The Hydrodynamics of River Ecosystems: Towards an Objective and Ecologically Relevant Classification of Mesohabitats

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To Geoffrey Arthur Wilkes, 'Gramps', for showing me the beauty of the natural world and the creative spirit required to capture it.

Abstract

This thesis brings together three recent trends in river research, namely the mesohabitat concept, the hydrodynamics of river ecosystems and the development of bioenergetic models, in order to drive progress in key river management applications. These applications include river habitat assessment, modelling and rehabilitation and the conservation of key biota. The identification of mesohabitats, defined as mesoscale (10^0-10^2 m) units of instream habitat (*e.g.* pool, run, glide, riffle), has become central to many river research and management activities due to its practicality and efficiency, yet the ecological and theoretical bases for mapping and classifying them are currently weak. Evidence on the ecological relevance and physical distinctiveness of mesohabitats is uncertain. The application of community-level modelling and the measurement of turbulence within mesohabitats are identified as means to strengthen these bases.

The use of community-level analysis showed that fish assemblages were structured at the mesoscale, strengthening the ecological basis for the mesohabitat concept. Turbulence is a ubiquitous phenomenon in river ecosystems and, as morphologically distinctive units of habitat, mesohabitats are expected to exhibit contrasting hydrodynamic characteristics. This is due to the relationships between turbulent flow structure and river morphology (*i.e.* morpho-hydrodynamic relationships) at different scales. Using classification trees it was shown that mesohabitats could be identified objectively using a set of hydrodynamic variables describing the intensity, periodicity, orientation and scale of turbulent flow in a model that sees pools as relatively quiescent habitats with a simple flow structure and riffles as highly turbulent with complex flow composed of eddies of different sizes. Two other mesohabitats common to lowland rivers, glides and runs, complete the gradient between these two extremes. Though this hydrodynamic classification was able to explain up to 82.9% of variation between mesohabitats, its ecological relevance remained to be tested. Evidence on the strength and direction of the relationship between turbulence and aquatic biota, for example, is equivocal even for a relatively well-researched species, Atlantic salmon (*Salmo salar*). By observing the position choice of Atlantic salmon parr in relation to turbulence in an artificial habitat, it was shown that a negative relationship between turbulence and habitat selection exists for this species and life-stage due to the energetic costs of swimming in turbulent flow. The findings have the potential to improve approaches to river habitat assessment, modelling, rehabilitation and conservation by providing an objective means of classifying mesohabitats within an ecologically relevant framework.

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Glossary of mathematical terms

Symbol	Description
h	Flow depth
y	Height above bed datum
A	Cross-sectional area of flow
P	Wetted perimeter
R	Hydraulic radius = A/P
S	Longitudinal bed slope
ρ	Fluid density of water
g	Acceleration due to gravity
k	Height of surface roughness elements
v	Kinematic viscosity
U	Mean streamwise velocity
Fr	Froude number $= U/\sqrt{gh}$
Re	Bulk flow Reynolds number $= Uh/v$
τ	Shear stress (section- or reach-averaged) = $pgRS$
U_*	Shear velocity or friction velocity $= \sqrt{\tau/\rho}$
$Re*$	Roughness Reynolds number $= U_* k/v$
δ	Thickness of laminar sublayer $= 11.5v/U_*$
D	Particle size
V_{max}	Burst swimming speed
V_{sust}	Sustained swimming speed
TKE	Turbulent kinetic energy
u	Instantaneous streamwise velocity component
v	Instantaneous vertical velocity component
w	Instantaneous lateral velocity component
i'	Turbulent residual velocity in given velocity component (i)
SD_i	Turbulence intensity (standard deviation) in given component (i)
TI_i	Relative turbulence intensity in given component (i) = SD_i/U
RMS_i	Turbulence intensity (root-mean-square) in given component (i) $= \sqrt{\frac{1}{n}(i'^2_1 + i'^2_2 + \cdots + i'^2_n}$
τ_{ij}	Reynolds stress in given plane (ij) $= \rho\overline{i'\,j'}$
TKE	Turbulent kinetic energy $= 0.5(RMS_u{}^2 + RMS_v{}^2 + RMS_w{}^2)$
$AvInt$	Average intensity given two components $= 0.5(RMS_u{}^2 + RMS_w{}^2)$
ITS_i	Integral time scale $= \int_0^\infty r(\tau)d\tau$
ILS_i	Integral length scale $= ITS_i U$
$r(\tau)$	Normalised autocorrelation function
$d\tau$	Time lag over which the velocity is highly correlated to itself
L	Characteristic length scale
t	Time scale
η	Kolmogorov's micro-scale $= (\upsilon^3 \varepsilon)^{1/4}$
ε	Rate of turbulent energy dissipation
λ	Taylor's micro-scale
G	Turbulent energy generation
f_i	Eddy frequency in a given component (i)

L_i	Eddy length in a given component (i)
S_l	Theoretical diameter of body responsible for eddy shedding
S	Strouhal number
h_s	Bedform height
$T_{Qp}T_{H:q}$	Time in given quadrant (p) for given hole size (q)
$\tau_{uvQp}T_{H:q}$	Contribution to Reynolds shear stress for given quadrant (p) and given hole size (q)
U_c	Convective velocity
f_D	Digitisation rate
f_N	Nyquist frequency $=0.5f_D$
D_s	Characteristic length of velocity sensor
RL	Record length of time series $=f_D t$
Kurti	Kurtosis of the instantaneous velocity in a given component (i)
Skewi	Skewness of the instantaneous velocity in a given component (i)
$G_{i,x}$	Gini index, a measure of node impurity $=1-p_j^2-p_0^2$ where p_j is the fraction of samples from class j out of the total samples p_0 at node i for variable x
I_x	Variable importance for variable $x=\left[\sum_{k=500}^{n} G_{i,x}\right]-G_{\max}$
bl	Fish body length
Π_e	Maximum angular eddy momentum $=\frac{m_e\Gamma_e}{4\pi}$
m_e	Eddy mass
Γ_e	Eddy angular velocity
FTSC	Forces swimming costs, $\log FTSC=0.96\log M+0.23\log U+0.67\log T-1.85$
CR	Turbulent swimming costs, $\log CR=0.23\log T+0.64\log M+2.43\log U+0.67\log SDu-4.06$
M	Fish body mass
T	Temperature
V_{grad}	Spatial velocity gradient
CO_{xy}	Cell occupancy for given fish ($fish_i$) for cell $xy=\sum_{i=1}^{n} fish_{i,xy}$
SI_{xy}	Habitat selection index for cell $xy=\frac{CO_{xy}}{CO_{\max}}$
g	Link function

List of abbreviations

ACF	Autocorrelation Function
ADV	Acoustic Doppler Velocimeter
AIC	Akaike Information Criterion
BAP	Biodiversity Action Plan
BSW	Broken Standing Waves
CART	Classification and Regression Tree
CCA	Canonical Correspondence Analysis
CFS	Coherent Flow Structure
CGU	Channel Geomorphic Unit
CH	Chute
CU	Channel Unit
CVRE	Cross-validated Relative Error
EA	Environment Agency
EC	European Commission
ECM	Electromagnetic Current Meter
EVHA	Evaluation of Habitat
FB	Flow Biotope
FF	Freefall
FH	Functional Habitat
HB	Hydraulic Biotope
HEP	Hydroelectric Power
HMS	Habitat Modification Score
HMU	Hydromorphic Unit
HPC	Habitat Preference Curve
HPI	Habitat Probabilistic Index
HQA	Habitat Quality Assessment
HSC	Habitat Suitability Curve
HSI	Habitat Suitability Index
IBM	Individual Based Model
IFIM	Instream Flow Incremental Methodology
IPOS	Intensity, Periodicity, Orientation and Scale
IQR	Inter-quartile Range
IRBM	Integrated River Basin Management
KDA	Kernel Discriminant Analysis
LB	Leigh Brook
MPST	Modified Phase-space Thresholding
MRT	Multivariate Regression Tree
MTR	Mean Trophic Rank
MU	Morphological Unit
MVDISP	Multivariate Dispersion
NB	Near-bed
NMDS	Non-metric Multidimensional Scaling
NP	No Perceptible Flow
OOB	Out-of-bag
P6	Point-six depth

PB	Physical Biotope
PCA	Principal Components Analysis
PHABSIM	Physical Habitat Simulation System
PIV	Particle Imaging Velocimetry
PST	Phase-space Thresholding
RA	River Arrow
RBMP	River Basin Management Plan
RDA	Redundancy Analysis
RE	Relative Error
RF	Random Forests
RHABSIM	River Habitat Simulation
RHS	River Habitat Survey
RHYHABSIM	River Hydraulics and Habitat Simulation
RIVPACS	River Invertebrate Prediction and Classification System
RP	Rippled
SAC	Special Area of Conservation
SC	Swimming Costs
SERCON	System for Evaluating Rivers for Conservation
SFT	Surface Flow Type
SM	Smooth/Smooth Boundary Turbulent
SNR	Signal-to-noise Ratio
SPA	Special Protection Area
SSSI	Site of Special Scientific Interest
UP	Upwelling
USW	Unbroken Standing Waves
WFD	Water Framework Directive
WSS	Within-group Sum of Squares
WUA	Weighted Useable Area
WUV	Weighted Useable Volume
ZINB	Zero-inflated Negative Binomial

1

Introduction

Chapter overview

This chapter introduces key concepts and establishes the context and motivation for the research. The thesis combines three parallel trends in river research, namely the mesohabitat concept, the hydrodynamics of river ecosystems and bioenergetics, in order to drive progress in key areas of river management. These key management activities include river habitat assessment, modelling, rehabilitation and the conservation of key biota. The mesohabitat concept in particular has become central to these activities but the theoretical and ecological bases for its application are still relatively weak. The overall aim of the research, therefore, is to strengthen these bases through an approach that is best described as 'hydroecological'. This approach requires the combination of reductionist and holistic methods within the interdisciplinary areas of ecohydraulics and hydromorphology in order to address ecological degradation caused by damaging management practices such as channelisation and flow regulation. Ecohydraulic research has identified relationships between flow related forces and the ecology of biota at all levels of the ecosystem, including Atlantic salmon (*Salmo salar*) which is considered a model organism in river ecology, but major knowledge gaps remain in the understanding and/or application of knowledge in river management. In habitat assessment there is a need for more quantitative, robust and ecologically explicit methods. Consolidation of mesoscale, multivariate and bioenergetic approaches is required to improve habitat modelling techniques. Design criteria for a range of habitat types and rapid measures of performance are needed to support river rehabilitation activities. Finally, the identification of key mechanistic biophysical linkages is crucial to making effective management decisions designed to conserve key biota.

1.1 Research aim and objectives

In recent decades there have been **parallel trends in river research and management** which have led to an increasing focus on mesoscale (10^0-10^2 m) habitats (**mesohabitats**) (Newson & Newson, 2000), the **hydrodynamics** (turbulent flow) of river ecosystems (Nikora, 2010) and a proliferation in the development of **bioenergetic** models for key biota (*e.g.* Dunbar *et al*., 2012). This thesis seeks to combine the principles of contemporary river science arising from these recent trends in order to **drive progress in river habitat assessment, modelling, rehabilitation and conservation** (Figure 1.1).

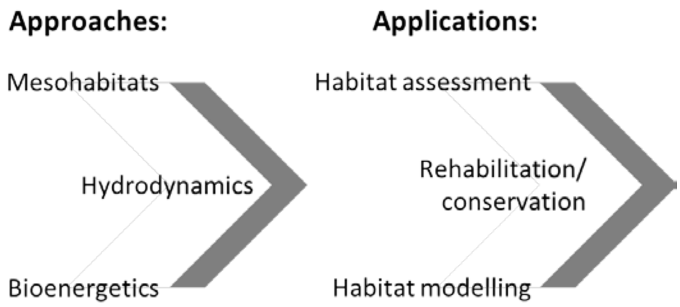


Figure 1.1 – River research approaches and management applications associated with this thesis.

The overall aim of the research is:

> *to strengthen the theoretical and ecological bases for mesoscale approaches to river habitat assessment, modelling and rehabilitation by developing a new, ecologically relevant and readily applicable hydrodynamic classification of mesohabitats*

This aim is addressed though five specific research objectives which are associated with a range of methodological approaches (Table 1.1).

1.2 Thesis structure

This thesis is structured according to the research aims and objectives outlined above. The current chapter establishes the research context (S 1.3) and identifies historical river management (S 1.3.2), ecological degradation (S 1.3.3) and the requirements of river-related legislation (S 1.3.4) as strong justificatory factors for this project. It then moves on to outline several key concepts that describe the strong biophysical linkages in river ecosystems (S 1.4.1) and provide the foundation for the hydraulic-biotic (ecohydraulic) relationships (S 1.4.2) that underpin many contemporary river research and management activities, particularly those focusing on Atlantic salmon populations (S 1.4.3). The chapter concludes by highlighting four key priorities in river research and management (S 1.5), namely habitat assessment (S 1.5.1), habitat modelling (S 1.5.2), river restoration (S 1.5.3) and the conservation of Atlantic salmon (*Salmo salar*) populations (S1.5.4), in order to further justify the approaches taken in subsequent chapters. This information is relatively detailed due to the breadth and richness of applied research areas relevant to the project.

Table 1.1 – Research objectives with associated methods and chapters.

Research objective	**Methods**	**Chapter**
1. Clarify the relationships between existing mesohabitat classifications and review their ecological and theoretical bases	Critical review, synthesis	Chapter 2
2. Strengthen the ecological basis for mesohabitat classification	Data collection and community-level analysis of fish assemblage structure	Chapter 3
3. Review the theory, structure and measurement of turbulence in rivers	Critical review, synthesis	Appendix C
4. Construct a hydrodynamic classification of mesohabitats	Measurement of turbulence in representative mesohabitats of two rivers over a range of discharges	Chapter 4
5. Test the ecological relevance of the hydrodynamic classification	Flume study of habitat selection by Atlantic salmon (*Salmo salar*) parr in relation to swimming energetics	Chapter 5

Chapter 2 introduces the concept of mesohabitats (S 2.1), broadly defined as mesoscale (10^0-10^2 m) units of instream habitat exhibiting a coherent set of physical conditions and a distinctive biological assemblage, and reviews the relationships between a confusing array of river habitat classifications in an attempt to clarify the situation (S 2.2). It then examines the ecological relevance of mesohabitats, by assessing the consistency of habitat associations exhibited by plants, macroinvertebrates and fish, and identifies community-level modelling as a way forward in strengthening the ecological basis for the mesohabitat concept (S 2.3). Finally, a critique of existing approaches to the hydraulic calibration of mesohabitats is presented (S 2.4).

In Chapter 3 the results of an analysis of fish community structure within mesohabitats of a large river, the San Pedro River, Chile, is presented. The chapter seeks to strengthen the ecological basis for mesohabitat classification and begins by introducing the knowledge gaps and challenges associated with mesoscale and community-level analyses in relatively large rivers before identifying the aims and objectives required to overcome them (S 3.1). It then outlines the novel methods used to reach those aims and objectives (S 3.2). Results are then presented (S 3.3) and the implications for river research and management discussed (S 3.4).

Appendix C presents a review of turbulence theory, structure and measurement. Based on this information, potential implications for the classification of physical biotopes (PBs), a particular type of mesohabitat, are explored in order to contextualise the approach taken in Chapter 4. Aims and hypotheses for a study which examines the hydrodynamic distinctiveness of PBs are then formulated (S 4.1) before site descriptions, field methods and data analysis techniques are described (S 4.2). Detailed results are then presented within a systematic structure (S 4.3) and discussed within the context of the research problem (S 4.4). Finally, a new hydrodynamic habitat classification is proposed (S 4.5).

Chapter 5 seeks to test the ecological relevance of the new hydrodynamic habitat classification using novel data on the habitat use of juvenile Atlantic salmon. It begins with a review of extant research on the links between turbulence and the swimming performance (S 5.1.1) and habitat selection (S 5.1.2) of river-dwelling fish, with an emphasis on juvenile salmonids. Aims and hypotheses are then formulated (S 5.1.3) before laboratory and data analysis methods are outlined (S 5.2). Results are then described (S 5.3) and discussed (S 5.4) with regards to the role of turbulence in the habitat selection of Atlantic salmon parr and the applicability of the new classification. The thesis then concludes with Chapter 6, which focuses on the implications of the findings for river research and management.

1.3 The research context

1.3.1 Some definitions at the interface between key river-related disciplines

Interdisciplinarity has become a theme of much academic research in recent decades (Morillo *et al*., 2003) and river science is no exception to this. The complexity and dynamicity of river systems, the strength of their biophysical linkages and the need to respond to adverse anthropogenic impacts has led to the emergence of several key interdisciplinary areas (Figure 1.2). These areas lie at the interface of traditional river related disciplinary boundaries and are required to bridge the gap between pure, strategic and applied research (Hannah *et al*., 2007). Although the use of different names for sub-disciplines varies between researchers, the overarching term used to describe this group of interdisciplinary sciences is '**hydroecology**'. Dunbar and Acreman (2001, p.1) define hydroecology as "*the linkage of knowledge from hydrological, hydraulic, geomorphological and biological/ecological sciences to predict the response of freshwater biota and ecosystems to variation of abiotic factors over a range of spatial and temporal scales*". Wood *et al*. (2007) provide an outline of the 'target elements' of hydroecology in which they emphasise the bi-directional nature of physical-ecological interactions and the need to identify causal mechanisms rather than merely establishing statistical links between biota, ecosystems and environments. Such causal mechanisms operate in the realm of the '**physical habitat**' (Figure 1.2).

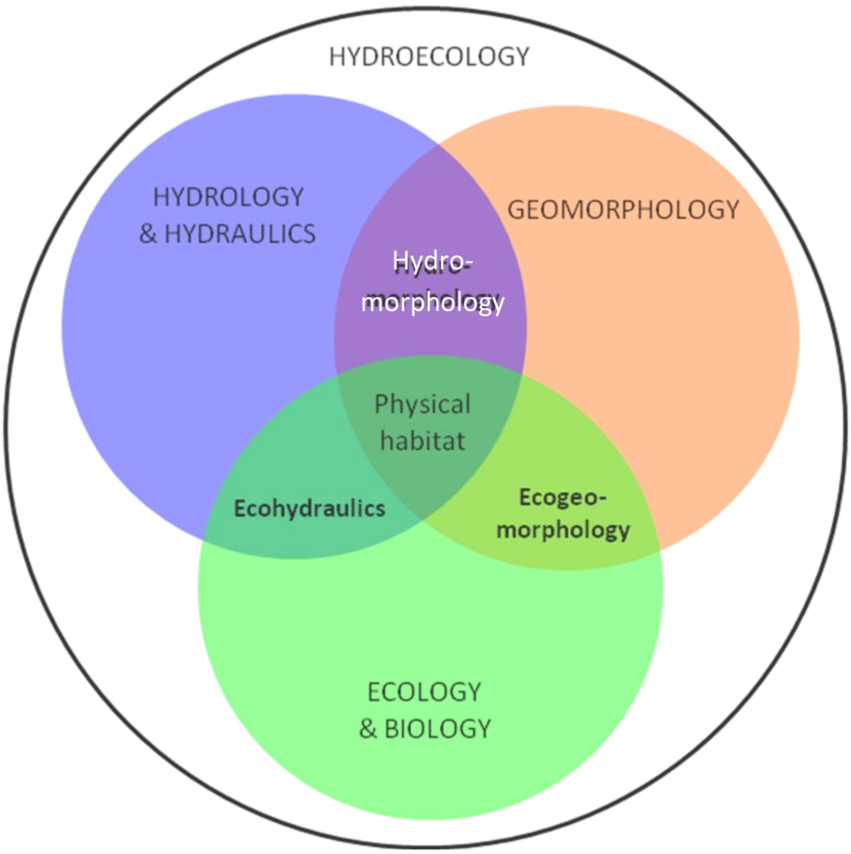


Figure 1.2 – Hydroecology, associated disciplines and the definition of physical habitat.

Two key sub-disciplines of hydroecology are worthy of particular note: hydromorphology and ecohydraulics. '**Hydromorphology**' was first used to refer to aquatic environments in European-level legislation, namely in the Water Framework Directive (WFD) (European Commission, 2000), where it was broadly defined as "*the hydrological and geomorphological elements and processes of waterbody systems*" (Vogel, 2011, p.147). The term has now become firmly established in the river research literature (*e.g.* Newson & Large, 2006; Orr *et al*., 2008) and more specific definitions have emerged. Vaughan *et al*. (2009, p.114), for example, define hydromorphology as "*the geomorphology and hydrology of a river system, their interactions, and their arrangement and variability in space and time*". They further outline the key elements of the sub-discipline as: flow and sediment transport regimes; channel and floodplain dimensions; topography and substratum; continuity and connectivity in three dimensions; and human modifications to these forms and processes.

'**Ecohydraulics**' has emerged from scientific literature in the fields of hydraulic engineering and ecology (Nestler *et al*., 2007) and, as a contemporary science, has its roots in the 'hydraulic stream ecology' paradigm (Stazner *et al*., 1988). Ecohydraulics is a sub-discipline of hydroecology and lies at the interface of **hydraulics and ecology** where new approaches to research are required to reconcile **the contrasting conceptual frameworks** underpinning these sciences, which can be seen respectively as Newtonian (**reductionist**) and Darwinian (**holistic**) (Hannah *et al*., 2007). Harte (2002) has identified 'elements of synthesis' for integrating these disparate traditions as: the use of simple, falsifiable models; the search for patterns and laws; and the focus on science of place. Newman *et al*. (2006) suggested that hierarchical scaling theory, whereby **reductionist explanations are considered at different levels of organisation**, could be used to integrate these two approaches, an idea taken up by Dollar *et al*. (2007) to address the challenges of scale associated with interdisciplinary river research. In hydroecology, the mesoscale (10^0-10^2 m) is the level of organisation at which explanations are increasingly sought for management purposes (Newson & Newson, 2000). This intermediate scale has often been neglected yet it is important for linking the outcomes of ecological research to the effective management of river ecosystems (Fausch *et al*., 2002).

1.3.2 A history of river management and associated impacts on hydromorphology

The major ways in which humans have altered the physical structure of river channels can be categorised into six broad chronological phases, each characterised by a set of management methods (Table 1.2). These methods have impacted on channel processes and morphology either directly (*e.g.* through dam construction and channel engineering) or indirectly (*e.g.* through land

Table 1.2 – Six chronological phases of anthropogenic influence on river channels. Modified from Downs and Gregory (2004).

Chronological phase	Characteristic developments	Management methods employed
1. Hydraulic civilisations	• River flow regulation • Irrigation • Land reclamation	• Dam construction • River diversions • Ditch building • Land drainage
2. Pre-industrial revolution	• Flow regulation • Drainage schemes • Fish weirs • Water mills • Navigation • Timber transport	• Land drainage • In-channel structures • River diversions • Canal construction • Dredging • Local channelisation
3. Industrial revolution	• Industrial mills • Cooling water • Power generation • Irrigation • Water supply	• Dam construction • Canal building • River diversions • Channelisation
4. Late nineteenth to mid-twentieth century	• River flow regulation • Conjunctive and multiple use river projects • Flood defence	• Large dam construction • Channelisation • River diversions • Structural revetment • River basin planning
5. Second part of twentieth century	• River flow regulation • Integrated use river projects • Flood controls • Research into effects of river channel management methods • Conservation management • Re-management of rivers	• Large dam construction • River basin planning • Channelisation • Structural and bioengineered revetments • River diversions • Mitigation, enhancement and restoration techniques
6. Late twentieth century to date	• Conservation management • Re-management of rivers • Sustainable use river projects	• Integrated river basin planning • Re-regulation of flow • Mitigation, enhancement and restoration techniques • Hybrid and bioengineered revetments

management practices) with concomitant changes in flow processes, sediment supplies, erosion and deposition (Downs & Gregory, 2004). Flow impacts include the magnitude, frequency and timing of floods and droughts, as well as local changes to flow depths and velocities (Gregory, 2006). This is not to mention the consequences of human activities for water quality (*e.g.* eutrophication, temperature changes, toxic effluents) (Sweeting, 1994), as well as the potential impacts of anthropogenic climate change (Kay *et al*., 2006; Johnson *et al*., 2009; Milner *et al*., 2012), which lie outside the scope of this thesis.

Of the most damaging human activities directly affecting lowland river channels over the past century, channelisation has received particular attention. Channelisation has been applied for the purposes of flood management, erosion control, land drainage and navigation using hard engineering methods such as bed and bank resectioning (widening, deepening), straightening, embanking, stabilising banks, dredging and clearing the channel of trash and woody debris (Downs & Gregory, 2004). The result is often a uniform channel with a trapezoidal cross-section and few, if any, overbank flows (Brookes, 1988). Although these management techniques have been in use for centuries, their application proliferated during the nineteenth century so that by 1900 most of the large European rivers had been channelised (Petts, 1989). Further so called 'improvement' works in the UK throughout the twentieth century, and particularly in the agricultural productivist period after World War II, meant that very few rivers in England and Wales were unmodified. Up to 96% of all rivers in lowland Britain were channelised to some extent by 1990 (Brookes *et al*., 1983; Brookes & Long, 1990).

