = 26.729$, $p < 0.001$) and LV control (> 50% CPP after the 1st attempt) ($W_s(1) = 31.593$, $p < 0.001$), but was not different between the LV and MV control (Figure 5.6a). For lamprey, *number of attempts before upstream passage* was higher under HV control (0% CPP despite up to 50 attempts) than the LV control (> 50% CPP after the 1st attempt) ($W_s(1) = 29.176$, $p < 0.001$) (Figure 5.6b). *Number of attempts before upstream passage* was lower under the HV treatment than control for both large eel (> 50% CPP after the 2nd attempt; $W_s(1) = 18.275$, $p < 0.001$) and lamprey (30.6% CPP after the 2nd attempt; $W_s(1) = 45.702$, $p < 0.001$) (Figure 5.6). There was no influence of treatment under the MV or LV regime (Figure 5.6).

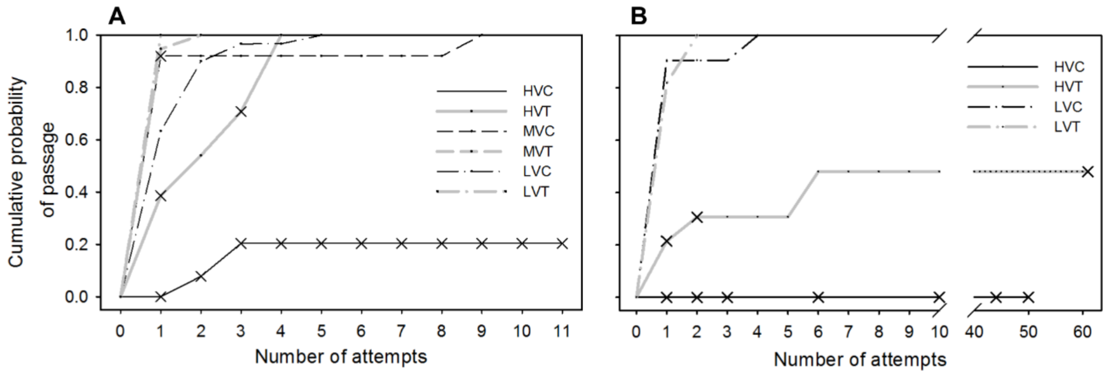


Figure 5.6 Cumulative Probability of Passage (CPP) upstream with number of attempts for large eel (A) and lamprey (B) with (treatment: grey lines) and without (control: black lines) bristle passes installed under the low (LV), medium (MV), and high (HV) velocity regimes. Crosses represent right censored data.

For large eel, *delay* was longer under the HV control (17.2% CPP after 330 minutes) than the MV (50% CPP after 13.3 minutes) ($X^2_{mc}(1) = 44.974$, $p < 0.001$) and LV control (50% CPP after 5.36 minutes) ($X^2_{mc}(1) = 69.399$, $p < 0.001$), and longer under MV control than the LV control ($X^2_{mc}(1) = 22.837$, $p < 0.001$) (Figure 5.7a). For lamprey, *delay* was longer under HV control (0% CPP after 330 minutes) than the LV control (50% CPP after 19.28 minutes) ($X^2_{mc}(1) = 38.767$, $p < 0.001$) (Figure 5.7b). *Delay* was shorter under the HV treatment than control for both large eel (50% CPP after 115 minutes: $X^2_{mc}(1) = 16.260$, $p < 0.001$) and lamprey (35.7% CPP after 330 minutes: $X^2_{mc}(1) = 6.730$, $p < 0.01$) (Figure 5.7). There was no influence of treatment under the MV or LV regime (Figure 5.7).

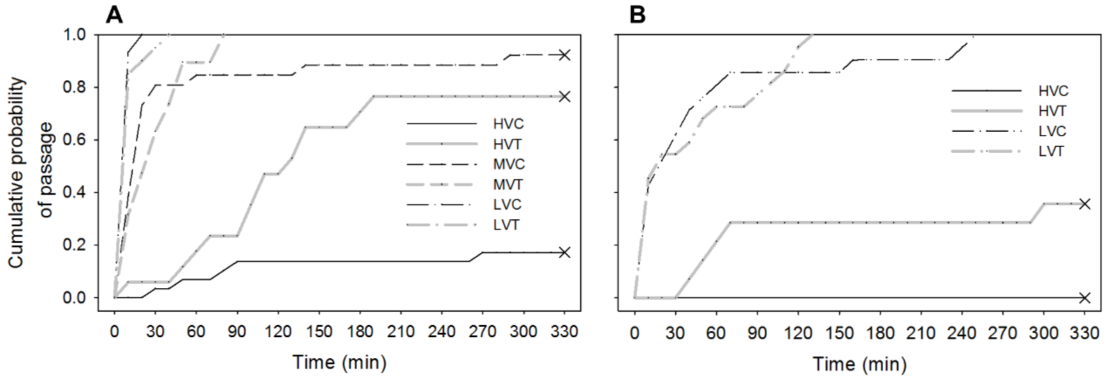


Figure 5.7 Cumulative Probability of Passage (CPP) upstream against time for large eel (A) and lamprey (B) with (treatment: grey lines) and without (control: black lines) bristle passes installed under the low (LV), medium (MV), and high (HV) velocity hydrodynamic regimes. Crosses represent right censored data.

Neither *percentage attachments* (34.2%) nor *number of attachments* (μ ± S.E.: 16.0 ± 6.8) were influenced by hydrodynamic regime or treatment. *Mean attachment duration* was influenced by hydrodynamic regime ($F(1, 8) = 7.807$, $p < 0.05$) but not by treatment, being longer under the HV (150.7 ± 27.0s) than LV regime (46.5 ± 19.6s).

Lamprey were not as proficient at navigating the bristled substrate as eel, often struggling to make progress through the passes. Lamprey were observed to have striated marks along the length of their body after exiting the bristle passes (Figure 5.8).These were temporary and disappeared within 24 hours. Eel showed no obvious physical external effects of bristle pass use.

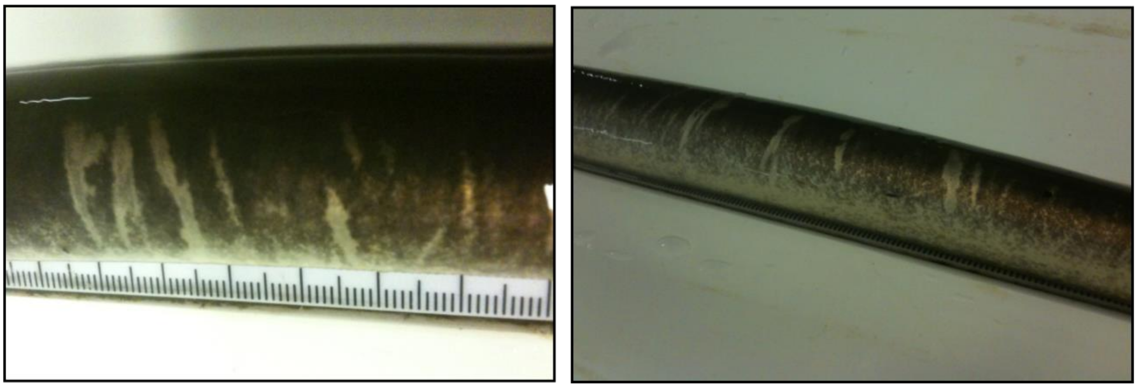


Figure 5.8 Two examples of striated marks on the flanks of lamprey caused by bristle pass use. Scale is in mm.

5.5 Discussion

This study experimentally assessed the efficiency of a side-mounted vertically oriented bristle pass for improving upstream passage of European eel and river lamprey at a low-head gauging weir. Eel and lamprey were highly motivated to explore their surroundings and move upstream as was evident by the high proportion of fish that attempted to pass under all conditions. Significant increases in passage efficiency and success and decreases in delay and the number of attempts before passage for both species under the high velocity treatment indicate that the bristle passes improved the ability of eel and lamprey to pass upstream when high flow velocities and turbulence restricted passage. However, interspecific variation in efficacy was apparent with the passes promoting a higher passage efficiency and success for eel than for lamprey.

Barriers can block or impede the movement of fish between essential rearing and spawning habitat (Lucas and Baras, 2001). Excessive energetic costs during migration can compromise the physiological and behavioural processes necessary for sexual maturation and successful reproduction (Mesa *et al.,* 2003). Delayed migration can increase predation risk (Peake *et al.,* 1997; Rieman *et al.,* 1991), physiological stress, and susceptibility to disease (Loge *et al.,* 2005). For adult lamprey, as for most anadromous species, additional energetic costs during upstream movement to spawning grounds cannot be compensated as feeding ceases during migration (Lucas and Baras, 2001). In this study, bristle passes mitigated to some extent these negative effects by providing higher passage success and efficiency, shorter delay, and fewer failed attempts for both eel and lamprey as they passed the model crump weir. However, the majority of barriers where bristle passes are likely to be installed are larger than the model weir used in this experiment (e.g. increased head difference and distance for traversal). Larger scale flume trials would provide useful information of the effects of increased barrier size but the facilities to undertake such experiments are rare. In addition, flume trials cannot adequately account for the numerous confounding variables that occur *in situ*. The next step in validating the effectiveness of side-mounted vertically oriented bristle passes is to undertake robust field studies at larger barriers.

A key concern in the design of the experiment was to allow fish sufficient time to pass the obstruction. As such, a single 5.5 hour long trial was undertaken per night. This, in combination with the limited duration of the experimental period, resulted in a low number of replicates. As such, the statistics presented could be considered conservative with a high chance of a type II error (i.e. only large effects being detected as significant). Although not statistically significant the measured mean and variance values indicate that bristle passes may also be affecting the number of upstream passes per night and having further beneficial influences on passage efficiency outside of those identified through the inferential statistics. For example, in addition to the bristle passes significantly improving passage efficiency for small and large eel under the HV regime, the data indicate they may have also improved passage efficiency for lamprey, and for small and large eel under the medium and low velocity regime. Further experimental data would have to be collected to validate these trends.

In good years, juvenile European eel are recruited into the lower catchment of freshwater systems in large numbers (Moriarty, 1990). As there is a causal relationship between body length and absolute swimming performance (Beamish, 1978; Clough *et al.,* 2004) small juvenile eel are particularly susceptible to velocity barriers. In this study, bristle passes facilitated the upstream passage of eel as small as *ca.* 100 mm. Enhanced dispersal of this life-stage is particularly important as it is likely that density-dependent mortality (see Vøllestad and Jonsson, 1988) would limit system productivity unless early upstream colonisation is achieved.

In comparison to small eel, a higher percentage of large eel passed over the weir directly, rather than via a bristle pass under each hydrodynamic regime. Possibly because bristle spacing was less appropriate for larger eel (restricted manoeuvring space) or their higher absolute swimming capability enabled them to more easily ascend the weir. Similarly, a lower percentage of both large and small eel passed the weir via the bristle passes under the low compared to high velocity treatment; probably due to it being easier for all sizes to ascend the weir directly under these conditions. Few lamprey passed through the bristle passes under any treatment. Those that did exhibited cutaneous abrasions, which can increase a fish's susceptibility to bacterial infection (Bader *et al.,* 2006). For this species, further research to investigate how design alterations, such as increasing bristle spacing, may improve passage success and reduce abrasion is warranted. The implication of such design modifications on eel passage should be considered in parallel.

Poor attraction efficiency is known to limit the overall effectiveness of fish passes (Bunt *et al.,* 2001; Moser *et al.,* 2002). In this study, limited downstream area, long trial duration, and the highly active nature of both species resulted in a very high chance of individuals encountering the entrance of a bristle pass. In addition, both eel and lamprey tended to move upstream along the flume walls further increasing their chances of encountering a pass entrance. Actively migrating juvenile eels tend to migrate on mass in the shallow low velocity regions along the banks of estuaries and rivers (Tesch*,* 2003), and passes located along channel boundaries generally catch more individuals than those in the centre (Piper *et al.,* 2012). As such, the configuration of bristle pass tested in this study (attached directly to the wing wall of a gauging structure) probably represents the optimal location to maximise attraction efficiency. However, it is acknowledged that at complex sites the low flow through this type of pass may limit attraction. In such cases extra attraction flow should be provided (see Piper *et al.,* 2012).

Unlike eel, lamprey lack paired fins and struggle to maintain stability in turbulent conditions (see Liao, 2007). A lower percentage of lamprey attempted to pass the weir under the high compared with low velocity regime, possibly because turbulent conditions associated with the hydraulic jump inhibited upstream movement. Lamprey also frequently attached to the face of the weir and attempted to pass using a burst-attach-rest mode of locomotion thought to enhance performance (Kemp *et al.,* 2011; Quintella *et al.,* 2004). Previous studies indicate that lamprey vary their attachment behaviour in response to hydrodynamic conditions (Kemp *et al.,* 2011), an observation supported by the results of this study in which mean duration of attachment was longer under the high velocity regime, presumably to facilitate recovery.

This study provides: 1) evidence that bristle passes improve the upstream passage of both eel and lamprey under experimental conditions and 2) a mechanistic understanding of how they function which will help improve future pass design. When high velocity and turbulence restricted passage, bristle passes increased the passage success of large eel and lamprey to 76.5 and 36.5%, respectively. For catadromous European eel, such levels may be adequate to maintain a stable population due to the extended duration of their diffusive upstream migration (i.e. a high probability of being able to pass during a high-flow event). For anadromous river lamprey, which are energetically and temporally constrained during their upstream migration, such levels will likely limit system productivity. It is recommended that new fish passage technologies for both species continue to be investigated. However, for a small barrier the configuration of bristle pass tested would seem to represent a viable low-maintenance and low-cost option to improve habitat connectivity for European eel. For river lamprey, while the wing-wall bristle media shows potential for assisting passage, further studies over a wider range of obstacle heights and bristle spacing are needed to determine whether this approach has merit.

CHAPTER 6

6 Masking an accelerating velocity gradient with turbulence: Application to improving the downstream migration of fish through bypass systems at anthropogenic barriers.

6.1 Summary

According to Signal Detection Theory (SDT), the ability to detect a signal (discriminability) decreases with increasing levels of internal and/or external noise. Brown trout (*salmo trutta*), were used to test whether external noise could be used to mask the detection of a signal that induced an unwanted response. On encountering a velocity gradient (VG), a feature commonly associated with river infrastructure (e.g. fish passes and screens), downstream moving fish generally switch orientation to face into the flow and actively reject (by swimming back upstream) the abrupt near field hydrodynamic transition. Such avoidance negatively impacts the efficiency of bypass systems designed to mitigate for reduced habitat connectivity at anthropogenic barriers (e.g. dams). An experiment was conducted to quantify trout behaviour in the presence or absence of an accelerating VG (constricted or unconstricted channel, respectively) under two levels of background hydrodynamic noise (low and high Turbulent Kinetic Energy - *TKE*). The proportion of trout that approached and passed, orientation, nature of response (orientation switch or rejection), delay and discriminability were quantified. When the channel was unconstricted trout generally approached and passed oriented downstream (*ca.* 67%), a high proportion passed (*ca.* 91%), and delay was short (Median: 0.13 minutes). In comparison, when the channel was constricted trout generally approached and passed the VG oriented into the flow (*ca.* 64%), fewer passed (*ca.* 43 %), and delay was longer (Median: >20 minutes). The level of hydrodynamic noise did not influence the proportion of fish that passed, time to pass, or the distance or absolute velocity at which trout responded to the VG. Discriminability both increased and decreased in response to hydrodynamic noise level depending on whether coarse or fine scale behavioural responses were assessed. Fine scale discriminability and, to some extent, the other passage metrics, seemed to be influenced by the high propensity of the fish to exhibit responsive behaviours during trials. Coarse scale

discriminability decreased under high levels of hydrodynamic noise indicating that some masking did occur. Increasing the level of noise used to mask the signal may produce a more noticeable effect in future experiments. Despite mixed results, the use of masking as a wildlife management technique is conceptually valid and the findings of this experiment present a useful stepping stone for future research.

6.2 Introduction

Psychophysics, a branch of psychology that deals with physical stimuli and mental phenomena, has been successfully utilised for over a century to analyse animal behaviour (Fechner, 1860; Graham, 1934; Akre and Johnsen, 2014). Signal Detection Theory (SDT), a key concept within psychophysics, considers the relationship between the magnitude and perceived intensity of a stimulus (signal) and the ability to discern between the signal and noise (discriminability) (Kemp *et al.,* 2012). An important premise within SDT is that discriminability decreases with increasing levels of background noise (internal or external). This 'masking' effect (defined as a change in the likelihood of perception of one signal in the presence of a second - Gelfand, 2010), has been shown to occur for diverse range of species and numerous sensory modalities (e.g. sound – Wollerman and Wiley, 2002; Lohr *et al.,* 2003, vibration – Wu and Elias, 2014, vision – Woo *et al.,* 2009, hydrodynamic signal detection - Engelmann *et al.,* 2002; Kröther *et al.,* 2002, Basset *et al.,* 2006). Indeed, vibrational masking is actively used by the male tree hopper, *Tylopelta gibbera*, to inhibit the localisation of its competitors by females (Legendre *et al.,* 2012). However, to this author's knowledge, masking has never been directly used as a management tool to limit the detection of a signal for conservation purposes.

The ability to manipulate behaviour has important implications for the conservation of vulnerable species, especially if the stimulus to which animals are responding to is anthropogenic. There are a diverse range of anthropogenically induced stimuli that disrupt animal behaviour. For example: European robins, *Erithacus rubecula*, are unable to use their internal magnetic compass in the presence of urban electromagnetic noise (Engels *et al.,* 2014), the sea-finding behaviour of hatchling loggerhead turtles, *Caretta caretta*, is disrupted by artificial lighting (Berry *et al.,* 2013), and intense hydrodynamic gradients induced by anthropogenic river infrastructure delay the migration of Atlantic salmon smolts, *Salmo salar*, and Juvenile American shad, *Alosa sapidissima* (Haro *et al.,* 1998). In many cases it is unfeasible to remove detrimental signals so mitigation measures must be taken. The ability to mask such signals and directly mitigate for anthropogenic impacts without costly, more intensive, conservation measures such as relocation (Green *et al.,* 2010) or population supplementation (Hedrick *et al.,* 2000) is an appealing concept.

Due to their high fecundity, short generation time, small size, ease of care, and relatively simplistic behaviour repertoire, fish make ideal model organisms for use in experimental research (e.g. in genetics, embryology and disease - Lieschke and Curie, 2007, physiology -

Briggs, 2002, and behaviour - Norton and Bally-Cuif, 2010). In relation to psychophysics, the downstream migrating life phase is of particular interest as their progress is more strongly mediated by behaviour than swimming performance (a significant factor for upstream migrating individuals) (Katopodis and Williams, 2012; Williams *et al.,* 2012). In addition, many populations are increasingly threatened by environmental change, making them of direct conservation concern (Allibone *et al.,* 2010; Dudgeon *et al*., 2005; Wilson *et al.,* 2008).

For downstream migrating fish, high levels of mortality occur during passage through hazardous routes at hydropower facilities (e.g. turbines and overspills) (Taylor and Kynard, 1985; Stokesbury and Dadswell, 1991; Heisey *et al.,* 1992; Navarro *et al.,* 1996; Winter *et al*., 2006, Calles *et al.,* 2010), of which there are an estimated 15,000 plants worldwide (World Energy Council, 2013). Sources of mortality include: blade strike, pressure change, gas supersaturation, and vertical drops, and indirectly: stress, disorientation, and increased susceptibility to predation and disease (see Cada *et al.,* 1990; Coutant and Whitney, 2000; Abernathy *et al.,* 2001; Budy *et al.,* 2002; Larinier, 2008). To mitigate for these adverse effects physical or behavioural screens are often used to direct downstream migrating fish away from deleterious routes to more desirable bypass channels (Larinier, 2008). However, the efficiency of these systems is often very low (Kynard and O'Leary, 1993; Johnson *et al.,* 2000; Calles *et al.,* 2012) with fish actively avoiding bypass intakes (Kynard and Buerkett, 1997).

Bypass entrances are synonymous with an accelerating velocity gradient (VG), decreasing area and increasing darkness (Haro *et al.,* 1998). Numerous studies have analysed fish behaviour as they encounter a VG (Haro *et al.,* 1998; Kemp *et al.,* 2005; 2006; 2008; Enders *et al.,* 2009; 2012; Russon and Kemp, 2011a; Vowles and Kemp, 2012; Vowles *et al.,* 2014), but relatively little attention has been given to the development of methods to reduce rejection rates (*exceptions:* Haro *et al.,* 1998; Vowles and Kemp, 2012). On encountering a VG downstream migrating fish typically switch orientation to face into the flow and actively avoid (reject) the abrupt near field hydrodynamic transition by swimming back upstream (Atlantic salmon smolts*:* Haro *et al.,* 1998; Pacific salmon smolts, *Oncorhynchus* spp.*:* Kemp *et al.,* 2005; European eel, *Anguilla anguilla:* Piper *et al.,* 2015; Newbold *et al.,* 2015). Partial success in reducing the rejection rate at a bypass entrance has been achieved by altering the intake design and minimising the intensity of the VG that fish experience as they pass (i.e. reducing the signal strength - Haro *et al.,* 1998). However, physical alterations that sufficiently reduce the intensity of a VG may not always be possible. Vowles and Kemp (2012) tested the effect of localised illumination on rejection rates and found that responsiveness (avoidance) and delay of brown trout, *Salmo trutta*, increased rather than decreased when multimodal stimuli were present. Further exploration of behavioural methods to improve passage efficacy through bypass systems is required if the adverse effects of anthropogenic barriers are to be mitigated for.

Kemp *et al.,* 2012 utilised SDT to analyse behavioural response of fish to different velocity gradients and highlighted its usefulness as a tool for understanding, quantifying and potentially manipulating fish behaviour. Building on the results of Kemp *et al.,* (2012) it is hypothesised that if hydrodynamic noise in the vicinity of an accelerating velocity gradient were increased then the discriminability of the signal and the probability of rejection will decrease. This was experimentally tested by assessing the behaviour of brown trout in the presence or absence of an accelerating VG (constricted or unconstricted channel, respectively) under two levels of background hydrodynamic noise (low and high Turbulent Kinetic Energy - *TKE*). The proportion of fish that approached and passed, orientation, nature of response (orientation switch or rejection), time to pass, and discriminability were quantified.

6.3 Methodology

6.3.1 Experimental setup

Experiments were undertaken in an indoor recirculating flume (21.40 m long, 1.38 m wide and 0.60 m deep) at the International Centre for Ecohydraulics Research (ICER), University of Southampton, UK (50° 57’42.6”N, 1°25’26.9”W). The experimental area consisted of a centrally located 2 metre section of the channel (Figure 6.1). Different treatments were created by changing two factors; *velocity gradient* (present or absent - factor A) and *hydrodynamic noise* (low or high *TKE*- factor B). Factor A was manipulated by either leaving the channel unmodified (absent) or gradually constricting the downstream end of the experimental area to 36.4% of its original width (present) (Figure 6.1). Factor B was manipulated by screening the upstream extent of the experimental area with either a flow straightening device (100 mm thick polycarbonate screen with elongated tubular porosity – 7 mm diameter) (low *TKE*) or a large diameter grid (orthogonally aligned and equally spaced wooden batons – 33 mm wide x 18 mm thick, M = 122 mm) (high *TKE*) (Figure 6.2). As such, four treatments were created: Absent low (AL), absent high (AH), present low (PL), and present high (PH).

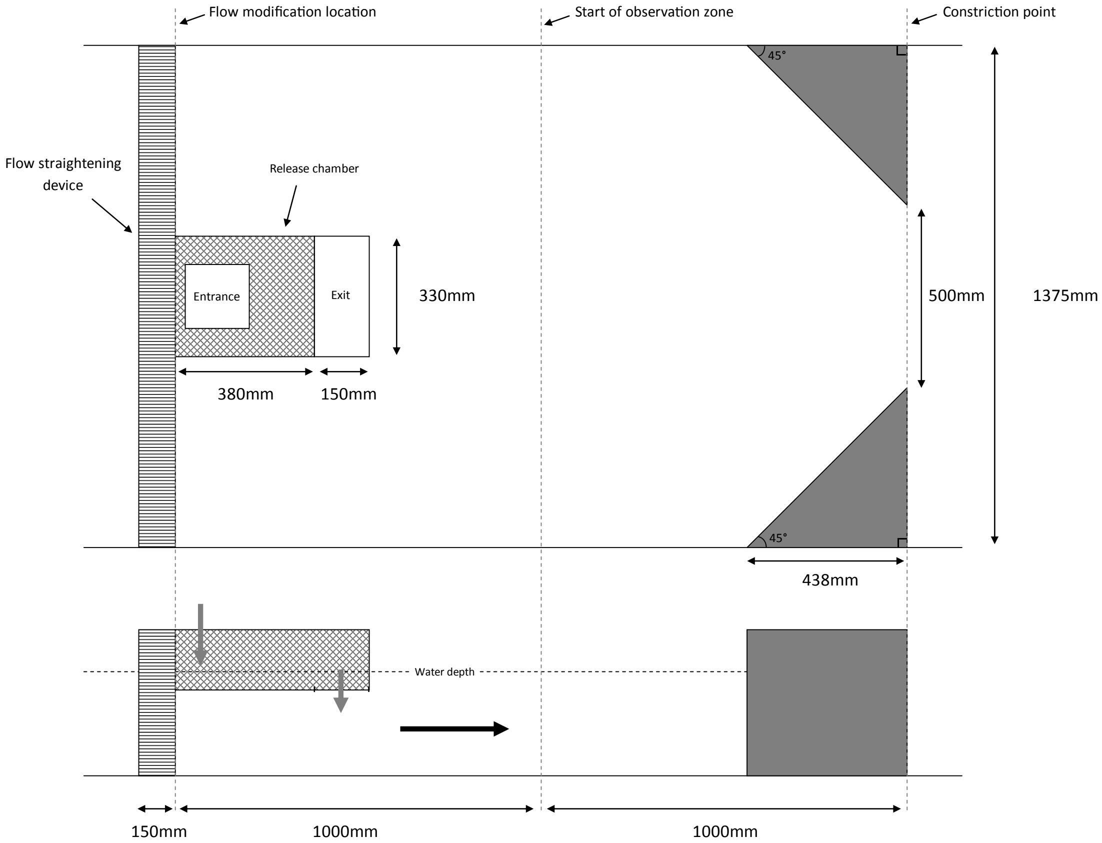


Figure 6.1 Schematic representation of the experimental area with velocity gradient present under low levels of hydrodynamic noise (TKE) (PL treatment). Thick grey arrows indicate the entrance and exit of the release chamber. Thick black arrow indicates bulk flow direction. Grey dashed lines indicate the flow modification location, the start of the observation zone, and the constriction point.

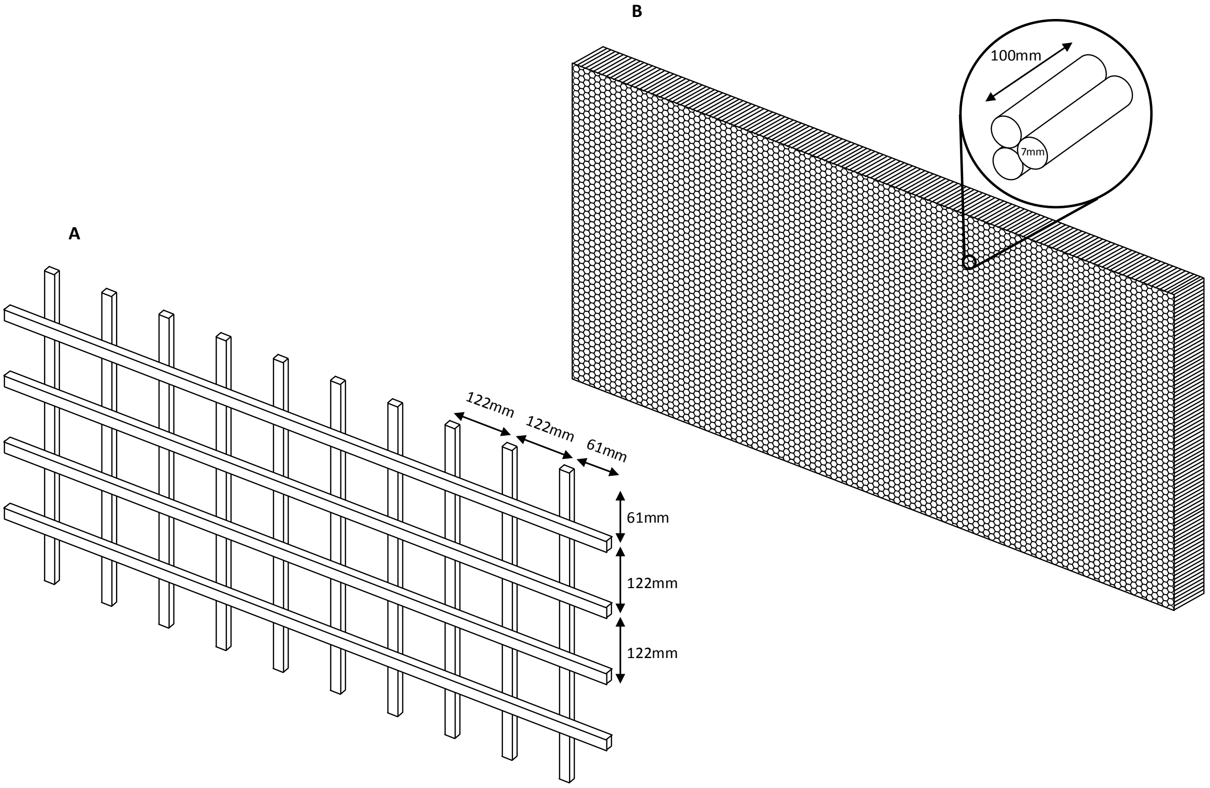


Figure 6.2 A) The grid utilised to increase turbulence intensities in the high turbulence treatments: constructed of equally spaced (*M* = 122m) wooden batons (33 mm x 18 mm). B) The flow straightening device used to reduce turbulence intensities in the low turbulence treatments: 100 mm thick polycarbonate screen with elongated tubular porosity – 7 mm diameter.

Discharge was constant in each treatment (0.09 $m^3 s^{-1}$). The free stream velocity (U_f - across channel mean measured 1 m upstream from the constriction point at 150 mm depth) was set to be similar in each treatment (*ca.* 0.27 m s^{-1}) (Table 6.1) by adjusting an overshot weir at the downstream end of the channel. Due to the blockage effect, water depth was slightly deeper when the velocity gradient was present versus absent (288 and 280 mm, respectively) (Table 6.1). A surface mounted release chamber (mesh cage - 0.53 m long, 0.33 m wide, 0.15 m deep), protruding 60 mm below the surface, allowed fish to volitionally enter the experimental area through a central orifice (0.15 m long, 0.33 m wide) located 1.62 metres upstream of the constriction point (Figure 6.1). Fish were prevented from exiting the experimental area upstream by the flow straightening device or by a fine wire mesh (12 mm diameter) attached to the upstream face of the grid. Fish could freely pass downstream beyond the constriction point (Figure 6.1). Experiments were undertaken at night with a 1 metre section upstream of the constriction point, the observation zone (Figure 6.1), illuminated with infrared light and monitored using a low-light overhead CCTV camera.

Table 6.1 Conditions encountered by brown trout, *Salmo trutta*, in experimental trials undertaken to assess their behavioural response to a velocity gradient (Factor A) under different levels of hydrodynamic noise (Factor B). *TKE* is the mean Turbulent Kinetic Energy recorded within the observation zone and *U* is the mean across channel velocity measured 1 metre upstream of the constriction point (150 mm depth).

Treatment	***Factor A (Velocity gradient)***	***Factor B (Hydrodynamic noise)***	***TKE* (μ ± σ) ($J\ m^{-3}$)**	***U* (μ ± σ) ($m\ s^{-1}$)**	***Depth* (μ ± σ) (mm)**	***Replicates***	***Temperature* (μ ± σ) (°C)**	***Fork Length* (μ ± σ) (mm)**
AL	Absent	Low	0.23 ± 0.00	0.27 ± 0.01	280	22	10.46 ± 0.00	153.1 ± 12.1
AH		High	1.52 ± 0.18	0.26 ± 0.00	280	21	10.45 ± 0.04	147.1 ± 11.8
PL	Present	Low	0.23 ± 0.03	0.26 ± 0.01	288	21	10.68 ± 0.05	147.3 ± 10.6
PH		High	1.61 ± 0.07	0.26 ± 0.01	288	21	11.24 ± 0.07	146.1 ± 11.7

Water velocities were measured in each treatment (*n* = 132, 132, 507, and 521 in the AL, AH, PL, and PH treatment, respectively) using an Acoustic Doppler Velocimeter (ADV) (Vectrino, Nortek, AS - frequency 50 Hz, sample volume 0.05 cm^3, depth 150 mm, record length 90 sec). Mean velocity (*U*) ($m\ s^{-1}$) (Eq. 6.1) and *TKE* ($J\ m^{-3}$) (Eq. 6.2) were calculated from filtered ADV data (3D cross correlation filter - see Cea *et al.,* 1997):

$$\mathrm{V} = (\bar{\mathrm{u}}^2 + \bar{\mathrm{v}}^2 + \bar{\mathrm{w}}^2)^{0.5} \qquad \text{Eq. 6.1}$$

$$\mathrm{TKE} = 0.5\rho\left(\overline{\mathrm{u}'^2} + \overline{\mathrm{v}'^2} + \overline{\mathrm{w}'^2}\right) \qquad \text{Eq. 6.2}$$

Where u, v and w are the instantaneous velocity values corresponding to the x, y and z spatial coordinates, overbar and prime denote time-averaged and deviation from mean, respectively, and ρ is density ($kg\ m^{-3}$). Within the hydrodynamically mapped region, conditions were linearly interpolated (1 mm resolution). Outside of the hydrodynamically mapped region (30 mm area adjacent to the flume walls) boundary layer conditions were calculated (1 mm resolution) by fitting a 3rd order polynomial between the two measured points closest to the wall and a zero point at the wall. In the presence and absence of the VG, velocities ranged from *ca.* 0.13 - 1.03

and *ca.* 0.24 - 0.29 m s^{-1}, respectively (Figure 6.3). Mean *TKE* recorded in the observation zone for each treatment are reported in Table 6.1. The VG was not noticeably influenced by hydrodynamic noise, with the area where velocity was at least 10% greater than free stream similar under both low and high *TKE* (Figure 6.3).

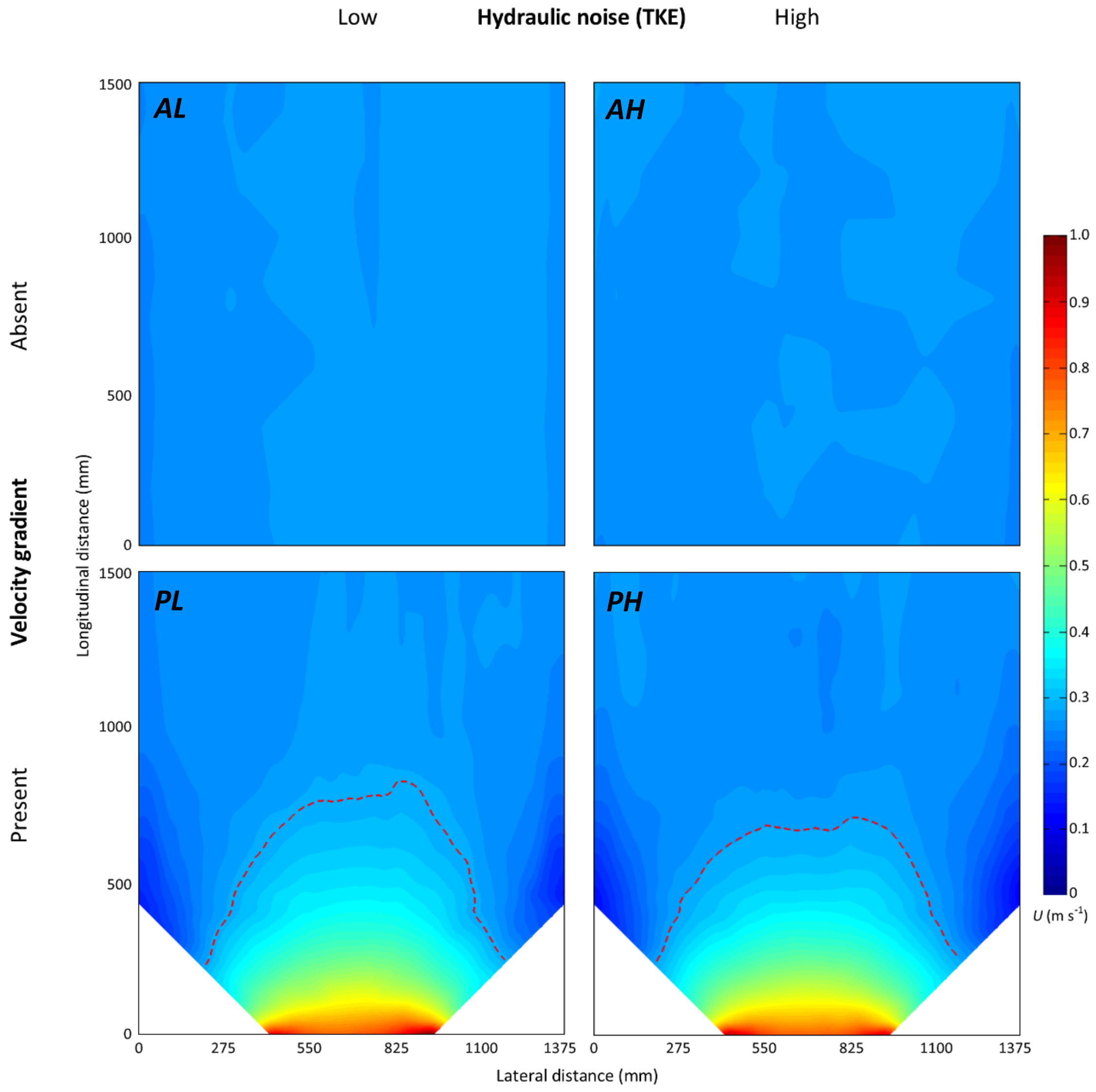


Figure 6.3 Colour intensity plots of velocity (m s^{-1}) under the four treatments (AL, AH, PL, and PH) created by manipulating *velocity gradient* (present or absent) and *hydrodynamic noise* (low or high *TKE*), for which the behavioural response of brown trout, *salmo trutta*, was assessed. Red dashed line delineates the extent of the accelerating velocity gradient (zone where velocity was at least 10% greater than background levels).

6.3.2 Experimental procedure

Brown trout (*N* = 85, μ = 148 mm, σ = 11.7 mm, range = 128 - 169 mm) were transported in an aerated tank from Leckford Estate trout fishery (51° 07’ 55.9” N, 1° 28’ 31.9” W) to the ICER facility on 11th October 2012.They were held in filtered and aerated 3000 litre external holding tanks (pH: 7.8, Ammonia: 0, Nitrite: 0, Nitrate: < 40, 50% weekly water change) at ambient temperature (μ = 7.76 °C, σ = 1.40 °C).

Eighty five trials were undertaken between 1st and 4th of November, 2012 (flume temperature: μ = 10.67°C, σ = 0.27C) (Table 6.1). Prior to each trial fish were placed in a porous container in the flume and allowed to acclimatise for at least 1 hour. Each trial commenced when a single fish was placed in the release chamber and ended when it had either passed downstream beyond the constriction point or after 20 minutes. Each trout was used only once and weighed (g) and measured (fork length) (mm) under anaesthetic after each trial (2-Phenoxy-1-ethanol, 0.2 ml l^{-1}).

6.3.3 Fish behaviour

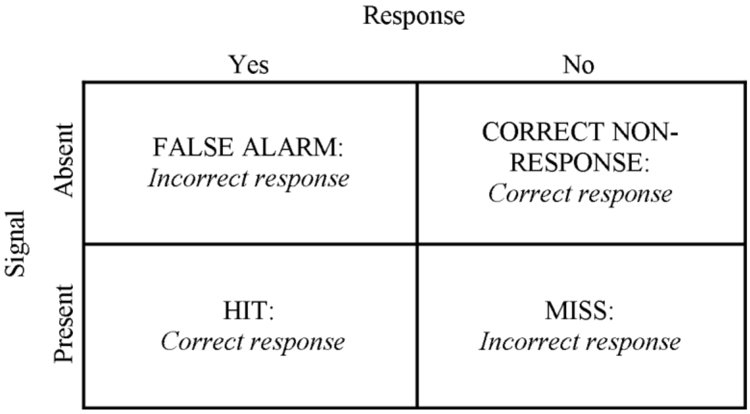
Following the methodology of Vowles and Kemp (2012) downstream passage was described in terms of 1) *approach*, 2) *pass*, 3) *orientation*, 4) *nature of response*, and 5) *time to pass* (see Table 6.2). Two distinct behavioural responses were defined: (a) *orientation switch* and (b) *rejection* (see Table 6.2). The head and tail position of the fish immediately prior to each behavioural response were obtained from the video footage (LoggerPro v.3.8.2 – Vernier Software and Technology, USA) and used to obtain the 6) *distance of initial response* (R_d) from the constriction and 7) *velocity at initial response* (R_v) (see Table 6.2). Mean R_d and R_v values were only calculated in the presence of the velocity gradient and when part or all of the fish was within the zone where the constriction was directly causing flow speeds to increase; considered to be the zone where velocity was at least 10% greater than background levels (see Figure 6.3).

Table 6.2 Definition of passage metrics obtained for brown trout, *Salmo trutta*, as they passed downstream through the experimental area and the statistical tests used.

Metric	**Definition**		**Statistical test**
1. Approach	Proportion of fish that entered the observation zone – 1 m section upstream of the constriction point (Figure 6.1).		*Pearson's Chi-square (X^2) tests*
2. Pass	Proportion of fish that passed downstream beyond the constriction point.		*Pearson's Chi-square (X^2) tests*
3. Orientation	Proportion of fish positively or negatively orientated as they approached or passed.		*Pearson's Chi-square (X^2) tests*
4. Nature of response	Proportion of fish that displayed either: a) *Orientation switch* - change from negative to positive rheotaxis or *vice versa*, or b) *Rejection* - cessation of downstream movement followed by upstream movement of at least half a body length.		*Pearson's Chi-square (X^2) tests*
5. Time to pass	Time between *approach* and *pass.*		Kaplan-Meier product-limit estimator and the Log Rank (Mantel-Cox) statistic (X^2_{mc}).
6. Distance of initial response (R_d)	Distance from the constriction at which fish displayed their initial response.	Extrapolated from the closest point (fish head or tail position) to the constriction.	Student t-tests and robust bootstrapped (n=2000) bias corrected and accelerated (BCa) confidence intervals (CI) (95%)[A].
7. Velocity at initial response (R_v)	Flow velocity at which fish displayed their initial response.		
8. Discriminability (d')	$d' = Z_H - Z_{FA}$	Where Z_H and Z_{FA} are the standard deviation units (Z scores of the unit normal Gaussian distribution) of the probability of a Hit and False Alarm. *Fine scale assessment:* *Hit*: Exhibited a behavioural response in the presence of the VG. *False alarm:* Exhibited a behavioural response in the absence of the VG. *Coarse scale assessment:* *Hit:* Did not pass downstream in the presence of the VG. *False alarm:* Did not pass downstream in the absence of the VG.	N/A
9. Response criterion (c)	$c = -\frac{Z_H + Z_{FA}}{2}$		

A. See *Efron and Tibshirani (1993).*

In addition, SDT, which accounts for response bias (e.g. the tendency for fish to react as though a velocity gradient was present even if one was not), was used to assess the 8) *discriminability* (*d'*) of the velocity gradient by the fish and 9) *response criterion* (*c*) of the fish - the level at which an internal response produces a behavioural response (see Table 6.2) (for comprehensive review of SDT see: Kemp *et al.,* 2012). This was achieved by assessing the correct and incorrect proportion of fish that *passed* downstream (course scale assessment) and the correct and incorrect proportion of fish that displayed a behavioural response when encountering the velocity gradient (fine scale assessment) in the constricted and unconstricted treatments. For the course scale assessment fish were considered to have correctly responded (from a biological perspective) to the velocity gradient, a potential deleterious passage route, if they failed to pass downstream in the constricted treatments (Hit) and incorrectly responded if they failed to pass downstream in the unconstricted treatments (False Alarm) (see Figure 6.4). For the fine scale assessment fish were considered to have correctly responded to the velocity gradient if they displayed a behavioural response (either an *orientation switch* or *rejection* – both behaviours that are indicative of an avoidance reaction) upon encountering the velocity gradient in the constricted treatment (Hit) and incorrectly responded if they displayed a behavioural response at any point in the unconstricted treatments (False Alarm) (Figure 6.4).



Signal	Response: Yes	Response: No
Absent	FALSE ALARM: *Incorrect response*	CORRECT NON-RESPONSE: *Correct response*
Present	HIT: *Correct response*	MISS: *Incorrect response*

Figure 6.4 The four potential signal-response outcomes that may occur in the presence or absence of a specific environmental stimulus. In this study, the signal is the presence or absence of the velocity gradient and the response is the choice not to pass downstream during a trial (course scale assessment) or displaying a behavioural response (fine scale assessment).

SDT states that in the presence of increased noise (external or internal) and with a completely unbiased *response criterion* (equal probability of a False Alarm or a Miss), the probability of a false alarm increases in the presence of noise (N) alone and the probability of an incorrect non-response increases in the presence of the signal + noise (S+N); hence the *discriminability* of a signal decreases (see Figure 6.5). The metric *d'* (Eq. 6.3) is a measure, in standard deviation units (*Z* scores), of the separation between the means of the N and S+N frequency distributions (assumed to be normally distributed with similar variance) (see Figure 6.5) and can be calculated from the Hit Rate (HR) and False Alarm Rate (FAR):

$$d' = Z_{HR} - Z_{FAR} \quad \text{Eq. 6.3}$$

where Z_{HR} and Z_{FAR} are the standard deviation units (Z scores of the unit normal Gaussian distribution) of the HR and FAR. Its primary virtue and the reason that it is so widely used in psychophysical analysis (Swets, 1996), is that its value does not depend upon the *criterion* the subject is adopting, but instead it is a true measure of internal response. *d'* values of 1 and 2 are equivalent to one and two standard deviations of separation, respectively, with higher values representing higher levels of signal discriminability. The metric *c* (Eq. 6.4) is a measure, in standard deviation units (*Z* scores), of the distance of the response criterion from being unbiased (equal probability of a False Alarm or a Miss – see Figure 6.5) (see Stanislaw and Todorov, 1999; Wickens, 2002) and is calculated as:

$$c = -\frac{Z_{HR}+Z_{FAR}}{2} \qquad \text{Eq. 6.4}$$

If the *response criterion* is unbiased, *c* has a value of 0. Negative values of *c* signify a bias toward responding *yes* (the criterion lies to the left of its unbiased location in Figure 6.5) whereas positive values signify a bias toward responding *no* (the criterion lies to the right of its unbiased location in Figure 6.5 – not depicted). The value of SDT is that is allows for *d'* and *c* to be calculated for an organism based on responses observed (False Alarms and Hits) under control (noise alone) and treatment (signal and noise) conditions, respectively, with no direct invasive physiological assessment of the organism.