1.3.3 Ecological impacts of channelisation

The effects of channelisation are extremely pervasive and include changes to water quality and ecological communities, as well as direct morphological adjustment (Brookes, 1988). Biota at all levels of the ecosystem (*e.g.* plants, invertebrates, fish) are affected (Table 1.3). Much of the evidence for this comes from research conducted in the 1970s and 80s, a period of increasing environmental awareness. Channel resectioning and realignment has been found to reduce the biomass and diversity of aquatic macrophyte communities, as well as changing the species composition compared to unmodified control reaches (Brookes, 1987; Hey, 1994; Pedersen *et al*., 2006). Macroinvertebrate communities have also been affected. In general, the overall density of macroinvertebrates can return to previous levels rapidly after channelisation but community composition does not recover where the nature, complexity and stability of the substrate is significantly altered and particular habitats eliminated (Brooker, 1985; Yount & Niemi, 1990; Negishi *et al*., 2002).

Table 1.3 – Examples of effects of channelisation on key aquatic biota.

Biotic group	Type of channel modification	Impacts	Reference
Aquatic macrophytes, semi-aquatic vegetation	Resectioned	No recovery of biomass and species composition within two years	Brookes (1987)
	Resectioned, realigned, concrete-lined	Lowest diversity of flora out of 18 flood alleviation schemes	Hey (1994)
	Channelisation	Lower species diversity, significantly different floristic composition	Pedersen *et al*. (2006)
Macroinvertebrates	Realigned, riparian vegetation cleared	No recovery of biomass to pre-disturbance levels after 5 years	Moyle (1976, cited in Yount & Niemi, 1990)
	Dredging	No difference in densities compared to natural streams, reduction of Ephemeroptera and Trichoptera populations, elimination of Plectoptera	Schmal & Sanders (1978, cited in Brookes, 1988).
	Straightened, concrete-lined	Lower total biomass, lower resistance and resilience of community to floods due to loss of flow refugia	Negishi *et al*. (2002)
Fish	Channelisation for flood alleviation	90% reduction in fish densities and 85% reduction in total biomass 3 months after works, loss of brown trout	Swales (1982)
	Embanking, straightening, installation of weirs	Reduction of recruitment by species associated with plants and fast-flowing habitats	Jurajda (1995)
	Channelisation	Reduction in the number of native species	Corbacho and Sánchez (2001)
	Channelisation	Reduction in abundance and composition of juveniles	Langler & Smith (2001)
Salmonid fish	Dredging	Increased fry mortality due to high concentrations of suspended solids	Toner *et al*. (1965, cited in Brooker, 1985)
	Channelisation for flood alleviation	Ratio of salmonids to coarse species changed from 14:1 (before) to 1:5 (after)	McCarthy (1981, cited in Brooker, 1985)
	Deepening	Skew of population structure towards older fish	Kennedy *et al*. (1983)

Research into the response of fish communities to channelisation is more developed than for other biota, although relatively few studies on British rivers exist (Brooker, 1985). Most notable among these is Swales (1982), who found a 90% reduction in overall fish densities and an elimination of brown trout (*S. trutta*) shortly after channelisation of the River Soar, with the principal factor cited as a loss of instream cover. Densities and age structures of salmonid populations appear to be particularly sensitive to channelisation. Kennedy *et al*. (1983), for example, found that deepened sections of the River Camowen in Northern Ireland had greater numbers of older salmonids than in unmodified reaches. In the Republic of Ireland, Toner *et al*. (1965) reported increased juvenile Atlantic salmon mortality due to high concentrations of suspended solids after dredging and McCarthy (1981) found that channelisation of the River Boyne was associated with a shift from a salmonid-dominated community to one composed mainly of coarse species. Other European studies on channelised rivers include that by Jurajda (1995) into fish recruitment in the River Morava, a large floodplain river in the Czech Republic. Channelisation served to disconnect the river from its floodplain and to isolate backwater channels, reducing the recruitment of a range of fish species through the loss of hydraulic conditions suitable for nursery habitat. Many more examples of the adverse effects of channelisation on fish communities can be found in the North American literature, with **reductions in total biomass, species richness, diversity and loss of salmonid species commonly reported** (Brookes, 1988).

Although biological degradation may be caused or aggravated by chemical pollution and changes in key water quality parameters (*e.g.* temperature and dissolved oxygen levels) (Brookes, 1988), the most commonly cited factor in the decline of lotic communities after channelisation is a reduction in physical habitat quality (*e.g.* Swales, 1982; Jurajda, 1995). Coupled with the hydrological changes associated with flow regulation through damming, hydroelectric power (HEP) generation and abstraction, such impacts are severe and widespread (Petts, 1984). This is **because of the strong links which exist between physical and biological systems in rivers** (S 1.4) (Harper & Everard, 1998; Hart & Finelli, 1999). Recent trends towards ecologically sensitive river management recognise this and acknowledge aquatic biota as legitimate 'users' of water in a multi-purpose ecosystem services approach to river management (Postel & Richter, 2003). Current management techniques should seek to relate local problems (*e.g.* sedimentation, flooding, erosion, ecological degradation) to basin-wide phenomena, through Integrated River Basin Management (IRBM) (Logan, 2001; Mance *et al*., 2002), and apply solutions which are 'designed-with-nature' (Downs & Gregory, 2004; Poff *et al*., 1997). This requires multidisciplinary involvement and interdisciplinary research at the interface of hydrological, hydraulic, geomorphological, biological and ecological sciences. Thus, driven by recent environmental legislation (S 1.3.4), **the contemporary approach to river channel management is best described as hydroecological, focusing on hydromorphological form and process as these constitute the habitat template for biota** (S 1.4.1).

1.3.4 River-related legislation

The main legislative driver of attempts to assess and, where necessary, improve the hydromorphological quality of British rivers is currently the European Commission (EC) **Water Framework Directive** (EC, 2000). The directive requires member states to implement measures to ensure that all water bodies (rivers, lakes, transitional and coastal waters) achieve 'good status', or 'good ecological potential' for heavily modified and artificial water bodies (*e.g.* urban rivers, canals, reservoirs), by December 2015. 'Good' status is the fourth classification on a five point scale from 'bad' to 'high' based on biological (plants, invertebrates, fish), physico-chemical and hydromorphological elements (Table 1.4). For rivers, **hydromorphology encompasses the physical habitat components of hydrology, morphology and continuity** (Table 1.5). The WFD provides several specific reasons for assessing hydromorphological (habitat) quality (Boon *et al*., 2010): (a) to establish 'type-specific hydromorphological conditions' (Annex II, 1.3); (b) to identify hydromorphological pressures that may be causing a water body to fail to reach its objectives (Annex II, 1.4); (c) to classify 'high status' water bodies and ensure that hydromorphology is 'consistent with the achievement of' other levels of ecological status (Annex V, 1.1); (d) to define maximum ecological potential for hydromorphology with respect to heavily modified and artificial water bodies (Annex V, 1.2); and (e) to produce 'programmes of measures' for enhancing hydromorphological quality to meet environmental objectives (Article 11). The WFD does not require a classification of hydromorphology in the five classes used for ecological status. For a water body to be at high status, however, hydromorphology as well as other elements must be classified at 'high'.

The WFD is by no means the only legislative driver for the ecologically sensitive management of British rivers. The **Sites of Special Scientific Interest** (SSSI) system designates rivers predominantly on the basis of diversity, naturalness and representativeness (Boon, 1991). In England and Wales, for instance, a total length of 1953 km of rivers over 5 m wide was contained within SSSIs by 1990, 1078 km of which was specifically mentioned in statutory citations whilst 526 km was the main focus of the designation (Holmes *et al*., 1990). Many river-based SSSIs are also designated as **Special Areas of Conservation** (SACs) under the **EC Habitats Directive** (EC, 1992), **Special Protection Areas** (SPAs) under the **EC Birds Directive** (EC, 1979), or **Ramsar sites** under the **Wetland Convention 1971** (UNESCO, 1994). Each of these designations carries certain requirements in terms of the conservation and rehabilitation of important habitats and species. The EC Habitats Directive, for instance, requires member states to designate sites as SACs where running waters exhibit 'natural or near-natural dynamics' or where Atlantic salmon occur. Appropriate conservation measures to maintain or restore listed habitats and species and to avoid potentially damaging activities are required within such designated sites. The Convention on Biological Diversity also recognises rivers as important habitats and signatories, including the UK, are committed to develop and enforce **Biodiversity Action Plans** (BAPs) at national and regional levels.

Table 1.4– Quality elements for the classification of water body status under the WFD. From Newson & Large (2006).

Quality element	Description
Biological elements	• Composition and abundance of aquatic flora • Composition and abundance of benthic invertebrate fauna • Composition, abundance and age structure of fish fauna

Hydromorphological elements supporting biological elements	• Hydrological regime:
	  • Quantity and dynamics of flow
	  • Connection to groundwater bodies
	• Morphological conditions:
	  • River depth and width variation
	  • Structure and substrate of the river bed
	  • Structure of the riparian zone
	• River continuity

Chemical and physico-chemical elements supporting the biological elements	• Thermal conditions • Oxygenation conditions • Salinity • Acidification status • Nutrient conditions • Specific pollutants • Pollution by all priority substances • Pollution by other substances

Table 1.5 - Hydromorphological quality elements and their description as given in the EC Water Framework Directive. From Boon *et al*. (2010).

Hydromorphological quality elements	WFD description of 'high status'
Hydrological regime	The quantity and dynamics of flow, and the resultant connection to groundwaters, reflect totally, or nearly totally, undisturbed conditions
Morphological conditions	Channel patterns, width and depth variations, flow velocities, substrate conditions and both the structure and condition of the riparian zones correspond totally or nearly totally to undisturbed conditions
River continuity	The continuity of the river is not disturbed by anthropogenic activities and allows undisturbed migration of aquatic organisms and sediment transport

1.4 Biophysical linkages in river ecosystems

1.4.1 Key concepts in river ecology

The word *ecology* is derived from the Greek *oikos*, meaning 'household', and *logos*, meaning 'to study'. Thus ecology is the study of the members of the 'household' as well as the functional processes which make the 'house' habitable (Odum & Barrett, 2005). The earliest formal definition of *ecology* was provided by Haeckel (1869, p.362) as "*the study of the natural environment including the relations of organisms to one another and their surroundings*". The fundamental link between organisms and 'their surroundings' is given by the concepts of *habitat* and *niche*. *Habitat* is "*the locality, site and particular type of local environment occupied by an organism [or population]*" (Lincoln *et al*., 1998, p.142). Rivers are strongly hierarchical (Poole, 2002; Parsons & Thoms, 2007) and, as such, **river habitats may be defined at a number of spatial scales** (Figure 1.3) (Frissell, *et al*., 1986). If *habitat* is the location of an organism in physical space then *niche* can be seen as its place in conceptual multi-dimensional space, where the coordinates represent the particular set of environmental conditions (*e.g.* temperature range, flow velocity range) under which the organism persists in reality (*realised niche*) or could occupy in the absence of biotic interaction (*fundamental niche*) (Hutchinson, 1978). Often, however, *habitat* is also used in a wider sense to refer to *niche* (*i.e.* niche dimensions = habitat preferences) and *microhabitat* is used to describe the particular set of conditions experienced by an organism at the point where it is situated. *Microhabitat* may also be used as an explicit reference to the scale of observation (*e.g.* 10^{-2}-10^{-1} m^2) in a similar way to *mesohabitat* (10^0-10^2 m). A related term is *biotope*, which should be used to refer to the community level equivalent of *habitat* (Udvardy, 1959), although *habitat* is often used as a generic term.

The habitat provides the template within which an organism must realise a niche if it is to persist. Southwood (1977, 1988) formalised this idea with the **habitat template concept**. Such templates are useful for predicting species distributions and life-history strategies from the abiotic environment and typically have axes based on disturbance frequency and productivity or stress (*e.g.* Figure 1.4). Temporal variation in the physical environment over timescales relevant to biota, in other words *disturbance*, is particularly marked in river systems (Figure 1.5) and often an overriding factor in the organisation of lotic communities. This is demonstrated by the applicability of the **patch dynamics concept** (White & Pickett, 1985) to river ecosystems (Pringle *et al*., 1988; Townsend, 1989). Stream productivity is largely determined by water quality, the energy budget (*e.g.* temperature regime, organic matter, nutrients), the physical structure of the channel and the flow regime (Stalnaker, 1979). The latter two factors constitute hydromorphology and, therefore, determine the *physical habitat* available for instream biota (Maddock, 1999; Rosenfeld *et al*., 2007).

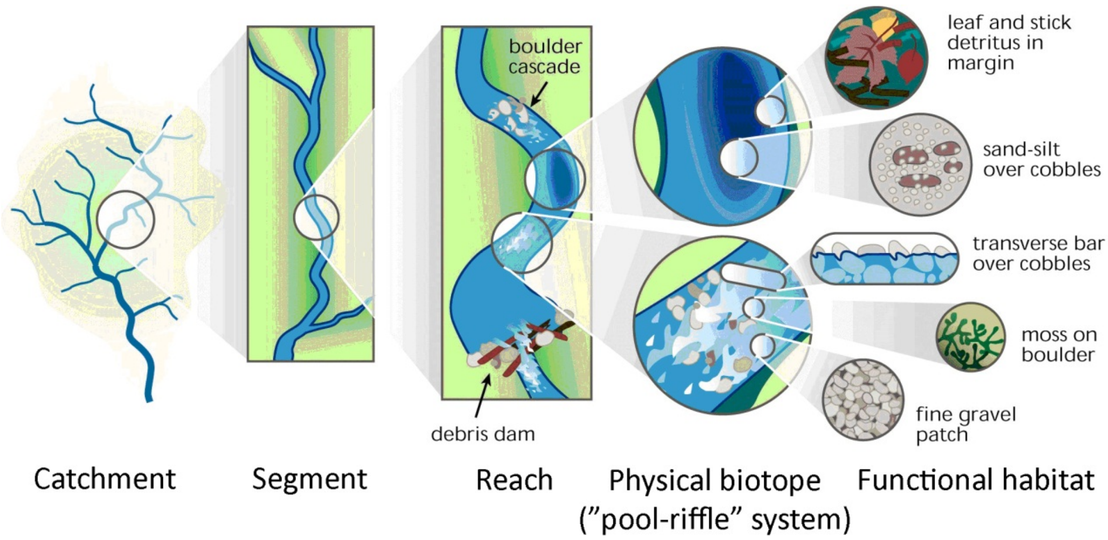


Figure 1.3 – Nested hierarchy of stream habitats. Modified from FISWRG (1998), Frissell et al. (1986).

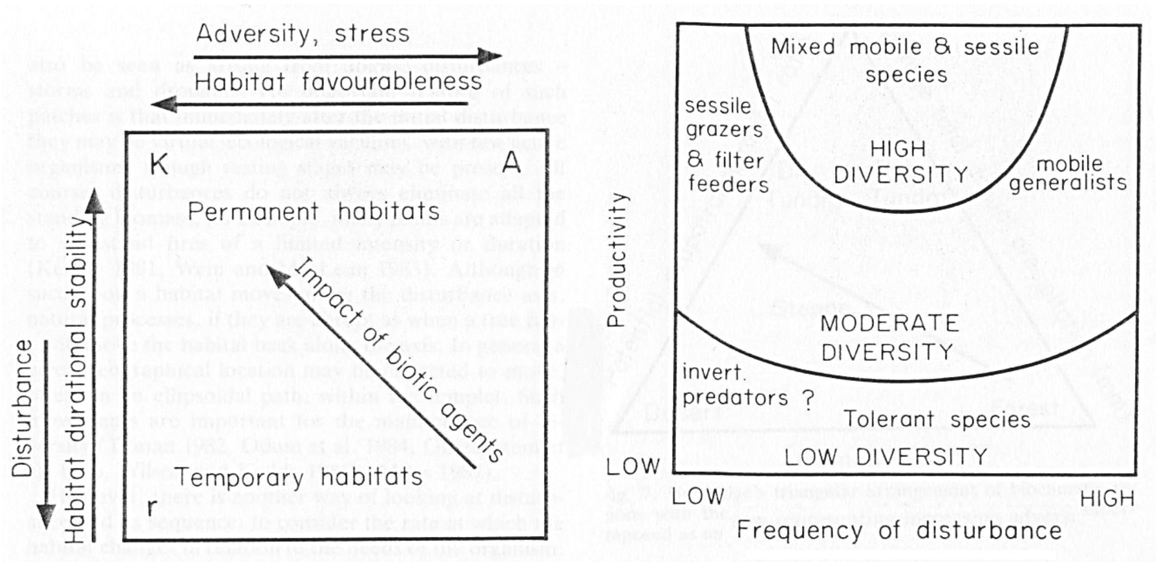


Figure 1.4 – The Southwood-Greenslade habitat template (left, where r, K and A represent different life-history strategies) and the Hildrew & Townsend (1987) template for benthic macroinvertebrate communities (right). From Southwood (1988).

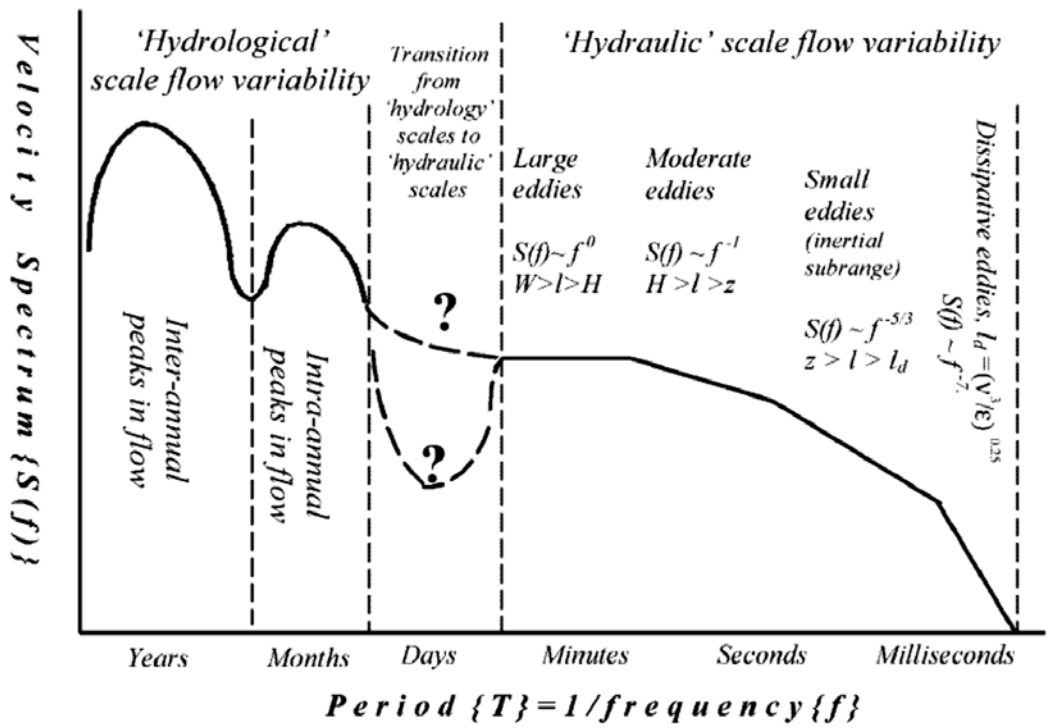


Figure 1.5 - A frequency spectrum for water velocity variation of flow in an idealised river. S(f)=velocity variation, W=width of the river, H=depth. From Biggs *et al*. (2005).

Several other key concepts emphasise the strong biophysical linkages in lotic ecosystems, which occur in four dimensions (Ward, 1989). In the longitudinal direction, the **river continuum concept** (Vannote *et al*., 1980) proposed a physical-biological relationship based on channel width, bank and riparian structure, water depth and suspended sediment concentration. In recognition of the longitudinal discontinuities present in river systems, particularly in the face of flow regulation, the **serial discontinuity concept** has been used to show that physical impacts of interruptions to the river continuum result in predictable consequences for biota downstream (Ward & Stanford, 1983; 1995; Stanford & Ward, 2001). In the lateral dimension, the **flood pulse concept** emphasises the importance of floodplain inundation to the energy balance through terrestrial-aquatic subsidies and for the availability of suitable nursery habitat and flow refugia for fish (Junk *et al*., 1989). In the vertical dimension, the **hyporheic corridor concept** recognises the importance of the hyporheic zone for the processing of organic matter and pollutants, as well as its role in determining spawning habitat quality for lithophilous fish and benthic organisms (Brunke & Gonser, 1997). The final dimension, time, is incorporated into stream ecological theory through the patch dynamics concept, which also emphasises the importance of spatial habitat heterogeneity (Townsend, 1989). A relatively new paradigm in river science, **fluvial landscape ecology**, brings together the above concepts (Poole, 2002) into a framework which integrates pattern and process (Ward *et al*., 2001, 2002a, 2002b; Wiens, 2002) and recognises the hierarchical nature of physical-biological associations in river ecosystems (Poff, 1997; Parsons & Thoms, 2007). Landscape ecology may provide a particularly helpful framework for fish research and conservation (Figure 1.6) (Schlosser, 1991; Fausch *et al*., 2002; Vaughan *et al*., 2009) (*e.g.* the **riverine ecosystem synthesis**; Thorp *et al*., 2006), including the management of anadromous salmonid populations (Kim & Lapointe, 2011; Flitcroft *et al*., 2012).

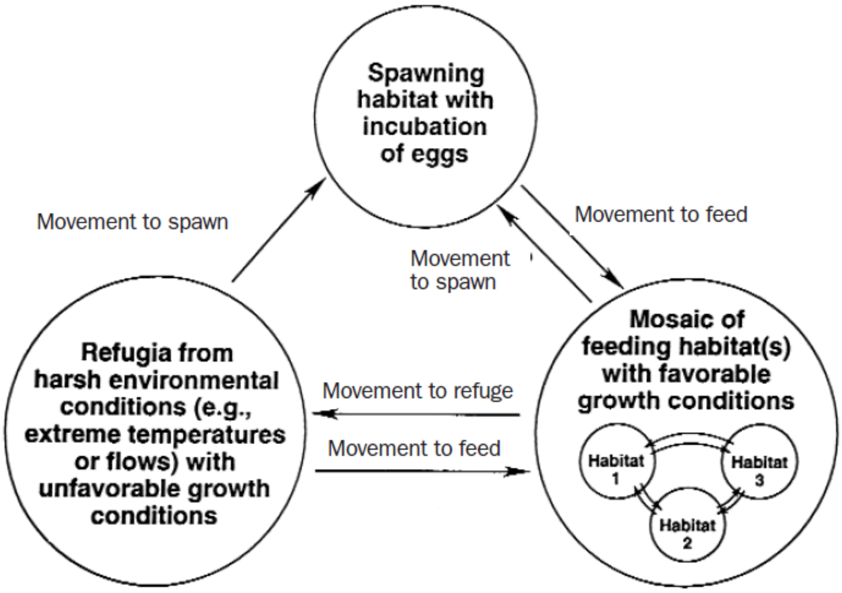


Figure 1.6 – A dynamic landscape model of lotic fish life-history. Fish require temporally-dependent and spatially connected habitats for different activities. From Schlosser and Angermeier (1995).

1.4.2 Ecohydraulic relationships

Whilst the importance of chemical, physico-chemical and interactive biological factors (*i.e.* interference, competition, predation) cannot be denied (Kohler, 1992; Sweeting, 1994; Lancaster & Downes, 2010), there has often been a **greater emphasis on the effects of physical stressors in rivers due to their physical dynamism** (Thompson & Lake, 2010). Vaughan *et al*. (2009, p.114) suggested that "*hydromorphological integrity is central to conservation since it provides the template upon which all other ecological structures and functions are built*". Much hydroecological research is founded on the premise that **hydromorphological quality and diversity are effective surrogates for biological quality and diversity** (Harper & Everard, 1998; Newson & Large, 2006), an assumption that is believed to represent a valid working principle in ecology (Newson & Newson, 2000). Thus, the discussion herein is limited to the physical component of river habitats. Within this physical realm, hydraulic conditions have received particular attention due to the pervasive effects of flow related forces (Statzner *et al*., 1988; Hart & Finelli, 1999). In the case of European freshwater fish species, for example, Blanck *et al*. (2007) reported that hydraulics play a more important role in the habitat template than physico-chemical variables such as temperature and dissolved oxygen. In particular, flow velocity, and its vertical profile through the water column, exerts friction and pressure related drag and lift forces on organisms. Numerous morphological and physiological adaptations have evolved to cope with these forces (*e.g.* dorsoventral flattening, substrate attachment mechanisms, behavioural avoidance) (Vogel, 1994; Allan, 1995). These same forces also have indirect consequences for biota by entraining and transporting sediment (Graf, 1984), thereby changing the structure of their habitat.

Much research has focused on the relationship between instream biota and the **'standard ecohydraulic variables'** of flow depth (h), mean streamwise velocity (U) and combinations of these. U is typically measured at 'point six' depth (y/h=0.4, where y is height above the bed) and (ensemble) averaged over 10-60 s. This reflects a continuation of standard practice used to measure stream discharge for traditional water resources compliance and research purposes (Gordon *et al*., 2004). Other commonly used variables describing the bulk flow are Froude number (Fr, ratio of inertial to gravitational forces) and Reynolds number (Re, ratio of inertial to viscous forces) (Table 1.6). These are dimensionless variables representing gradients from tranquil (sub-critical) to shooting (super-critical) and laminar to fully developed (turbulent) flow respectively. Because the flow environment experienced by benthic organisms living very close to the bed differs markedly to that further up in the water column (Statzner *et al*., 1988), near-bed flow has often been characterised by a different set of variables. They include bed shear stress (τ), shear velocity (U_*), roughness Reynolds number ($Re*$) and the thickness of the laminar sublayer (δ). U_* is related to τ (Table 1.6) which, in turn, is responsible for the appearance of a mean gradient in the vertical velocity profile. U_* can be interpreted as a velocity scale for near-bed flow. $Re*$ describes the 'roughness' of the near-bed flow environment. Finally, δ approximates the thickness of the laminar sublayer where viscous forces predominate over inertial forces. In rivers with coarse bed material (*i.e.* gravel-bed rivers) which are characterised by hydraulically rough flow ($Re*$>70), however, δ is typically very small in comparison to roughness size (k) (Davis & Barmuta, 1989; Kirkbride & Ferguson, 1995), rendering it irrelevant to the study of all but the smallest organisms (Allan, 1995).

Flow forces have been found to control the processes of dispersal, reproduction, habitat use, resource acquisition, competition and predation (Table 1.7) (Hart & Finelli, 1999). The passive dispersal of aquatic organisms is controlled by the same mechanisms as sediment transport (Nelson *et al*., 1995; McNair *et al*., 1997), although many benthic organisms actively enter the water column and are able to swim back to the substrate (Waters, 1972; Mackay, 1992). Hydraulic limitations to fish migration are related to body depth and burst swimming speeds (V_{max}), which vary considerably between species and with water temperature (Beamish, 1978). h and U are key factors in the segregation of rheophilic species (*e.g.* Bisson *et al.*, 1988), whilst the distribution of benthic organisms has been related to δ, Fr, τ and Re^* (*e.g.* Statzner, 1981a, 1981b; Scarsbrook & Townsend, 1993; Brooks *et al.*, 2005). **Most aquatic biota exhibit a subsidy-stress response to flow** as resources (*e.g.* food, nutrients, oxygen) may be limiting at low U, whilst at high U drag disturbance and mass transfer may be the limiting factor (Hart & Finelli, 1999; Nikora, 2010). Thus, for example, periphyton biomass is found to be maximised at intermediate U (Biggs, 1996) and the net energetic intake of feeding for juvenile salmonids is negatively related to U (e.g. Godin & Rangeley, 1989). These studies show that a strong link exists between the flow environment and ecological patterns and processes, a link exemplified by the natural history and habitat requirements of Atlantic salmon, a species which is considered a model organism in this respect (Aas *et al.*, 2011).

Table 1.6 – Common terms used to describe the flow environment. From Wilkes *et al*. (2013).

Term	Description	Notes
h	Flow depth	
y	Height above bed datum	
A	Cross-sectional area of flow	
P	Wetted perimeter	
R	Hydraulic radius $= A/P$	
S	Longitudinal bed slope	
ρ	Fluid density of water	Taken as 1000 kg m^{-3}
g	Acceleration due to gravity	9.81 m s^{-2}
k	Height of surface roughness elements	Various methods to quantify k provided by Statzner et al. (1988)
v	Kinematic viscosity	1.004 x 10^{-6} m^2 s^{-1} at 20°C
U	Mean streamwise velocity	Typically measured at y/h=0.4 and averaged over 10-60 s or measured anywhere in the water column to describe focal point of organism
Fr	Froude number $= U/\sqrt{gh}$	Fr <1 → sub-critical flow Fr =1 → critical flow Fr >1 → super-critical flow
Re	Bulk flow Reynolds number $= Uh/v$	Re <500 → laminar flow 500< Re<10^3-10^4 → transitional flow Re>10^3-10^4 → turbulent flow
τ	Shear stress (section- or reach-averaged) = $pgRS$	Point measurements can be made using Fliesswasserstammtisch (FST) hemispheres
U_*	Shear velocity or friction velocity $= \sqrt{\tau/\rho}$	Calculated from point measurements of shear stress or estimated from near-bed velocity profile
Re^*	Roughness Reynolds number $= U_* k / v$	Re^* <5 → hydraulically smooth flow 5< Re^*<70 → transitional flow Re^*>70 → hydraulically rough flow
δ	Thickness of laminar sublayer $= 11.5v/U_*$	δ/k <1 → hydraulically smooth flow δ/k >1 → hydraulically rough flow

Table 1.7 – Some examples of flow-biota links identified. From Wilkes *et al*. (2013).

Reference	Variable(s)	Species/community/process influenced by variable
Dispersal and reproduction		
Silvester & Sleigh (1985); Reiter & Carlson (1986); Biggs & Thomsen (1995)	τ, U_*	Positively correlated with loss of biomass of filamentous and matt-forming algal communities
Stevenson (1983); Peterson & Stevenson (1989)	U	Negatively correlated with diatom colonisation rates on clean ceramic tiles
Deutsch (1984); Becker (1987) cited in Statzner *et al*. (1988)	Re, Fr	Certain caddis fly (Trichoptera) genera select ovipostion sites based on Re and Fr
McNair *et al*., (1997)	U_*	Transport distance positively related to Rouse number ($= V_S / U_*$, where V_s is settling velocity)
Beamish (1978); Crisp (1993); Hinch & Rand (2000)	h, U	Fish migration inhibited when h<<body depth and/or when $U >> V_{max}$
Habitat use		
Biggs (1996)	U	Growth rate and organic matter accrual of periphyton and macrophytes enhanced at intermediate U
Scarsbrook & Townsend (1993); Lancaster & Hildrew (1993)	τ	Macroinvertebrate community structure related to spatial and temporal variation in τ
Statzner (1981a)	δ	Body length of freshwater snails (Gastropoda) and shrimps (Gammarus) positively correlated with δ
Statzner (1981b)	δ, Fr	Abundance of *Odagmia ornata* (Diptera:Simuliidae) negatively correlated with δ and positively correlated with Fr
Statzner *et al*., (1988)	$Re > U > \delta > Re^* > Fr$	Order of best explanatory variables to predict distribution of water bug *Aphelocheirus aestivalis*
Brooks *et al*. (2005)	Re^*	Strongest (negative) correlation with macroinvertebrate abundance and species richness
Bisson *et al*. (1988); Lamouroux *et al*. (2002); Moir *et al*. (1998. 2002); Sagnes & Statzner (2009)	h, U, Fr	Fish species and life stages segregated by hydraulic variables due to morphological and ecological traits
Resource acquisition, competition and predation		
Wiley & Kohler (1980); Eriksen *et al*. (1996); Stevenson (1996)	U, δ	U controls the delivery of limiting resources for periphyton. Laminar sublayer (δ) limits rate of molecular diffusion. At low U some invertebrates actively circulate water past respiratory organs to decrease δ and enhance rate of gas exchange
Godin & Rangeley (1989); Hayes & Jowett (1994); Heggenes (1996); Smith *et al*.(2006)	U, h	Velocity positively correlated with prey delivery and negatively correlated with capture rates for salmonids; velocity gradients determine energetic costs of drift-feeding by insectivorous fish; high h provides refuge from predators and competition.
Peckarsky *et al*. (1990); Malmqvist & Sackman (1996); Hart & Merz (1998);	U	High U serves as a refuge from predators for blackflies (Simuliidae) and stoneflies (Plecoptera)
Poff & Ward (1992, 1995); DeNicola & McIntire (1991)	U	Negatively correlated with rates of algal consumption by snails and certain caddis flies (Trichoptera)
Matczak & Mackay (1990); Hart & Finelli (1999)	U	Higher U reduces competition and increases carrying capacity of filter-feeding macroinvertebrates

1.4.3 Atlantic salmon: the model organism

Atlantic salmon is an iconic species with high social, economic and ecological value (S 1.5.4). The consensus among fisheries managers is that the most important physical habitat variables (niche dimensions) for Atlantic salmon are h, U, substrate size (D) and cover (Armstrong *et al*., 2003). Each freshwater life stage has certain limits and preferences for these variables, as established by a wealth of research conducted in the late 20th century (Table 1.8), although many other abiotic factors are directly or indirectly involved in habitat selection (Figure 1.7). Adults migrate from the sea to freshwater to spawn during autumn or winter, burying eggs in 'redds' (nests). Depending on water temperature, eggs hatch within 60-200 days and the newly emerged 'alevins' remain within the gravel matrix. Some weeks after hatching the alevins 'swim-up' into the water column, at which time they are known as 'fry'. Free-swimming juveniles are later known as 'parr' and remain in fresh water for two winters or more before undergoing physiological changes in a process known as 'smoltification'. When ready, 'smolts' migrate downstream and spend one or more years in the North Atlantic before returning to freshwater to spawn.

The values given in Table 1.8 are only approximate due to considerable among and within population variability (Heggenes, 2002), ontogenetic shifts and seasonal changes in habitat use (Heggenes, 1996; Maki-Petays *et al*., 1997; Hayes *et al*., 2000). The maximum flow velocity that an individual can maintain position in for short (V_{max}) or sustained (V_{sust}) periods is largely a function of body length and temperature (Figure 1.8). During all freshwater life stages, salmonids require access to a range of cover elements (*e.g.* deep water, woody debris) to seek refuge from high U and to provide visual isolation from predators and competitors (Campbell & Neuner, 1985; Fausch, 1992). They also require a suitable spatial arrangement of habitat conditions at different scales (Fausch *et al*., 2002). For example, at the mesoscale over small multiples of body length (Guensch *et al*., 2001), drift-feeding parr exhibit territorial behaviour, selecting a 'home rock' behind which they 'hold station' in a microhabitat with a relatively low mean velocity before 'attacking' prey in adjacent, faster flow (Cunjak, 1988; Guay *et al*., 2000). At a landscape scale, individuals must be able to move between suitable spawning, rearing, feeding and resting habitats in order to complete their life cycle (Schlosser & Angermeier, 1995). Variation over hydrological and hydraulic timescales is also important for Atlantic salmon. At hydrological scales, discharge fluctuations change local hydraulic conditions (Biggs *et al*., 2005) and provide cues for migration (*e.g.* Tetzlaff *et al*., 2008). **Recent field and laboratory work with salmonids suggests that short-term, turbulent fluctuations in flow also have direct relevance to the habitat selection of juveniles** (Chapter 5) (Figure 1.7).

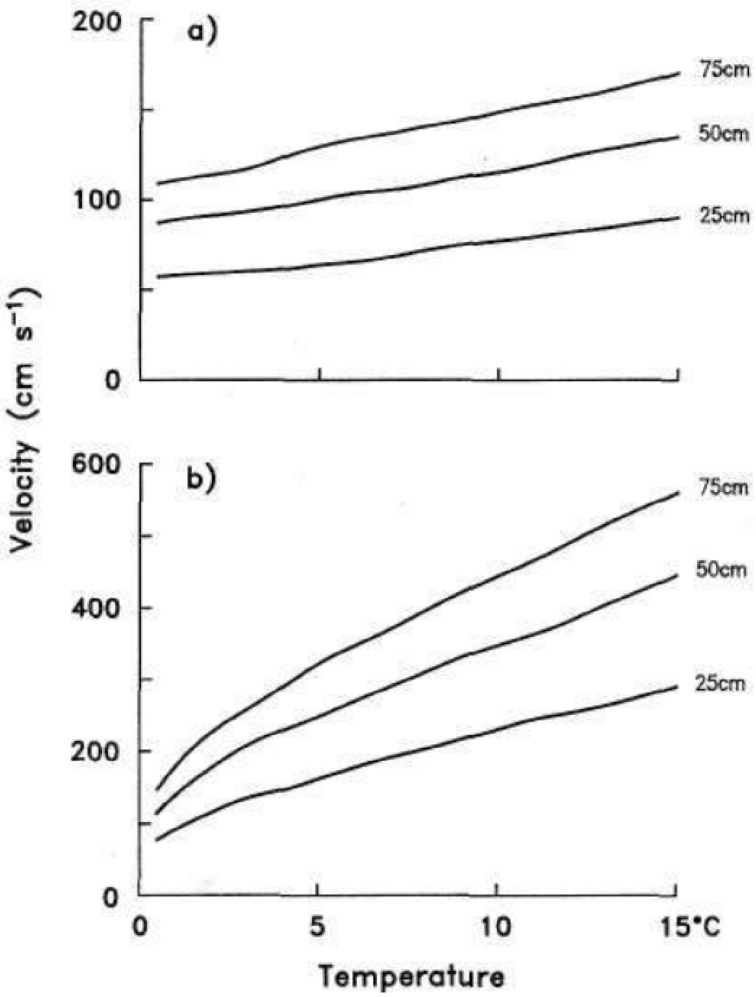


Figure 1.8 –Sustained swimming speed (V_{sust}) (a) and burst swimming speed (V_{max}) (b) based on temperature for fish of three different lengths. From Crisp (1993).

1.5 Priorities in river research and management

1.5.1 Habitat (hydromorphological) assessment

The importance of assessing physical habitat quality as part of a multi-indicator approach to river health assessment (Boulton, 1999) has been made clear (Harper & Everard, 1998), and is now a requirement under the WFD (EC, 2000), yet the development of appropriate methods has been slow in comparison to those for water quality and biological assessment (Maddock, 1999). A number of stream reconnaissance methods have been developed from a geomorphological perspective (*e.g.* Downs & Brookes, 1994; Newson, 1997; Thorne, 1998) but these are typically at a broad scale, lack ecological relevance (Vaughan *et al*., 2009) and require expert knowledge in order to interpret channel features and underlying processes (Downs & Gregory, 2004). Habitat mapping surveys are often used for habitat assessment and stream inventory applications and rely upon classifications of pools, riffles and other habitat units (Chapter 2) (Bisson *et al*., 1982; Hawkins *et al*., 1993).

Table 1.8 – Approximate physical habitat characteristics of locations inhabited by freshwater life stages of Atlantic salmon (0+, 1+, 2+ represent age classes of juveniles). *Based on spawning adult length of 75 cm (Crisp, 1993).

Life stage	Habitat variable	Measure	Values	References
Spawning adult/egg /alevin	U (point-six)	Mean	40 cm s^{-1}	Heggberget (1991)
			53 cm s^{-1}	Beland *et al*. (1982); Moir *et al*. (1998);
		Range	15-150 cm s^{-1}	Crisp & Carling (1989); Crisp (1993)
	h	Mean	50 cm	Heggberget (1991)
			38 cm	Beland *et al*. (1982)
			25 cm	Moir *et al*. (1998)
		Range	15*-76 cm	Beland *et al*. (1982); Crisp (1993)
	Substrate	Median diameter	22 mm	Kondolf & Wolman (1993)
			37 mm*	Crisp (1993)
		Mean diameter	20.7 mm	Moir *et al*. (1998)
		Gravel depth	15-25 cm	Bardonnet & Bagliniere (2000)
		% material <1 mm by volume	2.3-8%	Moir *et al*. (1998)
			<15 %	Crisp (1993); O'Connor & Andrew (1998)
	Cover	Proximity to deep pools		White (1942); Kennedy (1984)
0+ fry and parr	U (focal point)	Range	5-15 cm s^{-1}	Morantz *et al*. (1987)
	U (point-six)	Range	10-30 cm s^{-1}	DeGraaf & Bain (1986)
		Mesohabitat range	5-100 cm s^{-1}	Crisp (1993, 1996); Heggenes (1990); Heggenes *et al*. (1999)
	h	Preference (fry)	<10 cm	Heggenes *et al*. (1999)
		Range (fry)	20-40 cm	Morantz *et al* (1987)
		Preference (parr)	<25 cm	Symons & Heland (1978); Kennedy & Strange (1982); Morantz *et al*. (1987); Heggenes (1990)
		Range	5-65cm	Heggenes (1990)
	Substrate	Range (diameter)	16-256 mm	Symons & Heland (1978)
	Cover	Overhanging or submerged vegetation, undercut banks, submerged structures (*e.g.* logs, boulders), broken water surface, deep water, coarse substrate		Gibson & Power (1975); Gibson (1978); Fausch (1993)
≥1+ parr	U (focal point)	Range	0-50 cm s^{-1}	Rimmer *et al*. (1984); Morantz *et al*. (1987); Heggenes *et al*. (1999)
	U (point-six)	Range	10-120 cm s^{-1}	Symons & Heland (1978); Morantz *et al*. (1987); Heggenes (1990); Heggenes *et al*. (1999)
	h	Range	20-70 cm	
	Substrate	Range (diameter)	64-512 mm	
	Cover	(See 0+ cover)		

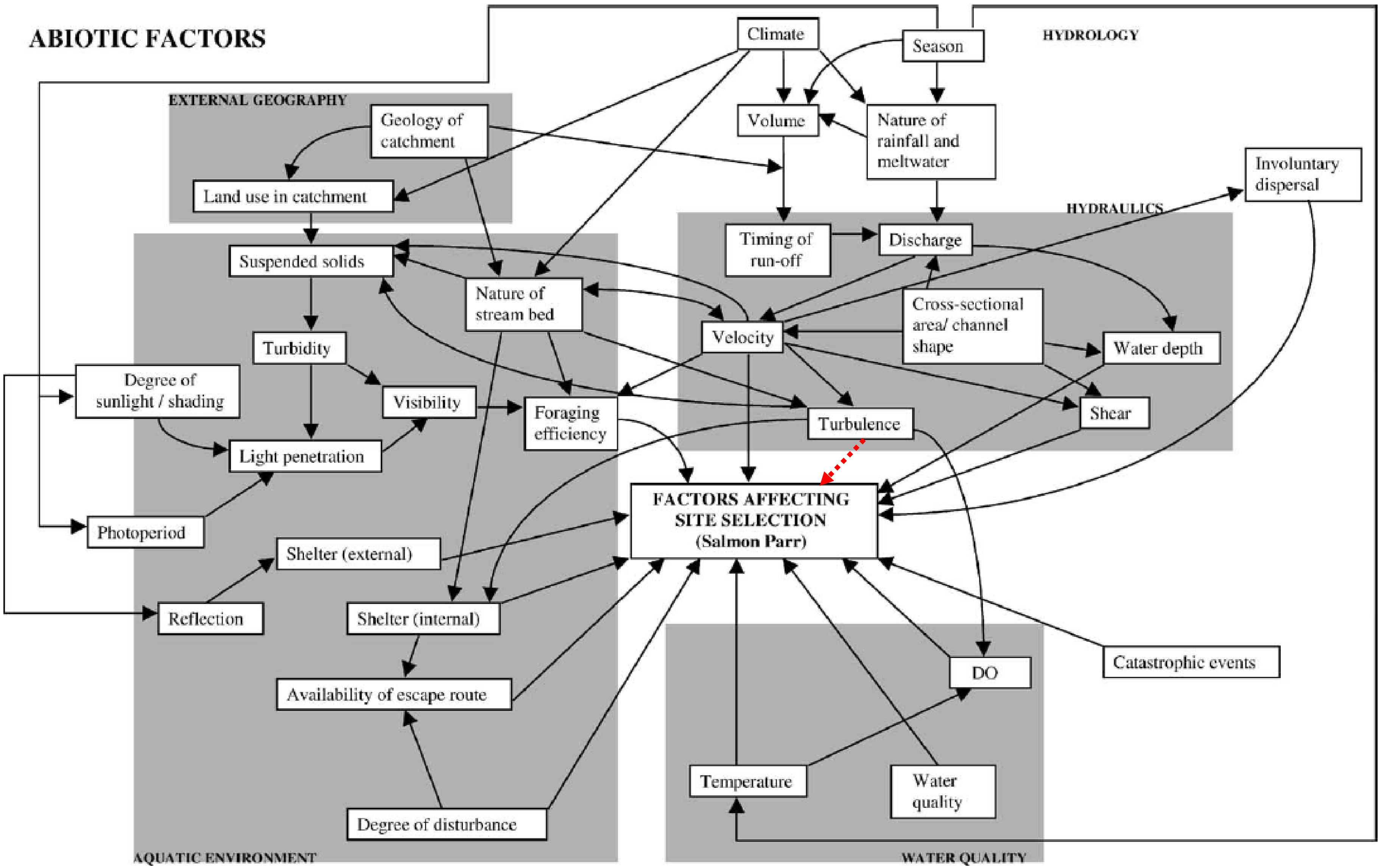


Figure 1.8 – Abiotic factors affecting Atlantic salmon parr habitat selection. From Armstrong *et al*. (2003) except dashed arrow.

These surveys range from rapid visual techniques (*e.g.* Hankin & Reeves, 1988), which lack repeatability, precision and transferability (Roper & Scarnecchia, 1995; Poole *et al*., 1997; Roper *et al*., 2002), to quantitative methods based on point measurements of hydraulic characteristics followed by numerical classification (*e.g.* cluster analysis) (Emery *et al*., 2003; Inoue & Nakano, 1999), which are time consuming and sensitive to subtle differences in data analysis techniques (Legleiter & Goodchild, 2005; Wallis *et al*., 2012).

Specific methods exist for the evaluation of fish (*e.g.* HABSCORE; Milner *et al*., 1998), macroinvertebrate (*e.g.* River Invertebrate Prediction and Classification System, RIVPACS; Wright *et al*., 1998) and macrophyte (*e.g.* Mean Trophic Rank, MTR; Holmes *et al*., 1998) habitat. These involve comparing observed densities of target biota to those expected based on physical and chemical conditions. Such methods may lack transferability outside of the region in which they were developed (Maddock, 1999) and make assumptions about the link between species and their environment, which is evaluated using correlative techniques rather than through the identification of causal mechanisms (Raven *et al*., 1998a). The System for Evaluating Rivers for Conservation (SERCON), a more general approach to habitat assessment, incorporates measures of physical habitat along with biological and catchment scale features to assess the conservation value of British rivers (Boon *et al*., 1997, 1998) and has been used to identify sites for designation as SSSIs. The basis for scoring sites in SERCON, however, relies on subjective criteria such as naturalness and representativeness (Raven *et al*., 1998a).

In England, the Environment Agency (EA) has adopted the River Habitat Survey (RHS) as its standard approach to habitat assessment and uses the technique for catchment evaluations, determining habitat suitability for key species, targeting sites for restoration and assessing the impacts of flood defence works (Elliott, 2005). RHS is a systematic method for qualitatively assessing the character and habitat quality of rivers based on valley, bank and in-channel characteristics at 10 transects along a 500 m reach (Figure 1.9) (Raven *et al*., 1997, EA, 2003a). The advantages of RHS are that it is rapid, calibrated by benchmark (top quality) sites, requires little expert training and is supported by a national database to aid comparisons with other sites in the same geographical area or of the same river type (Raven *et al*., 1998b; Harvey *et al*., 2008). Outputs in the form of Habitat Quality Assessment (HQA) and Habitat Modification Scores (HMS) make the results easily interpretable and further indices can be derived to describe more specific aspects of the physical habitat (Vaughan, 2010). Concerns raised regarding RHS include its oversimplification of complex physical and ecological phenomena (Clifford *et al*., 2006), underrepresentation of certain habitat types (*e.g.*

marginal deadwaters, chutes, glides) (Padmore, 1997a; Newson *et al*., 1998) and insensitivity to small scale (~1 m^2) spatial heterogeneity and discharge related variability in physical habitat conditions (Townsend *et al*., 1997; Padmore, 1998). **There remains an urgent need for a more quantitative, robust, transferable and ecologically explicit approach to habitat assessment in order to achieve targets set by the WFD and to support ongoing river research and management activities** such as habitat modelling (S 1.5.2), river rehabilitation (S 1.5.3) and the conservation of key biota (S 1.5.4) (Newson & Large, 2006; Vaughan *et al*., 2009; Boon *et al*., 2010).

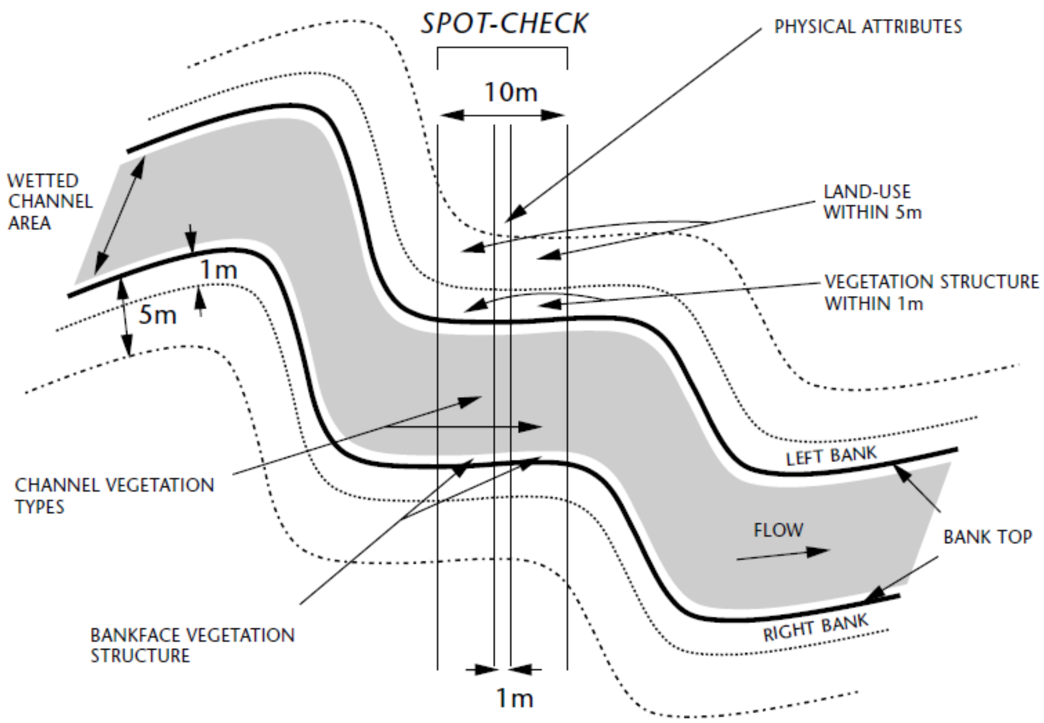


Figure 1.9 – Dimensions and characteristics recorded at cross-sections ('spot-checks') when carrying out RHS. From Environment Agency (2003a).