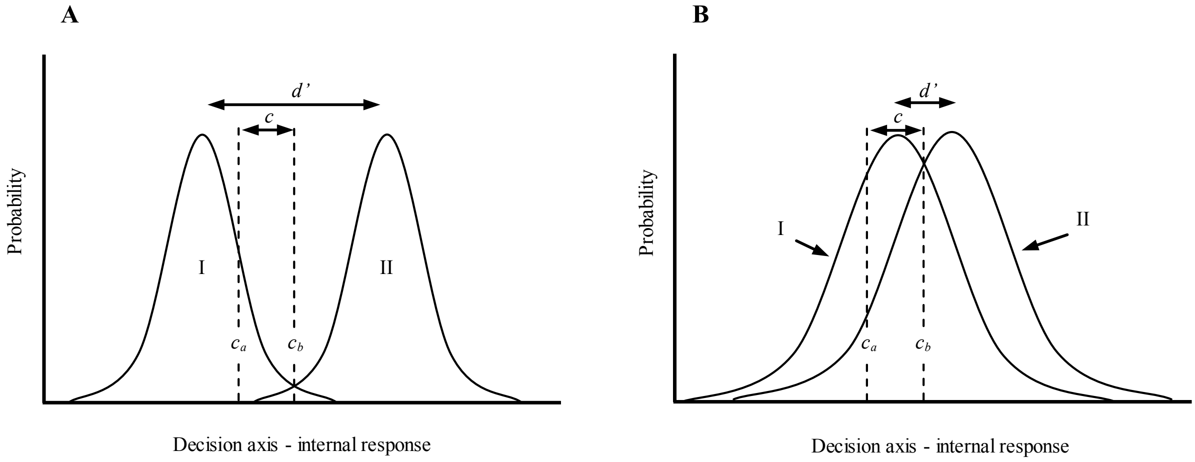


Figure 6.5 Gaussian probability distributions illustrating internal response probability density functions for noise-alone (I) and for signal-plus-noise (II) under low noise (A) and high noise (B) conditions. The dashed vertical lines illustrate the position of the *response criterion* if the response was completely unbiased (c_b) (equal probability of a False Alarm or a Miss) or if there was a negative bias (c_a) (tendency to respond *yes* – higher probability of False Alarm than a Miss). The value *c* is the distance of the *response criterion* from being unbiased (illustrated by criterion c_b). *Discriminability*, *d'*, is the distance between the means of the distributions for noise-alone (I) and signal-plus-noise (II).

SDT theory results, specifically *d'* and *c* values, are usually visualised using Receiver Operating Characteristic (ROC) curves (Figure 6.6). ROC curves are plots of the proportion of Hits against

False Alarms and illustrate the full range of possible HR-FAR pairs that can be achieved using different internal response thresholds. If the internal response threshold (*c*) is high (representing a conservative bias), then both FAR and HR will be low (Figure 6.6). If *c* is lower (and the bias becomes more liberal), then the FAR and HR will increase. If the strength of a signal is increased (or noise decreased), then a stronger internal response will be exhibited resulting in greater separation between the probability of occurrence curves (see Figure 6.5) and an organisms decisions will become increasingly accurate, and the HR will increase relative to FAR (i.e. *d′* increases) (Figure 6.6).

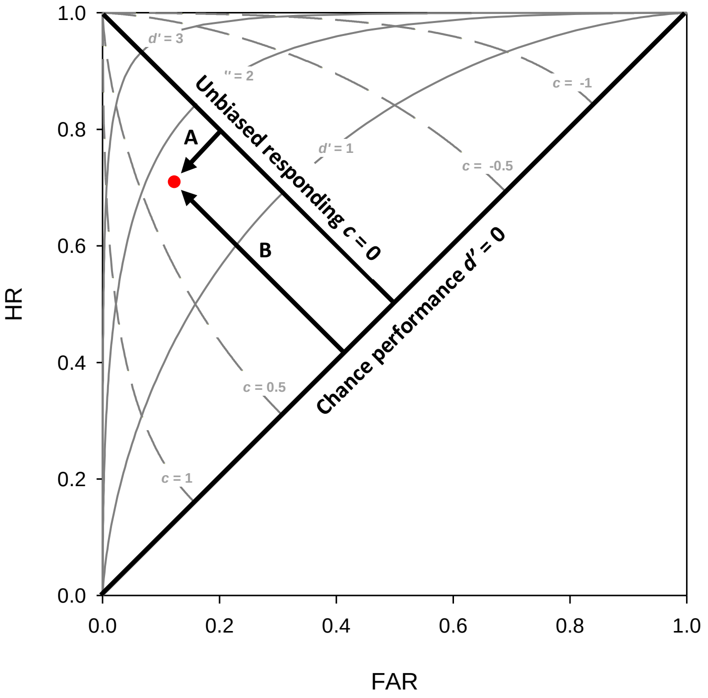


Figure 6.6 Example Receiver Operating Characteristic (ROC) curve. The diagonal, *d′* = 0, represents chance response. The diagonal, *c* = 0, represents unbiased response. The point illustrates a hypothetical response for which *d′* is between 1.0 and 2.0 and *c* is between 0 and 0.5 (a slightly conservative response bias). Movements in the **A** direction (increasing *c* value) represent an increasingly conservative response bias (i.e. increased tendency to respond *no*). Movements in the **B** direction (increasing d′ value) represent an increasing discriminability of the signal either through higher signal intensity or reduced background internal or external noise.

The influence of *velocity gradient*, *hydrodynamic noise*, and *approach orientation* (where applicable) on each metric was assessed using appropriate statistical techniques (Table 6.2). Time to pass was assessed using time to event analysis (Singer and Willet, 2003) (Table 6.2); a method that provides unbiased estimates compared to conventional statistical techniques by including fish that fail to pass downstream (right-censored individuals) in a probability function (reported in this study as: Cumulative Probability of Passage) at any given time (see Castro-Santos and Haro, 2003). Data manipulation was undertaken using Matlab v7.10.0.499, statistical analysis using SPSS v.20.0.0, and figures produced using Matlab, SigmaPlot v12.5.038 and Microsoft Publisher v14.0.7106.5003.

6.4 Results

All fish exited the release chamber within 5.83 minutes (Mdn duration: 0.15 minutes). The proportion of fish that approached was not influenced by velocity gradient or by hydrodynamic noise, with only one trout in the AL treatment failing to approach. The proportion of fish that passed was influenced by velocity gradient ($X^2(1) = 22.014$, $p < 0.001$), but not by approach orientation or by hydrodynamic noise, with more trout passing downstream when the velocity gradient was absent (90.7%) versus present (42.9%) (Figure 6.7).

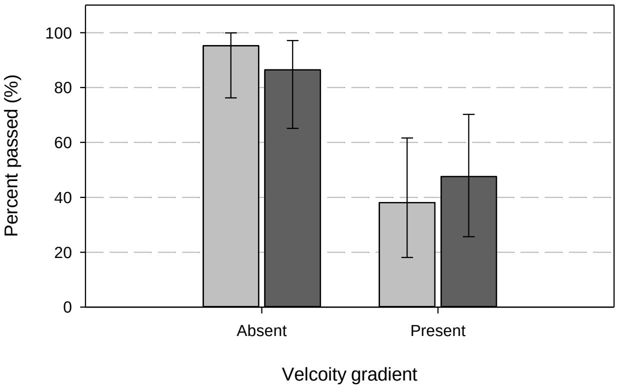


Figure 6.7 Proportion of brown trout, *Salmo trutta*, that passed downstream when velocity gradient was absent and present under low (light grey bars) and high (dark grey bars) levels of hydrodynamic noise (*TKE*). *N* = 22, 21, 21 and 21 for the AL, AH, PL, and PH treatment, respectively. Error bars are 95% confidence intervals.

The orientation of trout as they approached and passed was influenced by velocity gradient ($X^2(1) = 5.765$, $p < 0.05$ and $X^2(1) = 6.510$, $p < 0.05$, respectively) but not by hydrodynamic noise. Trout typically approached and passed oriented facing upstream when the velocity gradient was present (61.9 and 69.2%, respectively) but facing downstream when it was absent (64.3 and 66.7%, respectively). When the velocity gradient was absent pass orientation was influenced by approach orientation (FET: $p < 0.05$), with trout more likely to pass downstream facing in the same direction as they approached. Pass orientation was not influenced by approach orientation when the velocity gradient was present.

Within the observation zone the majority of trout (*ca.* 64%) switched orientation at least once (Table 6.3). The proportion of fish that switched orientation wasn't influenced by approach orientation, hydrodynamic noise, or by velocity gradient (Table 6.3). The proportion of trout that rejected at least once was influenced by velocity gradient ($X^2(1) = 16.045$, $p < 0.001$), but not by approach orientation or by hydrodynamic regime, with a higher proportion of trout rejecting when the velocity gradient was present (85.7%) versus absent (44.2%) (Table 6.3).

Table 6.3 Proportion (%) of trout that were oriented positively as they *approached* and *passed* and exhibited an orientation switch or rejection at least once whilst within the observation zone for each treatment.

Treatment	**Orientation (% positive)**		**Orientation switch (%)**	**Rejection (%)**
	Approach	Passage		
AL	40.0	45.0	65.0	55.0
AH	31.8	15.8	54.5	36.4
PL	66.7	75.0	66.7	90.5
PH	57.1	60.0	71.4	81.0

Time to pass was influenced by approach orientation ($X^2_{MC}(1) = 4.707$, $p < 0.05$) and by velocity gradient ($X^2_{MC}(1) = 31.599$, $p < 0.001$) but not by hydrodynamic noise, with delay tending to be longer when the velocity gradient was present (Mdn: >20 minutes) versus absent (Mdn: 0.13 minutes) (Figure 6.8a) and longer for individuals that approached facing upstream (Mdn: 5.18 minutes) compared to downstream (Mdn: 0.16 minutes) (Figure 6.8b).

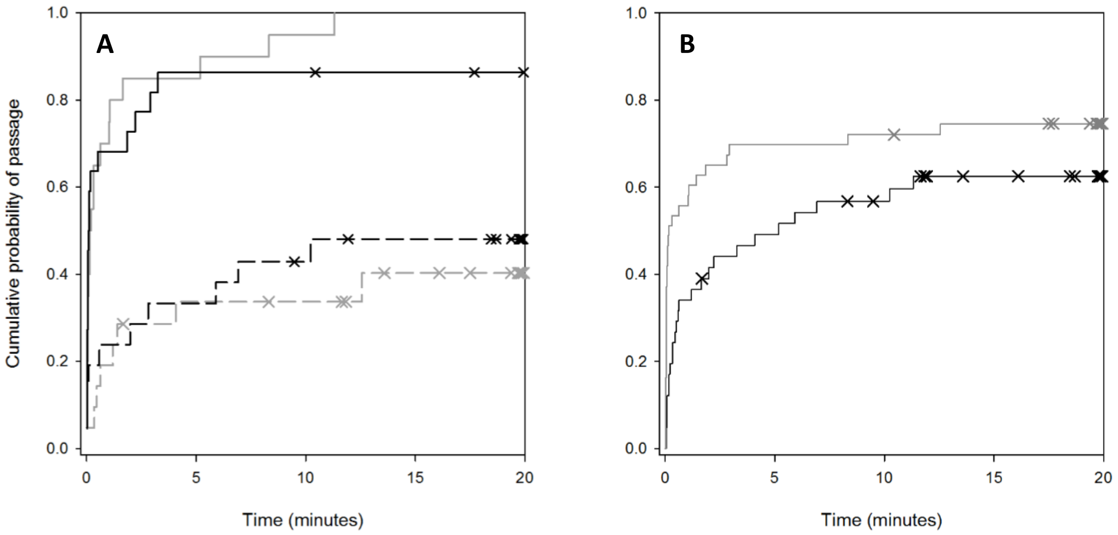


Figure 6.8 A) Cumulative probability of passing downstream against time (minutes) for brown trout, *Salmo trutta*, when the velocity gradient was absent (solid lines) and present (dashed lines) under low (grey) and high (black) levels of hydrodynamic noise. B) Cumulative probability of passing downstream against time (minutes) for brown trout that entered the observational zone facing upstream (positive approach rheotaxis - black line) and downstream (negative approach rheotaxis - grey line) (aggregated data for constricted and unconstricted treatments). Crosses denote instances of right censored data.

Trout switched orientation further away (R_D = *ca.* 340 mm) (µ diff.: +262 mm, BCa CI: [154, 374], $t(36) = 4.492$, $p < 0.001$) and at a lower velocity (R_V = *ca.* 0.38 m s^{-1}) (µ diff.: -0.28 m s^{-1}, BCa CI: [-0.18, -0.40], $t(36) = -5.396$, $p < 0.001$) than they rejected (R_D = *ca.* 85mm and R_V = *ca.* 0.59 m s^{-1}) (Figure 6.9 and Figure 6.10). However, R_D and R_v weren't influenced by hydrodynamic noise (Figure 6.9 and Figure 6.10).

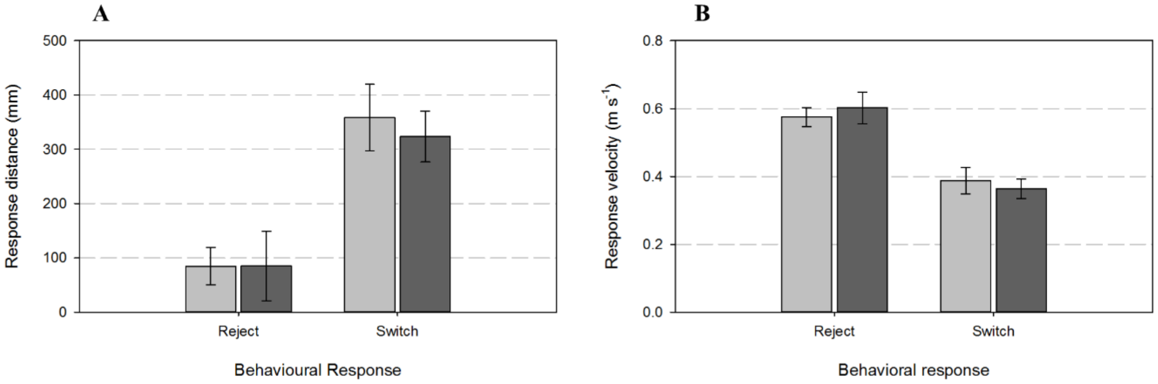


Figure 6.9 Response distance (R_d) (mm) (A) and response velocity (R_v) (m s^{-1}) (B) at which brown trout, *salmo trutta*, responded (rejection or orientation switch) when the velocity gradient was present under low (light grey bars) and high (dark grey bars) levels of hydrodynamic noise (*TKE*).

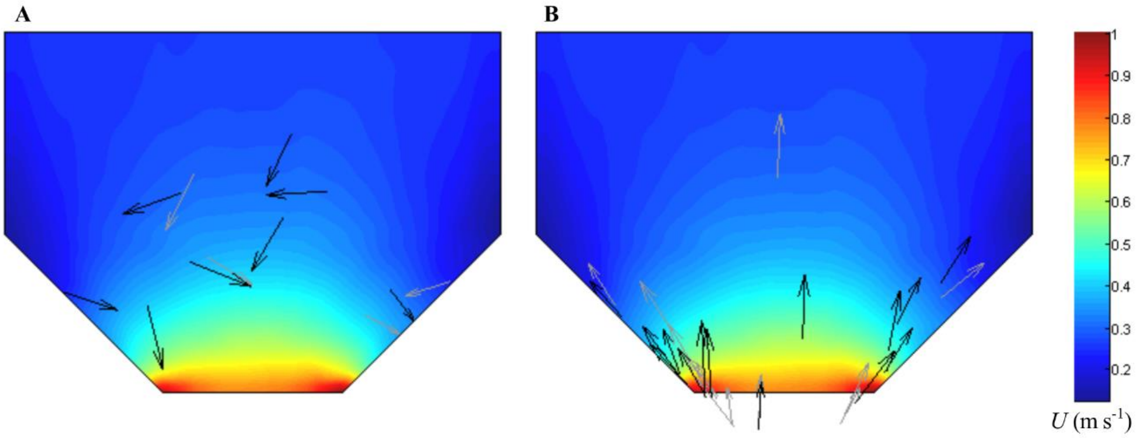


Figure 6.10 Location of initial orientation switch (A) and rejection (B) when the velocity gradient was present under low (grey arrows) and high (black arrows) levels of hydrodynamic noise (*TKE*) superimposed onto colour intensity plots of flow velocity (m s^{-1}). Arrow head indicates head position of trout.

Coarse scale *discriminability* was lower under high (*d′* = 1.16) compared to low (*d′* = 1.97) levels of hydrodynamic noise (Figure 6.11). The coarse scale *response criterion* was positive and similar under low and high levels of hydrodynamic noise (*c* = 0.68 and 0.52, respectively), indicating a general bias to towards passing downstream (Figure 6.11). Counterintuitively however, fine scale *discriminability* was higher under high (*d′* = 0.81) compared to low (*d′* = 0.13) levels of hydrodynamic noise (Figure 6.11). The fine scale *response criterion* was negative and similar under low and high levels of hydrodynamic noise (*c* = -0.75 and -0.52, respectively), indicating a general bias towards exhibiting a behavioural response (Figure 6.11).

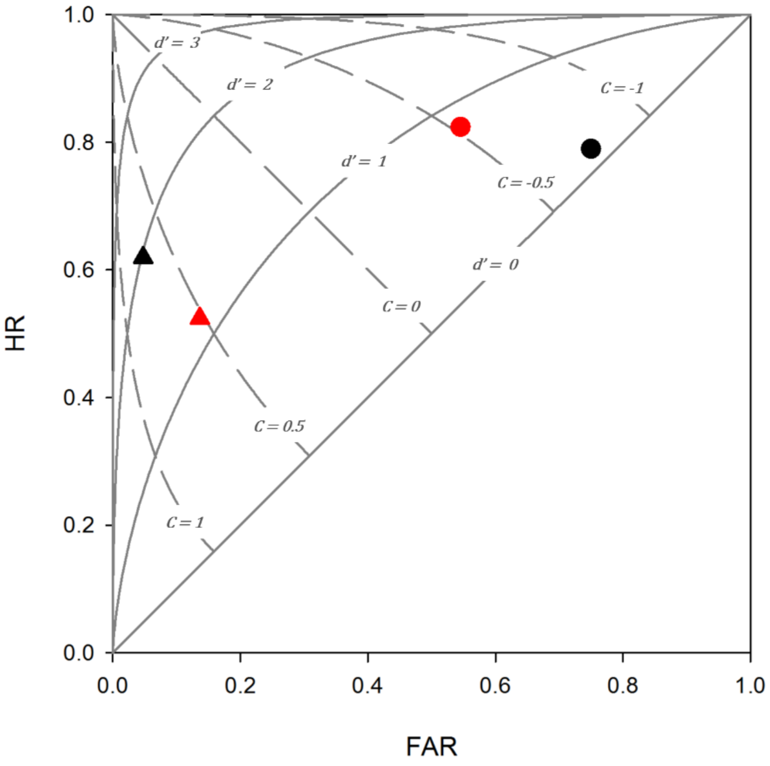


Figure 6.11 Receiver-Operating Characteristics (ROC) plot of Hit Rate (HR) against False Alarm Rate (FAR) for coarse (triangles) and fine (circles) scale assessment of the behavioural responses of brown trout, *Salmo trutta*, to a velocity gradient under low (black data points) and high (red data points) levels of hydrodynamic noise (*TKE*). Reference discriminability (*d′* = 0, 1, 2, 3) and response criterion (*c* = -1, -0.5, 0, 0.5, 1) lines are shown (solid and dashed grey lines, respectively). Increases in *d′* represent greater signal discriminability and increases in *c* represent greater bias towards responding.

6.5 Discussion

Trout displayed behaviours typical of actively migrating salmonids smolts; approaching and passing whilst facing downstream in the unconstricted channel, but facing upstream and displaying more frequent rejections when the VG was present (*as seen by*: Haro *et al.,* 1998; Kemp *et al.,* 2005, 2006; Enders *et al.,* 2009b). Vowles *et al.* (2014) directly linked such behaviours (e.g. rejections) with increased delay and distance travelled before downstream passage. Similar links were evident in this study, with a lower proportion of passes and increased delay when the channel was constricted. However, increased hydrodynamic noise did not influence the conventional passage metrics measured (i.e. proportion that passed and time to pass) and from a management perspective, it would seem that increasing background hydrodynamic noise has no beneficial influence on passage at an accelerating VG. In addition there were discrepancies in the influence hydrodynamic noise had on signal discriminability depending on whether it was assessed using coarse or fine scale behavioural responses.

During experiments, trout had a high propensity to display responsive behaviours (i.e. orientation switches and rejections) even when the hydrodynamic conditions where relatively homogenous (unconstricted conditions). The seeming random nature of these responses may have introduced a high level of error into the fine scale assessment of discriminability. The coarse scale assessment of discriminability, which could be considered more robust, was lower under high levels of hydrodynamic noise, indicating that masking may have occurred at some level. However, this result should be interpreted with caution as it did not translate to a significant effect on the other passage metrics. It is likely that either the signal was too intense or the level of noise was too weak for masking to significantly affect passage. Further reductions in discriminability, by reducing the intensity of the VG or using greater intensities of turbulence, may be needed before biologically significant improvements in passage occur. However, turbulence rapidly dissipates after generation and inducing sufficiently high levels of turbulence at an accelerating VG without physically interfering with fish movement may be difficult. The use of grids with larger bar width and spacing to generate larger scales of turbulence that permeate downstream further (see Mohsen and LaRue, 1990) or using boundary roughness prior to and directly at the intake (see Raupach *et al.,* 1991) may provide a solution.

Trout exhibited a negative response criterion when assessment was undertaken on coarse scale behaviours, indicating that they were biased towards passing downstream. Bias has important ecological consequences. For example, if predation pressure increases, fitness may be improved by temporarily becoming more cautious (see Lima and Bednekoff, 1999; but also Ferrari *et al*., 2009; 2010). For downstream migrating fish a bias towards passing downstream is logical, as, although it is necessary to avoid deleterious passage routes, individuals ultimately need to progress downstream. If fish were biased towards more frequently rejecting the hydrodynamic conditions associated with potential passage routes then a higher proportion of fish may fail to complete their life cycle essential downstream migrations. Further increasing complexity, an individual's bias to pass downstream may change depending on complex factors such as context (Jelbert *et al.,* 2014), selective attention (Paulk *et al.,* 2014), and emotion (Giske *et al.,* 2014), which are observed in even the smallest of animals, or by broad scale factors such as motivation, swimming performance, or sensory perception. The influence of such broad scale factors is evident in observed differences in the VG response thresholds between Chinook salmon (Enders *et al.,* 2009b) and brown trout (Vowles and Kemp, 2012) and in the rejection rates of Atlantic salmon smolts versus American shad (Haro *et al.,* 1998).

The findings of this study further highlight the importance of fish behaviour at downstream bypass facilities. Although, at a coarse scale, discriminability of the accelerating VG was lower in the presence of increased noise, no improvements in downstream passage occurred. These findings suggest that masking may have occurred but that the reduction in discriminability wasn't sufficient to elicit a significant improvement in passage. Further reductions may be achieved through the use of a higher level of background hydrodynamic noise. Masking could still prove to be an effective management tool and has potential widespread application but changes in signal discriminability need to be sufficient to elicit the desired response.

CHAPTER 7

---

7 Thesis discussion

Worldwide, barriers to the movement of fish within rivers system are extant. For example, in England and Wales, the Environment Agency has classified 25,935 potential barriers to fish movement, including waterfalls, weirs, dams, barrages and locks (Environment Agency, 2010b). In South America, 68,800 separate impoundments have been identified, primarily for irrigation and hydropower projects, of which 50 have reservoirs covering > 10,000 ha and 520 > 1,000 ha (Larinier, 2001). To be able to effectively mitigate for such extensive longitudinal fragmentation, fisheries managers must have suitable technologies at their disposal to facilitate the free movement of fish past barriers. However, technologies that can re-establish connectivity for the complete fish community, across a range of environmental conditions, at all barrier types, do not currently exist (Noonan *et al.,* 2012; Bunt *et al.,* 2012). The experimental research conducted as part of this thesis was undertaken to advance scientific knowledge to aid in the development of methods to improve fish passage at migration barriers. This chapter discusses the key findings of this research, including the fundamental knowledge gained, its application to improving fish passage and limitation/benefits of the methods used.

The literature review revealed that low-head barriers can prevent the upstream movement of non-salmonid weaker swimming fish. This was confirmed in Chapter 5, in which a relatively small barrier (320 mm high Crump weir, 230 mm hydraulic head difference) in an open channel flume severely restricted the upstream movement of the critically endangered European eel, *Anguilla anguilla*, and river lamprey, *Lampetra fluviatilis,* which is heavily in decline. Hydrodynamic assessment along with fine scale observations of fish behaviour indicated that the primary factor limiting passage was the high flow velocity that occurred along the downstream face of the weir (2.43 m s^{-1}) but that high levels of turbulence generated at the hydraulic jump may have also had an effect. Weir passability was tested under a range of hydrodynamic conditions and the results will help fisheries managers to accurately assess the transparency of similar structures for the upstream movement of European eel and river lamprey *in situ*; ultimately allowing for more informed mitigation decisions to be made.

The predicted burst swimming speed of a 660 mm (TL) European eel at a comparable temperature to that used in Chapter 5 (16° C) is 1.3 m s^{-1} (90% Confidence Interval: 1.1 - 1.5 m s^{-1}) (SWIMIT Model v.3.3). However, a small proportion (17.2%) of large eel (320 – 660 mm) could pass over the Crump weir when maximum velocity at the trailing edge reached 2.43 m s^{-1}. This finding is in agreement with previous studies that have reported eel achieving higher than predicted swimming speeds to overcome velocity barriers (Russon and Kemp, 2011b; Newbold *et al.,* 2015). Burst swimming speeds, the maximum speed that a fish can maintain for 20 seconds, are generally ascertained through forced swimming experiments performed in sealed swim chambers (Beamish, 1978; Clough *et al.,* 2004). Such swim chambers, due to their small size, do not allow fish to exhibit performance enhancing compensatory behaviours such as burst-glide swimming (Tudorache *et al.,* 2007). In addition, the duration over which burst speeds are measured brings into question their applicability in relation to spatially small velocity barriers that fish can pass in much less than 20 seconds. However, burst swimming speeds are often the only performance metric indicative of maximum swimming speed available (e.g. SWIMIT Model v.3.3; also see Haro *et al.,* 2004). It is likely that volitional passage experiments undertaken under realistic flow conditions, like those in Chapter 5, provide more relevant swimming performance data which are better suited to influence management decision than those ascertained in swim-tunnels.

There is very little data available on the swimming performance of river lamprey but they can pass an experimental undershot weir with peak velocities ranging from 1.75 - 2.12 m s^{-1} (temp.: μ = 12.6°C, S.E. = 0.4) (Russon and Kemp, 2011b). In Chapter 5, no lamprey passed over the weir when maximum velocity at the base of the weir was 2.43 m s^{-1} despite a high proportion of attempts (62.5%) (temp.: μ = 8.8°C, σ = 1.5). This finding, alongside those of Russon and Kemp (2011b), indicate that the maximum swimming speed that adult migratory river lamprey can attain at *ca.* 10 °C is likely between 2.12 - 2.43 m s^{-1}. The results obtained in Chapter 5, not only shed light on the passage of eel and lamprey over a model Crump weir, but provide valuable information regarding the swimming performance of both species in relation to velocity barriers. Such information will help in the future assessment of the transparency of a range of barriers, not just Crump weirs, and further help guide mitigation decisions.

In general, there is a causal relationship between body length and absolute swimming performance (Beamish, 1978; Clough *et al.,* 2004; Peake *et al.,* 1997). In Chapter 5 a large size range of European yellow eel were used (82 - 660 mm TL) and differences in swimming performance were evident in the ability of large eel (320 - 660 mm TL) to pass the model Crump weir under high velocity control conditions when small eel (82 - 320 mm TL) could not. Similar results were observed in Chapter 4 with small trout tending to swim for a shorter duration than larger individuals, presumably because their decreased absolute swimming performance resulted in a higher rate of fatigue (e.g. Tudorache *et al.,* 2008). In addition smaller trout exhibited a greater preference to hold position with their tail against the downstream screen; a behaviour that required no visible body undulation and was probably the most energetically efficient method of holding station whilst maintaining rheotaxis under the conditions provided. The length range of lamprey utilised in Chapter 5 was small (291 - 401 mm TL) (a sub sample of the migratory population). However, for other migratory populations of lamprey, length has been shown to significantly affect passage efficiency, with larger specimens being 2 - 4 times more likely to pass than smaller individuals (Pacific lamprey, *Lampetra tridentata* - Keefer *et al.,* 2009). In Chapter 5, no size related swimming performance differences for lamprey were observed, predominantly because 0 and 100% passed under the high and low velocity control conditions, respectively. Differences in lamprey swimming ability may have been evident if the medium velocity treatment had been undertaken for this species. Results from both Chapter 4 and 5 highlight the importance of physical characteristics, such as fish length, on energetics, and consequently, swimming performance and behaviour.

Frequently, experimental research is undertaken on a scale that is not representative of field conditions (e.g. using small open channel flumes - Tyler and Gilliam, 1995; Servais, 2006; or swim chambers - Tudorache, 2008), a factor that can reduce the applicability of results (i.e. a lack of realism: see Rice *et al.,* 2010). For example, as already mentioned, large open flumes allow fish to display more natural compensatory behaviours (e.g. burst-glide swimming) that can influence swimming performance (Tudorache *et al.,* 2007). The absence of these behaviours has been linked with the limited applicability of experimental data ascertained in small spaces (Haro *et al.,* 2004). The use of a large open-channel flume during this research enabled hydrodynamic conditions and fish behaviour to be assessed at scales relevant to those encountered in the field. For example, low-head gauging structures are often utilised on small rivers and streams (Figure 7.1), meaning the hydrodynamic characteristics created in Chapter 5, are likely to be comparable in terms of magnitude and scale to some barriers found in the field (although this author acknowledges that much larger barriers also exist). In addition, although not applied research, the other two experiments were also undertaken at a representative scale to *in situ* conditions. For example, the experimental area (2.94 x 1.38 m) used to assess space use of brown trout in

Chapter 4 was comparable in size to the pool areas of many technical fish passes (e.g. Stuart and Berghuis, 2002; Stuart and Mallen-Cooper, 1999; Knaepkens *et al.,* 2006) and the constricted flume section (1.38 m reduced to 0.50 m wide) used to create an accelerating velocity gradient in Chapter 6 was of similar size to many downstream bypass entrances (e.g. Croze, 2008). As such, the results of this research, in certain situations, are applicable without having to take into account scaling issues.

Figure 7.1 Small Crump weir on the River Isbourne (4.5 m wide, 0.5 m high channel walls implying head differences of < 500 mm). Copyright David Stowell and licensed for reuse under the Creative Commons Licence

In the experiments undertaken as part of Chapter 5 the upstream movement of European eel and European river lamprey was assessed at a single barrier. However, river systems are frequently disrupted by multiple barriers which have can have cumulative impacts on the proportion of fish that reach lifecycle essential habitat (e.g. Lucas *et al.,* 2009). Although fish become fatigued after attempting to pass a velocity barrier multiple times (Quintella *et al.,* 2004), there is also evidence that they do not volitionally swim to physiological exhaustion when attempting to traverse a velocity barrier (Haro *et al.,* 2004). Hence, although it is logical that there are cumulative energetic costs associated with passing barriers, it is currently unknown whether pre-existing fatigue could be a factor impacting future passage success/efficiency. Further work is required to ascertain whether the passage efficiency of fish (e.g. eel and lamprey) over a Crump weir would be impacted by previous barrier traversal and what is the minimum recovery time (i.e. distance between barriers) required to mitigate for this.

Legault (1992) whilst investigating the effectiveness of bristle passes with different bristle spacings (7 mm, 14 mm and 21 mm) found no clear size selectivity between passes but did find that that the proportion of European eel that utilised the smallest bristle spacing was less than those using the largest. In addition, it was noted that an adjacent eel lift was used, on average, by larger eel, suggesting that they may be avoiding the bristle passes all together. In Chapter 5 a similar effect was observed with large eel preferentially selecting to pass the weir directly rather than using the bristle passes. It is not clear if this reflects inappropriate bristle spacing or whether little advantage was gained in using the passes as they were capable of negotiating the structure directly. Small eel showed a higher preference for using the bristle passes to pass the weir than large eel under all hydrodynamic regimes. Although Chapter 5 provides no conclusive evidence of size selectivity, the findings, in agreement with indirect evidence from Legault (1992), suggest that this may be a potential limitation of the technology. Further work should be undertaken to assess if bristle passes are efficient for larger eel when alternative routes of passage are not available. Under all treatment conditions, very few lamprey passed over the weir using a bristle pass. For lamprey (and possibly large eel) small design alterations such as increasing the bristle spacing could improve passage success, especially as individuals appeared to struggle to make progress through the stiff bristles.

Alternative substrates are available to promote the passage of eel over migration barriers (see Environment Agency, 2011). One type consists of a 500 mm^2 polycarbonate board moulded with two different sizes and densities of protruded pegs, commonly referred to as an ‘eel tile’ (Figure 7.2). Similar peg like protrusions have been used in eel ladders previously (e.g. McGrath *et al.,* 2003; Verdon *et al.,* 2003; Schmidt *et al.,* 2009) and are often referred to as ‘stud’ or ‘boss’ substrates. As with bristle boards, eel tiles are currently being attached to low-head weirs and barriers to facilitate the upstream passage of eel and other anguilliform morphotype species (pers. comm. Fishtek consultancy ltd.; Berry and Escott Engineering Ltd.). Dr Andrew Vowles recently tested the efficiency of eel tiles for improving the upstream passage of European eel and river lamprey over a low-head weir at the ICER facility in a similar configuration to that undertaken in Chapter 5 (vertically oriented and attached to the wing walls of the flume) (unpublished data). Observation of lamprey attempting to use the substrate indicated that the small spacing between the pegs and their off-parallel alignment with the weir face inhibited river lamprey from ascending (pers. comm. Andrew Vowles). This finding, in conjunction with those reported in Chapter 5, suggest that substrate density and arrangement are important factors governing passage efficiency of lamprey through this type of pass, possibly because lamprey have a weaker crawling/climbing ability in comparison to eel (personal observation). As such, in addition to informing fisheries managers on the efficiency of side-mounted vertically oriented bristle passes for upstream moving European eel and river lamprey, the direct observations of fish behaviour undertaken in Chapter 5, in combination with that undertaken by Dr Vowles, will aid in the rapid improvement of anguilliform morphotype passage substrate technologies, something that coarser field evaluations would not have allowed.

Figure 7.2 Commercially available multi-density eel tile available from Berry & Escott Engineering Ltd. (photo from www.berryescott.co.uk).

At hydrometric weirs a major consideration for installation of fish passes is the effect that the pass has on the gauging accuracy of the structure (White *et al.,* 2006). Other common eel passage technologies such as ‘up and over’ or ‘pumped’ passes (see Environment Agency, 2011) do not interfere with the flow over a gauging weir and the water abstracted to feed them is negligible, but they require frequent checks and regular maintenance. Although ‘pumped’ passes are considerably cheaper than other conventional fish passes there are still logistic and economic restrictions precluding the installation of them at every low head-barrier in the UK. The new configuration of bristle pass tested in Chapter 5 represents a cost-effective, easy to install, non-mechanical, low-maintenance and hydrodynamically unobtrusive (Environment Agency, 2010a) alternative to standard eel passes at low-head structures. However, it is acknowledged that this type of pass will likely only facilitate the passage of anguilliform morphotype species and possibly other very small fish or invertebrates. Although ideally a single structure that facilitates the passage of all species/lifestages is desirable (i.e. to reduce costs), in reality it is likely that combinations of pass types are necessary to achieve this (e.g. Schwalme *et al.,* 1985). The low cost of this type of bristle pass make it a viable option for installation alongside conventional more-costly technical passes that target alternate species (e.g. Denil, pool and weir, Larinier).

In the experiments undertaken in Chapter 4, although individual fish appeared to use areas where entraining, Kármán gaiting, and bow riding behaviours could be expressed for a high proportion of each trial, they were not consistently used by all trout. These behaviours represent energetically favourable strategies for holding station in a flow (Taguchi and Liao, 2011). Liao (2006) observed brown trout within an illuminated experimental area containing a single vertically oriented 'D' shaped half-cylinder to Kármán gait, entrain and bow ride for *ca.* 82%, 2%, and, 0% of a 60 minute trial, respectively. Przybilla *et al.* (2010) in a very similar experimental setup observed trout to Kármán gait, entrain, and bow ride for *ca.* 8%, 28%, and 28% of a trial, respectively. In Chapter 4, trout of comparable length (small hatchery trout) to those used by Liao (2006) and Przybilla *et al.* (2010), spent a mean of only 0.4% (range: 0 - 2.1%), 3.4% (range: 0 - 64.2%), and 0.1% (range: 0 - 0.6%) of each trial in zones where they could Kármán gait, entrain and bow ride, respectively. Even large hatchery trout, which were more inclined to use drafting and bow riding zones than smaller fish, spent a mean of only 2.6% (range: 0 - 9.4%), 3.7% (range:0 - 37.4%), and 0.6% (range: 0 - 3.0%) of each trial in these zones, respectively. Differences in the proportion of time that these behaviours were expressed in Chapter 4 compared to that found by either Liao (2006) or Przybilla *et al.* (2010) likely stem from the use of a larger and more hydrodynamically heterogeneous experimental area. In addition, circular cylinders were utilised, which tend to produce less discrete vortex shedding than D-section cylinders (Blevins, 1990), and experiments were undertaken at night under low levels of illumination, a factor that has been noted to reduce the likelihood of fish Kármán gaiting (Liao, 2006). However, the differences in the results recorded by Liao (2006) and Przybilla *et al.* (2010), in which experimental setups were almost identical, indicate that there is also a high level of individual variability in the expression of these behaviours. This high level of individual variability was also observed in Chapter 4 within each group. It is likely that, although it is possible for fish to use specialised behaviours to hold station, they may be more inclined to do so under very stable, coherent flow conditions. Such conditions are much rarer under natural conditions than in the laboratory (Roy *et al.,* 1999). Currently there is no direct kinematic evidence that fish use such behaviours *in situ*; probably because kinematic assessment of fish swimming is difficult to obtain in the field (Liao, 2007). However, observations of fish holding station around bluff bodies are numerous (McMahon and Hartman, 1989; Fausch, 1993; Schuler *et al.,* 1994). The experimental results of Chapter 4 in combination with others (Liao, 2006; Przybilla *et al.,* 2010) indicate that trout are either less able or less inclined to exhibit behaviours that rely on stable, or predictably shed, flow properties when flow conditions are complex compared to under more simplistic conditions (e.g. like those created behind a single 'D' section cylinder). However, this assessment should be interpreted with caution as fish evidently regularly associate with bluff bodies *in situ* and it is likely that they are very adept at finding and using space that enables them to exhibit specialised behaviours and reduce energetic costs.

The experiment presented in Chapter 4, to this author's knowledge, represents the highest resolution assessment of space use by fish under complex hydrodynamic conditions to date. As such, a key limitation of previous studies, spatial sampling resolution, has been heavily reduced. For example, previous laboratory experiments that have linked fish behaviour with hydrodynamic conditions have often done so at a coarse spatial resolution. For example: Smith *et al.* (2006) measured experimental hydrodynamic conditions at high spatial resolution but then used a whole flume spatial average to draw comparisons with the density of rainbow trout, *Oncorhynchus mykiss*, residing in the experimental area. Silva *et al.,* (2011; 2012a; 2012b) in multiple studies in a model pool and weir fish pass investigated correlations between space use of Iberian Barbell, *Luciobarbus bocagei*, and hydrodynamic conditions averaged within 333 mm wide by 380 mm long sections. And Hockley *et al.* (2014) linked space use of the guppy, *Poecilia reticulate*, in a complex flow field to spatially averaged hydrodynamic conditions in zones selected based on broad scale flow features (e.g. recirculating or the high-velocity zones). The reason for such spatial averaging is likely because measuring hydrodynamic conditions and space use of fish at very fine scales, and the analysis required to link the two, is time consuming and complicated. However, spatial averaging can result in the loss of important information. For example, if similar sized sections as used by Silva *et al.* (2011; 2012a; 2012b) had been used to describe the flow conditions created in Chapter 4, certain individual zones would have incorporated multiple turbulent flow structures and almost the full range of horizontal Reynolds shear stress (*ca.* -15 to 15 N m^{-2}), turbulent kinetic energy (*ca.* 0 to 80 J m^{-3}), and turbulent drag (*ca.* 0 to 0.5) measured throughout the whole experimental area (see Figure 4.5). As such, the applicability of linking space use by trout to average hydrodynamic metrics at this scale would have been questionable.

The smallest scale of flow variability that provides environmental information to fluvial animals is currently unknown (see review in Johnson and Rice, 2014) and as such there is a lack of information on the sampling resolution required to resolve ecologically important hydrodynamic flow features. For example, the scale of the smallest turbulent fluctuation is governed by fluid viscosity, is estimated by the Kolmogorov (spatial) microscale $\eta = ({k_v}^3/\varepsilon)^{1/4}$, and is of the order of *ca.* 0.1 mm (Lacey *et al.,* 2012). Where k_v (m^2 s^{-1}) is the kinematic viscosity and ε (m^2 s^{-3}) is the energy dissipation rate per unit mass. However, although fluctuations at or near η may have an effect on performance via changes in skin friction (Vogel, 1996) whether they influence fish behaviour is unknown. Fish use surface and canal neuromasts (sensory hair cells) to perceive minute changes in regional flow and pressure (Montgomery *et al.,* 2000) and many species have a dense and complex covering of these sensory cells across their body (Coombs *et al.,* 1989). These enable fish to resolve spatial hydrodynamic information from complex flow phenomenon smaller than their body length (e.g. vortex rings - Chagnaud *et al.,* 2006). However the information that animals perceive and what they respond to may differ. The influence of turbulence on fish swimming performance and behaviour has been observed to be most critical when eddy diameters are equivalent to fish length (Tritico and Cotel, 2010). Hence, there is an argument that this scale of turbulence is important and that hydrodynamic measurements should be undertaken to resolve flow structures that are proportional to fish size. Further work is required to ascertain what an adequate sampling resolution is. In the experiment presented in Chapter 4, hydrodynamic measurements were undertaken at a spatial resolution to clearly resolve the major flow features (Figure 4.3) and then interpolated down to 1mm^2 grid before being linked to fish behaviour. As such, in the regions with high flow heterogeneity, sampling resolution was much smaller than fish length.

Excessive turbulence has been implicated as a key factor hindering effective fish passage at mitigation structures designed to improve connectivity in anthropogenically fragmented rivers (Barry and Kynard, 1986; Haro and Kynard, 1997; Lucas *et al*., 1999; Bunt *et al*., 2000; Mallen-Cooper and Brand, 2007; Foulds and Lucas, 2013), presumably because it can increase energetic expenditure (Enders *et al.,* 2003; 2004; 2005a) and, if of an equivalent scale to fish length, can reduce stability (Tritico and Cotel, 2010). However it has also been suggested that the judicial use of turbulence could enhance fish passage (Castro-Santos *et al*., 2009). The literature review highlighted that upstream fish passage research will benefit from a better understanding of the fundamental principles of how fish utilise complex flows (Castro-Santos *et al.,* 2009), and the hydrodynamic metrics that are most appropriate from a biological perspective to describe those flows (Lacey *et al.,* 2012; Vowles *et al.,* 2013). Chapter 4 tackled these issue and the results indicate that in a complex hydrodynamic flow field, space use by trout is predominantly governed by the selection of areas where they can reduce energetic expenditure, through either exhibiting specialised behaviours or by selecting low drag regions. This finding is in agreement with others that have found fish to use energy conservation strategies during lifecycle essential upstream migrations (*in situ* telemetry studies with pallid sturgeon, *Scaphirhynchus albus*: McElroy et al., 2012; *in situ* observations of sockeye salmon (*Oncorhynchus nerka*): Hinch and Rand, 2000) and when approaching fish pass entrances (flume experiment with Atlantic salmon, *Salmo salar*: Guiny *et al.,* 2005). These results indicate that where feasible, fish passes should provide low-turbulence low-drag pathways for fish to ascend but also areas with spatial and temporal flow variations that enable fish to express specialised behaviours to rest in between intermittent bouts of movement. Such flow structures could be introduced using appropriately sized bluff bodies. However, although information on the range of hydrodynamic conditions under which fish can express specialised behaviours is starting to be accumulated (e.g. Akanyeti and Liao, 2012) further work is required.

To date Liao's (2007) review on 'fish swimming mechanics and behaviour in altered flows' is the most up to date compilation of information on the subject. Liao (2007) highlights that a detailed description of how fish interact with the immediate spatial and temporal features of flow are necessary if we are to understand behaviour across different hydrodynamic environments. Although the experiments undertaken as part of Chapter 4 did not deal with temporal flow variability (time averaged metrics are measured) the results represent the highest spatial resolution data available on fish space use in a complex flow field. Importantly, the focus of the research progressed from simply investigating correlative links between biota, ecosystems and environments and attempted to establish a causal link between fish behaviour and complex flow conditions. As such, the results are easy to interpret and to relate to conservation and management issues. Although it is acknowledged that further research is required before these experimental results can be effectively used to improve fish passage they offer an important improvement in fundamental knowledge of how fish use space under hydrodynamically complex flow conditions. In addition, a new metric to the field of Ecohydraulics is described and tested that should have direct applicability - turbulent drag (D_t).

Recent improvements in technology have led to the development of commercially available high-frequency three-dimensional acoustic velocity meters that can be used in the field (e.g.

Enders *et al.,* 2009a). This means that metrics such as D_t are easily measured in the field as well as in the laboratory. It is acknowledged that D_t does not incorporate the influence of periodicity, orientation or scale of turbulence, factors that have been identified as important in relation to fish behaviour and swimming performance (e.g. IPOS framework - Lacey *et al.,* 2012). However, it does combine the influence of mean flow velocity and turbulence intensity within a single metric that relates to the energetic cost of swimming in a flow, which should be more relevant to lotic organisms than a separate measure of the two. As such, it represents a potentially useful tool that should enable fisheries managers and scientists to assess complex hydrodynamic environments in a more biologically relevant manner.

Turbulence intensity, periodicity, orientation and scale can be inferred from high frequency three-dimensional temporal velocity data but it is a complicated process (see Chapter 4). Direct measurements of spatial flow phenomenon are possible through other advanced techniques, such as particle image velocimetry (PIV) (e.g. Tritico and Cotel, 2010), but only recently have field versions been developed (Tritico *et al.,* 2007). It is likely that in the future a combination of both point-measurements (e.g. ADV's) and optical spatial techniques (e.g. PIV) will provide the most productive path towards a reliable quantitative description of turbulent flows with adequate temporal and spatial resolution (Cotel and Webb, 2012). Until then, the best available option for the wider research and management community to measure hydrodynamic conditions is with time averaged three-dimensional velocity meters such as ADVs. The results of Chapter 4 provide useful information regarding the fundamental links between fish and space use using time-averaged metrics and provide an important step towards understanding what hydrodynamic conditions are most biologically relevant.