1.5.2 Habitat modelling

A great number of different types of ecological model have been developed such that a detailed review is not possible here. In the context of river ecosystems they have predominantly been applied to fish populations, although many can also be used for other biota such as macroinvertebrates (*e.g.* Gore *et al*., 1998) and macrophytes (*e.g.* Hearne *et al*., 1994). The two main types of model focus on population distribution and population ecology respectively (Frank *et al*., 2011). The former of these model types typifies the conventional approach in hydroecological research and river management (Jowett, 1997; Lamouroux & Capra, 2002). These 'habitat-hydraulic' models combine hydromorphological assessment, hydraulic modelling and knowledge of the habitat preferences of target biota in order to predict the quantity of suitable habitat at a given flow stage. The Physical Habitat Simulation system (PHABSIM; Milhous *et al*., 1984) has been the most popular of these models for the last three decades (Jowett, 1997; Petts, 2009). PHABSIM has been used to assess changes in species-specific habitat associated with impoundment (*e.g.* Gibbins & Acornley, 2000), abstraction (*e.g.* McPherson, 1997), channelisation (*e.g.* Booker & Dunbar, 2004) and river rehabilitation (*e.g.* Acreman & Elliott, 1996). The technique involves the collection of detailed data on channel topography, h, U and D at 'representative cross-sections' over a range of discharges to describe the microscale physical habitat conditions within a 'representative reach'. The topographic and hydraulic data are then fed into a hydraulic model to provide information on physical habitat availability across a range of discharges based on real or hypothetical hydrographs. The preferences of target biota for each physical habitat variable are represented as Habitat Preference Curves (HPCs) or Habitat Suitability Curves (HSCs) which are derived empirically for the site being modelled, usually through snorkel (*e.g.* Guay *et al*., 2000) or electrofishing surveys (*e.g.* Remshardt & Fisher, 2009), or taken from the literature (*e.g.* Bovee, 1982). PHABSIM outputs are in the form of a Weighted Useable Area (WUA) versus discharge relationship for the chosen site and target species (Figure 1.10).

Despite their widespread application, PHABSIM and other similar techniques (*e.g.* River HABitat SIMulation, RHABSIM – Payne & Associates, 1994; EValuation of HAbitat, EVHA – Ginot, 1998; River HYdraulics and HABitat SIMulation, RHYHABSIM – Jowett, 2004), known as Habitat Suitability Index (HSI) based models, have been criticised for a number of reasons:

- *Data intensiveness*. As microhabitat methods they require intensive field data collection to calibrate the hydraulic model (Parasiewicz & Dunbar, 2001).
- *Transferability*. HPCs lack transferability due to differences in habitat availability, ontogenetic shifts in habitat use and the strong genetic and phenotypic variation among populations (Heggenes, 1996; Frank *et al*., 2011). For reliable results, therefore, expensive and time consuming site-, species- and life stage-specific HSCs must be developed through empirical observation of fish locations (Gore & Nestler, 1988; Heggenes, 2002).
- *Predictions*. They are generally poor predictors of species requirements (Scott & Shirvell, 1987; Bourgeois *et al*., 1996; but see Orth & Maughan, 1982; Bovee *et al*., 1998) as they assume that organisms respond in a predictable and continuous manner to changes in habitat availability, yet there is no evidence for a linear relationship between WUA and fish

biomass (Mathur *et al*., 1985; Gore & Nestler, 1988) and individual responses are known to vary (Murchie *et al*., 2008).

- *Interpretation*. Their outputs are not probabilistic (Lancaster & Downes, 2010) but are often treated as such (Mathur *et al*., 1985). WUA combines habitat quantity and quality into a single index (Scott & Shirvell, 1987) but these components should be assessed separately (Newson & Large, 2006). It can be difficult to base management decisions on the results due to uncertainty associated with their meaning (*e.g.* what does a decline of 50% in WUA mean for resident biota?) (Raven *et al*., 1998b; Maddock, 1999; Booker & Dunbar, 2004).
- *Restrictiveness*. They are restricted in their utility to cases where physical habitat is the factor limiting the size and structure of the target population (Hardy, 1998; Guensch *et al*., 2001) as they do not include other potentially limiting factors like water quality (Castleberry *et al*., 1996; Van Winkle *et al*., 1997; Booker & Dunbar, 2004).
- *Physical habitat characterisation*. Even in the above cases, they may not adequately characterise the physical habitat available due to the crude application of 'representative transects' (Parasiewicz, 2001; Clifford *et al*., 2002; Lancaster & Downes, 2010). Additionally, they often neglect important physical variables like cover (*e.g.* overhanging vegetation, undercut banks), velocity gradients and turbulence, factors which are particularly important for juvenile salmonids (S 1.4.3, Appendix C) (Hayes & Jowett, 1994; Heggenes, 1996; Smith *et al*., 2006).
- *Ecological realism*. They ignore biological interactions (*e.g.* competition, predation, food availability) (Nislow *et al*., 1999; Guay *et al*., 2003; Lancaster & Downes, 2010). They do not model the spatial dynamics (*e.g.* size, configuration and connectivity) of habitat patches (Maddock, 1999; Murchie *et al*., 2008). They are univariate and assume that fish select physical habitat variables (*e.g.* depth, velocity, substrate) independently, yet significant interactions may exist (Mathur *et al*., 1985; Gore & Nestler, 1988; Heggenes, 1996). They also assume that fish track preferred habitats as discharge increases but there is evidence that some fish may be site-attached (Kemp *et al*., 2003). They generally rely on one-dimensional hydraulic models which oversimplify the flow environment and have limited temporal resolution (Gordon *et al*., 2004; Clifford *et al*., 2002; Booker & Dunbar, 2004). They do not operate over ecologically relevant space and time scales (Railsback *et al*., 1999; Dunbar *et al*., 2011). Furthermore, they assume that U_m influences habitat choice, yet instantaneous flow velocities (e.g. turbulent flow properties, Chapter 3) at the focal position of an organism are more important (Scott & Shirvell, 1987; Heggenes, 2002; Armstrong *et al*., 2003).

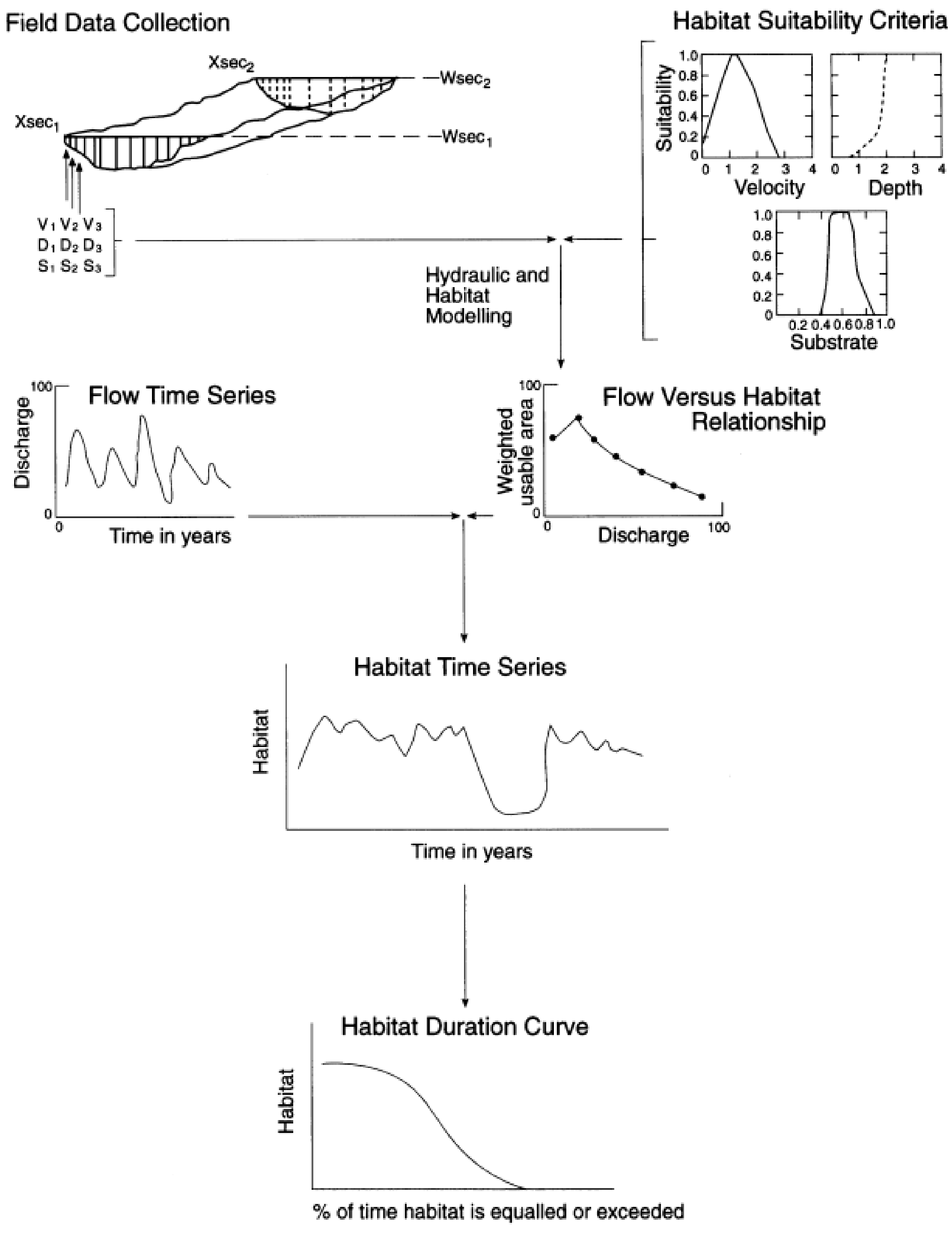


Figure 1.10 – The basis of PHABSIM showing the integration of hydraulic measurements and habitat suitability criteria to define the flow vs. habitat relationship. This can be combined with a flow time series to produce a habitat time series and habitat duration curve. From Nestler *et al*. (1989), Maddock (1999).

A number of alternatives to traditional HSI-based models have been suggested, although none represents a panacea for the above problems (Table 1.9). Three-dimensional hydraulic simulations can be used with different types of habitat models to increase ecological realism and better characterise physical habitat conditions by providing spatially explicit hydrodynamic information at a scale relevant to biota and providing output in the form of weighted useable volume (WUV) rather than WUA (Mader *et al*., 2005; Mouton *et al*., 2007a). Two- and three-dimensional hydraulic models also require less calibration than one-dimensional versions, thereby minimising data collection requirements (Austin & Wentzel, 2001; Parasiewicz & Dunbar, 2001). Microscale alternatives to univariate HSI-based models include fuzzy and multivariate approaches, which allow for interaction between habitat variables. The Computer Aided Simulation for Instream Flow Requirements (CASIMIR) model employs a three-dimensional 'river bed model' to simulate near-bed flow forces and uses fuzzy rules to combine preferences for h, U, D and cover into a categorical (low, medium, high) suitability index (Giesecke *et al*., 1999). A drawback is that the model relies on subjective 'expert knowledge' on the preferences of target species to define fuzzy membership levels (Jorde *et al*., 2001). Multivariate models are capable of integrating a wider range of ecological variables, including cover types and water quality parameters, by using logistic regression to provide truly probabilistic results (Parasiewicz *et al*., 1999; Ayllón *et al*., 2009). Using one such multivariate model, Guay *et al*. (2000, 2003) found that a Habitat Probabilistic Index (HPI) gave more accurate and transferrable predictions than a univariate HSI when applied to the Atlantic salmon populations of two Canadian rivers. Results from multivariate models, however, can be difficult to interpret (Parasiewicz & Dunbar, 2001; Lancaster & Downes, 2010).

The pressure on river management agencies to evaluate habitat quality rapidly across extensive river systems has led to the development of models at larger scales than traditional microhabitat models (Kershner & Snider, 1992). Mesoscale models involve classifying and mapping mesohabitats (Chapter 2) in an attempt to 'upscale' predictions from representative reaches to whole rivers. Such models better reflect the spatial dynamics of physical habitat conditions (Parasiewicz & Dunbar, 2001) but suffer from varying levels of subjectivity associated with the classification of habitat types (Eisner *et al*., 2005). They can be used with multivariate (*e.g.* MesoHABSIM) or fuzzy (*e.g.* MesoCASIMIR) analyses of habitat preference to combine the advantages of both approaches, often leading to better predictions. For instance, in a comparison between MesoHABSIM, PHABSIM and HARPHA, Parasiewicz and Walker (2007) found that only MesoHABSIM predictions were significantly correlated with the abundances of five coarse fish species in a section of the Quinebaug River, USA.

Others have incorporated mesoscale habitat mapping into studies utilising PHABSIM for the purposes of selecting representative reaches and transects (Kershner & Snider, 1992; Maddock *et al*., 2001), but these do not constitute mesoscale models *per se*. At the reach-scale, Lamouroux *et al*. (1998) used a rapid multivariate technique requiring simple average hydromorphic input variables (discharge-dependent width and depth, bed particle size) to explain up to 95% of the variance in fish community structure in the Rhône River, France. Lamouroux and Jowett (2005) found that this 'generalized' method was highly transferrable between rivers in France and New Zealand, despite very different biogeoegraphic and geomorphic contexts. This reach scale approach, however, is incapable of predicting the abundance of separate size classes for each species (Lamouroux *et al*., 1999) and is associated with a loss of information in comparison to microscale models (Lamouroux & Jowett, 2005).

One of the most common criticisms of HSI-based models is that they lack a mechanistic basis for their predictions (*e.g.* Mathur *et al*., 1985; Scott & Shirvell, 1987; Nislow *et al*., 1999; Vaughan *et al*., 2009; Lancaster & Downes, 2010). This is a problem which is not addressed by the alternatives outlined above. Instead, bioenergetic models founded on optimal foraging theory (*e.g.* Hughes & Dill, 1990) and Individual-Based Models (IBM) incorporating a range of biotic and water quality parameters (*e.g.* INSTREAM; Railsback *et al*., 2009) can be used over ecologically relevant timescales (Railsback *et al*., 1999). Such models can be combined with three-dimensional hydraulic models (*e.g.* Booker *et al*., 2004) to offer more transferrable, mechanistic and easily interpretable results. The ultimate aim for habitat modellers, particularly those studying salmonids, is to integrate detailed and spatially explicit ecological, demographic and genetic information into demogenetic models to assess biological responses to a range of management and conservation activities (Lancaster & Downes, 2010; Frank *et al*., 2011). The development of such sophisticated models, however, is not at a stage where they can replace more traditional methods. Lamouroux *et al*. (2010) have argued that correlative techniques provide relatively good predictions in the absence of sufficient knowledge for widespread application of new integrative models. **A realistic priority for hydroecological research, therefore, is to improve mesoscale multivariate models by identifying the key habitat variables that biota respond to at this scale and linking with bioenergetic models and IBMs to provide a more mechanistic basis for predicting the outcome of management actions** (*e.g.* river rehabilitation).

Table 1.9 – Alternative habitat-hydraulic models and their advantages over traditional HSI-based methods in relation to the criticisms in the text ('remedial properties' indicated by •).

		Remedial properties						
Model type	**Examples**	Data intensiveness	Transferability	Predictions	Interpretation	Restrictiveness	Physical habitat characterisation	Ecological realism
2D and 3D hydraulic models	2D model (Austin & Wentzel, 2001) 3D HAbitat MOdelling SOFTware (HAMOSoft) (Mader *et al*., 2005; Mouton *et al*., 2007a)	•					•	•
Fuzzy microscale	Computer Aided SIMulation for Instream flow Requirements (CASIMIR) (Giesecke *et al*., 1999; Jorde *et al*., 2000, 2001; Mouton *et al*., 2007b)							•
Multivariate microscale	Habitat probabilistic model (Guay *et al*., 2000, 2003); Hybrid Approach for Riverine Physical HAbitat (HARPHA) (Parasiewicz *et al*., 1999); Resource Selection Function (RSF) Ayllón *et al*., 2009)		•	•		•	•	•
Mesoscale	MesoHABSIM (Parasiewicz, 2001, 2007) MesoCASIMIR (Schneider *et al*., 2005) Norway Mesohabitat Classification Method (NMCM) (Borsányi *et al*., 2004; Halleraker *et al*., 2005)	•		•				•
Reach scale ('generalized')	Lamouroux *et al*. (1998, 1999); Lamouroux & Capra (2002); Lamouroux & Jowett (2005)	•	•					
Bioenergetic and individual-based (IBM) models	Hughes & Dill (1990); Addley (1993); Clark & Rose (1997); Van Winkle *et al*. (1998); 3D hydraulic-bioenergetic model (Booker *et al*., 2004); INdividual-based Stream Trout Research and Environmental Assessment Model (INSTREAM) Railsback *et al*., 2009)		•		•	•	•	•

1.5.3 River restoration and rehabilitation

The restoration of British rivers began in earnest in the 1980s (Adams *et al*., 2004; Ormerod, 2004), boosted by influential publications (*e.g.* Purseglove, 1988) and key events such as the 1990 River Conservation and Management conference in York (Boon *et al*., 1992). The practice has now become a lucrative industry in the USA (Bernhardt *et al*., 2005) and, in Europe, it is a key objective in achieving targets set by the WFD and other legislation (S 1.2.3) (Newson, 2002; Clarke *et al*., 2003; Skinner & Bruce-Burgess, 2005). Despite this, there is still no consensus as to the definition of river restoration (Large & Newson, 2005; but see Brookes & Shields, 1996). Bradshaw's (1984) model (Figure 1.11) illustrates the true meaning of restoration as a return to the original or 'natural' (pre-industrial) ecosystem. Due to the lack of detailed information on historical or natural 'reference' conditions and the processes which maintain them (Ward *et al*., 2001), many commentators prefer to use the term 'river rehabilitation' (*e.g.* Brierley *et al*., 2010), which may be defined as any attempt to improve the ecological integrity of a river system (Palmer *et al*., 2005). This represents a pragmatic approach to improving hydromorphological form and process that avoids unproductive debates about 'nature' and relies on the assumption that physical habitat diversity equates with biological diversity (Osborne *et al*., 1993; Newson & Large, 2006). Biogeographical and ecological factors (Bond & Lake, 2003), however, together with our incomplete understanding of natural form and process (Ward *et al*., 2001) may mean that biota do not respond to physical habitat rehabilitation (*e.g.* Pretty *et al*., 2003; Jähnig & Lorenz, 2008).

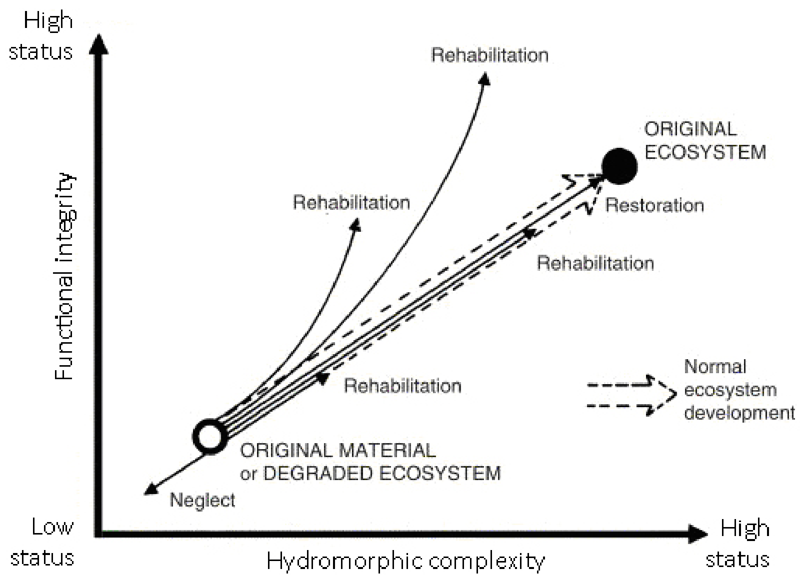
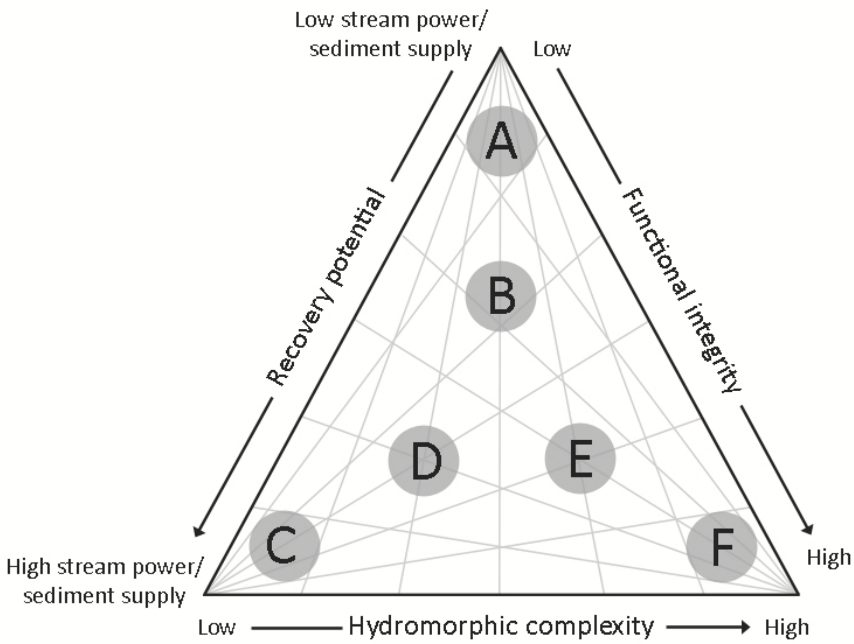


Figure 1.11 – The processes of river restoration and rehabilitation from a hydromorphological perspective. Modified from Bradshaw (1984), Newson and Large (2006).

Rehabilitation options for river managers depend on the levels of structural and functional degradation exhibited by the site in question, as well as its recovery potential (Figure 1.12), which is a function of stream power and sediment supply (Brookes, 1992). The rehabilitation of flow and sediment regimes is necessary where abstraction or impoundment limits recovery potential. Tools for river managers include bottom-up decision making frameworks based on the results of habitat modelling, such as the Instream Flow Incremental Methodology (IFIM; Bovee & Milhous, 1978; Bovee, 1982) within which PHABSIM operates, and top-down approaches driven by the belief that indices reflecting hydrological alteration integrate the complexity of ensuing biological responses (*e.g.* Richter *et al*., 1996). Solutions must incorporate a range of hydrological features critical for ecological functioning (*e.g.* flushing, channel maintenance, floodplain flows) (Petts, 1996; Poff *et al*., 1997; Bragg *et al*., 2005; Petts, 2009) based on comprehensive, river-type specific environmental flow assessments (Arthington *et al*., 2006).



Condition	Options to achieve good ecological status
A	Non-structural methods; rehabilitate flow and sediment regimes; prompted recovery; morphological reconstruction
B	Non-structural methods; rehabilitate flow and sediment regimes; prompted recovery
C	Non-structural methods or natural recovery
D	Non-structural methods
E	Non-structural methods; rehabilitate flow and sediment regimes
F	Good status – mitigate against degradation

Figure 1.12 – Options for rehabilitating degraded river channels. Based on Brookes (1992), Downs & Gregory (2004) and Newson & Large (2006).

Prompted recovery using instream structures (*e.g.* boulder clusters, vanes, deflectors) (Brookes & Shields, 1996) may be required in order to encourage the development of local patterns of scour and sediment deposition at sites affected by hydromorphological modification such as overwidening or other forms of channelisation. Other potential instream works include the introduction of features with specific ecological functions such as woody debris (Crook & Robertson, 1999) or fish passes

(Larinier & Marmulla, 2004), or the removal of barriers (*e.g.* weirs) (Garcia de Leaniz, 2008; Kemp & O'Hanley, 2010). Wholesale morphological reconstruction may be the only acceptable solution at severely degraded sites (*e.g.* Pedersen *et al*., 2007), particularly those in urban areas (Bernhardt & Palmer, 2007; *e.g.* Biggs *et al*., 1998). In such cases care should be taken to rehabilitate key geomorphic processes (*e.g.* sediment storage and transport) in order to ensure long-term sustainability (Sear, 1994; Clarke *et al*., 2003; Wohl *et al*., 2005). Non-structural measures such as strategic land-use planning at the catchment scale (*i.e.* IRBM), the establishment of valley floor wetlands (*e.g.* Sear *et al*., 1994) or the planting of riparian buffer strips (Haycock *et al*., 1997), may suffice to assist natural recovery without local intervention where recovery potential is evident. Where time and space is available to allow a river with sufficient recovery potential to adjust naturally then the best approach may be to do nothing (Brookes, 1992).

The above techniques represent broad options for river rehabilitation but, as Hynes (1975, p.12) stated, "*every stream is likely to be individual*". The uniqueness of river systems (Poole, 2002) precludes the use of 'off-the-shelf' rehabilitative solutions. Flexible design criteria are required and, although comprehensive manuals of restoration techniques have been developed (*e.g.* River Restoration Centre, 2002), such criteria are hard to come by (Biron *et al*., 2004; Skinner & Bruce-Burgess, 2005; Miller & Hobbs, 2007; but see Newson, 2002). Suitable channel design dimensions may be estimated using simple rules from regime theory (Hey, 1997) or hydraulic geometry (Rosgen, 1994, 1996) and some progress has been made on the geomorphic characteristics and hydraulic functioning of designed pool-riffle sequences (*e.g.* Table 1.10) (Clifford & French, 1998; Clifford *et al*., 2002; Emery *et al*., 2003; Pasternack *et al*., 2008), but other habitat types (*e.g.* runs, glides, marginal habitats) have been neglected (Brierley *et al*., 2010). Two further criticisms of river rehabilitation projects have been their ignorance of spatial and temporal dynamics (Clarke *et al*., 2003; *e.g.* Harrison *et al*., 2004) at ecologically relevant scales (Lake *et al*., 2007) and the lack of pre- and post-project monitoring undertaken (Ormerod, 2004; Berhardt *et al*., 2005, 2007; Giller, 2005; Souchon *et al*., 2008).