In Chapter 6, although, at a coarse scale, discriminability of the accelerating VG was lower in the presence of increased hydrodynamic noise, no improvements in relevant downstream passage statistics for brown trout were observed. It is likely that either the signal was too intense or the level of noise was too weak for masking to significantly affect passage. Further reductions in discriminability, by reducing the intensity of the VG or using greater intensities of turbulence may be needed before biologically significant improvements in passage occur. Although the brown trout used in the experiment displayed behaviours typical of actively migrating salmonid smolts (e.g. '*switch orientation*' or '*rejection*' – see Table 6.2) (Haro *et al.,* 1998; Kemp *et al.,* 2005, 2006; Enders *et al.,* 2009b), they had a high propensity to exhibit these behaviours when the velocity gradient was both present and absent. This influenced the calculation of fine scale discriminability as the number of false alarms was high. This ‘erratic’ behaviour could relate to a number of factors acting in isolation or combination, such as “naïve” farmed fish expressing a more cautious strategy on encountering abrupt hydrodynamic transitions for the first time (as suggested by Vowles and Kemp, 2012) or lack of motivation to conserve energy or reduce delay during downstream passage. Actively migrating wild salmonid smolts that are more motivated to move downstream with the bulk flow might not display such ‘erratic’ behaviour and this should be investigated further.

Another consideration is that the mechanosensory lateral line might not be the only sensory system that provides information on a velocity gradient. The mechanosensory lateral line is used to detect flow over the surface of the body and has the appropriate anatomical distribution and physiological properties to identify the strength and direction of a flow and, hence, contribute to the detection of regional differences over deferent parts of the body (Montgomery *et al.,* 2000). However, the inner ear can also provide information on changes in flow by detecting whole-body accelerations (e.g. Pavlov and Tjurjukov, 1995). The inner ear is a highly sensitive accelerometer (Sand and Karlsen, 2000) and, it is possible that a fish would be able to gain additional information on the presence and magnitude of a velocity gradient it encountered via this sensory organ. The relative contribution of the inner ear or the lateral line to detecting flow variations is unknown but this sensory input combination should be considered during future experimentation. Despite a lack of definitive results and uncertainties as to the key sensory modality for detecting a velocity gradient, signal detection theory provided a useful framework to analyse fish behaviour as it accounts for internal bias. The research presented in Chapter 6 provides a useful stepping stone for future studies to continue investigating novel behavioural manipulation techniques for improving fish passage at bypass entrances.

7.1 Future research

The results obtained through assessing space use of brown trout in a hydrodynamically complex experimental environment need to be applied to improving fish passage. A similar methodology as used in Chapter 4 should be used to assess the movement of a representative salmonid through an experimental fish pass, with an aim to test whether fish use pathways via which energetic costs can be reduced; specifically by linking space use during passage with turbulent drag and specialised behaviours. If this prediction is confirmed then fish passes can be developed that provide low drag pathways and locations where fish can use specialised behaviours to rest between intermittent bouts of movement. Future work should also focus on expanding the results of Chapter 4 to other species and body/fin forms to ascertain if energy conservation strategies govern space use for a wide range of fish.

Investigations into the impact of biotic factors on space use are also warranted. For example, salmonids have been observed to exhibit a hierarchal population structure within fluvial environments with dominant individuals using optimal habitat patches (e.g. food intake - Kemp *et al.,* 2005). Further investigation should be undertaken to ascertain if hierarchal dominance extends to the use of 'optimal' hydrodynamic space (e.g. areas of low drag or where specialised behaviours can be exhibited). Individual salmonids have a territory size dependent on complicated factors such as visual isolation (Imre *et al.,* 2002) and population density (Wood *et al.,* 2010). It is likely that in the experimental area created in Chapter 4, which was relatively large and complex, that there are multiple locations where energy conservation behaviours are possible and that if territory size is small that subordinate individuals may not be impacted. Trials with several fish may be necessary before the lowest ranked individual is forced to occupy sub-optimal hydrodynamic space.

In addition, the hydrodynamic processes that enable trout to hold position against a boundary and slightly downstream from a cylinder (termed wall holding in Chapter 4), a behaviour believed to be analogous to entraining, needs to be assessed. A hydrodynamic model and experimental methodology akin to that used by Przybilla *et al.,* (2010) would be appropriate for this research. The proximity of fish to a boundary can lead to effects which can theoretically increase the thrust of an individual by tens of percentages without additional energy expenditure (see Liao, 2007). The potential energy savings of such a boundary effect during wall-holding should be investigated.

To validate the results of Chapter 5 trials need to be undertaken to ascertain the efficiency of side-mounted and vertically oriented bristle passes for European eel and river lamprey at a representative low-head structure *in situ*. Such research will shed light on the impact of confounding environmental variables on passage statistics in addition to enabling assessment of the attraction efficiency of this pass type. Further, experimental research should also be undertaken to optimise bristle pass efficiency by trialling different bristle spacings; primarily larger bristle spacings to facilitate the easier passage of river lamprey. However, the potential negative effects that larger bristle spacing has on the upstream movement of small European eel (*ca.* < 150 mm) should be considered concurrently. Alternatively some light could be shed on this issue by trialling the current bristle spacing (30 mm) with a smaller species of lamprey. For example, brook lamprey, *Lampetra planeri*, are a potamodromous species of lamprey, which undertake short distance migrations (Malmqvist, 1980) and for which low head barriers are also likely to impact habitat connectivity.

In Chapter 6 the level of background hydrodynamic noise used did not have a biologically significant impact on downstream passage and had an ambiguous impact on signal discriminability. Further experimentation should be carried out to ascertain whether higher background levels of hydrodynamic noise will sufficiently reduce the discriminability of an accelerating velocity gradient to the point that downstream passage is improved. However, various factors need to be addressed prior to further experimentation: 1) Small methodological alterations, such as limiting a fish's exposure to the physical structures should be considered, possibly through restricting them to the central section of the channel using a mesh cage. 2) A selection of wild actively migrating salmonid smolts should be used to test if these individuals exhibit clearer behavioural responses to a velocity gradient than hatchery reared fish. 3) Consideration should be given to whether fish use an alternate sensory system to detect and inform decision making in regards to velocity gradients. This could be achieved by repeating the experiment undertaken in Chapter 6, in which brown trout showed a clear behavioural response to an accelerating velocity gradient, but with the lateral line blocked (e.g. Karlsen and Sand, 1987).

7.2 Conclusion

The aim of this thesis was to 'advance scientific knowledge to aid in the development of methods to improve fish passage at migration barriers'. To meet this aim, experimental research was undertaken to address three knowledge gaps: 1) A poor understanding of the explanatory mechanisms that underpin interactions between fish and their hydrodynamic environment. 2) A lack of research focussed on the upstream passage of non-salmonid, weaker swimming species, for which standard technical fish passes often perform poorly and even very low-head barriers can prevent upstream movement. 3) A lack of effective methods to stop downstream moving fish actively avoiding bypass entrances.

Although turbulence is likely to be causing poor passage efficiency, definitive evidence is lacking because the impact it has on behaviour and ecology is poorly understood. In Chapter 4 this was addressed by returning to first principles and investigating hydrodynamic space use by brown trout under a controlled experimental setting in which key confounding variables (e.g. visual cues, food, predators and conspecifics) were absent. Numerous previous studies have attempted to find statistical links between patterns of fish distribution/movement and one or more of any number of turbulent flow characteristics, such as turbulence intensity (TI), relative turbulence intensity (k), turbulent kinetic energy (TKE), turbulent length scale (TLS), or Reynolds shear stresses (τ) (e.g. Smith *et al*., 2005; 2006; Russon *et al*., 2011 Silva *et al*., 2011; 2012a; 2012b; Duarte *et al*., 2012). However, often, the biophysical interpretation of these statistical links is obscure. This issue was overcome by using a reductionist approach and investigating space use in-line with the general principle that it should be dictated by energy conservation, or more specifically, strategies to minimise the costs of swimming. A simple, robust and biologically relevant hydrodynamic descriptor of drag (D_t) that incorporated both mean and fluctuating velocity components provided a proxy for the energetic cost of holding station. Specialised behaviours (entraining, bow riding, drafting, wall holding and tail holding) that could not be described by this proxy were indirectly accounted for by analysing and removing space use in key zones. As predicted, under controlled experimental conditions in which density dependent (conspecifics) and other confounding factors (e.g. visual cues, food, predators) were absent, fish adopted energy conservation strategies through the selection of low drag areas or where they could exhibit specialised performance enhancing behaviours. Two new specialised behaviours were identified (wall-holding and tail holding), as well as a correlative link between fish length and the size of an object that they preferentially choose to entrain upon. The results of Chapter 4 represent a step forward in the understanding of fish behaviour in hydrodynamically complex environments and will have direct implications for fisheries management and conservation. Pending further research, the findings of this study suggest that, where feasible, fish passes should be designed to provide low-turbulence low-drag pathways for fish to ascend and resting areas that are conducive to energy conservation through the expression of specialised behaviours.

Historically there has been a bias towards designing fish passes to facilitate the passage of commercially important species (usually stronger swimming salmonids) (Katopodis and Williams, 2012). In Chapter 5 the efficiency of a new configuration of bristle pass for improving upstream passage of European eel and European river lamprey at an experimental Crump weir was quantified. This pass type is non-mechanical, low-cost, low-maintenance, and hydrodynamically unobtrusive. When high velocity and turbulence restricted passage, bristle passes increased the passage success of large eel (> 320 mm) and lamprey to 76.5 and 36.5%, respectively, and reduced delay and the number of attempts before passage for both species. Bristle passes also improved passage efficiency of small eel (< 320 mm), facilitating the passage of individuals as small as *ca.* 100 mm. For catadromous European eel, such levels may be adequate to maintain a stable population due to the extended duration of their diffusive upstream migration (i.e. a high probability of being able to pass during a high-flow event). For anadromous river lamprey, which are energetically and temporally constrained during their upstream migration, such levels will likely limit system productivity. It is recommended that new fish passage technologies for both species continue to be investigated. However, for a small barrier the configuration of bristle pass tested would seem to represent a viable low-maintenance and low-cost option to improve habitat connectivity for European eel. For river lamprey, while the wing-wall bristle media shows potential for assisting passage, further studies are needed to refine the technology and determine whether this approach has merit. Fine scale observation of fish behaviour during experimentation indicated that small bristle spacing (30 mm) may be limiting the passage of lamprey due to their observed weaker climbing/crawling ability. Further experimentation with larger bristle spacing is warranted.

Efficiency of downstream passage facilities is being impacted by fish rejecting accelerating velocity gradients associated with bypass entrances (Kynard and Buerkett, 1997). According to Signal Detection Theory (SDT), the ability to detect a signal (discriminability) decreases with increasing levels of internal and/or external noise. As such, it was hypothesised that if hydrodynamic noise in the vicinity of an accelerating velocity gradient were increased then the discriminability of the signal and the probability of rejection would decrease. This was experimentally tested by assessing the behaviour of brown trout in the presence or absence of an accelerating VG (constricted or unconstricted channel, respectively) under two levels of background hydrodynamic noise (low and high Turbulent Kinetic Energy - TKE). During the experiment fish displayed behaviour similar to actively migrating salmonid smolts (e.g. Haro *et al.,* 1998; Kemp *et al.,* 2005, 2006; Enders *et al.,* 2009b). However, although, at a coarse scale, discriminability of the accelerating VG was lower in the presence of increased noise, no improvements in relevant downstream passage statistics for brown trout were observed. It is likely that either the signal was too intense or the level of noise was too weak for masking to significantly affect passage. Further reductions in discriminately, by reducing the intensity of the velocity gradient or using greater intensities of turbulence, may be needed before biologically significant improvements in passage occur. Despite mixed results, the use of masking as a wildlife management technique is conceptually valid and the findings of this experiment present a useful stepping stone for future research. Potential limitations of the study have been highlighted and discussed.

7.3 Research impact, management application, and societal importance

The literature review highlighted that although fish passage research is a growing area of fisheries science (Roscoe and Hinch, 2010) there are many challenges still to overcome if vulnerable freshwater species are to be conserved. This body of experimental research attempted to tackle some of these challenges and as a result numerous novel contributions to science have been made. This section outlines these contributions and discusses their research impact, management application, and societal importance.

Novel contributions to science produced from experimental research undertaken meet objective 2 (see Chapter 4):

- A new metric for describing hydrodynamic conditions was presented and tested – turbulent drag (D_t). D_t *is a* simple, robust, and biologically relevant hydrodynamic descriptor that incorporates both mean and fluctuating velocity components and can be used as a proxy to infer the relative energetic cost of holding station. Previously there has been uncertainty as to what hydrodynamic metrics are appropriate for describing fish behaviour (Lacey *et al.,* 2012; Vowles *et al.,* 2013). D_t is easy to calculate from commercially available three dimensional flow meters of which both laboratory and field versions are available. As such, it is readily accessible to both scientific researchers and fisheries managers to assess space use by fish.
- It was shown that under controlled experimental conditions fish adopt energy conservation strategies through the selection of low drag areas or where they can exhibit specialised performance enhancing behaviours. Importantly, this study moved on from investigating solely correlative links between fish and hydrodynamic metrics, a major limitation of previous studies (Johnson and Rice, 2014), consequently the results are easier for scientists and fisheries managers to interpret and apply.
- Two new specialised behaviours for holding station were observed and described (wall holding and tail holding). Wall holding is of particular interest as the mechanisms that enable a fish to hold position in this location with apparent reduced body undulating are unclear and it was the only behaviour that was frequently expressed which didn't rely on physical contact with a structure to maintain position (e.g. tail holding). Animals have

evolved extremely efficient locomotory styles and humans often seek to replicate these to develop more efficient technologies (e.g. Fish *et al.,* 2011). Although fine scale evaluation of the hydrodynamic forces that enable fish to hold position in these locations was beyond the scope of this thesis, these types of specialised behaviours are of interest to ecologists and biomimicists and pending further investigation may help scientists develop bioinspired modes of efficient transport.

- Assessment of space use by brown trout revealed the first volitional evidence that fish choose to entrain on objects proportional in size to their body length. This finding will help to improve often ineffective habitat restoration schemes, where bluff bodies are used to increase hydrodynamic heterogeneity and fish densities within rivers (Palmer *et al.,* 2010).

A paper based on the results of Chapter 4 is in the final preparation stages for submission in the Journal of Experimental Biology.

Novel contributions to science produced from experimental research undertaken to meet objective 3 (see Chapter 5):

- The efficiency of side-mounted vertically oriented bristle passes for improving upstream passage of European eel (*Anguilla anguilla*) and river lamprey (*Lampetra fluviatilis*) at an experimental Crump weir was quantified. Bristle passes helped European eel and river lamprey pass upstream but interspecific variation in efficacy was evident. For a small barrier the configuration of bristle pass tested would seem to represent a viable low-maintenance and low-cost option to improve habitat connectivity for European eel. For river lamprey, the bristle passes would need to be optimised before they could be considered an effective passage solution. This section of the research was part funded by the Environment Agency and the experimental results have directly impacted local management decisions. For example, it has steered current research efforts and funding towards alternate substrate types that may be more appropriate for both species (e.g. the aforementioned studded tiles that Dr Andrew Vowles [ICER] recently evaluated at Southampton University). As such the experimental results have been instrumental in steering fisheries management decisions that seek to investigate new methods to improve upstream passage of fish at anthropogenic barriers.
- Fine scale observations of fish behaviour indicated that small bristle spacing was impeding the upstream passage of river lamprey. This observation along with data from

similar passage experiments (e.g. by Dr Andrew Vowles) will aid in the efficient development of fish passage substrate technologies for this species.

- River lamprey were observed to be have light physical marks on their flanks after bristle pass use. This is the first documented evidence that this type of pass could injure fish and possibly have further negative health implications.

The results of this experimental research have been presented at two international conferences:

- *"Efficiency of eel passes for upstream moving river lamprey (Lampetra fluviatilis) at an experimental Crump weir." IFM Annual Conference, Liverpool, UK, October 2014.*
- *"Efficiency of a vertically oriented bristle pass for upstream moving European eel (Anguilla anguilla) and river lamprey (Lampetra fluviatilis) at an experimental Crump weir." Fish Passage 2015, Groningen, Netherlands, May 2015.*

By invitation, at a national conference:

- *"Efficiency of eel passes for upstream moving River lamprey (Lampetra fluviatilis) at an experimental Crump weir." IFM Lamprey Conference, York, UK, May 2014.*

And at a regional conference:

- *"Upstream passage of anguilliform fish over low-head barriers". Chalkstream Research Conference, Southampton, UK, June 2013.*

In addition a paper summarising these findings, titled 'Efficacy of a side-mounted vertically oriented bristle pass for improving upstream passage of European eel (Anguilla anguilla) and river lamprey (Lampetra fluviatilis) at an experimental Crump weir', has been accepted (with minor revisions) for publication in the journal 'Ecological Engineering'.

Novel contributions to science produced from experimental research undertaken to meet objective 4 (see Chapter 6):

- A potential new behavioural manipulation method is presented and discussed: Masking a velocity gradient with turbulence to reduce rejection rates of downstream moving fish at bypass intakes.
- Although the experimental results were inconclusive this is the first attempt to use Signal Detection Theory as a management tool to manipulate animal behaviour to help conserve vulnerable species. As such it provides a useful platform for future research.

In addition, knowledge gained during research undertaken for this thesis has contributed towards:

- A book chapter: Vowles, A.S., Eakins, L.R., Piper, A.T., Kerr, J.R. and Kemp, P.S. **2013**. Developing realistic fish passage criteria: An integrated approach. *In:* Maddock, I., Harby, A., Kemp, P. and Wood, P (eds.), Ecohydraulics: An Integrated Approach, John Wiley & Sons Ltd., pp. 464.
- A research letter, which is in preparation to be submitted to the journal Trends in Ecology and Evolution (TREE) and is titled: 'Proportional processing in migratory fish' (authors in order: Kerr, J.R, Vowles, A.S., Goodwin, R.A. and Kemp, P.S.). The letter is a comment piece on an article by Akre and Johnson (2014). In the letter, the use of psychophysical concepts in fisheries science and research on the behaviour of migratory fish are discussed that support the concept that animals compare stimuli based on proportional rather than absolute differences in magnitude.

The findings of this thesis will help increase the transparency of anthropogenic barriers and reduce the impact of habitat fragmentation on vulnerable fish species. The re-establishment of habitat connectivity has been shown to increase system productivity (Cloern, 2007), gene flow between populations (Mech and Hallett, 2001) and increase species diversity by re-opening previously isolated habitat to transient individuals (Shuman, 1995). Improvements in fish passage will also directly benefit society by promoting sustainable populations and re-establishing harvestable stocks for subsistence and trade. An important factor considering fish are often the major and the only source of animal protein for low income families in many less economically developed countries (Briones *et al.,* 2004) and they are an important source of income for many fishermen worldwide (e.g. Lymer *et al.,* 2008; Kelly and King, 2001). The persistence of migratory fish stocks is also critically important for the hugely lucrative industry of recreational angling. For example, in England and Wales alone, if current salmon stocks were to severely decline, the annual loss in income is estimated to be *ca.* £350 million annually (Mawle and Peirson, 2009). Many migratory fish populations also promote human welfare by providing opportunities for leisure activities (e.g. angling) and via cultural heritage (e.g. the importance of the pacific lamprey to the indigenous people of the Columbian planes - Close *et al.,* 2002). Hence, the maintenance of healthy, genetically robust and sustainable populations of freshwater fish is hugely important for human subsistence, economics, cultural heritage, and wellbeing.

The research undertaken as part of this thesis is of interest to scientists working in a diverse range of research fields (e.g. ecology, ecohydraulics, biomimicry, and psychophysics) and to fisheries managers and policy makers who are seeking to improve fish passage both directly and through law. Many of the key findings have been, or are in the process of, being disseminated and, in one case, has already directly influenced fish passage research. Ultimately the changes brought about as a result of this research should aid in the conservation of vulnerable fish species, something that will, in turn, help promote productive and resilient ecosystems that benefit society.

References

Aarestrup, K,. Lucas, M.C. and Hansen, J.A. **2003**. Efficiency of a nature-like bypass channel for sea trout (*Salmo trutta*) ascending a small Danish stream studied by PIT telemetry. *Ecology of Freshwater Fish*, **12**, 160-168.

Abernethy, C.S., Amidan, B.G. and Čada, G.F. **2001**. Laboratory studies of the effects of pressure and dissolved gas supersaturation on turbine-passed fish. PNNL-13470, Pacific Northwest National Laboratory, Richland, WA. pp. 61.

Agostinho, A.A., Gomes, L.C., Fernandez, D.R. and Suzuki, H.I. **2002**. Efficiency of fish ladders for neotropical ichthyofauna. *River Research and Applications*, **18**, 299-306.

Agostinho, A.A., Pelicice, F.M. and Gomes, L.C. **2008**. Dams and the fish fauna of the Neotropical region: Impacts and management related to diversity and fisheries. *Brazilian Journal of Biology,* **68**(s4), 1119-1132.

Akanyeti, O. and Liao, J.C. **2012**. The effect of flow speed and body size on Kármán gait kinematics in rainbow trout. *Journal of Experimental Biology*, **216**, 3442-3449.

Akilli, H., Akar, A. and Karakus, C. **2004**. Flow characteristics of circular cylinders arranged side-by-side in shallow water. *Flow Measurement and Instrumentation,* **15**, 187-197.

Akre, K.L. and Johnsen, S. **2014**. Psychophysics and the evolution of animal behaviour. *Trends in Ecology and Evolution*, **29**(5), 291-300.

Allibone, P., David, B., Hitchmough, R., Jellyman, D., Ling, N., Ravenscroft, P. and Waters, J. **2010**. Conservation status of New Zealand freshwater fish, 2009. *New Zealand Journal of Marine and Freshwater Research,* **44**(4), 271-287.

Anderson, E.J., McGillis, W.R. and Grosenbaugh, M.A. **2001**. The boundary layer of swimming fish. *The Journal of Experimental Biology,* **204**, 81-102.

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.

Aparicio, E., Vagras, M.J., Olmo, J.M. and de Sostoa, A. **2000**. Decline of native freshwater fishes in a Mediterranean watershed on the Iberian Peninsula: A quantitative assessment. *Environmental Biology of Fishes*, **59**, 1-19.

Archer, S., Hope, A. and 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, J.D., Kemp, P.S., Kennedy, G.J.A., Ladle, M. and Milner, N.J. **2003**. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research*, **62**(2), 143-170.

Armstrong, G.S., Aprahamian, M.W., Fewings, G.A., Gough, P.J., Reader, N.A. and Varallo, P.V. **2010**. Environment Agency Fish Pass Manual. Guidance notes on the legislation, selection and approval of fish passes in England and Wales. Document – GEHO 0910 BTBP-E-E. pp. 369.

Bachman, R.A. **1984**. Foraging behaviour of free-ranging wild and hatchery brown trout in a stream. *Transactions of the American Fisheries Society*, **113**(1), 1-32.

Bader, J.A., Moore, S.A. and Nusbaum, K.E. **2006**. The effect of cutaneous injury on a reproducible immersion challenge model for *Flavobacterium columnare* infection in channel catfish (*Ictalurus punctatus*). *Aquaculture*, **253**, 1-9.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J-S., Nakashizuka, T., Raffaelli, D. and Schmid, B. **2006**. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, **9**, 1146-1156.

Baran, E., Jantunen, T. and Chong, C.K. **2007**. Values of inland fisheries in the Mekong River Basin. WorldFish Center, Phnom Penh, Cambodia. pp. 76.

Baras, E. and Jeandrain, D. **1998**. Evaluation of surgery procedures for tagging eel *Anguilla anguilla* (L.) with biotelemetry transmitters. *Hydrobiologia*, **371/372**, 107-111.

Barry, T. and Kynard, B. **1986**. Attraction of adult American shad to fish lifts at Holyoke Dam, Connecticut River. *North American Journal of Fisheries Management,* **6**, 233-241.

Basolo, A.L. and Alcaraz, G. **2003**. The turn of the sword: length increases male swimming costs in swordtails. *Proceedings of the Royal Society of London B*, **270**, 1631-1636.