River rehabilitation should now be approached from a 'design-with-nature' perspective (Downs & Gregory, 2004) according to the principles of landscape ecology (Palmer *et al*., 1997). Solutions should recognise the importance of creating, or assisting natural recovery (Brookes & Sear, 1996; Newson *et al*., 2002) of spatially complex and temporally dynamic hydromorphic conditions (Brookes, 1996; Biggs *et al*., 2005; Thoms *et al*., 2006; Palmer *et al*., 2007) typical of the reach type in question (Montgomery & Buffington, 1997; Newson *et al*., 1998). Any approach incorporating dynamicity is inherently uncertain (Hillman & Brierley, 2005; Perrow *et al*., 2008) and, therefore, adaptive management based on ongoing monitoring is necessary (Palmer *et al*., 2005; Gregory & Downs, 2008; Skinner *et al*., 2008). Since relatively little funding is made available for Post Project Appraisal (PPA) (Clarke *et al*., 2003; Bernhardt *et al*., 2007) **there is an urgent need for rapid measures of rehabilitation performance** (Ormerod, 2004; Wohl *et al*., 2005) **that integrate and quantify complex hydromorphic factors** (*e.g.* flow dynamics, substrate size and structure, cover) **as part of a systematic, standardised protocol** (Bernhardt *et al*., 2005; Vaughan *et al*., 2009; *e.g.* Woolsey *et al*., 2007).

Table 1.10 – Geomorphic design and location for pools and riffles. From Brookes & Sear (1996).

Pools	• slower water often asymmetrical in cross-section, even in straight channels • floored by loose, mixed sandy gravels • often up to 25% narrower than riffle sections at all discharges of a minimum 3 m depth • located at apexes of meanders • associated with gravel shoals/bars exposed at low discharges • ecologically important for aquatic macrophytes and fish species • recreational importance – fish/boating/tranquillity • may periodically fill with sediments, particularly when there is an excessive sediment load derived from upstream. Sediments may later scour out during a flood event
Riffles	• locally steep, shallow section of river profile, generally symmetrical in cross-section • characterised by rapid, turbulent flow at low discharges • often up to 25% than pools at all discharges • located at cross-over points in meanders or spaced between three and ten widths (higher slope – shorter spacing) • mixed gravel substrate with a coarser, tightly packed, surface armoured layer. Larger stones should be spaced over the riffle surface to break up low flow patterns and induce turbulence • expected to fill with sediment after flood events which scour upstream pools. Excess sediment will be moved into downstream pool during subsequent lower flood discharges

1.5.4 Conservation and rehabilitation of Atlantic salmon populations

Atlantic salmon has a high conservation status in the UK due to its environmental, economic and social importance. It is also recognised as a threatened species (IUCN, 2011) and is protected under the Habitats Directive (EC, 1992). As an anadromous fish Atlantic salmon is a keystone species, bringing marine-derived nutrients to nutrient-poor environments (Jonsson & Jonsson, 2003; Naiman & Latterell, 2005) and providing food for range of predatory fish, birds and mammals (Wilson & Halupka, 1995). The socioeconomic value of the species is well established. Angling is the most popular sport in England and Wales, with 1.18 million rod licenses purchased in 2002/03 (EA, 2004) and, although salmon fishing represents only a small proportion of this, the value of the species to the economies of England and Wales is disproportionately large. Commercial and recreational fishing for Atlantic salmon and sea trout (*S. trutta*) contributed an estimated £550 million yr^{-1} combined in the 1980s and 1990s (Simpson & Mawle, 2001; Murray & Simcox, 2003). Angling also has social benefits, connecting people with their environment and providing positive experiences for young people from deprived areas (Peirson *et al.*, 2001). Furthermore, Atlantic salmon are an iconic species to which art and culture have attached great meaning (*e.g.* Hughes, 1983).

Despite the multiple values placed on Atlantic salmon, a number of European populations have declined or disappeared in recent decades (Figure 1.13) and many fisheries are now entirely dependent on restocking through hatchery releases (Parrish *et al*., 1998). Data from a range of sources (*e.g.* rod catch records, fish traps, counters, commercial catch data) show that conservation limits (minimum target level of spawning to sustain population) set by the EA were not met (‘at risk’) in 36% of principal English and Welsh rivers in 2010, including designated SSSIs and SACs (*e.g.* River Wye), with a further 25% ‘probably at risk’ of failing to comply (Figure 1.14). The major reasons for population declines and extirpations have been cited as overexploitation, poor water quality (*e.g.* nutrient enrichment, temperature and dissolved oxygen changes; pesticides, toxic spillages), modified flow regimes (*e.g.* land drainage, flow regulation), structural modification (*e.g.* channelisation, siltation), barriers to migration (*e.g.* weirs, dams, culverts), predation by increasing numbers of predatory birds (*e.g.* cormorant, *Phalacrocorax sp.*), introduction of non-native predators (*e.g.* zander, *Stizostedion lucioperca*), and the effects of hatchery releases and salmon farm escapees (*e.g.* competition, disease, genetic interbreeding) (Hendry *et al*., 2003; Roberge *et al*., 2008; Jonsson & Jonsson, 2009). The effects of these factors on salmon populations are complex, often indirect and occurring in combination over multiple scales (Armstrong *et al*., 1998; Ruckelshaus *et al*., 2002; Ormerod, 2003). The most common factor in the failure, or threat of failure, of English and Welsh rivers to comply with conservation limits is physical habitat degradation (NASCO, 2009). Human activities have altered hydromorphic conditions, reducing the quantity and quality of habitat suitable for different freshwater life stages (S 1.3.2, S 1.4.3).

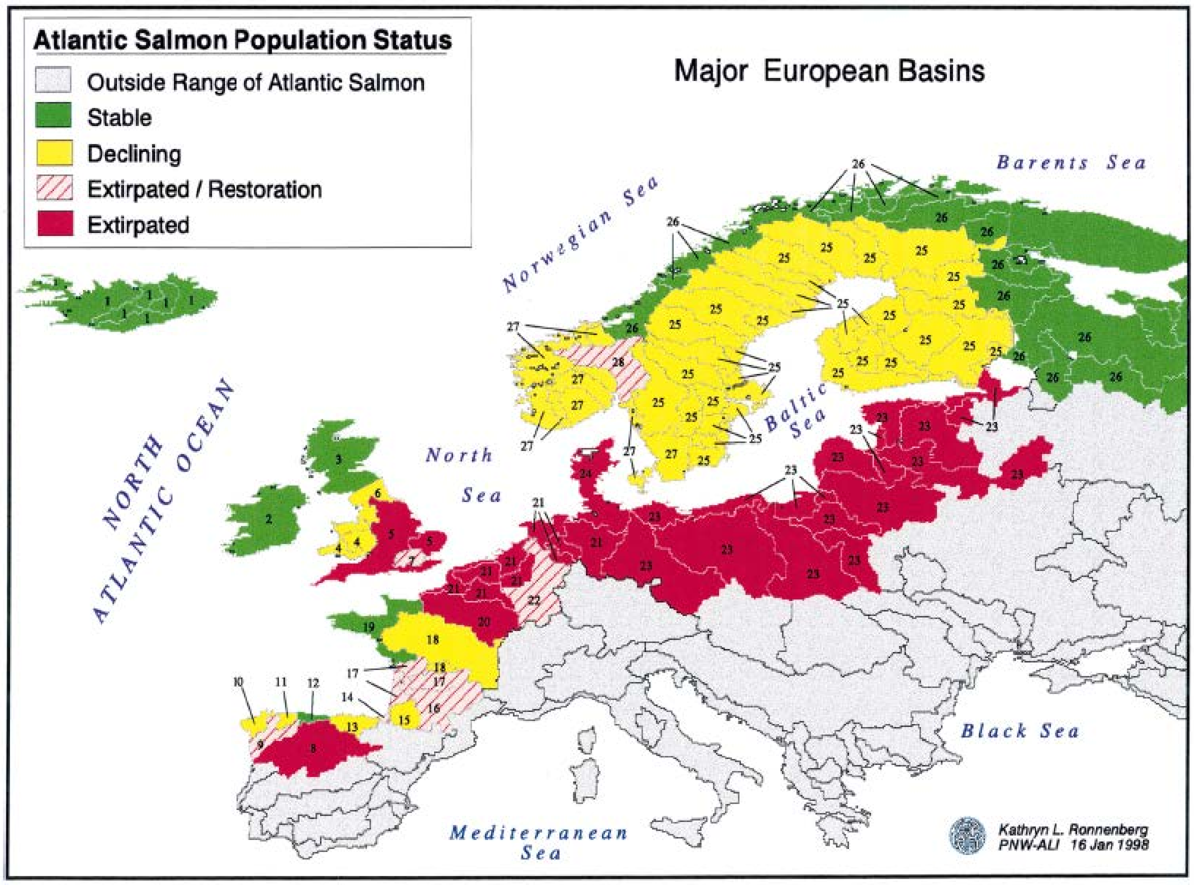


Figure 1.13 – Atlantic salmon population status for major watershed throughout its European range. Categories are extirpated (no returns for >10 years), extirpated with restoration (no returns for >10 years followed by reintroduction), declining (decreasing trend for >10 years) and stable (no consistent decline for 10 years). Categorisation based on expert knowledge. Note Iceland and Russia not to scale and some rivers have recovered since publication. From Parrish *et al*. (1998).

The EA's response to the decline of Atlantic salmon populations has been in the form of Salmon Action Plans (SAPs) for key salmon river basins and, more recently, the identification of salmon management needs in River Basin Management Plans (RBMPs) for 11 major catchments in England and Wales. SAPs and RBMPs attempt to identify the causes of failure to comply with environmental objectives and set out management actions to address them (NASCO, 2009). Such management plans have emphasised the need to address limiting factors for juveniles at the intragravel and free-swimming stages (*e.g.* EA, 2003b). Limiting factors at critical periods, or 'bottlenecks', include poor physical habitat quality for drift-feeding parr (Nislow *et al*., 1999, 2004; Armstrong, 2005). The River Wye SAP, for example, identifies actions such as improving juvenile habitat through cleaning gravels, excluding livestock and planting riparian vegetation (EA, 2003b). Many salmonid conservation and rehabilitation schemes involve restocking with hatchery reared eggs, fry or parr, often with limited success in achieving self-sustaining populations due to the reduced performance of hatchery bred fish and/or the continuing influence of poor physical habitat quality (Crozier *et al*., 1997; Ritter, 1997; Carr *et* al., 2004; Frankham, 2008; Fraser, 2008). Indeed, hatchery releases may well have detrimental effects on wild Atlantic salmon populations if not undertaken with knowledge of population dynamics (Armstrong, 2005; Einum *et al*., 2008). Research using genetic analyses and tagging have shown that, where habitat conditions have been improved, population recovery can occur through natural recolonisation by straying adults from neighbouring populations (Fraser *et al*., 2007, Dillane *et al*., 2008; Griffiths *et al*., 2011).

The general view now is that habitat rehabilitation is preferred to stocking when attempting to rejuvenate salmon populations (Jonsson & Jonsson, 2009; Griffiths *et al*., 2011). Previous attempts to improve physical habitat quality for salmonids and other fish, however, have not always been successful. The most commonly cited reasons for the perceived failure of projects, such as those listed in Table 1.11, are the inappropriate scale and hydromorphic characteristics of installed features (Pretty *et al*., 2003; Koed *et al*., 2006) and the inadequate design of project monitoring protocols (Baldigo & Warren, 2008; Summers *et al*., 2008; Jähnig *et al*., 2011). Many rehabilitation projects are founded on the assumption that increased physical habitat complexity will yield enhanced population numbers as a result of simple behavioural effects (*e.g.* reduced territory size) (Kalleberg, 1958). Results from controlled laboratory tests on parr, however, suggest that enhancing habitat complexity through the addition of instream structures decreases foraging rates and increases energy expended on swimming, energetic costs which may offset any potential benefits of increased habitat complexity (Kemp *et al*., 2005). In order to address the continuing decline of many Atlantic salmon populations, it is crucial that conservation and rehabilitation projects have a sound scientific basis, clear goals and adequate monitoring. **The identification of key biophysical linkages determining juvenile salmonid production, such as the energetic costs** (Enders *et al*., 2003) **and/or benefits** (Liao *et al*., 2003a) **of swimming in turbulent flow** (Appendix C, Chapter 5) **will assist in the suitable design of management plans**.

Table 1.11 – Summary of outcomes of physical habitat rehabilitation projects targeted at fish. Refers to effects on Atlantic salmon unless stated otherwise.

Site	Management action	Outcome	Reference
13 rivers in lowland Britain	Installation of riffles and flow deflectors	No significant improvement of total fish abundance, species richness or equitability. No Atlantic salmon individuals found	Pretty *et al*. (2003)
Six streams in Vermont, USA	Addition of large instream structures (woody debris, boulders)	Increased availability of suitable foraging locations for parr in spring but not summer	Nislow *et al*. (1999)
River Skjern, Denmark	Removing dykes, re-meandering, lake construction	Increased mortality of smolts due to bird predation mediated by constructed lake	Koed *et al*. (2006).
River Nidelva, River Daleeva, Norway	Addition of spawning gravels at four sites	Increased number of redds at two sites over four years. Failure due to scour during floods at two sites	Barlaup *et al*. (2008)
River Piddle, Devil's Brook, Dorset, England	Fencing to exclude livestock and pool excavation at three sites	Increased abundance of juvenile brown trout at two sites. Decreased abundance at one site	Summers *et al*. (2008)
26 projects in piedmont and lowland rivers in Germany	Addition of gravels, wood placement, installation of flow deflectors and morphological reconstruction	Over 50% of projects did not result in improved fish communities. 84% of restored reaches still not achieving good ecological status under the WFD.	Jähnig *et al*. (2011)
Brierly Brook, Nova Scotia, Canada	Addition of large instream structures (artificial woody debris, deflectors)	Increased spawning, fry and parr densities. Direct observations of juveniles using structures	Floyd *et al*. (2009)
Four streams in New York, USA	Morphological reconstruction, rehabilitation of sediment regimes	Increased densities of brown trout and brook trout (*Salvelinus fontinalis*). Increased richness of fish community. No Atlantic salmon found	Baldigo *et al*. (2008)
Müggelspree, Germany	Morphological reconstruction (remeandering)	Decreased densities of rheophilic and lithophilic species. No effect on richness and diversity of fish community. No salmonids found	Wolter (2010)
River Spree, Berlin, Germany	Installation of artificial backwaters and marginal nursery habitat	Increased densities of rheophilic and phyto-lithophilic species. No effect on richness and diversity of fish community. No salmonids found	Wolter (2010)

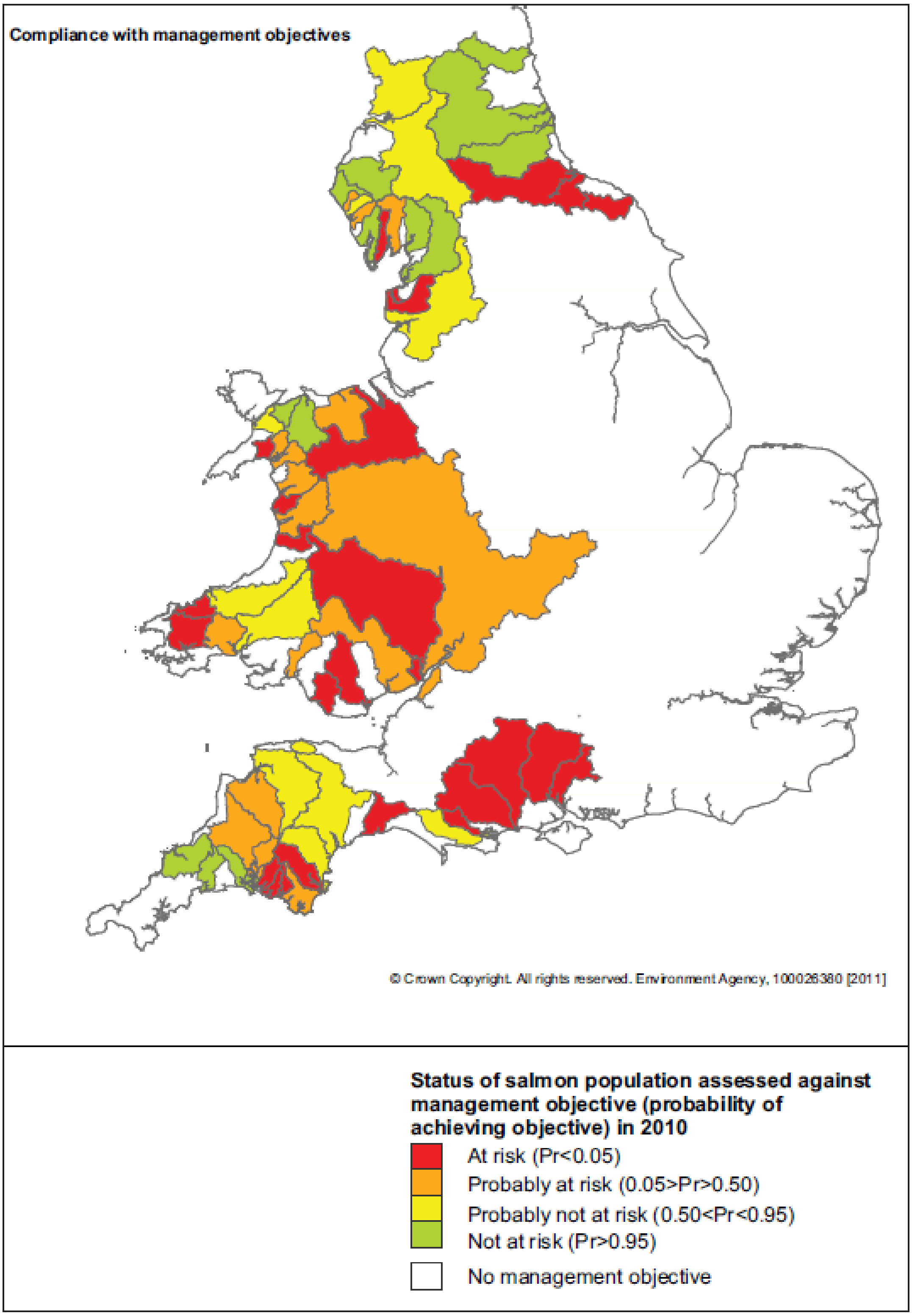


Figure 1.14 – Conservation status of principal salmon rivers in England & Wales. Risk categories indicate probability that river basin has achieved or exceeded its conservation limit (see text for explanation). Note, only includes rivers with Salmon Action Plans. From EA (2011).

In conclusion, river research and management in the past 50 years has progressed from hard engineering of river channels (S 1.3.2) to evidence-gathering on the ecological effects of channelisation and other harmful management techniques (S 1.3.3) to the enactment of high-level, ecologically sensitive legislation (S 1.3.4). The identification of ecohydraulic relationships (S 1.4) has informed current approaches to river habitat assessment (S 1.5.1), modelling (S 1.5.2), rehabilitation (S 1.5.3) and conservation (S 1.5.4) but **additional work is required to develop more quantitative, ecologically explicit, mechanistic and generalisable approaches to these management activities**. This thesis attempts to address knowledge gaps in these areas.

2

A critique of the mesohabitat concept

Chapter overview

Despite their importance to river research and management, mesohabitats are poorly defined. A typology of existing mesohabitat classifications is presented to combat confusion arising from a lack of common terminology. One such mesohabitat classification is that of 'physical biotopes'. Common physical biotopes include pools, riffles, glides and runs. As classifications of habitat for stream-dwelling biota, mesohabitats should be biologically distinct yet only loose associations between single species, families or guilds and these habitat units have been identified. Community-level analysis is suggested as a way forward in this area. Manifestations of the habitat template concept in river ecology have generally focused on hydraulics due to the pervasive nature of flow related forces. On this basis it would be expected that mesohabitats are hydraulically distinct but existing hydraulic calibrations are weak and heavily reliant on relatively simple, time-averaged descriptions of the bulk flow (*e.g.* mean velocity, Froude number) known as 'standard hydraulic variables'. Recent research has begun to show that the morphological characteristics of mesohabitats give rise to distinctive patterns of turbulent flow. A hydrodynamic classification of mesohabitats, therefore, is identified as a way to strengthen the mesohabitat concept and aid the objective identification of habitat types.

2.1 Introduction

Chapter 1 described how the classification of mesohabitats, defined as mesoscale units of instream habitat exhibiting a coherent set of physical conditions and a distinctive biological assemblage, has become central to contemporary approaches to habitat assessment and modelling due to its practicality and efficiency (Newson *et al*., 1998). RHS, for instance, involves the qualitative assessment of dominant substrate and hydraulics (surface flow type) at equally spaced transects and counting the number of pools and riffles present along the survey reach (EA, 2003a) (S 1.5.1). The habitat models MesoHABSIM (Parasiewicz, 2001, 2007) and MesoCASIMIR (Schneider *et al*., 2005) characterise physical conditions in mesohabitats classified predominantly on the basis of hydraulic, substrate and cover conditions (S 1.5.2). Knowledge of the hydraulic functioning and hydromorphic characteristics of mesohabitats is also important for the appropriate design of river rehabilitation projects (Newson *et al*., 1998; Brierley *et al*., 2010) (S 1.5.3) and essential to eliciting the desired response from biota (Pretty *et al*., 2003; Koed *et al*., 2006) (*e.g.* S 1.5.4).

2.2 Relationships between mesohabitat classifications: biota, hydraulics and morphology

Despite their importance in river research and management, **mesohabitats classifications are only very loosely defined and a common terminology is lacking** (Wadeson & Rowntree, 1998; Newson *et al*., 1998; Clifford *et al*., 2006). Confusion over the use of different classifications such as Channel Geomorphic Unit (CGU), Channel Unit (CU), Morphological Unit (MU), HydroMorphic Unit (HMU), Physical Biotope (PB), Flow Biotope (FB), Hydraulic Biotope (HB), Surface Flow Type (SFT) and Functional Habitat (FH) hampers any attempt to synthesise the extant literature. The naming of mesohabitat classifications has also progressed without regard to ecological definitions of habitat and biotope (S 1.4.1). Functional 'habitats' are, strictly speaking, functional 'biotopes' in the sense that they are defined by resident biological communities. Conversely, 'physical biotope' may be used erroneously in the context of a single species (*i.e.* habitat), yet the alternative use of 'physical habitat' is too ambiguous due to its broader meaning. Indeed, the term 'mesohabitat' can refer to biotopes. Semantic problems hinder attempts to synthesise the literature and make direct comparisons between studies difficult (S 2.4) but these aside, Figure 2.1 attempts to provide a consistent typology of the multiple, often conflicting terms used to describe mesoscale habitat units in order to aid in reviewing the literature.

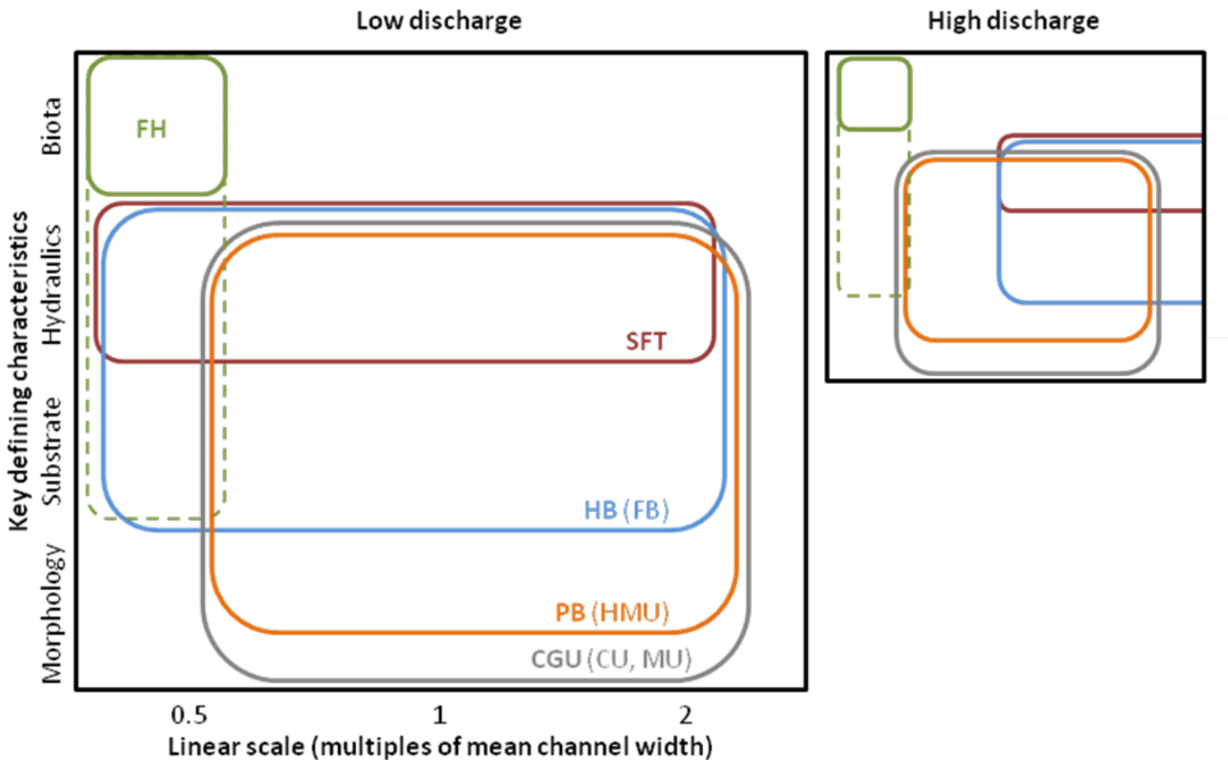


Figure 2.1 – A typology of mesoscale habitat classifications. Acronyms (see text) in bold refer to the preferred terminology used herein, those in parentheses refer to alternative terms. 'Morphology' includes local lateral and longitudinal channel topography. Dashed line indicates that functional habitats (FHs) may be described, yet are not defined, by substrate and hydraulics.