Bassett, D.K., Carton, A.G. and Montgomery, J.C., **2006**. Flowing water decreases hydrodynamic signal detection in a fish with an epidermal lateral-line system. *Marine and Freshwater Research*, **57**, 611-617.

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, MAFF Directorate of Fisheries Research, **78**, pp. 46.

Beamish, F.W.H. **1978**. Swimming Capacity, in: Hoar, W.S., Randall, D.J. (Eds.), Fish Physiology Vol. 7 Locomotion. Academic Press Inc., New York, pp. 187.

Bell, M. 1991. Fisheries handbook of engineering requirements and biological criteria. U.S. Army Corps of Engineers, North Pacific Division, Portland, Oregon. pp. 352.

Bellanger, A., Huon, S., Steinmann, P., Chabaux, F., Velasquez, F., Vallès, V., Arn, K., Clauer, N., Mariotti, A. **2004**. Oxic–anoxic conditions in the water column of a tropical freshwater reservoir (Peña-Larga dam, NW Venezuela). *Applied Geochemistry,* **19**, 1295-1314.

Bentley, W.W. and Raymond, H.L. **1976**. Delayed migrations of yearling Chinook salmon since completion of lower monumental and little goose dams on the Snake River. *Transactions of the American Fisheries Society*, **105**(3), 422-424.

Berry, M., Booth, D.T. and Limpus, C.J. **2013**. Artificial lighting and disrupted sea-finding behaviour in hatchling loggerhead turtles (*Caretta caretta*) on the Woongarra coast, south-east Queensland, Australia. *Australian Journal of Zoology*, **61**, 137-145.

Beyer, H.L, Haydon, D.T., Morales, J.M., Frair, J.L., Hebblewhite, M., Mitchell, M. and Matthipoulos, J. **2010**. The interpretation of habitat preference metrics under use–availability designs. *Philoshophical Transactions of the Royal Society A*, **365**, 2245-2254.

Biewener, A.A. **2003**. Animal locomotion. Oxford University Press, New York. pp. 285.

Blevins, R. D. **1990**. Flow Induced Vibration, 2nd edition. Krieger Publishing Company, Malabar, Florida. pp. 410.

Bonhommeau, S., Blanke, B., Tréguier, A., Grima, G., Rivot, E., Vermard, Y., Greiner, E. and Le Pape, O. **2009**. How fast can the European eel (*Anguilla anguilla*) larvae cross the Atlantic Ocean*? Fisheries Oceanography*, **18**(6), 371-385.

Boon, P.J. **1988**. The impact of river regulation on invertebrate communities in the UK. *Regulated Rivers: Research and Management,* **2**, 389-409.

Bovee, K.D. **1986**. Development and evaluation of habitat suitability criteria for use in the instream flow incremental methodology. Instream Flow Information Paper #21 FWS/OBS-86/7. Washington, DC: USDI Fish and Wildlife Service. pp. 235.

Briand, C., Fatin, D. and Legault, A. **2002**. Role of eel odour on the efficiency of an eel, *Anguilla anguilla*, ladder and trap. *Environmental Biology of Fishes*, **65**, 473-477.

Briand, C., Fatin, D., Fontenelle, G., Feunteun, E. **2005**. Effect of re-opening of a migratory pathway for eel (*Anguilla anguilla*, L.) at a watershed scale. *Bulletin Francais de la Peche et de la Pisciculture,* **378-379**, 67-86.

Briggs, J.P. **2002**. The zebrafish: A new model organism for integrative physiology. *American Journal of Physiology - Regulatory, Integrative and Comparative Physiology*, **282**, R3-9.

Briones, M., Dey, M.M., and Ahmed, M. **2004**. The future for fish in the food and livelihoods of the poor in Asia. *NAGA, WorldFish Center Quarterly*, **27**(3/4), 48-50.

Brown, L.R., Moyle, P.B. and Ronald, M. **1994**. Historical decline and current status of coho salmon in California. *North American Journal of Fisheries Management*, **14**(2), 237-261.

Budy, P., Thiede, G.P, Bouwes, N., Petrosky, C.E. and Schaller, H. **2002**. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. *North American Journal of Fisheries Management*, **22**, 35-51.

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

Bunt, C. M., Katopodis, C., McKinley, R.S. **1999**. Attraction and passage efficiency of white suckers and smallmouth bass by two Denil fishways. *North American Journal of Fisheries Management,* **19**, 793-803.

Bunt, C.M., Cooke, S.J. and McKinley, R.S. **2000**. Assessment of the Dunnville Fishway for passage of walleyes from Lake Erie to the Grand River, Ontario. *Journal of Great Lakes Research*, **26**(4), 482-488.

Bunt, C. M., van Poorten, B.T. and Wong, L. **2001**. Denil fishway utilization patterns and passage of several warm water species relative to seasonal, thermal and hydraulic dynamics. *Ecology of Freshwater Fish,* **10**, 212-219.

Bunt, C.M., Castro-Santos, T. and Haro, A. **2012**. Performance of fish passage structures at upstream barriers to migration. *River Research and Applications*, **28**, 457-478.

Burkhead, N.M. **2012**. Extinction rates in North American freshwater fishes, 1900–2010. *BioScience*, **62**(9), 798-808.

Cada, G.F. **1990**. A review of studies relating to the effects of propeller-type turbine passage on fish early life stages. *North American Journal of Fisheries Management*, **10**, 418-426.

Calles, E.O. and 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, O., Olsson, I.C., Comoglio, C., Kemp, P.S., Blunden, L., Schmitz, M. and Greenburg, 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., Karlsson, S., Hebrand, M. and Comoglio, C. **2012**. Evaluating technical improvements for downstream migrating diadromous fish at a hydroelectric plant. *Ecological Engineering*, **48**, 30-37.

Castro-Santos, T. and Haro, A. **2003**. Quantifying migratory delay: a new application of survival analysis methods. *Canadian Journal of Fisheries and Aquatic Science*, **60**, 989-996.

Castro-Santos, T., Cotel, A. and Webb, P. **2009**. Fishway evaluations for better bioengineering: An integrative approach. American Fisheries Society Symposium, **69**, 557–575.

Caudill, C.C., Daigle, W.R., Keefer, M.L., Boggs, C.T., Jepson, M.A., Burke, B.J., Zabel, R.W., Bjornn, T.C. and Peery, C.A. **2007**. Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: delayed negative effects of passage obstacles or condition-dependent mortality? *Canadian Journal of Fisheries and Aquatic Science,* **64**, 979-995.

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

Cederholm, C.J., Kunze, M.D., Murota, T. and Sibatani, A. **1999**. Pacific Salmon Carcasses: Essential Contributions of Nutrients and Energy for Aquatic and Terrestrial Ecosystems. *Fisheries*, **24**(10), 6-15.

Chesney, E.J. **1989**. Estimating the food requirements of striped bass larvae Morone saxatilis: effects of light, turbidity and turbulence. *Marine Ecology Progress Series*, **53**, 191-200.

Chagnaud, B.P., Bleckmann, H. and Engelmann, J. **2006**. Neural responses of goldfish lateral line afferents to vortex motions. *The Journal of Experimental Biology*, **209**, 327-342.

Clay, C.H. **1995**. Design of fishways and other fish facilities. Second edition. CRC Press, Inc., Boca Raton, Florida. pp. 249.

Cloern, J.E. **2007**. Habitat connectivity and ecosystem productivity: implications from a simple model. *The American Naturalist*, **169**(1), E21-E33.

Close, D.A., Fitzpatrick, M.S. and Li, H.W. **2002**. The ecological and cultural importance of a species at risk of extinction, Pacific lamprey. *Fisheries*, **27**(7), 19-25.

Clough, S.C., Lee-Elliott, I.H., Turnpenny, A.W.H., Holden, S.D.J., Hinks, C. **2004**. Swimming speeds in fish: Phase 2. R&D Technical Report No. W2-026/TR3, Environment Agency, Bristol, pp. 82.

Clough, S.C., Turnpenny, A.W.H. **2001**. Swimming speeds in fish. Phase 1. R&D Technical Report No. W2-026/TR1&2, Environment Agency, Bristol, pp. 94.

Colgan, P. **1993**. The motivational basis of fish behaviour. In Pitcher, T.J. (ed.) Behaviour of Teleost Fishes, 2nd Edition, Chapman and Hall, London, pp. 715.

Cooke, S.J., Bunt, C.M., Hamilton, S.J., Jennings, C.A., Pearson, M.P., Cooperman, M.S., Markle, D.F. **2005**. Threats, conservation strategies, and prognosis for suckers (Catostomidae) in North America: insights from regional case studies of a diverse family of non-game fishes. *Biology Conservation,* **121**, 317-331.

Coombs, S., Gorner, P. and Munz, H. **1989**. The Mechanosensory Lateral Line: Neurobiology and Evolution. Springer-Verlag, New York. pp. 724.

Coombs, S. **1999**. Signal detection theory, lateral-line excitation patterns and prey capture behaviour of mottled sculpin. *Animal Behaviour*, **58**, 421-430.

Costanza, R., d'Arge, R., de Groot, R., Farberk, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., Raskin, R.G., Sutton, P. and van den Belt, M. **1997**. The value of the world's ecosystem services and natural capital. *Nature*, **387**, 253-260.

Costello, M.J. **2009**. How sea lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. *Proceedings of the Royal Society B*, **276**, 3385-3394.

Cotel, A.J., Webb, P.W. and Tritico, H. **2006**. Do brown trout choose locations with reduced Turbulence? *Transactions of the American Fisheries Society*, **135**, 610-619.

Cotel, A.J. and Webb, P.W. **2012**. The challenge of understanding and quantifying fish response to turbulence-dominated physical environments. In: Childress, S., Hosoi, A., Schultz, W. and Wang, Z.J. (Eds.), Natural locomotion in fluids and on surfaces. Swimming, flying and sliding. Spinger Science + Business Media, New York. pp. 316.

Coutant, C.C. and Whitney, R.R. **2000**. Fish behavior in relation to passage through hydropower turbines: A review. *Transactions of the American Fisheries Society*, **129**, 351-380.

Croze, O. **2008**. Assessment of downstream fish bypasses for Atlantic salmon smolts at four hydroelectric facilities on the Ariège River (France). *American Fisheries Society Symposium*, **61**, 123-140.

Croze, O. and 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 Rodére Ram. *Bulletin Francais de la Peche et de la Pisciculture*, **353/354**, 141-156.

Crump, E.S. **1952**. A new method of gauging stream flow with little afflux by means of a submerged weir of triangular profile. *Proceedings of the Institution of Civil Engineers*, **1**, 223-242.

Daniel, T.L. **1981**. Fish mucus: *In situ* measurements of polymer drag reduction. *Biological Bulletin*, **160**, 376-378.

Dean, B. and Bhushan, B. **2010**. Shark-skin surfaces for fluid-drag reduction in turbulent flow: a review. *Philosophical Transactions of the Royal Society A*, **368**, 4775-4806.

DeGraaf, D.A. and Bain, L.H. 1986. Habitat use by and preferences of juvenile Atlantic salmon in two Newfoundland Rivers. *Transactions of the American Fisheries Society*, **115**(5), 671-681.

Dekker, W. **2003a**. Status of the European eel stock and fisheries. *In: Aida K., Tsukamoto K. and Yamauchi K. (editors)*. Eel Biology. Springer-Verlag. Tokyo. Pages 237-254.

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

Dekker, W., Pawson, M. and Wickström, H. **2007**. Is there more to eels than slime. An introduction to papers presented at the ICES Theme Session in September 2006. *ICES Journal of Marine Science,* **64**(7), 1366-1367.

Denil, G. **1909**. Les échelles à poissons et leur application aux barrages de Meuse et d'Ourthe (Fish ladders and their use at the Meuse and Ourthe dams). Bulletins Académie Royale de Belgique., 1221-1224.

Denil, G. **1938**. La mécanique du poisson de rivière (The mechanics of riverine fish). Annales des Travaux Publics de Belgique, Bruxelles, Belgique. pp. 395.

Dodds, W. and Whiles, M. **2010**. Freshwater Ecology: Concepts and Environmental Applications of Limnology. Elsivier Inc., London, UK. pp. 829.

Donoho, D.L. and Johnstone, I.M. **1994**. Ideal spatial adaptation by wavelet shrinkage. *Biometrika*, **81**(3), 425-455.

Duarte, B.A.F., Romos, I.C.R. and Santos, H.A. **2012**. Reynolds shear-stress and velocity: Positive biological response of neotropical fishes to hydraulic parameters in a vertical slot fishway. *Neotropical Ichthyology*, **10**(4), 813-819.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z-I., Knowler, D.J., Lévéque, C., Naiman, R.J., Prieur-Richard, A-H., Soto, D., Stiassny, M.L.J. and Sullivan, C.A. **2006**. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Review*, **81**, 163-182.

Dupont, S., Brunet, Y. and Finnigan, J.J. **2008**. Large-eddy simulation of turbulent flow over a forested hill: Validation and coherent structure identification. *Quarterly Journal of the Royal Meteorological Society*, **134**, 1911-1929.

Erkan, D.E. **2002**. Strategic plan for the restoration of anadromous fishes to Rhode Island coastal streams. Rhode Island Department of Environmental Management, Division of Fish and Wildlife, Wakefield, RI. pp. 83.

Efron, B. and Tibshirani, R. **1993**. An Introduction to the bootstrap. *New York: Chapman and Hall.* pp. 456.

Enders, E.C., Boisclair, D. and Roy, A.G**. 2003**. The effect of turbulence on the cost of swimming for juvenile Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 1149-1160.

Enders, E.C., Boisclair, D. and Roy, A.G. **2004**. The cost of habitat utilization of wild, farmed, and domesticated juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Science,* **61**, 2302-2313.

Enders, E.C., Boisclair, D. and Roy, A.G. **2005a**. A model of total swimming costs in turbulent flow for juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Science,* **62**, 1079-1089.

Enders, E.C., Roy, M.L., Ovidio, M., Hallot, E.J., Boyer, C., Petit, F. and Roy, A.G. **2009a**. Habitat choice by Atlantic salmon parr in relation to turbulence at a reach scale. *North American Journal of Fisheries Management,* **30**, 1819-1830.

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

Enders, E.C., Gessel, M.H., Anderson, J.J. and Williams, J.G. **2012**. Effects of decelerating and accelerating flows on juvenile salmonid behavior. *Transactions of the American Fisheries Society*, **141**(2), 357-364.

Engelmann, J., Hanke, W. and Bleckmann, H. **2002**. Lateral line reception in still- and running water. *Journal of Comparative Physiology A*, **188**, 513-526.

Engels, S., Schneider, N-S., Lefeldt, N., Hein, C.M., Zapka, M., Michalik, A., Elbers, D., Kittel, A., Hore, P. J. and Mouritsen, H. **2014**. Anthropogenic electromagnetic noise disrupts magnetic compass orientation in a migratory bird. *Nature*, **509**, 353-561.

Environment Agency. **2010a**. Field evaluation of the effect of elver passes on measuring structures. Draft Report, J2578/1.

Environment Agency. **2010b**. Mapping hydropower opportunities and sensitivities in England and Wales. Technical Report. ea/br/e/std/v1. pp. 74.

Environment Agency. **2011**. Elver and eel passes: A guide to the design and implementation of passage solutions at weirs, tidal gates and sluices. *GEO0211BTMV-E-E*.

Facey, D.E. and Grossman, G.D. **1992**. The relationship between water velocity, energetic costs, and microhabitat selection use in four North American Stream fishes. *Hydrobiologia*, **239**, 1-6.

FAO, 2014. The state of the world fisheries and aquaculture: Oportunities and challenges. Food and Agriculture Organization of the United Nations. Rome. pp. 243.

Fausch, K.D. **1993**. Experimental analysis of microhabitat selection by juvenile steelhead (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) in a British Columbia stream. *Canadian Journal of Fisheries and Aquatic Sciences,* **50**, 1198-1207.

Fausch, K.D., Togersen, C.E., Baxter, C.V. and Li, H.W. **2002**. Landscapes to Riverscapes: Bridging the Gap between Research and Conservation of Stream Fishes. *BioScience*, **52**(6), 483-498.

Fay, R.R., **1988**. Hearing in Vertebrates: A Pyschophysics Databook. Hill-Fay, Winnetka, IL.

Fay, R.R. and Popper, A.P. **1974**. Acoustic stimulation of the ear of the goldfish (*Carassius auratus*). *Journal of Experimental Biology*, **61**, 243-260.

Fechner, G. T. **1860**. Elementa der psychophysik. Breitkopf and Hartel, Leipzig. In translation: 1966. Elements of Psychophysics. HE Adler, DH Howes, and EG Boring, editors. Holt, Rinehart and Winston. *Inc., New York*. pp. 286.

Feldkamp, S.D. **1987**. Swimming in the California Sea Lion: Morphometrics, drag and energetics. *Journal of Experimental Biology*, **131**, 117-135.

Ferrari, M.C.O., Sih, A and Chivers, D.P., **2009**. The paradox of risk allocation: a review and prospectus. *Animal Behaviour*, **78**, 579-585.

Ferrari, M.C.O., Elvidge, C.K., Jackson, C.D., Chivers, D.P. and Brown, G.E., **2010**. The responses of prey fish to temporal variation in predation risk: sensory habituation or risk assessment. *Behavioural Ecology,* **21**, 532-536.

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

Ficke, A.D., Myrick, C.A. and Kondratieff, M.C. **2012**. The effects of PIT tagging on the swimming performance and survival of three nonsalmonid freshwater fishes. *Ecological Engineering*, **48**, 86-91.

Fleming, I.A., Jonsson, B. and Gross, M.R. **1994**. Phenotypic divergence of sea-ranched, farmed, and wild salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**(12), 2808-2824.

Foulds, W.L. and Lucas, M.C. **2013**. Extreme inefficiency of two conventional, technical fishways used by the European river lamprey (*Lampetra fluviatilis*). *Ecological Engineering*, **58**, 423-433.

Fish, F.E., Weber, P.W., Murray, M.M. and Howle, L.E. **2011**. The tubercles on humpback whales' flippers: Application of bio-inspired technology. *Integrative and Comparative Biology*, **51**(1), 203-213.

Freyhof, J. **2013a**. *Lampetra fluviatilis*. The IUCN Red List of Threatened Species. Version 2014.1. <www.iucnredlist.org>. Accessed on 11 July 2014.

Freyhof, J. **2013b**. Salmo trutta. The IUCN Red List of Threatened Species. Version 2014.1. <www.iucnredlist.org>. Accessed on 14 July 2014.

Friedland, K.D., MacLean, J.C., Hansen, L.P., Peyronnet, A.J., Karlsson, L., Reddin, D.G., Ó Maoiléidigh, N., and McCarthy, J.L. **2009**. The recruitment of Atlantic salmon in Europe. *ICES Journal of Marine Science*, **66**, 289-304.

Friedland, K.D., Reddin, D.G., McMenemy, J.R. and Drinkwater, K.F. **2003**. Multidecadal trends in North American Atlantic salmon (*Salmo salar*) stocks and climate trends relevant to juvenile survival. *Canadian Journal of Fisheries and Aquaculture*, **60**, 563-583.

Gao, Y., Yu, D., Tan, S., Wang, X. and Hao, Z. **2010**. Experimental study on the near wake behind two side-by-side cylinders of unequal diameters. *Fluid Dynamics Research*, **42**(5), 1-13.

Gascuel, D. **1986**. Flow-carried and active swimming migration of the glass eel (*Anguilla anguilla*) in the tidal area of a small estuary on the French Atlantic coast. *Helgoland Marine Research*, **40**, 321-326.

Gelfand, S. A. **2010**. Hearing: An Introduction to psychological and physiological acoustics. 5th edn. New York: Taylor and Francis. pp. 392.

Gibson, F.A. **1953** Brook lamprey, *Lampetra branchialis Day*, in a Westmeath stream. Irish Naturalists' Journal, **11**, 86-9.

Giske, J., Eliassen, S., Fiksen, Ø., Jakobsen, P.J., Aksnes, D.L., Mangel, M. and Jørgensen. C. **2014**. The emotion system promotes diversity and evolvability. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 1096.

Goodwin, R. A., M. Politano, J. W. Garvin, J. M. Nestler, D. Hay, J. J. Anderson, L. J. Weber, E. Dimperio, D. L. Smith, and M. A. Timko. **2014**. Fish navigation of large dams emerges from their modulation of flow field experience. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 5277-5282.

Gordon, E., Meentemeyer, R.K. **2006**. Effects of dam operation and land use on stream channel morphology and riparian vegetation. *Geomorphology,* **8**2, 412-429.

Gosset, C. and Travade, F. **1999**. Devices to aid downstream salmonid migration: Behavioral barriers. *Cybium*, **23**(s), 45-66.

Goudie, A.S. **2013**. The human impact on the natural environment: Past, present, and future. 7th edn. Wiley-Blackwell, Oxford, UK. pp. 376.

Govardovskiĭ, V.I. and Lychakov, D.V. **1984**. Visual cells and visual pigments of the lamprey, *Lampetra fluviatilis*. *Journal of Comparative Physiology A*, **154**, 279-286.

Gowans, R.D., Armstrong, J.D. and Priede, I.G. **1999**. Movements of adult Atlantic salmon in relation to a hydroelectric dam and fish ladder. *Journal of Fish Biology*, **54**, 713-726.

Graham, C. H. **1934**. Psychophysics and behaviour. The Journal of General Psychology, **10**(2), 299-310.

Green, D.M. and Swets, J.A. **1966**. Signal Detection Theory and Psychophysics. New York: Wiley. pp. 455.

Green, B.S., Gardner, C., Linnane, A. and Hawthorne, P.J. **2010**. The good, the bad and the recovery in an assisted migration. *PLOS ONE*, **5**(11), e14160.

Greenberg, L.A., Calles, O., Andersson, J. and Engqvist, T. **2012**. Effect of trash diverters and overhead cover on downstream migrating brown trout smolts. *Ecological Engineering*, **48**, 25-29.

Gresh, T., Lichatowich, J. and Schoonmaker, P. **2000**. An estimation of historic and current levels of salmon production in the northeast pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. *Fisheries*, **25**(1), 15-21.

Gries, G. and Letcher, B.H. **2002**. Tag retention and survival of age-0 Atlantic salmon following surgical implantation with passive integrated transponder tags. *North American Journal of Fisheries Management*, **22**(1), 219-222.

Guiny, E., Ervine, D.A. and Armstrong, J.D. **2005**. Hydraulic and biological aspects of fish passes for Atlantic salmon. *Journal of Hydraulic Engineering*, **131**, 542-553.

Gustafson, R.G., Waples, R.S., Myers, J.M., Weitkamp, L.A., Bryant, G.J., Johnson, O.W. and Hard, J.J. **2007**. Pacific salmon extinctions: Quantifying lost and remaining diversity. *Conservation Biology*, **21**(4), 1009-1020.

Hadderingh, R.H., van der Stoep, J.W. and Habraken, J.M.P.M. **1992**. Deflecting eels from water inlets of power stations with light. In: Moriarty, C. (ed.) *Irish Fisheries Investigations*, Series A (Freshwater), **36**, 78-87.

Hadderingh, R.H., Van Aerssena, G.H.F.M., De Beijerb, R.F.L.J. and Van Der Veldeb, 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.

Hall, C.J., Jordaan, A. and Frisk, M.G. **2011**. The historic influence of dams on diadromous fish habitat with a focus on river herring and hydrologic longitudinal connectivity. *Landscape Ecology*, **26**, 95-107.

Hansen, M.M., Fraser, D.J., Meier, K. and Mensberg, K-L.D. **2009**. Sixty years of anthropogenic pressure: a spatio-temporal genetic analysis of brown trout populations subject to stocking and population declines. *Molecular Ecology*, **18**, 2549-2562.

Haro, A. and 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**(4), 981-987.

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

Haro, A., Castro-Santos, T., Noreika, J. and 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 Science*, **61**, 1590-1601.