One of the most apparent features of the typology outlined in Figure 2.1 is the separation of FHs from other habitat units. This represents a fundamental difference in the way that the problem of mesohabitat classification has been approached (Figure 2.2). FHs, also known simply as 'mesohabitats' (Pardo & Armitage, 1997) represent a biological, 'top-down' approach based on macroinvertebrate communities (*e.g.* Harper *et al*., 1992) (Table 2.1). FHs, therefore, are relatively static habitat units as their classification is not discharge dependent, although the biota found during and shortly after extreme flows may be different to those at lower discharges (Townsend *et al*., 1997). SFTs, HBs and PBs, on the other hand, are examples of 'bottom-up' approaches in that they are defined by the physical environment in light of species habitat requirements (Newson & Newson, 2000). SFTs are visually categorised hydraulic patches which reflect the water surface expression of the interaction between hydraulics and morphological characteristics, with the size (D), arrangement and relative roughness (h/k) of bed particles particularly important factors (Davis & Barmuta, 1989). SFTs can be seen as classes of surface roughness representing a gradient of 'hydraulic energy' and have been described in different ways (*e.g.* Table 2.2). Classification of HBs involves the visual assessment of SFT and D (Padmore, 1997a). HBs are largely analogous to SFTs, however, as D has little effect on the resulting classification in most cases (Table 2.3). The scale and identity (*e.g.* cascade, rapid) of SFTs and HBs is highly dependent on discharge (Figure 2.3), with high flows tending to result in fewer, larger units (Padmore, 1998; Hill *et al*., 2008).

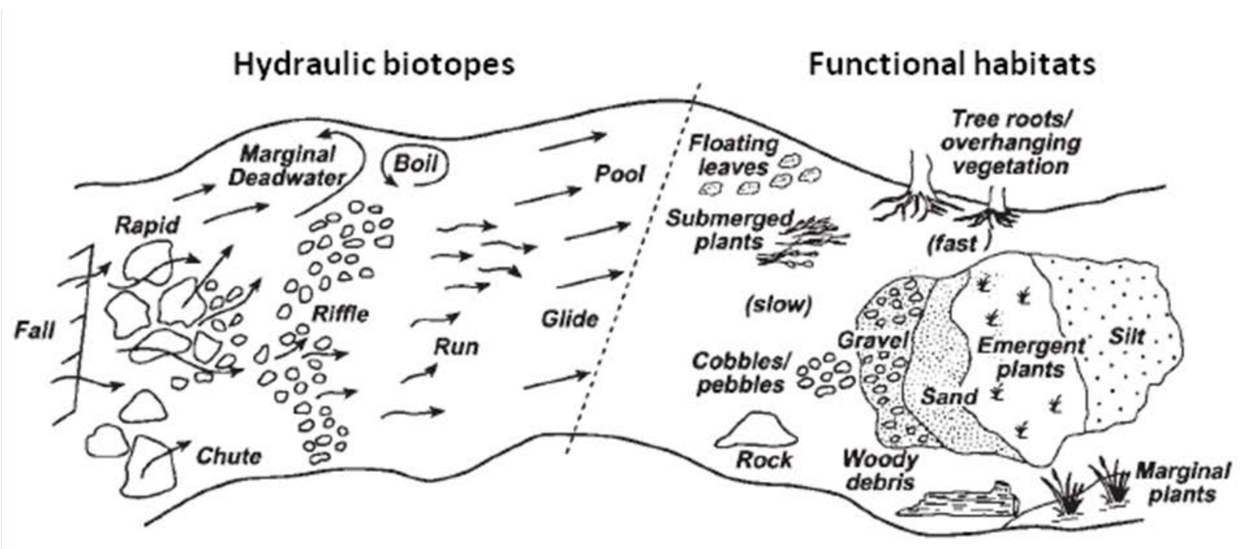


Figure 2.2 – A comparison of Hydraulic Biotopes (HBs) and macroinvertebrate Functional Habitats (FHs) in a hypothetical river. From Newson & Newson (2000).

Table 2.1 – Macroinvertebrate Functional Habitats (FHs) derived from Harper *et al*. (1992).

Functional habitat	Description
Rocks	Inorganic habitats
Cobbles	
Gravel	
Sand	
Silt	
Roots	Organic habitats
Trailing vegetation	
Marginal plants	
Leaf litter	
Woody debris	
Emergent macrophytes	
Floating-leaved macrophytes	
Submerged, fine-leaved macrophytes	
Submerged, broad-leaved macrophytes	
Mosses	
Macroalgae	

Table 2.2 – Surface Flow Types (SFTs) used in River Habitat Survey (RHS) (EA, 2003a), in order of 'hydraulic energy' (FF-NP), and their associated Hydraulic Biotopes (HBs) (Newson, 2002).

SFT (Code)	Description	Associated HB
Free Fall (FF)	Water falls vertically without obstruction; generally >1 m high	Water fall
Chute (CH)	Fast, low curving flow in contact with substrate	Cascade
Broken Standing Waves (BSW)	Tumbling 'white water' waves	Riffle; Rapid
Unbroken Standing Waves (USW)	Undular standing waves; crest faces upstream without breaking	Riffle
Rippled (RP)	Surface symmetrical ripples moving in general downstream direction	Run
Upwelling (UP)	Secondary flow cells visible as 'boils' or circular eddies	Boil
Smooth/Smooth Boundary Turbulent (SM)	Very little surface turbulence; small flow cells visible	Glide
No/Scarcely Perceptible Flow (NP)	No apparent downstream flow at surface; surface foam appears stationary	Pool

Table 2.3 – The Hydraulic Biotope (HB) matrix. – indicates combinations unlikely to occur in rivers. Modified from Wadeson & Rowntree (1998) to reflect RHS categories (Table 2.2).

	SFT							
Substrate (mm)	FF	CH	BSW	USW	RP	UP	SM	NP
Silt (<0.625)	-	-	-	-	-	Boil	Glide	Pool
Sand (0.625-2)	-	-	-	-	Run	Boil	Glide	Pool
Gravel (2-64)	-	-	Riffle	Riffle	Run	Boil	Glide	Pool
Cobble (64-256)	-	Cascade	Riffle	Riffle	Run	Boil	Glide	Pool
Boulder (>256)	-	Cascade	Rapid	Riffle	Run	Boil	-	Pool
Bedrock	-	Cascade	Rapid	Riffle	Run	Boil	Glide	Pool
Cliff	Waterfall	-	-	-	-	-		-

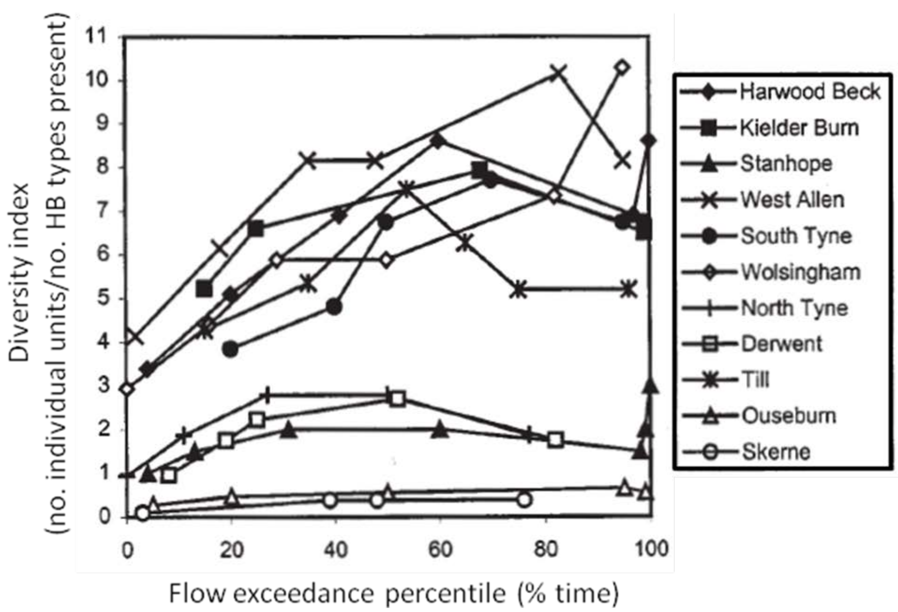


Figure 2.3 – Variation in Hydraulic Biotope (HB) diversity with discharge on 11 British rivers. Flood flows on the left, near-drought conditions on the right. From Padmore (1998).

CGUs and PBs are closely related but subtly different. As geomorphological units, CGUs (*e.g.* pool, riffle; Figure 2.4, Table 2.4) are not strictly mesohabitats as they are not delineated with regard to the requirements of biota, but are instead defined as "*having characteristic bed topography, water surface slope*" (Frissell *et al*., 1986, p. 206) and "*areas of relatively homogeneous depth and flow that are bounded by sharp gradients in both depth and flow*" (Hawkins *et al*., 1993, p.4). The most common CGUs in lowland streams are pools and riffles. These CGUs have been classified on the basis of numerous criteria, including hydraulics (Yang, 1971), D (Leopold *et al*., 1964; Mosley, 1982), substrate structure (Sear, 1996) and channel morphology (Richards, 1976; O'Neill & Abrahams, 1984). Hawkins *et al*. (1993) used a three-level hierarchy to separate CGUs into four groups based on qualitative categories of U, qualitatively assessed levels of turbulence (rough, smooth) and, for pool types, formative processes (Figure 2.5). Numerous CGU classifications have been used depending on geographical context and study purposes (*e.g.* compare Figure 2.4, Figure 2.5 and Table 2.4).

In the typology presented in Figure 2.1, similar to Harvey *et al*'s (2008) interpretation, **PBs are seen as a biologically-based, temporally dynamic analogue of CGUs, and a structurally persistent alternative to HBs**. They are classified on the basis of dominant SFT at low flow, following the classification of HBs (Table 2.2), but delineated by the morphological and sedimentological factors defining CGUs. The SFT of a PB, therefore, may change with discharge (*e.g.* USW-RP) but the habitat unit is always contained within the CGU. So, whereas SFTs and HBs may extend to many multiples of channel width as the hydraulic influence of bedforms is 'drowned out' at high discharges (Clifford *et al*., 2002; Emery *et al*., 2003), PBs retain spatial information on the structural influence of CGUs which can be important for inducing distinctive three-dimensional flow patterns (Booker *et al*., 2001; MacWilliams *et al*., 2006) and providing certain types and levels of cover for fish (*e.g.* undercut banks, submerged structures) (Beschta & Platts, 1986).

The similarities and differences between FHs, HBs and PBs can be seen as representing the relationships between biological communities (FHs), hydraulics (SFTs or HBs) and morphology (PBs). The strength and direction of these relationships are currently assumed in the application of mesoscale approaches to river management (*e.g.* RHS, MesoHABSIM). As RHS involves the collection of data relevant to all three mesohabitat classifications, albeit at a crude level, Harvey *et al*. (2008) were able to develop a model describing the interplay of morphology, hydraulics and biota in which assemblages of FHs are transferrable between HBs and combinations of HBs reflect reach scale morphology (Montogomery & Buffington, 1997) (Figure 2.6). Similarly loose associations between FHs and PBs were also reported by Kemp *et al*. (2000). Zavaldi *et al*. (2012) established links between SFT diversity of reach scale morphology, particularly depth variability. There is a strong indication from the studies reviewed above that **mesohabitat distributions reflect morphological variations along a reach but the widespread application of the mesohabitat concept may be premature, particularly in the case of large rivers** which do not necessarily contain well-defined, channel-spanning habitat units (*e.g.* pool, glide, run, riffle) (Chapter 3). Whilst **there is some evidence to suggest that the distributions of aquatic biota are organised according to PBs and other related mesohabitats** (S 2.3), **there is a dearth of studies employing community-level analyses, despite numerous advantages associated with this approach** (Chapter 3). Furthermore**, PB-hydraulic associations** (S 2.4) **may currently be too broad to warrant the use of mesoscale approaches** (Clifford *et al*., 2006).

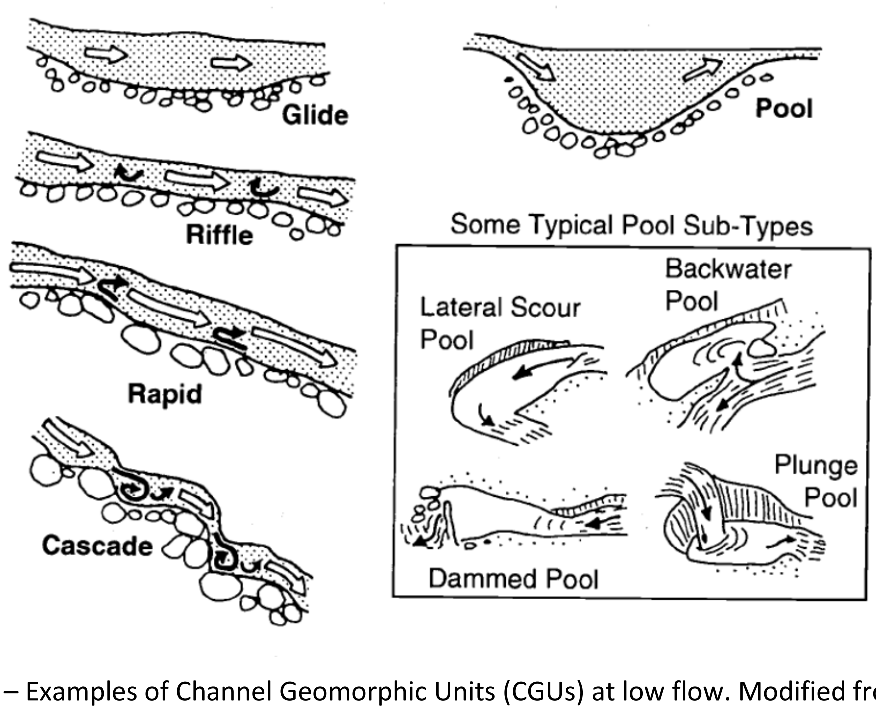


Figure 2.4 – Examples of Channel Geomorphic Units (CGUs) at low flow. Modified from Bisson *et al*. (1982), Frissell *et al*. (1986), Poole *et al*. (1997).

Table 2.4 – CGU classification used by Maddock *et al*. (2007).

CGU	Hydraulics	Brief Description
Fall	Turbulent & Very Fast	Vertical drops of water over a full span of the channel, commonly found in bedrock and step-pool stream reaches.
Cascade	Turbulent & Very Fast	Highly turbulent series of short falls and small scour basins, frequently characterised by very large substrate sizes and a stepped profile; prominent features of bedrock and upland streams.
Chute	Turbulent & Very Fast	Narrow steep slots or slides in bedrock.
Rapid	Turbulent & Fast	Moderately steep channel units with coarse substrate, but unlike cascades posses a planar rather than stepped profile.
Riffle	Turbulent & Moderately Fast	The most common type of turbulent fast water CGU's in low gradient alluvial channels. Substrate is finer (usually gravel) than other fast water turbulent CGU's, and there is less white water, with some substrate breaking the surface.
Run	Less Turbulent & Moderately Fast	Moderately fast and shallow gradient with ripples on the surface of the water. Deeper than riffles with little if any substrate breaking the surface.
Glide	Non-Turbulent Moderately Slow	Smooth 'glass-like' surface with visible flow movement along the surface; relatively shallow (compared to pools).
Pool	Non-Turbulent & Slow	Relatively deep and normally slow flowing, with finer substrate. Usually little surface water movement visible. Can be bounded by shallows (riffles, runs) at the upstream and downstream ends.
Ponded	Non-Turbulent & Slow	Water is ponded back upstream by an obstruction, e.g. weir, dam, sluice gate etc.
Other	Used in unusual circumstances where the feature does not fit any other type.	

2.3 Ecological relevance of mesohabitats

PBs and related mesohabitats have been reported to influence the structure of ecological communities at all levels from primary producers (*e.g.* Murphy, 1998) to predatory fish (*e.g.* Schwartz & Herricks, 2008) (Table 2.5). Haslam (1978) has detailed the habitat associations of macrophytes and Murphy (1998) has described how certain mesohabitats act as production areas for periphyton (*e.g.* riffles, runs) and others as detrital areas for sloughed algal cells (*e.g.* pools). The production and relative abundance of macroinvertebrate species has been related to various mesohabitat classifications. Huryn and Wallace (1978) found that Trichopteran feeding groups had affinities with certain PBs, with production by shredders dominating in pools (75% of total biomass) and a more even distribution of feeding groups in riffles. Working on a fourth-order stream in Australia, Reid and Thoms (2008) found that most SFTs had significantly different macroinvertebrate assemblages ($p<0.05$), although the differences were blurred along a continuum of 'hydraulic energy' represented by SFTs, with adjacent SFTs in the continuum (*e.g.* NP-SM, USW-BSW) exhibiting non-significant differences. In a similar study, Hill *et al*. (2008) mapped SFTs along reaches of six lowland rivers in the UK and collected macroinvertebrates from representative SFTs. Family level identification revealed that some macroinvertebrate families had strong affinities with certain SFTs. Tipulidae and Brachycentridae, for instance, were found exclusively in association with unbroken standing waves and smooth SFTs respectively.

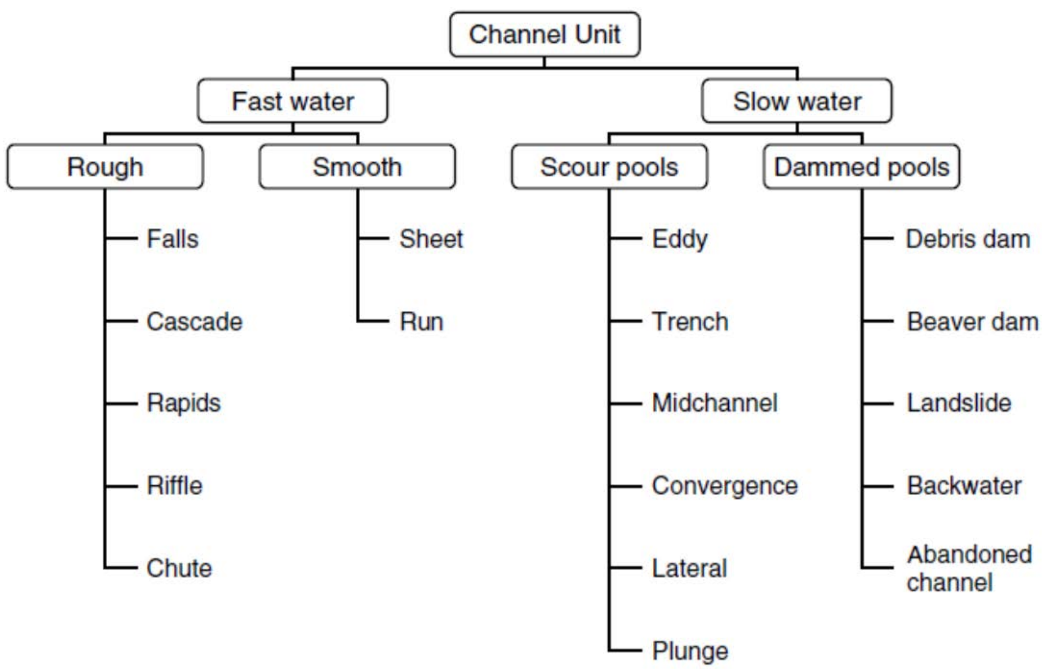


Figure 2.5 – Hierarchical subdivision of CGUs in streams. From Hawkins *et al*. (1993), Bisson *et al*. (2007).

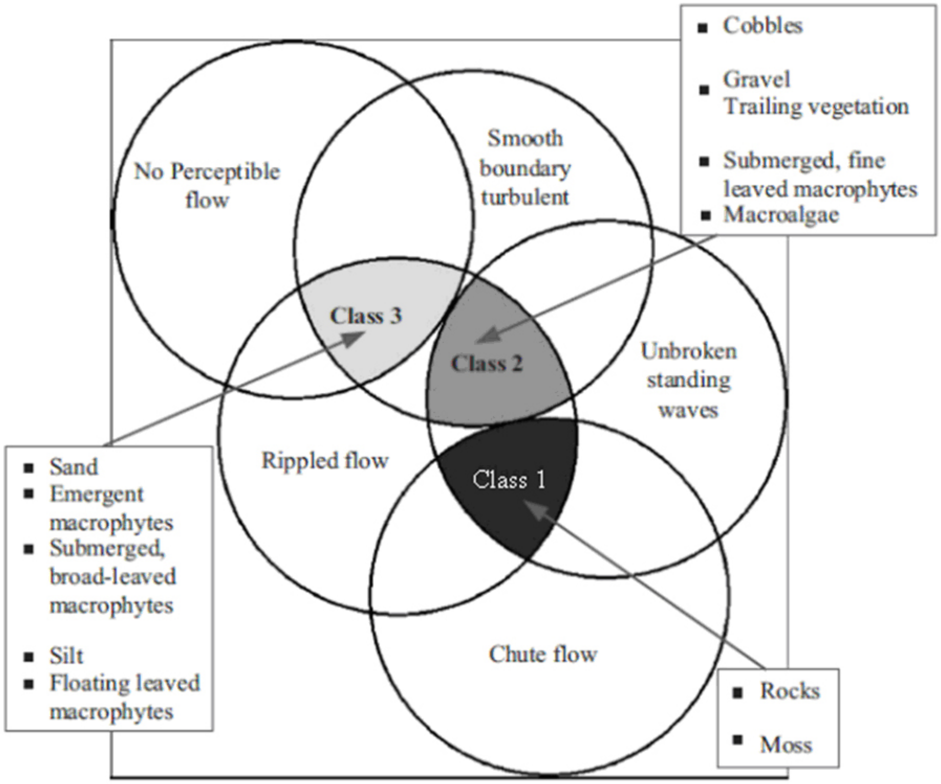


Figure 2.6 – Venn diagram to illustrate broad classification of HBs into 'classes' according to functional habitat preferences and reach scale morphology based on data from over 4000 RHS sites. Class 1 = step-pool morphology, class 2 = pool-riffle morphology, class 3 = glide-pool morphology. From Harvey *et al*. (2008).

Principe *et al*. (2007) investigated the HB associations of macroinvertebrate communities in four Argentinean mountain streams and concluded that "most of the hydraulic units we found in this study allocated different macroinvertebrate assemblages" (p.334). Halwas *et al*. (2005) were less optimistic about the distinctiveness of macroinvertebrate assemblages in several PB types of 13 steep, first-order reaches in British Columbia, although they did find that certain PBs (riffles, rapids) supported higher total macroinvertebrate abundance than others. All of the aforementioned studies on macroinvertebrate community-mesohabitat associations involved identification only to family level and would have benefited from employing a finer taxonomic resolution. Focusing on habitat units similar to FHs and identifying taxa generally to species level, Pardo and Armitage (1997) used indicator species analysis and found that 11 habitat units with particular substrate type and U combinations in an English chalkstream supported distinct macroinvertebrate communities.

Table 2.5 – Key studies examining the mesohabitat associations of instream biota.

Reference	Mesohabitat classification	Ecological relevance
Haslam (1978); Murphy (1998)	PB	Primary production, macrophyte and periphyton community composition
Huryn & Wallace (1987)	PB (riffles, pools)	Macroinvertebrate (Trichoptera) distributions
Pardo & Armitage (1997)	FH ('mesohabitats')	Macroinvertebrate community composition
Halwas *et al*. (2005)	PB	
Hill *et al*. (2008); Reid & Thoms (2008)	SFT	
Principe *et al*. (2007)	HB	
Bisson *et al*. (1982; 1988)	PB	Segregation of sympatric juvenile salmonid species
Modde *et al*. (1991)	CGU	Brown trout biomass
Inoue & Nakano (1999)	PB ('sub-units')	Juvenile masu salmon (*Oncorhychus masou*) abundance
Inoue & Nunokawa (2002)	PB ('sub-units')	Masu salmon and rosyface dace (*Leuciscus exoe*) abundance
Moir & Pasternack (2008)	PB ('morphological units')	Chinook salmon (*Oncorhynchus tshawytscha*) spawning locations
Schwartz & Herricks (2008)	PB	Fish community density and biomass; segregation of fish feeding guilds
Hauer *et al*. (2011)	PB ('hydromorphological units')	Habitat suitability for age classes of rheophilic fish

Research into the mesohabitat associations of fish has generally focused on habitat units at a similar scale to PBs. Bisson *et al*. (1982, 1988) found that juveniles of three pacific salmonid species, namely coho salmon (*Oncorhynchus kisutch*), steelhead trout (*S. gairdneri*) and cutthroat trout (*S. clarki*) have particular age-dependent preferences for mesohabitats analogous to PBs (Figure 2.7), with body morphology a key factor in determining particular species-habitat associations. Modde *et al*. (1991) reported that brown trout biomass could be categorised by CGU type, with a clear preference for trench and plunge pools, but brook trout (*Salvelinus fontinalis*) biomass could not. Several studies into fish habitat associations have focused on objective classifications of mesohabitats. Working in three small Japanese streams, Inoue and Nakano (1999) used hierarchical cluster analysis to define 'sub-unit patches' based on

h, U and D. Of the eight sub-unit types identified across all reaches they found that the summer baseflow preference of juvenile masu salmon (*O. masou*) was overwhelmingly for the deep and moderately fast sub-unit (Figure 2.8) and emphasised the importance of adjacency as most fish were found in areas close to faster sub-units. Inoue and Nunokawa (2002) used a similar approach to examine the habitat preferences of juvenile masu salmon and rosyface dace (*Leuciscus exoe*) in a third-order stream in Japan. Results for masu salmon were in general agreement with Inoue & Nakano (1999), whereas the abundance of rosyface dace was linked to the available area of marginal habitat characterised by high spatial variability in U.