Hedrick, P.W., Hedgecock, D., Hamelberg, S. and Croci, S.J. **2000**. The impact of supplementation in winter-run Chinook salmon on effective population size. *Journal of Heredity*, **91**(2), 112-116.

Heggenes, J., Northcote, T.G. and Peter, A. **1991**. Seasonal habitat selection and preferences by cutthroat trout (*Oncorhynchus clarki*) in a small coastal stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**(8), 1364-1370.

Heisey, P.G., Mathur, D. and Rineer, T. **1992**. A reliable tag-recapture technique for estimating turbine passage survival application to young-of-the-year American shad *Alosa sapidissima*. *Canadian Journal of Fisheries and Aquatic Sciences,* 49, 1826-1834.

Hinch, S.G. and Rand, P.S. **2000**. Optimal swimming speeds and forward-assisted propulsion: energy-conserving behaviours of upriver-migrating adult salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 2470-2478.

Hirt-Chabbert, J.A. and Young, O.A. **2012**. Effects of surgically implanted PIT tags on growth, survival and tag retention of yellow shortfin eels *Anguilla australis* under laboratory conditions. *Journal of Fish Biology*, **81**, 314-319.

Hockley, F.A., Wilson, C.A.M.E., Brew, A. and Cable, J. **2014**. Fish responses to flow velocity and turbulence in relation to size, sex and parasite load. *Journal of the Royal Scoiety Interface*, **11**, 20130814.

Hope, A.J., Partridge, J.C. and 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.

Hughes, N. F., and L. M. Dill. **1990**. Position choice by driftfeeding salmonids: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 2039-2048.

Ibbotson, A., Smith, J., Scarlett, P. and Aprahamian, M. **2002**. Colonisation of freshwater habitats by the European eel *Anguilla anguilla. Freshwater Biology*, **47**, 1696-1706.

ICES. **2012**. Report of the Joint EIFAAC/ICES Working Group on Eels (WGEEL), 3–9 September 2012, Copenhagen, Denmark. ICES CM 2012/ACOM:18. pp. 824.

Igoe, F., Quigley, D.T.G., Marnell, F., Meskell, E., O'Conner, W. and Byrne, C. **2004**. The sea lamprey *Petromyzon marinus* (L.), river lamprey *Lampetra fluviatilis* (L.), and brook lamprey *Lampetra planeri* (Bloch) in Ireland: General biology, ecology, distribution and status with recommendations for conservation. *Biology and Environment: Preceedings of the Royal Irish Academy*, **104B**(3), 43-56.

Imre, I., Grant, J.W.A. and Keeley, E.R. **2002**. The effect of visual isolation on territory size and population density of juvenile rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Science*, **59**, 303-309.

Jackson, C.D. and Brown, G.E. **2011**. Differences in antipredator behaviour between wild and hatchery-reared juvenile Atlantic salmon (*Salmo salar*) under seminatural conditions. *Canadian Journal of Fisheries and Aquatic Science,* **68**, 2157-2165.

Jacoby, D. and Gollock, M. **2014**. *Anguilla anguilla*. The IUCN Red List of Threatened Species. Version 2014.1. <www.iucnredlist.org>. Accessed on 14 July 2014.

Janetski, D.J., Chaloner, D.T., Tiegs, S.D. and Lamberti, G.A. **2009**. Pacific salmon effects on stream ecosystems: a quantitative synthesis. *Oecologia*, **159**, 583-595.

Jang, M.-H. and Lucas, M.C. **2005**. Reproductive ecology of the river lamprey. *Journal of Fish Biology*, **66**, 499-512.

Jelbert, S.A., Hurly, T.A., Marshall, R.E.S. and Healy, S.D. **2014**. Wild, free-living hummingbirds can learn what happened, where and in which context. *Animal Behaviour*, **89**, 185-189.

Jellyman, D.J. and Ryan, C.M. **1983**. Seasonal migration of elvers (*Anguilla* spp.) into Lake Pounui, New Zealand, 1974-1978. *New Zealand Journal of Marine and Freshwater Research,* **17**, 1-15.

Jenkins, A.R. and Keeley, E.R. **2010**. Bioenergetic assessment of habitat quality for stream-dwelling cutthroat trout (*Oncorhynchus clarkii bouvieri*) with implications for climate change and nutrient supplementation. *Canadian Journal of Fisheries and Aquatic Sciences*, **67**, 371-385.

Johnson, M.F. and Rice, S.P. **2014**. Animal perception in gravel-bed rivers: scales of sensing and environmental controls on sensory information. *Canadian Journal of Fisheries and Aquatic Science*, **71**, 945-957.

Johnson, G.E., Adams, N.S., Johnson, R.L., Rondorf, D.W., Dauble, D.D. and Barila, T.Y. **2000**. Evaluation of the prototype surface bypass for salmonid smolts in spring 1996 and 1997 Lower Granite Dam on the Snake River, Washington. *Transactions of the American Fisheries Society*, **129**, 381-397.

Jowett, I.G. and Richardson, J. **1995**. Habitat preferences of common, riverine New Zealand native fishes and implications for flow management. *New Zealand Journal of Marine and Freshwater Research*, **29**(1), 13-23.

Jungwirth, M. **1996**. Bypass channels at weirs as appropriate aids for fish migration in Rhithral rivers. *Regulated Rivers: Research and Management*, **12**, 483-492.

Junker, J., Peter, A., Wagner, C.E., Mwaiko, S., Germann, B., Seehausen, O. and Keller, I. **2012**. River fragmentation increases localized population genetic structure and enhances asymmetry of dispersal in bullhead (*Cottus gobio*). *Conservation Genetics*, **13**, 545-556.

Jutila, A., Saura, A., Kallio-Nyberg, A., Huhmarniemi, A. and Romakkaniemi, A. **2006**. The status and explotation of sea trout on the Finnish coast of the Gulf of Bothnia in the Baltic Sea. *In: Sea Trout: Biology, Conservation and Management* (eds. Harris, G. and Milner, N.). Blackwell Publishing Ltd, Oxford. pp. 520.

Karlsen, H.E. and Sand, O. **1987**. Selective and reversible blocking of the lateral line in freshwater fish. *Journal of Experimental Biolog*y, **133**, 249-262.

von Kármán, T. **1937**. On the statistical theory of turbulence*. Proceedings of the National Academy of Sciences of the United States of America,* **23**(2), 98-105.

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

Katz, J., Moyle, P.B., Quiñous, R.M., Israel, J. and Purdy, S. **2013**. Impending extinction of salmon, steelhead, and trout (Salmonidae) in California. *Environmental Biology of Fishes*, **96**, 1169-1186.

Keefer, M.L., Moser, M.L., Boggs, C.T., Daigle, W.R. and Peery, C.A. **2009**. Effects of body size and river environment on the upstream migration of adult Pacific lampreys. *North American Journal of Fisheries Management*, **29**(5), 1214-1224.

Keefer, M.L., Peery, C.A., Lee, S.R., Daigle, W.R. and Johnson, E.L. **2011**. Behaviour of adult Pacific lamprey in near-field flow and fishway design experiments. *Fisheries Management and Ecology*, **18**, 177-189.

Keefer, M.L., Clabough, T.C., Jepson, M.A., Johnson, E.L., Boggs, C.T., Caudill, C.C. **2012**. Adult Pacific lamprey passage: Data synthesis and fishway improvement prioritization tools. Technical report 2012-8. *Prepared for: Department of Fish and Wildlife Sciences College of Natural Resources, University of Idaho*. pp. 125.

Kelly, F.L. and 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*, **101(B)**, 165–185.

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

Kemp, P.S., Gessel, M.H., Sandford, B.P. and 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. and Williams, J.G. **2008**. Response of downstream migrant juvenile Pacific salmonids to accelerating flow and overhead cover. *Hydrobiologia*, **609**, 205-207.

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

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

Kemp, P.S., Anderson, J.J. and Vowles, A.S. **2012**. Quantifying behaviour of migratory fish: application of signal detection theory to fisheries engineering. *Ecological Engineering*, **41**, 22-31.

Kenyon, T.N., Ladich, F. and Yan, H.Y. **1998**. A comparative study of hearing ability in fishes: the auditory brainstem response approach. *Journal of Comparative Physiology A*, **182**, 307-318.

Kieffer, J.D. and Colgan, P.W. **1992**. The role of learning in fish behaviour. *Reviews in fish biology and fisheries*, **2**, 125-143.

Klemetsen, A., Amundsen, P-A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F. and Mortensen, E. **2003**. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish,* **12**, 1-59.

Knaepkens, G., Baekelandt, K. and 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.

Knudsen, F.R., Enger, P.S. and Sand, O. **1992**. Awareness reactions and avoidance responses to sound in juvenile Atlantic salmon, *Salmo salar* L. *Journal of Fish Biology* , **40**, 523-534.

Knudsen, F.R., Schreck, C.B., Knapp, S.M., Enger, P.S. and Sand, O. **1997**. Infrasound produces flight and avoidance responses in Pacific juvenile salmonids. *Journal of Fish Biology*, **51**, 824-829.

Krebs, J.R. **1978**. Optimal foraging: Decision rules for predators . In Krebs, J.R. and Davies, N.B. (eds.). Behavioural Ecology: An Evolutionary Approach. Sinauer Associates Inc., Sunderland, Massachusetts, pp. 23-63.

Kröther, S., Mogdans, J. and Bleckmann, H. **2002**. Brainstem lateral line responses to sinusoidal wave stimuli in still and running water. *The Journal of Experimental Biology*, **205**, 1471-1484.

Kruk, A. **2004**. Decline in migratory fish in the Warta River, Poland. *Ecohydrology and Hydrobiology*, **4**(2), 147-155.

Kusmic, C. and Gualtieri, P. **2000**. Morphology and spectral sensitivities of retinal and extraretinal photoreceptors in freshwater teleosts. *Micron*, **31**, 183-200.

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

Kynard, B. and O'Leary, **1993**. Evaluation of a bypass system for spent American shad at Holyoke Dam Massachusetts. *North American Journal of Fisheries Management*. **13**, 782–789.

Lacey, R.W.J., Neary, V.S., Liao, J.C., Enders, E.C. and Tritico, H. **2012**. The IPOS framework: linking fish swimming performance in altered flows from laboratory experiments to rivers. *River Research and Applications,* **28**, 429-443.

Laffaille, P., Caraguel, J-M. and Legault, A. **2007**. Temporal patterns in the upstream migration of European glass eels (*Anguilla anguilla*) at the Couesnon estuarine dam. *Estuarine, Coastal and Shelf Science,* **73**, 81-90.

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

Larinier, M. **2001**. Environmental issues, dams and fish migration. In: Marmulla, G. (ed.), Dams, fish and fisheries. Opportunities, challenges and conflict resolution. FAO Fisheries Technical Paper. No. **419**. Rome, FAO. pp. 166.

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

Larinier, M. and Boyer-Bernard, S. **1991**. Smolts downstream migration at Poutès Dam on the Allier River: Use of mercury lights to increase the efficiency of a fish bypass structure. *Bulletin Francais de la Peche et de la Pisciculture*, **323**, 129-148.

Larinier, M. and Travade, F. **2002**. Downstream migration: Problems and facilities. *Bulletin Francais de la Peche et de la Pisciculture*, **364**(s), 181-207.

Larinier, M. and Marmulla, G. **2004**. Fish Passes: Types, Principles and Geographical Distribution – An Overview. *In*: Welcomme, R., Petr, T. (Eds.), Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries Volume II. FAO Regional Office for Asia and the Pacific, Bangkok, Thailand. RAP Publication 2004/17, pp. 1-14.

Larinier, M., Chanseau, M., Bau, F. and Croze, O. **2005**. The use of radio telemetry for optimizing fish pass design. 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. 53-60.

Larsen, L. O. **1980**. Physiology of adult lampreys, with special reference to natural starvation, reproduction and death after spawning. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 1762-1779.

Lee, C.G., Farrell, A.P., Lotto, A., MacNutt, M.J., Hinch, S.G. and Healey, M.C. **2003**. The effect of temperature on swimming performance and oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. *Journal of Experimental Biology*, **206**, 3239-3251.

Legault, A. **1988**. Le franchissement des barrages par l'escalade de l'anguille; étude en Sèvre Niortais. *Bulletin Français de la Pêche et de la Pisciculture,* **308**, 1-10.

Legault, A. **1992**. Study of some selectivity factors in eel ladders. *Bulletin Français de la Pêche et de la Pisciculture*, **325**, 83-91.

Legendre, F., Marting, P.R. and Cocroft, R.B. **2012**. Competitive masking of vibrational signals during mate searching in a treehopper. *Animal Behaviour*, **83**, 361-368.

Liao, J.C. **2004**. Neuromuscular control of trout swimming in a vortex street: implications for energy economy during the Kármán gait. *Journal of Experimental Biology*, **207**(20), 3495-3506.

Liao, J.C. **2006**. The role of the lateral line and vision on body kinematics and hydrodynamic preference of rainbow trout in turbulent flow. *Journal of Experimental Biology*, **209**, 4077-4090.

Liao, J.C. **2007**. A review of fish swimming mechanics and behavior in altered flows. *Philosophical Transactions of the Royal Society B,* **362**, 1973-1993.

Liao, J.C., Beal, D.N., Lauder, G.V. and Triantafyllou, M.S. **2003a**. Fish exploiting vortices decrease muscle activity. *Science*, **302**, 1566-1569.

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

Lieschke, G.J. and Currie, P.D. **2007**. Animal models of human disease: zebrafish swim into view. *Nature Reviews Genetics*, **8**, 253-267.

Lima, S.L. and Bednekoff, P.A., **1999**. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *The American Naturalist*, **153**, 649-659.

Liu, Y., Olaussen, J.O. and Skonhoft, A. **2001**. Wild and farmed salmon in Norway - A review. *Marine policy*, **35**, 413-418.

Loge, F.J., Arkoosh, M.R., Ginn, T.R., Johnson, L.L. and Collier, T.K. **2005**. Impact of environmental stressors on the dynamics of disease transmission. *Environmental Science and Technology,* **39**(18), 7329-7336.

Lohr, B., Wright, T.F. and Dooling, R.J. **2003**. Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal. *Animal Behaviour*, **65**, 763-777.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D. and Wardle D.A. **2001**. Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science*, **294**, 804-808.

Loring, P.A. and Gerlach, C. **2010**. Food security and conservation of Yukon River Salmon: Are we asking too much of the Yukon River? *Sustainability*, **2**, 2965-2987.

Lopes, C.M., Almedia, F.S., Orsi, M.L., Britto, S.G.C., Sirol, R.N. and Sodre, L.M.K. **2007**. Fish passage ladders from Canoas Complex. Parapanema River evaluation of genetic structure maintenance of *Salminus brasiliensis* (Teleostei: Characiformes). *Neotropical Ichthyology,* **5**, 131-136.

Louhi, L., Mäki-Petäys, A. and Erkinaro, J. **2008**. Spawning habitat of Atlantic salmon and brown trout: General criteria and intragravel factors. *River Research and Applications*, **24**, 330-339.

Lucas, M.C., and 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., Mercer, T., Armstrong, J.D., McGinty, S. and Rycroft, P. **1999**. Use of a flat-bed passive integrated transponder antenna array to study the migration and behaviour of lowland river fishes at a fish pass. *Fisheries Research*, **44**, 183-191.

Lucas, M.C. and Baras, E. **2001**. Migration of Freshwater Fishes. Blackwell Science Ltd. Oxford. pp. 440.

Lucas, M.C., Bubb, D.H., Jang, M., Ha, K. and 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.

Lupandin, A.I. **2005**. Effect of flow turbulence on swimming speed of fish. *Biological Bulletin*, **32**(5), 461-466.

Lupandin, A.I. and Pavlov, D.S. **1996**. Effect of starvation on fish attitude to flows with different turbulence. *Journal of Ichthyology*, **36**(3), 416-419.

Lymer, D., Funge-Smith, S., Khemakorn, P., Naruepon, S. and Ubolratana, S. **2008**. A review and synthesis of capture fisheries data in Thailand. Large versus small-scale fisheries. RAP publication 2008/17. pp. 50.

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

Maitland, P.S. and Campbell, R.N. **1992.** Freshwater Fishes. Harper and Collins, London. pp. 368.

Mäki-Petäys, A., Muotka, T., Huusko, A., Tikkanen, P. and Kreivi, P. **1997**. Seasonal changes in habitat use and preference by juvenile brown trout, *Salmo trutta*, in a northern boreal river. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 520-530.

Mallen-Cooper, M. **1999**. Developing fishways for nonsalmonid fishes: a case study from the Murray River in Australia. In: M. Odeh (ed.) Innovations in Fish Passage Technology. Bethesda, MD: American Fisheries Society, 173–195.

Mallen-Cooper, M. and Brand, D.A. **2007**. Non-salmonids in a salmonid fishway: what do 50 years of data tell us about past and future fish passage? *Fisheries Management and Ecology*, **14**, 319-332.

Malmqvist, B. **1980**. The spawning migration of the brook lamprey, *Lampetra planeri* Bloch, in a South Swedish stream. *Journal of Fish Biology*, **16**(1), 105-114.

Marine Scotland, 2013. Sea trout fishery statistics – season 2012. Topic sheet No. 69, V4. <http://www.scotland.gov.uk/Publications/2013/09/5157/downloads>. Accessed on 5th November 2014.

Matzinger, A., Pieters, R., Ashley, K.I., Lawrence, G.A., Wüest, A. **2007**. Effects of impoundment on nutrient availability and productivity in lakes. *Limnology and Oceanography,* **52** (6), 2629-2640.

Mawle, G.W. and Peirson, G. **2009**. Economic evaluation of inland fisheries. Environment Agency managers report, SC050026/SR2. pp. 58.

Maynard Smith, J. **1978**. Optimization Theory in Evolution. *Anuual Review of Ecology and Systematics*, **9**, 31-56.

Mazur, M.M. and Beauchamp, D.A. **2006**. Linking piscivory to spatial–temporal distributions of pelagic prey fishes with a visual foraging model. *Journal of Fish Biology*, **69**, 151-175.

McElroy, B., DeLonay, A. and Jacobson, R. **2012**. Optimum swimming pathways of fish spawning migrations in rivers. *Ecology*, **93**(1), 29-34.

McGrath, K.J., Desrochers, D., Fleury, C. and Dembeck IV, J.M. **2003**. Studies of upstream migrant American eels at the Moses-Saunders Power Dam on the St. Lawrence River near Massena, New York. Pages 153-168. In D.A. Dixon (ed). Biology, management, and Protection of Catadromous Eels. American Fisheries Society Symposium 33, Bethesda, Maryland. pp.308.

McMahon, T.E. and Hartman, G.F. **1989**. Inlfuence of cover complexity and current velocity on winter habitat use by juvenile Coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1551-1557.

McNamara, J. M., Trimmer, P.C. and Houston. A.I. **2014**. Natural selection can favour 'irrational' behaviour. *Biology Letters*, **10**, 20130935.

Mech, S.G. and Hallet, J.G. **2001**. Evaluating the effectiveness of corridors: A genetic approach. *Conservation Biology*, **15**, 467-474.

Mesa, M.G., Bayer, J.M. and 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.

Mohsen, S.M. and LaRue, J.C. **1990**. The decay law in grid-generated turbulence. *Journal of fluid mechanics*, **219**, 195-214.

Montgomery, D., Carton, G., Voigt, R., Bake, C. and Diebel, C. **2000**. Sensory processing of water currents by fishes. *Philosophical Transactions of the Royal Society B*, **355**, 1325-1327.

Montgomery, D.R. **2003**. King of fish. The thousand-year run of salmon. Westview Press, Cambridge. pp 304.

Moore, J.W. **2006**. Animal Ecosystem Engineers in Streams. *BioScience*, **56**(3), 237-246.

Moorcroft, P.R. **2012**. Mechanistic approaches to understanding and predicting mammalian space use: recent advances, future directions. *Journal of Mammalogy*, **93**(4), 903-916.

Moriarty, C. **1986**. Riverine migration of young eels *Anguilla anguilla* (L.). *Fisheries Reseacrh,* **4**, 43-58.

Moriarty, C. **1990**. European catches of elver of 1928-1988. *International Review of Hydrobiology,* **75**(6), 701-706.

Moriarty, C. and Tesch, F.-W. **1996**. Possible increase in catch of Atlantic elver *Anguilla anguilla* in 1993 and 1994. *Ecology of Freshwater Fish*, **5**, 213-215.

Morita, K. and Yamamoto, S. **2002**. Effects of habitat fragmentation by damming on the persistence of stream-dwelling charr populations. *Conservation Biology,* **5**, 1318-1323.

Moser M.L., Ocker, P.A., Stuehrenberg, L.C. and Bjornn, T.C. **2002**. 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., Keefer, M.L., Pennington, H.T., Ogden, D.A. and Simonson, J.E. **2011**. Development of Pacific lamprey fishways at a hydropower dam. *Fisheries Management and Ecology,* **18**, 190-200.

Moyle, P.B., Katz, J.V.E. and Quiñones, R.M. 2011. Rapid decline of California's native inland fishes: A status assessment. *Biological Conservation*, **144**, 2414-2423.

Mueller, R.P., Neitzel, D.A., Mavros, W.V. and Carlson, T.J. **1998**. Evaluation of low and high frequency sound for enhancing the capacity of fish screening facilities to protect outmigrating salmonids. Contract Number DE-A179-86BP62611, Bonneville Power Administration, Portland, Oregon. pp. 36.

Mueller, R.P., Southard, S.S., May, C.W., Pearson, W.H. and Cullinan, V.I. **2008**. Juvenile coho salmon leaping ability and behavior in an experimental culvert test bed. *Transactions of the American Fisheries Society*, **137**(4), 941-950.

Muller, U.K., Smit, J., Stamhuis, E.J. and Videler, J.J. **2001**. How the body contributes to wake in undulatory fish swimming: Flow fields of swimming eel (*Anguilla anguilla*). *Journal of Experimental Biology,* **204**, 2751-2762.

Muir, W.D., Marsh, D.M., Sandford, B.P., Smith, S.G. and Williams , J.G. **2006**. Post-hydropower system delayed mortality of transported Snake River stream-type chinook salmon: Unraveling the mystery. *Transactions of the American Fisheries Society*, **135**(6), 1523-1534.

Nalpanis, P., Hunt, C.R.J. and Barret, C.F. **1993**. Saltating particles over flat beds. *Journal of Fluid Mechanis*, **251**, 661-685.

National River Flow Archive. <www.ceh.ac.uk/data/nrfa>. Accessed on 29 May 2015.

Naughton, G.P., Caudill, C.C., Keefer, M.L., Bjornn, T.C., Stuehrenberg, L.C. and 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.

Navarro, J.E., McCauley, D.J. and Blystra, A.R. **1996**. Turbine passage at four low-head hydroelectric facilities in northeast Michigan. *North American Journal of Fisheries Management*, **16**, 182-191.

Nelson, M.L., McMahonald, T.E. and Thurow, R.F. **2002**. Decline of the migratory form in bull charr, *Salvelinus confluentus*, and implications for conservation. *Environmental Biology of Fishes,* **64**, 321-332.

Newbold, L.R., Hockley, F.A., Williams, C.F., Cable, J., Reading, A.J., Auchterlonie, N. and Kemp, P.S. **2015**. Relationship between European eel *Anguilla anguilla* infection with non-native parasites and swimming behaviour on encountering accelerating flow. *Journal of Fish Biology*, **86**, 1519-1533.

Newby, N.C., Binder, T.R. and Stevens, E.D. **2007**. Passive integrated transponder (PIT) tagging did not negatively affect the short-term feeding behaviour or swimming performance of juvenile rainbow trout. *Transactions of the American Fisheries Society*, **136**, 341-345.

Nielsen, C., Aarestrup, K., Nørum, U. and Madson, S.S. **2003**. Pre-migratory differentiation of wild brown trout into migrant and resident individuals. *Journal of Fish Biology*, **63**, 1184-1196.

Nikora, V.I. and Goring, D.G. **1998**. ADV measurements of turbulence: Can we improve their interpretation? *Journal of Hydraulic Engineering*, **124**, 630-634.

Nilsson, C., Reidy, C.A., Dynesius, M. and Revenga, C. **2005**. Fragmentation and flow regulation of the world's large river systems. *Science*, **308**, 405-408.

Noonan, M.J., Grant, J.W.A. and Jackson, C.D. **2012**. A quantitative assessment of fish passage efficiency. *Fish and Fisheries,* **13**, 450-464.

Northcote, T.G. **1998**. Migratory behaviour of fish and its significance to movement through riverine fish passage facilities. In: M. Jungwirth, S. Schmutz & S. Weiss (eds), Fish Migration and Fish Bypasses. Oxford: Fishing News Books. Blackwell Science Publications, pp. 3-18.

Norton, W. and Bally-Cuif, N. **2010**. Adult zebrafish as a model organism for behavioral genetics. *BMC Neuroscience*, **11**, 90.

Odeh, M. **1999**. Innovations in Fish Passage Technology. American Fisheries Society, Bethesda, MA. pp. 212.

Oldani, N.O. and Baigún, C.R.M. **2002**. Performance of a fishway system in a major South American dam on the Parana River (Argentina-Paraguay). *River Research and Applications*, **18**, 171-183.

Ojutkangas, E., Aronen, K. and Laukkanen, E. **1995**. Distribution and abundance of River lamprey (*Lampetra fluviatilis*) ammocoetes in the regulated River Perhonjoki. *Regulated Rivers: Research and Management,* **10**, 239-245.

Palmer, M.A., Menninger, H.L. and Bernhardt, E. **2010**. River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? *Freshwater Biology*, **55**(S1), 205–222.

Parker, G.A. and Maynard Smith, J. **1990**. Optimality theory in evolutionary biology. *Nature*, **438**, 27-33.

Parsley, M.J., Wright, C.D., van der Leeuw, B.K., Kofoot, E.E., Peery, C.A. and Moser, M.L. **2007**. White sturgeon (*Acipenser transmontanus*) passage at the Dalles dam, Columbia River, USA. *Journal of Applied Ichthyology,* **23**, 627-635.

Parkyn, D.C. and Hawryshyn, C.W. **2000**. Spectral and ultraviolet-polarisation sensitivity in juvenile salmonids: A comparative analysis using electrophysiology. *The Journal of Experimental Biology*, **203**, 1173-1191.

Paulk, A.C., Stacey, J.A., Pearson, T.W.J., Taylor, G.J., Moore, R.J.D., Srinivasan, M.V. and van Swinderen, B. **2014**. Selective attention in the honeybee optic lobes precedes behavioral choices. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 5006-5011.

Pavlov, D.S., Skorobogatov, M.A. and Shtaf, L.G. **1982**. Effect of turbulence degree on the critical flow rate for fishes. *Doklady Akademii Nauk SSSR*, **267**(4), 1019-1021.

Pavlov, D.S. and Lupandin, A.I. **1994**. Reactions of fish to streams with different intensities of turbulence. *Doklady Biological Sciences,* **339**, 595-597.

Pavlov, D.S., Lupandin, A.I. and Skorobogatov, M.A. **1994**. Influence of flow turbulence on critical flow velocity for gudgeon (*Gobio gobio*). *Doklady Biological Sciences*, **336**, 215-217.

Pavlov, D.S., Lupandin, A.I. and Skorobogatov, M.A. **2000**. The effects of flow turbulence on the behaviour and distribution of fish. *Journal of Ichthyology*, **40**(2), S232-S261.

Pavlov, D.S. and Tjurjukov, S.N. **2005**. Reactions of dace to linear accelerations. *Journal of Fish Biology*, **46**, 768-774.

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

Pederson, L-F., Koed, A. and 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.

Pelicice, F.M. and Agostinho, A.A. **2008**. Fish-passage facilities as ecological traps in large neotropical rivers. *Conservation Biology*, **22**(1), 180-188.

Pess, G.R., McHenry, M.L., Beechie, T.J. and Davies, J. **2008**. Biological impacts of the Elwha River dams and potential salmonid responses to dam removal. *Northwest Scientific Association,* **82** (s1), 72-90.

Petts, G.E. **1980**. Long-term consequences of upstream impoundment. *Environmental Conservation,* **7** (4), 325-332.

Piper, A.T., Wright, R.M. and Kemp, P.S. **2012**. The influence of attraction flow on upstream passage of European eel (*Anguilla anguilla*) at intertidal barriers. *Ecological Engineering,* **44**, 329-336.

Piper, A.T., Manes, C., Siniscalchi, F., Marion, A., Wright, R.M. and Kemp, P.S. **2015**.Response of seaward-migrating European eel (*Anguilla anguilla*) to manipulated flow fields. *Proceedings of the Royal Society B*, **282**, 20151098.

Pompeu, P.S., Agostinho, A.A. and Pelicice, F.M. **2012**. Existing and future challenges: The concept of successful fish passage in South America. *River Research and Applications*, **28**, 504-512.

Pope, S.B. **2000**. Turbulent flows. Cambridge University Press, Cambridge. pp. 773.

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

Porto, L.M., McLaughlin, R.L. and Noakes, D.L.G. **1999**. Low-head barrier dams restrict the movements of fishes in two lake Ontario streams. *North American Journal of Fisheries Management*, **19**(4), 1028-1036.

Poudevigne, I., Alard, A.D., Leuvenb A.R.S.E.W. and Nienhuisb, P.H. **2002**. A systems approach to river restoration: A case study in the lower Seine Valley, France. *River Research and Applications*, **18**, 239-247.

Przybilla, A., Kunze, S., Rudert, A., Bleckmann, H. and Brücker, C. **2010**. Entraining in trout: a behavioural and hydrodynamic analysis. *Journal of Experimental Biology*, **213**, 2987-2996.

Qiwei, W. **2010**. *Psephurus gladius*. The IUCN Red List of Threatened Species. Version 2014.2. <www.iucnredlist.org>. Accessed on 19 August 2014.

Qiwei, W. Fu'en, K., Jueming, Z., Ping, Z., Junde, L., Rueqiong, Z. and Wenhua, Y. **1997**. Biology, fisheries, and conservation of sturgeons and paddlefish in China. *Environmental Biology of Fishes*, **48**, 241-255.

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

Quintella, B.R., Andrade, N.O., Koed, A. and 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.

Raupach, M.R., Antonia, R.A. and Rajagopalan, S. **2009**. Rough-wall turbulent boundary Layers. *Applied Mechanics Review*, **44**, 1-25.

Raymond, H.L. **1979**. Effects of Dams and Impoundments on Migrations of Juvenile Chinook Salmon and Steelhead from the Snake River, 1966 to 1975. *Transactions of the American Fisheries Society*, **108**(6), 505-529.

Reeves, P. **2003**. The cultural significance of fish in India: First steps in coming to terms with the contradictory positions of some key materials. ARI, Working Paper Series, No. 5. pp. 18.

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

Rice, S.P., Lancaster, J. and 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.

Rieman, B.E., Beamesderfer, R.C., Vigg, S. and Poe, T.P. **1991**. Estimated Loss of Juvenile Salmonids to Predation by Northern Squawfish, Walleyes, and Smallmouth Bass in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Scoiety,* **120**(4), 448-458.

Robinet, T., Guyet, S., Marquet, G., Mounaix, B., Olivier, J-M., Tsukamotot, K., Valade, P. and Feunteun, E. **2003**. Elver invasion, population structure and growth of marbled eels *Anguilla marmorata* in a tropical river on Réunion Island in the Indian Ocean. *Environmental Biology of Fishes,* **68**, 339-348.

Rodríguez, T.T., Agudo, J.P., Mosquera, L.P. and González, E.P. **2006**. Evaluating vertical-slot fishway designs in terms of fish swimming capabilities. *Ecological Engineering*, **27**, 37-48.

Roscoe, D.W. and Hinch, S.G. **2010**. Effectiveness monitoring of fish passage facilities: historical trends, geographic patterns and future directions. *Fish and Fisheries*, **11**, 12-33.

Roy, A.G., Biron, P.M., Buffin-Bélanger, T. and Levsseur, M. **1999**. Combined visual and quantitative techniques in the study of natural turbulent flows. *Water Resources Research*, **35**(3), 871-877.

Ruban, G. and Qiwei, W. **2010**. *Acipenser schrenckii*. The IUCN Red List of Threatened Species. Version 2015.2. <www.iucnredlist.org>. Accessed on 21 July 2015.

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.

Russon, I.J. and Kemp, P.S. **2011a**. Advancing provision of multi-species fish passage: behaviour of adult European eel (*Anguilla anguilla*) and brown trout (*Salmo trutta*) in response to accelerating flow. *Ecological Engineering*, **37**, 2018-2024.

Russon, I.J. and Kemp, P.S. **2011b**. Experimental quantification of the swimming performance and behaviour of spawning run river lamprey *Lampetra fluviatilis* and European eel *Anguilla anguilla. Journal of Fish Biology*, **78**, 1965-1975.

Russon, I.J., Kemp, P.S. and Lucas, M.C. **2011**. Gauging weirs impede the upstream migration of adult river lamprey *Lampetra fluviatilis*. *Fisheries Management and Ecology*, **18**, 201-210.

Sand, O. and Karlsen, H.E. **2000**. Detection of infrasound and linear acceleration in fishes. *Philosophical Transactions of the Royal Society B*, **355**, 1295-1298.

Sand, O., Enger, P.S., Karlsen, H.E. and Knudsen, F.R. **2001**. Detection of infrasound in fish and behavioural responses to intense infrasound in juvenile salmonids and European silver eels: A minireview. *American Fisheries Society Sympossium*, **26**, 183-193.

Santos, J.M., Ferreira, M.T., Godinho, F.N. and Bochechas, J. **2005**. Efficacy of a nature-like bypass channel in a Portuguese lowland river. *Journal of Applied Ichthyology*, **21**, 381-388.

Santos, J.M., Ferreira, M.T., Pinheiro, A.N. and Bochechas, J.H. **2006**. Effects of small hydropower plants on fish assemblages in medium-sized streams in central and northern Portugal. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **16**, 373-388.

Schill, D.J. and Elle, F.S. **2000**. Healing of electroshock-induced haemorrhages in hatchery rainbow trout. *North American Journal of Fisheries Management*, **20**(3), 730-736.

Schmidt, R.E., O'Reilly, C.M. and Miller, D. **2009**. Observations of American eels using an upland passage facility and effects of passage on the population structure. *North American Journal of Fisheries Management*, **29**(3), 715-720.

Shuler, S.W, Nehring, R.B. and Fausch, K.D. **1994**. Diel habitat selection by brown trout in the Rio Grande River, Colorado, after placement of boulder structures. *North American Journal of Fisheries Management,* **14**, 99-111.

Schultz, W.W. and Webb, P.W. **2002**. Power requirements of swimming: Do new methods resolve old questions? *Integrative and Comparative Biology*, **42**, 1018-1025.

Schwalme, K., Mackey, W.C. and 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., Porter, T.R. and Clarke, K.D. **2007**. Assessment of a retrofitted downstream fish bypass system for wild Atlantic salmon (*Salmo salar*) smolts and kelts at a hydroelectric facility on the Exploits River, Newfoundland, Canada. *Hydrobiologia*, **582**, 155-169.

Servais, S.A. **2006**. Physical modelling of low-cost modications 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. pp. 371.

Sfakiotakis, M., Lane, D.M. and Davies, B.C. **1999**. Review of fish swimming modes for aquatic locomotion. *IEEE Journal of Oceanic Engineering,* **24**(2), 237-252.

Shtaf, L.G., Pavlov, D.S., Skorobogatov, M.A. and Barekyan, A.S. **1983**. The influence of flow turbulence on fish behaviour. *Journal of Ichthyology*, **23**, 307-317.

Shuman, J.R. **1995**. Environmental considerations for assessing dam removal alternatives for river restoration. *Regulated Rivers: Research and Management*, **11**, 249-261.

Silva, A.T., Santos, J.M., Franco, A.C., Ferreira, M.T. and Pinheiro, A.N. **2009**. Selection of Iberian barbel *Barbus bocagei* (Steindachner, 1864) for orifices and notches upon different hydraulic configurations in an experimental pool-type fishway. *Journal of Applied Ichthyology*, **25**, 173-177.

Silva, A.T., Santos, J.M., Ferreira, M.T., Pinheiro, A.N. and Katopodis, C. **2011**. Effects of water velocity and turbulence on the behaviour of Iberian barbell (*Luciobarbus bocagei*, Steindachner 1864) in an experimental pool-type fishway. *River Research and Applications*, **27**, 360-373.

Silva, A.T., Katopodis, C., Santos, J.M., Ferreira, M.T. and Pinheiro, A.N. **2012a**.Cyprinid swimming behaviour in response to turbulent flow. *Ecological Engineering*, **44**, 314-328.

Silva, A.T., Santos, J.M., Ferreira, M.T., Pinheiro, A.N. and Katopodis, C. **2012b**. Passage efficiency of offset and straight orifices for upstream movemments of Iberian barbell in a pool-type fishway. *River Research and Applications*, **28**, 529-542.

Singer, J.D. and Willet, J.B. **2003**. Applied longitudinal data analysis: Modelling change and event occurrence. Oxford University Press, New York, pp. 672.

Skorobogatov, M.A, Pavlov and Lupandin, A.I. **1996**. Effects of current velocity and turbulence intensity on the distribution of the Roach *Rutilus rutilus* in a water stream. *Journal of Ichthyology*, **36**(8), 654-658. Translated from *Voprosy Ikhtiologii*, **36**(5), 687-692.

Slatick, E. and Basham, L.R. **1985**. The effect of Denil fishway length on passage of some nonsalmonid fishes. *Marine Fisheries Review,* **47**(1), 83-85.

Smith, D.L., Brannon, E.L. and Odeh, M. **2005**. Response of juvenile rainbow trout to turbulence produced by prismatoidal shapes. *Transactions of the American Fisheries Society*, **134**, 741-753.

Smith, D.L., Brannon, E.L., Shafii, B. and Odeh, M. **2006**. Use of the average and fluctuating velocity components for estimation of volitional rainbow trout density. *Transactions of the American Fisheries Society,* **135**, 431-441.

Sokal, R.R. and Rohlf, F.J. **1995**. Biometry: The priciples and practices of statistics in biological research, 3rd edition. W. H. Freeman and Co, New York, pp. 880.

Solomon, D. J. and Beach, M. H. **2004**. Fish pass design for eel and elver *(Anguilla anguilla*). R&D Technical Report W2-070/TR1. Environment Agency, Bristol, pp. 92.

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.

Stanislaw, H. and Todorov, N. **1999**. Calculation of signal detection theory measures. *Behaviour Research Methods, Instruments, and Computers,* **31**(1), 137-149.

Stokesbury, K.D. and Dadswell, M.J. **1991**. Mortality of juvenile clupeids during passage through a tidal, low-head hydroelectric turbine at Annapolis Royal, Nova Scotia. *North American Journal of Fisheries Management*, **11**, 149-154.

Stuart, I.G. and Mallen-Cooper, M. **1999**. An assessment of the effectiveness of a vertical-slot fishway for non-salmonid fish at a tidal barrier on a large tropical/subtropical river. *Regulated Rivers: Research and Management*, **15**, 575-590.

Stuart, I.G. and Berghuis, A.P. **2002**. Upstream passage of fish through a vertical-slot fishway in an Australian subtropical river. *Fisheries Management and Ecology*, **9**, 111-122.

Sumer, M. and Fredsøe, J. **1997**. Hydrodynamics around cylindrical structures. Advancing Series on Ocean Engineering, Volume 12. *World Scientific*. pp. 535.

SWIMIT Model v.3.3. Environment Agency. Excel spreadsheet for predicting swim speeds. Based on data from Clough and Turnpenny (2001) and Clough *et al.* (2004).

Taguchi, M. and Liao, J.C. **2011**. Rainbow trout consume less oxygen in turbulence: the energetics of swimming behaviours at different speeds. *The Journal of Experimental Biology*, **214**, 1428-1436.

Tanner, W.P. and Swets, J.A. **1954**. A decision-making theory of visual detection. *Psychological Review*, **61**, 401-409.

Tayler, J.A. and Gilliam, J.F. **1995**. Ideal free distributions of stream fish: a model and test with minnows, *Rhinicthys atratulus. Ecology,* **76**(2), 580-592.

Taylor, G.I. **1938**. The spectrum of turbulence. *Proceedings of the Royal Society of London*, **164**, 476-490.

Taylor, R.E. and Kynard, B. **1985.** Mortality of juvenile American shad and blueback herring passed through a low-head Kaplan turbine*. Transactions of the American Fisheries Society*, **114**, 430-435.

Tesch, F.-W. **2003**. The eel. Fifth edition, Blackwell publishing, Oxford. pp. 408.

Thiem, J.D., Binder, T.R., Dumont, P., hatin, D., Hatry, C., Katopodis, C., Stamplecoskie K.M. and Cooke, S.J. **2013**. Multispecies fish passage behaviour in a vertical slot fishway on the Richelieu River, Quebec, Canada. *River Research and Applications*. **29**, 582-592.

Travade, F. and Larinier, M. **2002**. Fish locks and fish lifts. *Bulletin Français de la Pêche et de la Pisciculture,* **364**(S), 102-118.

Tritico, H.M., Cotel, A.J. and Clarke, J.N. **1997**. Development, testing and demonstration of a portable submersible miniature particle imaging velocimetry device. *Measurement Science and Technology*, **18**, 1555-1562.

Tritico, H.M. and Cotel, A.J. **2010**. The effects of turbulent eddies on the stability and critical swimming speed of creek chub (*Semotilus atromaculatus). The Journal of Experimental Biology,* **213**, 2284-2293.

Tudorache, C., Viaenen, P., Blust, R. and 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. and De Boaeck, 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. and O'Keeffe, N. **2005**. Screening for intake and outfalls: a best practice guide. Environment Agency Science Report SC030231. pp. 154.

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

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

Verdon, R., Desrochers, D. and Dumont, P. **2003**. Recruitment of American eels in the Richelieu River and Lake Champlain: provision of upstream passage as a regional-scale solution to a large-scale problem. Pages 125-138. In: D.A. Dixon (editor). *Biology, Management, and Protection of Catadromous Eels*. American Fisheries Symposium Series **33**, Bethesda, Maryland.

Vogel, S. **1996**. Life in moving fluids: The physical biology of flow. Princeton University Press, New Jersey. pp. 469.

Vøllestad, L.A. and Jonsson, B. **1988**. A 13-year study of the population dynamics and growth of the European eel *Anguilla anguilla* in a Norwegian river: Evidence for density-dependent mortality, and development of a model for predicting yield. *Journal of Animal Ecology,* **57**, 983-997.

Voulgaris, G. and Trowbridge, J.H. **1998**. Evaluation of the Acoustic Doppler Velocimeter (ADV) for turbulence measurements. *Journal of Atmospheric and Oceanic Technology*, **15**, 272-289.

Vowles, A.S. and Kemp, P.S. **2012**. Effects of light on the behaviour of brown trout (*Salmo trutta*) encountering accelerating flow: application to downstream fish passage. *Ecological Engineering*, **47**, 247-253.

Vowles, A.S., Eakins, L.R., Piper, A.T., Kerr, J.R. and Kemp, P.S. **2013**. Developing realistic fish passage criteria: An integrated approach. In: Maddock, I., Harby, A., Kemp, P. and Wood, P (eds.), Ecohydraulics: An Integrated Approach, John Wiley & Sons Ltd., pp. 464.

Vowles, A.S., Anderson, J.J., Gessel, M.H., Williams, J.G. and Kemp, P.S. **2014**. Effects of avoidance behaviour on downstream fish passage through areas of accelerating flow when light and dark. *Animal Behaviour*, **92**, 101-109.

Wang, R.W. and Hartlieb, A. **2011**. Experimental and field approach to the hydraulics of nature-like pool-type fish migration facilities. *Knowledge and Management of Aquatic Ecosystems*, **400**, 05.

Webb, P.W. **1975**. Hydrodynamics and energetics of fish propulsion. *Bulletin of the Fisheries Research Board of Canada*, **190**, 1-159.

Webb, P.W. **1998**. Entrainment by river chub *Nocomis micropogon* and smallmouth bass *Micropterus dolomieu* on cylinders. *The Journal of Experimental Biology*, **201**, 2403-2412.

Webb, P.W. **2006**. Stability and manoeuvrability. In: Shadwick, R. and Lauder, G. (eds). Fish physiology: Fish biomechanics. Elsevier Academic Press, London. pp. 281-332.

Webb, P.W. and Cotel, A.J. **2010**. Turbulence: Does vorticity affect the structure and shape of body and fin propulsors. *Integrative and Comparative Biology*, **50**, 1155-1166.

Weihs, D. **1974**. Energetic advantages of burst swimming of fish. *Journal of Theoretical Biology*, **48**, 215-229.

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

Weyand, M., Redeker, M. and 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**(9), 77-84.

White, W.R., Iredale, R. and Armstrong, G. **2006**. Fishpasses at flow measurement structures. *Water Management*, **159**(3), 165-171.

Wickens, T.D. **2002**. Elementary Signal Detection Theory. Oxford University Press, New York. pp. 288.

Williams, J.G., Armstrong, G., Katopodis, C., Larinier, M. and Travade, F. **2012**. Thinking like a fish: a key ingredient for development of effective fish passage facilities at river obstructions. *River research and Applications*, **28**, 407–417.

Wilson, S.K., Fisher, R., Patchett, M.S., Graham, N.A.J., Dulvey, N.K., Turner, R.A., Cakacaka, A., Polunin, N.V.C. and Rushton, S.P. **2008**. Exploitation and habitat degradation as agents of change within coral reef fish communities. *Global Change Biology*, **14**, 2796-2809.

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

Winter, H.V., Jansen, H.M. and 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.

Wollerman, L. and Wiley, R. **2002**. Background noise from a natural chorus alters female discrimination of male calls in a Neotropical frog. *Animal Behaviour*, **63**, 15-22.

Woo, K.L., Burke, D. and Peters, R.A. **2009**. Motion sensitivity of the Jacky dragon, *Amphibolurus muricatus*: random-dot kinematograms reveal the importance of motion noise for signal detection. *Animal Behaviour*, **77**, 307-315.

Wood, J.L.A., Grant, J.W.A. and Belanger, M.H. **2010**. Population density and territory size in juvenile rainbow trout, *Oncorhynchus mykiss*: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Science,* **69**, 1121-1128.

World Commission on Dams, **2000**. Dams and development. A new framework the report of the world commission on dams for decision-making. Earthscan Publications Ltd., London, UK. pp. 404.

World Energy Council. **2013**. Word energy resources: 2013 Survey. World Energy Council, England and Wales. pp. 468.

Wu, C. and Elias, D. **2014**. Vibratory noise in anthropogenic habitats and its effect on prey detection in a web-building spider. *Animal Behaviour*, **90**, 47-56.

Xie, P. **2003**. Three-Gorges Dam: Risk to ancient fish. Science, **302**, 1149-1149.

Xu, K. and Milliman, J.D. **2009**. Seasonal variations of sediment discharge from the Yangtze River before and after impoundment of the Three Gorges Dam. *Geomorphology,* **104**, 276-283.

Yoshiyama, R.M., Fisher, F.W. and 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**(3), 487-521.

Yan, H.Y. and Popper, A.N. **1992**. Auditory sensitivity of the cichlid fish *Astronotus ocellatus* (Cuvier). *Journal of Comparative Physiology A*, **171**, 105-109.

Zhang, H.J. and Zhou, Y. **2001**. Effect of unequal cylinder spacing on vortex streets behind three side-by-side cylinders. *Physics of fluids*, **13**(12), 3675-3686.