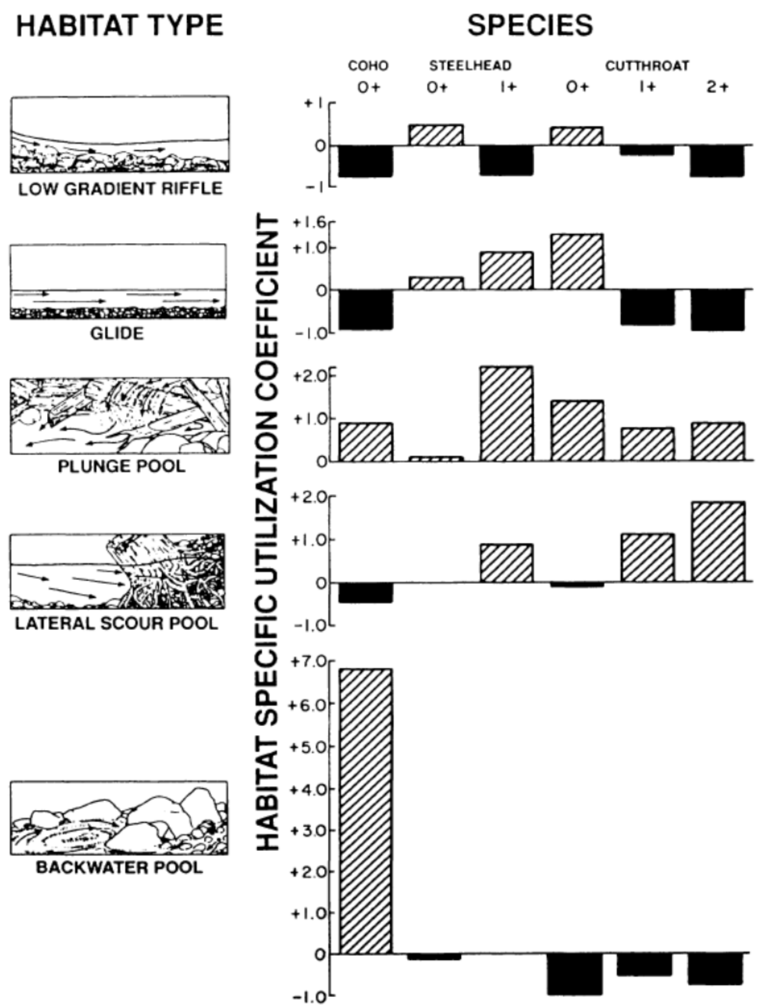


Figure 2.7 – Habitat utilisation of age classes of three pacific salmon species in five different Physical Biotopes (PBs). 'Habitat specific utilization coefficient' defined as $(D_h\text{-}D_r)/D_r$ where D_h and D_r are habitat specific density and average reach density respectively. Data from Bisson *et al*. (1988).

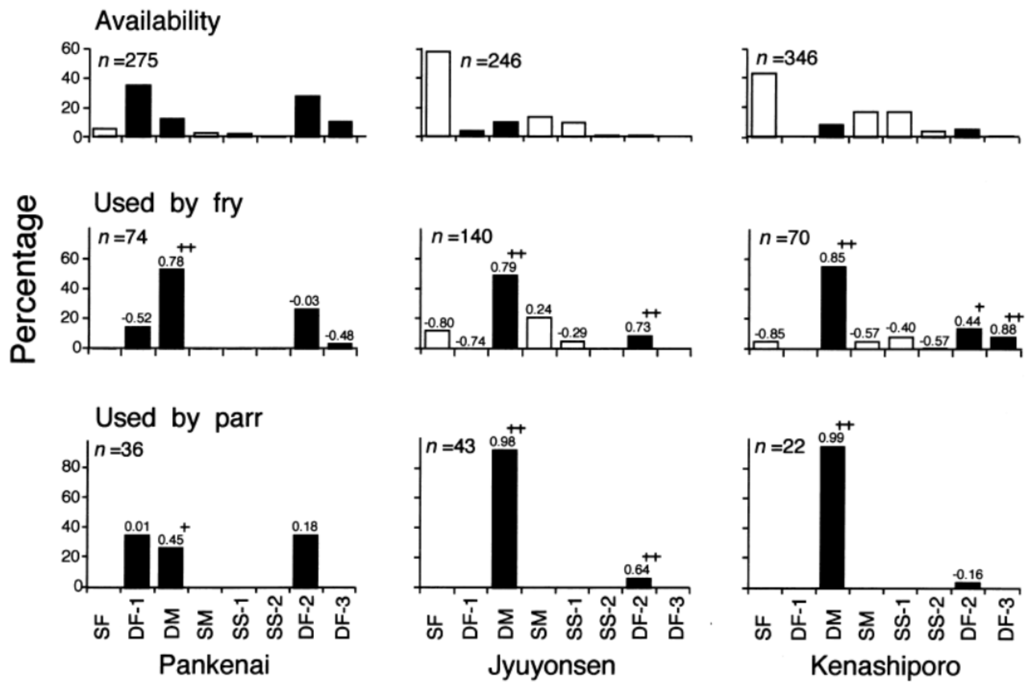


Figure 2.8 - Subunit-type composition of cells in each study reach (availability), and those used by fry and parr. Subunit types with relatively deep and shallow water are shown by solid and open columns, respectively: (SF) shallow-fast; (DF) deep-fast; (DM) deep-moderate;(SM) shallow-moderate; and (SS) shallow-slow. The selectivity index of Jacobs ([r±p]/[r+p±2rp]), where r and p are the proportions of the subunit type used by the fish and found throughout the reach respectively) is shown for each column. Positive selectivities are denoted by symbols for clarity: (+) values between 0.3 and 0.6; and (++) values >0.6. From Inoue & Nakano (1999).

Hauer *et al*. (2011) used an objective means of classifying PBs based on measurements of h, U and τ in eight reaches on Austrian rivers and reported contrasting mesohabitat associations for different life stages of rheophilic fish species, with most juveniles found in shallower and slower (backwater pool) habitats and adults in pools and runs. Schwartz and Herricks (2008) used the concept of fish guilds in a study which classified areas of a third-order stream in Illinois, USA as one of nine 'mesohabitat units' (Table 2.6). These mesohabitats are similar to PBs, except for the longitudinal subdivision of pools. By electrofishing the reach during summer baseflow and assigning each species to a fish guild, they were able to show that overall fish densities were greatest in the pool-front and scour pool units and certain fish feeding guilds had broad preferences for mesohabitat types. Insectivores, for example, were most abundant in pool-front, pool-mid and scour pool units, herbivores generally used glides and complex riffles, whereas piscivores were limited to pool units. Finally, Moir and Pasternack (2008) found that, of 10 subjectively assessed PBs, Chinook salmon (*O. tshawytscha*) overwhelmingly preferred to construct redds on riffles, with 79% of redds found in areas of convective flow acceleration associated with riffles and riffle entrances.

Table 2.6 – The mesohabitat classification used by Schwartz and Herricks (2008).

'Mesohabitat units'	**Description**
Pool-front	Entrance slope to pool; downward directed bed slope oriented with flow
Pool-mid	Topographic low along stream bed; level bed
Pool-rear	Exit slope to a pool; upward directed bed slope oriented with flow
Local scour pool	Small area of topographic low; length smaller than width
Glide	Intermediate bed elevation; level and uniform bed
Simple riffle ('run')	Topographic elevation intermediate-high; lateral bed diversity
Complex riffle	Topographic high; sinuous flow path through emergent substrate at low flow; diverse bed morphology
Submerged point bar	Lateral topographic high inside bend adjacent to pool and extending into riffle; alternate bars in straight channels
Channel expansion marginal deadwater	Intermediate bed elevation laterally positioned behind instream or bank structure; area in lee of obstruction

From the above review of studies seeking to establish the ecological relevance of mesohabitats it can be seen that **evidence on mesohabitat-biota links suggests loose associations between single species, families or guilds and particular habitat units**. There is a dearth of studies employing analyses that are truly conducted at the community-level. Most work has examined habitat associations using species-by-species (*e.g.* Modde *et al*., 1991; Inoue & Nakano, 1999) or reduced dimensionality (*e.g.* Halwas *et al*., 2005; Principe *et al*., 2007) approaches, neither of which adequately describe or integrate processes occurring within the whole community (*e.g.* interactions between predation or competition and physical habitat). **Further progress in establishing the ecological relevance of mesohabitat classifications may be made by using innovative community-level techniques, such as multivariate regression trees** (De'ath, 2002) (Chapter 3).

2.4 Hydraulic calibration of mesohabitats

There is some evidence to suggest that mesohabitats are biologically distinct (S 2.3). Thus if, as according to the prevailing consensus in river ecology, hydraulic conditions, together with food availability, water quality and biotic interactions (factors which are influenced by hydraulics), are among the most important habitat factors (S 1.4.2) then **the expectation is that PBs are hydraulically distinct**. The hydraulics of mesohabitats have generally been characterised and calibrated by h and U and combinations of these (*e.g.* Fr, $U{:}h$). These are the basic hydraulic parameters (h, U) used in many habitat models (S 1.5.2). One of the most commonly cited studies in this context is Jowett (1993), who focused on the ability of water surface slope and the above hydraulic variables to objectively discriminate between PB types (pool, run, riffle) in three reaches of a New Zealand river at low flow. During data collection, PB type was classified subjectively based on visual assessment of U, SFT and D. Despite finding significant differences ($p<0.001$) between PB types in relation to the mean values of all potential discriminatory variables, discriminant models from results of Linear Discriminant Analyses (LDA) correctly classified only 38-66% of PBs (Table 2.7), with 'correctness' measured as agreement with subjective assessment of PB type. It was concluded that $U{:}h$ and Fr were the best single discriminatory variables, yet there was much overlap in the bivariate h-U distributions of the three PB types, with runs occupying most of the combined distributions of pools and riffles (Figure 2.9). The reason for such overlap was attributed to either inconsistent subjective classification of PBs or the variable hydraulic characteristics of runs and riffles.

Moir and Pasternack (2008) also found considerable overlap in Fr between a range of habitat units similar to PBs and reported that joint h-U distributions discriminated between units more effectively. Using Kernal Discriminant Analysis (KDA) to objectively predict unit types (*e.g.* pool, riffle, run, chute) based on joint h-U distributions, however, correctly classified only 60.4% of units. One of the problems with the approach taken by both Jowett (1993) and Moir and Pasternack (2008) is that non-standard classifications were used, with the former only recognising three PBs and the latter using a bespoke set of 'morphological unit types'. Transferability of these results is further compromised by the fact that they are from single rivers at only one discharge.

Table 2.7 – Classification success (%) of discriminant models from Linear Discriminant Analyses (LDA). From Jowett (1993).

Model	Pool (n=187)	Run (n=760)	Riffle (n=165)	Overall (n=1112)
Fr	<0.18 (78%)	0.18-0.41 (50%)	>0.41 (60%)	56%
Water surface slope	<0.0039 (79%)	0.0039-0.0099 (21%)	>0.0099 (70%)	38%
$U{:}h$	<1.24 (84%)	1.24-3.20 (60%)	>3.20 (61%)	64%
Fr & slope	Fr < 0.18 (76%)	Fr ≥ 0.18 & slope ≤ 0.0099 (63%)	Fr ≥ 0.18 & slope ≥ 0.0099 (68%)	66%
$U{:}h$ & slope	$U{:}h$ < 1.24 (85%)	$U{:}h$ ≥ 1.24 & slope ≤ 0.0099 (59%)	$U{:}h$ ≥ 1.24 & slope ≥ 0.0099 (69%)	65%

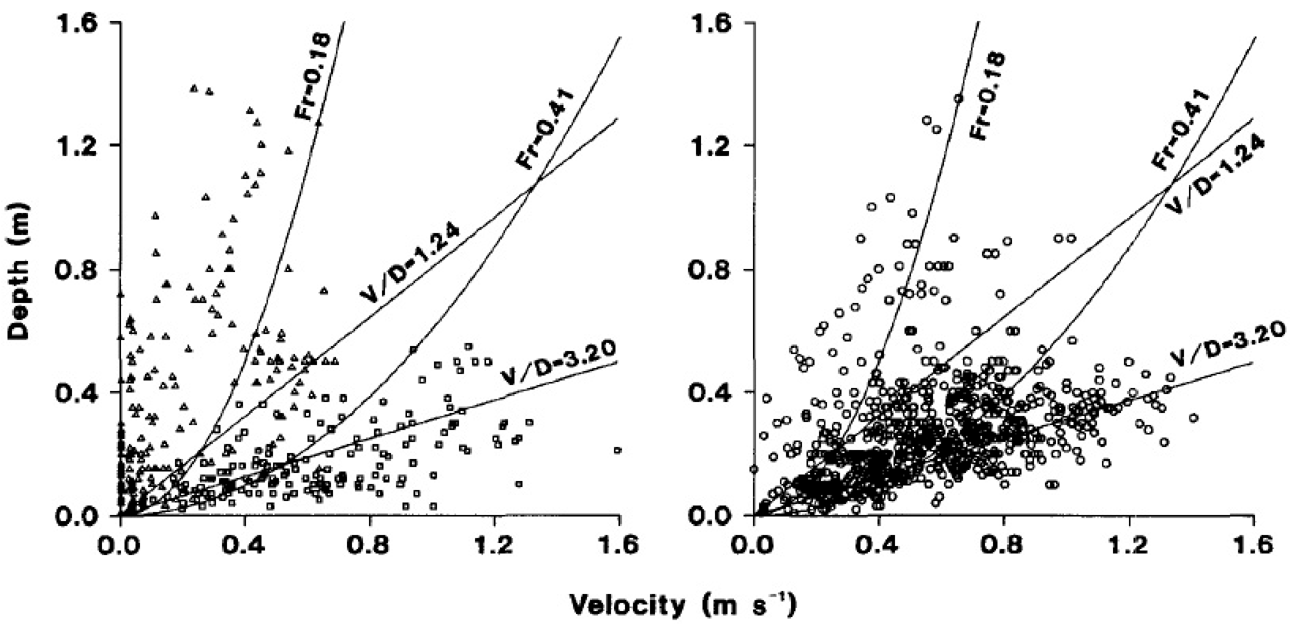


Figure 2.9 – Classification of pool (triangle), riffle (square) and run (circle) by velocity:depth (V/D) ratios and Froude (Fr) numbers. From Jowett (1993).

An early application of the HB concept was provided by Wadeson (1994, 1996) who investigated the validity of the HB 'matrix' (Table 2.3) based on hydraulic data from five third- to sixth-order reaches along the Buffalo River, South Africa. Hydraulic indices commonly used to describe mean flow in the water column ($U{:}h$, Fr, Re) and near-bed conditions (Re^*, U_*) (S 1.4.2) were derived from simple measures of U, h and k (Wadeson & Rowntree, 1998). Multiple range analysis was used to calculate intervals of differences between all possible pairs of means from HBs that were visually classified according to SFT and substrate. Where there is no significant difference (p=0.05) between the intervals, this test groups means together (Milliken & Johnson, 1984). Results indicated that most HBs were hydraulically distinct when all hydraulic indices were taken together, with the only substantive overlap occurring between rapids and cascades (Figure 2.10). The best discriminatory variables were found to be Fr, U_* and Re^*, although Fr was the only variable which provided consistent separation of HBs across all study reaches. Additional findings related to stage-dependent hydraulics, with 'higher energy' HBs (riffle, rapid, cascade) found to be more hydraulically 'stable' over a range of discharges than 'lower energy' HBs (pools, runs). Whilst it provides an important example of the hydraulic distinctiveness of HBs, this South African study is limited to a single river and used a protocol for naming HBs which does not translate directly to that used elsewhere (Table 2.2).

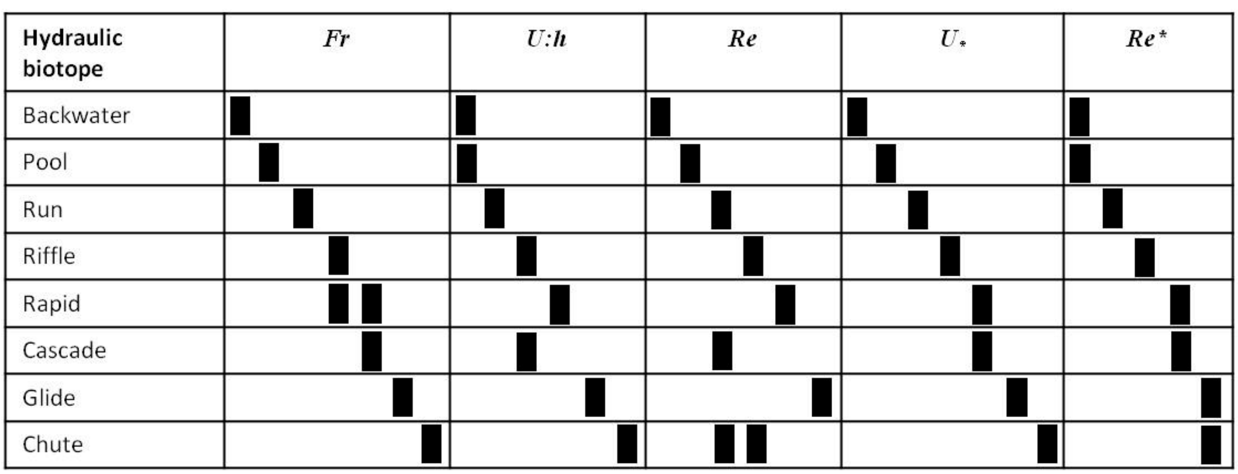


Figure 2.10 – Homogeneous Hydraulic Biotope (HB) groups according to results of multiple range analysis (confidence level = 95%). 'Backwater' refers to marginal biotopes with no net flow. Homogenous groups can be identified by shaded blocks occurring in the same column. From Wadeson & Rowntree (1998).

Further support for the efficacy of Fr as a primary discriminatory hydraulic variable was provided by Padmore (1997a, 1997b, 1998). Working on 11 rivers representing the range of geomorphological features and mesohabitats present in North-East England, Fr was identified from a set of hydraulic indices as the single best discriminator of SFTs across a range of discharges based on the results of stepwise discriminant analysis (Table 2.8). There was, however, much discharge related variability in the results, with relative exposure and turbulence indices ranked as more important discriminatory variables when 'mid' and 'high' discharges were analysed separately (Table 2.9). Furthermore, Clifford *et al*. (2006) have illustrated the considerable degree of overlap in a subset of Padmore's (1997a) data with regards to the Fr distributions of each SFT, even when using a relatively conservative means of plotting the data (Figure 2.11). Whilst highly relevant to the situation in Britain, this work was undertaken with little regard for the hydraulics of river flow. Results are compromised by the construction of 'turbulence', 'shelter' and 'relative exposure' indices (Table 2.8), which have no foundation in the fluid mechanics literature. A further confounding factor is the use of a stepwise method of analysis, which is associated with serious biases and inconsistencies (Whittingham *et al*., 2006).

Table 2.8 – Results of stepwise discriminant analysis for Surface Flow Types (SFTs) across three discharges. Numbers shown are F values indicating the relative importance of each hydraulic index in characterising the SFT (denoted by shading). SFT codes from Table 2.2 except SRip, an additional SFT used to distinguish shallow runs from deep runs (RP). D_{int} refers to the intermediate substrate diameter at the point of measurement. From Padmore (1997a).

	SFT							
Hydraulic index (formula)	NP	SRip	SM	RP	USW	BSW	CH	UP
Fr	1626	1305	1784	1301	1512	1504	2031	1327
U_*	72	19	12	18	42	77	190	19
Turbulence index (hU/D_{int})	19	11	67	17	24	18	18	17
Relative roughness (D_{int}/h)	-	163	-	10	-	-	44	-
Substrate (D_{int})	-	-	-	-	-	23	20	15
Shelter index (D_{int}/Fr)	128	-	-	-	15	-	-	-
Relative exposure (h/ D_{int})	-	-	55	-	9	-	-	-

Fr has also been implicated in the distribution of FHs. Kemp *et al*. (1999, p.159) initially applied an occurrence function to 100 point observations of U, h and FH type and suggested that '*in most cases, each habitat was associated with distinct depth-velocity classes*'. The same data were later re-examined by Kemp *et al*. (2000) who calculated the occurrence of FHs in arbitrary Fr classes. They found that eight out of the 14 FHs present occurred in the lowest Fr class (0-0.05), with the remaining FHs occurring along a gradient from Fr 0.05 to 0.85 (Figure 2.12). Clifford *et al*. (2006), however, have again demonstrated the large degree of overlap associated with the Fr distributions of these mesohabitats, despite using a conservative means of plotting the data (Figure 2.13). Several points compromise the validity of Kemp *et al*'s (2000) results (Clifford *et al*., 2006). Sampling was generally confined to a small range of low Fr and the method of data analysis meant that none of the FHs encountered had only positive or negative associations across the whole Fr range. Furthermore, the original U data were collected at y/h=0.7 (Kemp *et al*., 1999) rather than the more commonly used y/h=0.4 (S 1.4.2), introducing unnecessary uncertainties when calculating Fr and making comparisons with other studies problematic. There was also little control over seasonality and discharge, a problem common to most studies attempting to calibrate the hydraulics of mesohabitats (Clifford *et al*., 2006).

Table 2.9 – Results of stepwise discriminant analysis for all SFTs at three separate discharges. Numbers shown are F values indicating the relative importance of each hydraulic index in discriminating between SFTs. Shading denotes primary (dark) and secondary (light) discriminatory variables at each discharge. From Padmore (1997a).

Significant discriminating index	**'Low'**	**'Mid'**	**'High'**
Fr	209.5	52.8	112.8
Shelter index	84.4	3.0	7.1
Relative roughness	36.9	15.6	56.7
U_*	34.9	13.3	3.3
Relative exposure	30.7	61.6	197.7
Turbulence index	16.6	19.6	113.6
Substrate	13.9	28.8	49.3

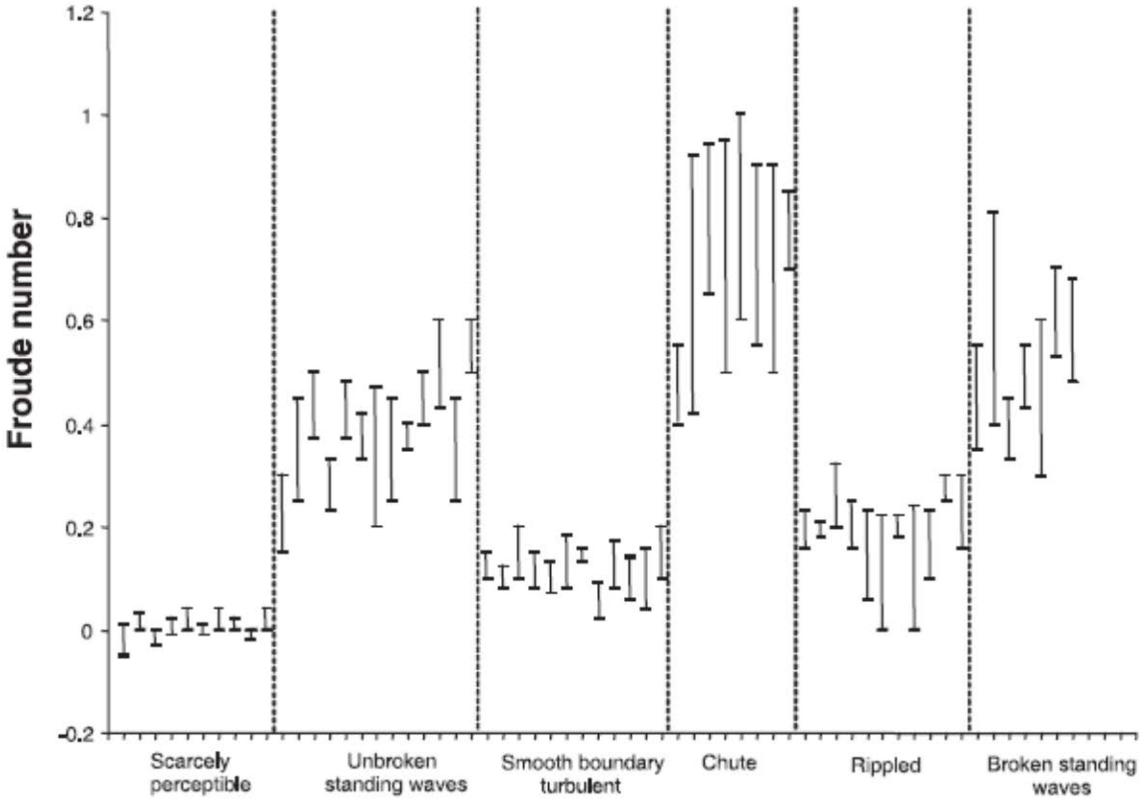


Figure 2.11 – Interquartile ranges of Froude number for several Surface Flow Types (SFTs). Each vertical bar represents results from one river or SFTs from the same river with a discrete Froude number range. Data from Padmore (1997a), Newson *et al*. (1998). From Clifford *et al*. (2006).

Fr is an appealing hydraulic index due to its non-dimensionality, making it transferable between mesohabitats and rivers of different sizes (Jowett, 1993; Moir *et al*., 1998). Clifford *et al*. (2006), however, have demonstrated how Fr can obscure important contrasts between very different mesohabitats. They used a highly objective means of classifying pools and riffles along a 120 m rehabilitated reach of the River Cole, Birmingham. Pools and riffles were classified as areas below the 25th and above the 75th percentiles of the bed topography respectively, after detrending by removing the mean slope of the reach centreline. High resolution collection of h and U data in these pools and riffles at 'low' (Q_{70}) and 'high' (Q_{13}) discharges revealed the main problem with Fr – that very different combinations of depth and velocity can exhibit similar Fr (Figure 2.14). By their very definition pools were deeper than riffles, yet they spanned a similar range of velocities at both discharges. Fr intervals cut across the bivariate h-U distributions of these very different mesohabitats, raising serious concerns regarding the power of Fr to

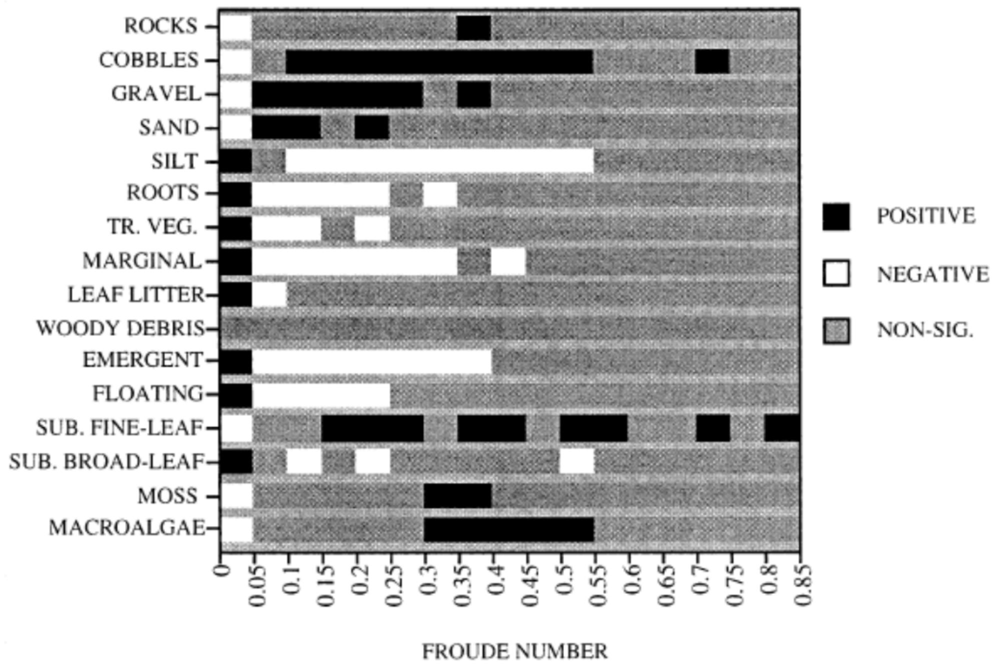


Figure 2.12 – Correlations between the occurrence of Functional Habitats (FHs) and Froude number classes (p=0.05). From Kemp *et al*. (2000).

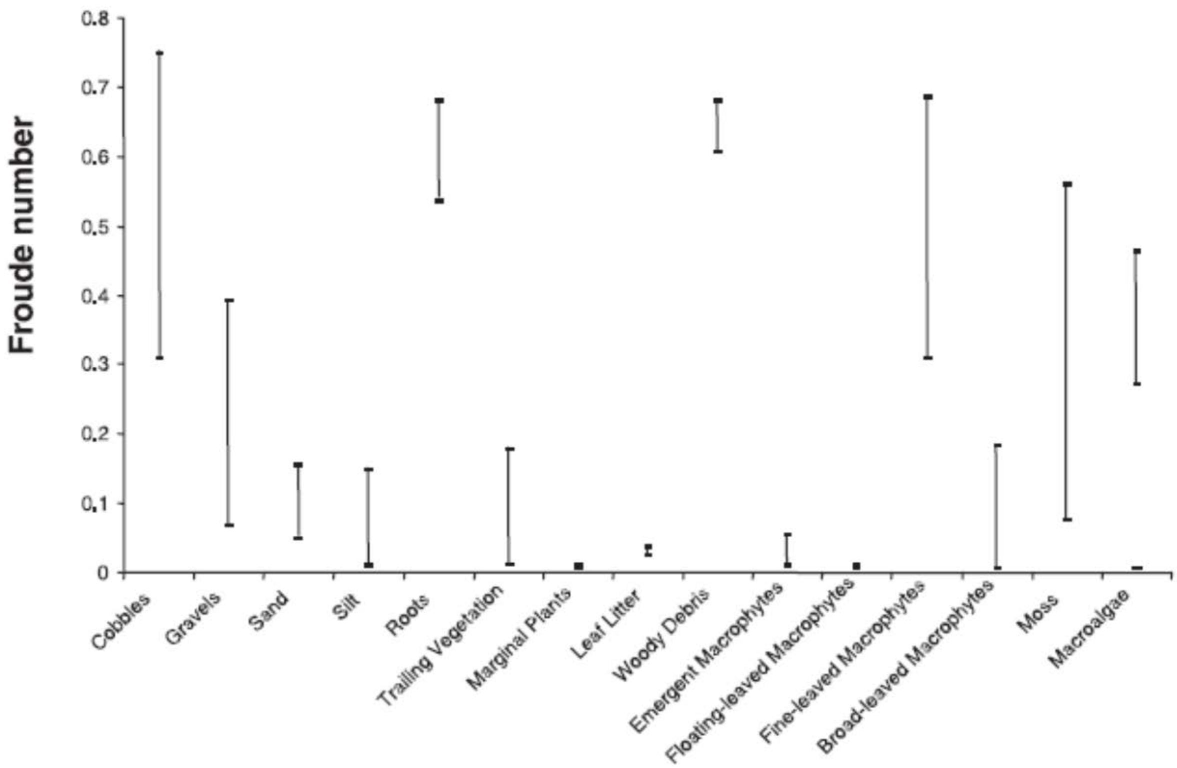


Figure 2.13 – 60% likelihood of occurrence limits for Functional Habitats (FHs). Data from Kemp *et al*. (2000). From Clifford *et al*. (2006).

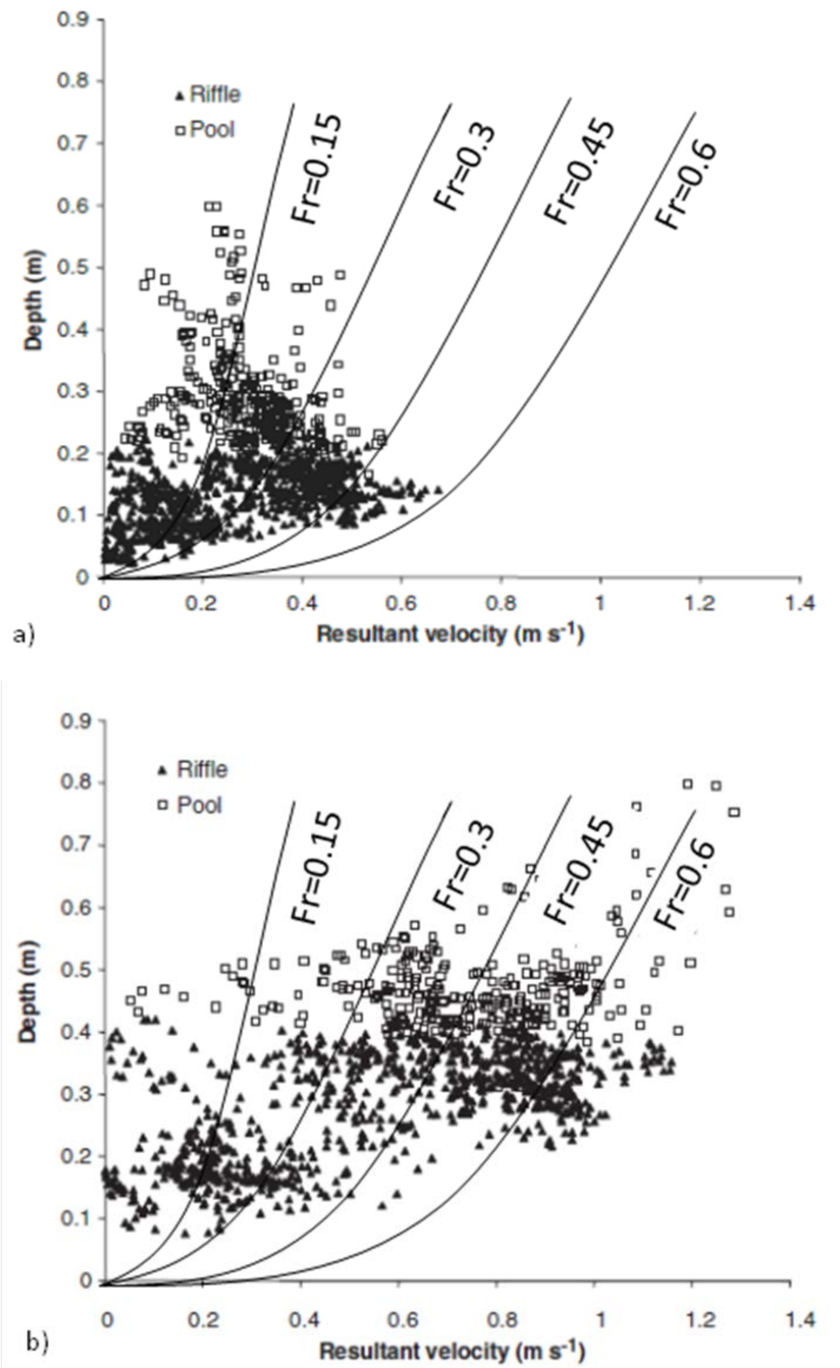


Figure 2.14 – Depth and velocity distributions of pools (lower 25th percentile of residual bed topography) and riffles (upper 25th) at Q_{70} (a) and Q_{13} (b) with Froude number (Fr) intervals. Modified from Clifford *et al*. (2006).

discriminate between mesohabitats. Hauer *et al*. (2011) also found that Fr could not be matched to the occurrence of PB-like mesohabitats over a range of discharges in pool-riffle reaches of eight Austrian rivers. In this case mesohabitats were objectively classified using the Mesohabitat Evaluation Model (MEM), which places areas of the channel into one of six 'hydromorphological units' (riffle, fast run, run, pool, backwater, shallow water) based on modelled hydraulic data or field measurements of h, U and τ (Hauer *et al*., 2009). Whilst these studies help to illustrate the problem with current approaches to calibrating the hydraulics of mesohabitats, the classification methods used make it difficult to compare the results to other studies and to assess the implications for river management applications, which generally involve rapid visual classification of a range of mesohabitats.

A novel approach to classifying channel morphology was presented by Stewardson and McMahon (2002). They used data on channel geometry and simple hydraulic measurements at cross-sections from 149 reaches with diverse morphologies in Europe, Australia and New Zealand. A stochastic model based on bivariate h-U distributions provided a useful tool for exploring the relations between reach scale morphology (*e.g.* plane-bed, pool-riffle) and fine scale hydraulic habitat conditions. This model relied on the effect of longitudinal and lateral variation in channel morphology on the relationship between h and U (Figure 2.15). Using data from 92 reaches in New Zealand, Schweizer *et al*. (2007) later reported that this relationship could be formulated in terms of the relative contributions of two end-member distributions, which were a function of reach-averaged hydraulic indices (*e.g.* mean Fr, Re). Working on a 1 km pool-riffle reach in British Columbia, Rosenfeld *et al*. (2011) found that the observed h-U distribution was consistent with that expected based on Figure 2.15. They further showed how reach scale h-U distributions were the result of a composite of narrower distributions in subjectively classified PBs. At low discharge, the relationships between h and U were similar to those expected at the reach scale, with some PBs exhibiting a weakly negative relationship (*i.e.* pools, glides) and others a positive correlation (*i.e.* riffles, runs) (Figure 2.16). They suggested, therefore, that because pools are dominated by longitudinal variation (*i.e.* shallow head and tail, deep mid-section) they should contain a wider variety of microscale hydraulic conditions . At high discharge, however, these relationships diminished and all habitats exhibited at least a weakly positive correlation between h and U, demonstrating the importance of controlling for discharge.

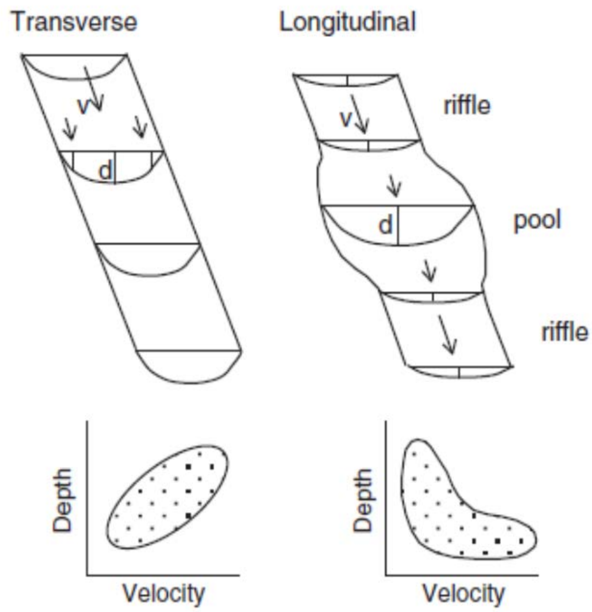


Figure 2.15 - Idealised effects of transverse and longitudinal variation in depth on joint velocity–depth frequency distributions. A positive relationship between velocity (v) and depth (d) is expected when transverse variation in depth dominates (left), and a negative relationship is expected when longitudinal variation dominates (right). From Rosenfeld *et al* (2011), Stewardson and McMahon (2002), Schweizer *et al*. (2007).

The emerging evidence suggests that bulk or time-averaged hydraulic variables (h, U, Fr), which have been used historically by river managers due to their simplicity and the lack of availability of advanced flow measurement devices (Appendix C)**, are not the most effective discriminators of mesohabitats** (Clifford *et al*., 2006; Hauer *et al*., 2011). Whilst Stewardson and McMahon (2002) demonstrated that probability distributions of these hydraulic variables yield more information than measures of central tendency (*e.g.* reach- or cross-section-averaged h and U), the functions used in their estimation may not be transferrable between sites (Rosenfeld *et al*., 2011). Habitat models based on such an approach are unlikely to improve upon predictions made using more traditional models (S 1.5.2) but, as rapid tools for reach scale assessment, they are appealing to river managers. **At the mesoscale, however, where many ecological processes operate, we require mechanistic knowledge about flow-**

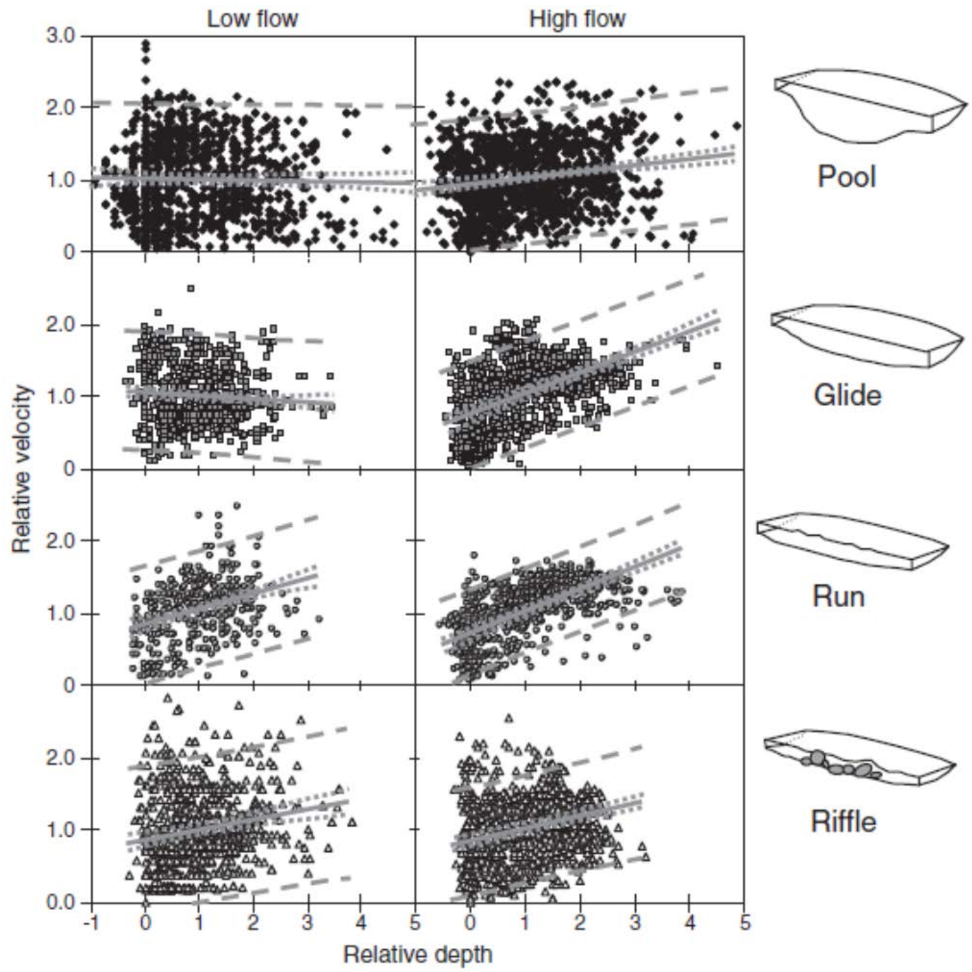


Figure 2.16 – Standardised (by average) velocity–depth distributions for pools, glides, runs, and riffles at low (left panels) and high flows (right panels). Solid grey lines represent the relationship between mean velocity and depth with 95% confidence intervals on the predicted mean as dotted grey lines. Broken grey lines represent 95% confidence intervals on all data points. From Rosenfeld *et al.* (2011).

biota interactions (Harper & Everard, 1998; Hart & Finelli, 1999; Newson & Newson, 2000; Lancaster & Downes, 2010). The most commonly used index for mesohabitat calibration, Fr, lacks ecological relevance. Whilst correlations between the distribution of certain biota and Fr have been identified, **there is no direct mechanistic relationship between organisms and Fr** (Allan, 1995). **Instead, indices describing turbulent flow derived from high-frequency hydraulic measurements** (Appendix C) **may be more ecologically relevant** (Chapter 5) **and provide greater power to objectively discriminate between PBs** (Harvey & Clifford, 2009).

3

A community-level, mesoscale analysis of fish assemblage structure in a large river using multivariate regression trees

Chapter overview

Despite the numerous advantages over traditional methods ascribed to community-level analyses, including the ability to rapidly predict the abundance of multiple species and the integration of complex biological interactions, very few applications to the mesoscale of river habitats can be found in the extant literature. Most previous work has been based on single species, species-by-species modelling or reduced dimensionality approaches. Community-level analyses have especially good properties for improving the understanding of habitat associations in large rivers where biological interactions are most intense and applications of the mesohabitat concept relatively sparse. This chapter seeks to test the ecological basis for applications of the mesohabitat concept in large rivers. Mesohabitats were mapped and their environmental characteristics recorded along a reach of the San Pedro River, Chile. A representative portion of the mesohabitats were selected for fish sampling and multivariate regression trees produced to predict community structure based on combinations of environmental variables. The analyses showed that fish assemblages were distinct at the mesoscale, with flow depth, bank materials, cover and woody debris the key predictor variables. The results support the application of the mesohabitat concept in this geographical context.

3.1 Introduction

Chapter 1 described how the mesohabitat concept has become central to many river research and management activities but Chapter 2 showed how its ecological relevance is still questionable and identified community-level modelling as a means to progress in this area. **Traditionally, fish habitat models have considered individual species** (*e.g.* Guay *et al*., 2000) or, if multiple species have been considered, community-environment relationships have been modelled separately (*e.g.* Lamouroux *et al*., 1999; Garcia *et al*., 2011). **The benefits of true community-level modelling**, however, include the ability to **rapidly model many species** simultaneously, including **infrequent species**, and enhanced capacity to produce results which are **readily interpretable**. Furthermore, consideration of the whole assemblage allows for the **detection of indicator species, species groups and predictive mapping of species distributions** on a regional scale (Ferrier & Guisan, 2006). Many community-level methods involve the classification or ordination of the biological data, without any reference to environmental factors, before synthetic community indices are modelled as a function of environmental predictors (*e.g.* Johnson & Jennings,1998). Alternatively, biological and environmental data can be considered together, using constrained classification or ordination (*e.g.* Fladung *et al*., 2003), to quantify the relative importance of abiotic variables in structuring the community. Such information is invaluable for river managers attempting to predict and monitor the impact of anthropogenic alterations, such as flow regulation for HEP generation.

There have been very few studies that have examined the response of whole riverine fish assemblages to environmental factors at the mesoscale. Johnson and Jennings (1998) used cluster analysis to group mid-channel islands in the Upper Mississippi based on their mesohabitat characteristics and species composition separately and found that each produced similar results. Erös *et al*. (2005) examined correlations between the abundance of gobiid species and axis scores from a principal components analysis (PCA) of mesohabitat characteristics in the River Danube, Hungary. Two studies have combined non-metric multidimensional scaling (NMDS) with multivariate versions of the univariate ANOVA (*e.g.* ANOSIM, PERMANOVA) to compare fish assemblages among pre-defined mesohabitats in large rivers (Boys & Thoms, 2006; Loisl *et al*., 2013). Others have used constrained methods to produce a truly multivariate, multiresponse output. Among these are Fladung *et al*. (2003) and Li and Gelwick (2005) who used canonical correspondence analysis (CCA) to model the habitat preferences of fish assemblages in shoreline habitats of the lowland Elbe River, Germany, and the Brazos River, Texas, respectively. One such constrained method, known as **'multivariate regression trees'** (MRTs), is related to the classification and regression tree (CART) approach (Breiman *et al*., 1984) and has been found to have particularly good qualities for applied ecosystem management as it **produces a community classification and a set of environmental rules for predictive mapping** (De'ath, 2002). By considering all species and environmental variables together, **MRTs also integrate the effects of biological interactions** (*e.g.* competition, predation) between species in the community (Larsen & Speckman, 2004). This is particularly important in larger rivers where the relative influence of biotic factors is often higher than in lower order streams (Zalewski & Naiman, 1985; Schlosser, 1987). Despite these advantages, to the authors' knowledge there have been no attempts to apply this method to the problem of modelling riverine fish communities.

Regression trees involve the recursive partitioning of a single quantitative response variable (*e.g.* species abundance) using a set of environmental variables. MRTs extend this method to allow the prediction of a multivariate response (*e.g*. an ecological community). An MRT is produced by combining two procedures: constrained partitioning of the data followed by cross-validation of the results (De'ath, 2002). The first of these procedures repeatedly splits the data into two groups at different levels in the tree and retains the solution which minimises the within-group variability. This can lead to a tree with many nodes and end-groups or 'leaves' that is overfitted to the data. To avoid this, and in doing so improving predictive rather than explanatory power, the cross-validation procedure iteratively builds trees based on a subset of data (training set) and validates the results using the remaining data (test set), allowing the user to decide at which level the tree should be 'pruned'. A detailed explanation of the procedure can be found in Borcard *et al*. (2011). MRT results can be submitted to IndVal (Dufrêne and Legendre, 1997) to search for indicator species in each leaf. This method assesses the significance of indicator values based on specificity (large mean abundance in one group compared to others) and fidelity (presence in most sites of that group). The results of MRTs can be further subjected to PCA in order to visualise tree splits and provide information on the strength of the community-environment relationship.

In summary, MRTs have the potential to contribute significant understanding of the spatial distribution of fish communities in aquatic ecosystems, particularly in large rivers where this knowledge is severely limited. This is because traditional concepts of river habitat (S 1.4.1) cannot be easily applied to large river-floodplain systems where biological complexity is high and patterns of habitat use (*e.g.* for feeding, spawning and refuge) are dynamic, being linked to the interplay of hydrology and bank/floodplain morphology (Junk *et al*., 1989; Nestler *et al*., 2012). **The aim of this**

chapter is to test the ecological relevance of the mesohabitat concept using MRTs to determine the relative influences of environmental factors within mesoscale shoreline habitats of the San Pedro River, Chile, on fish assemblages. The chapter also serves to define reference communities prior to the planned construction of a HEP plant some 12 km downstream of the study reach. In order to achieve these aims, mesohabitats along a reach were mapped and classified on the basis of hydromorphological characteristics before fish were sampled within a representative selection of these mesohabitats. The results represent both a novel application of MRTs in predictive mapping of riverine fish assemblages and a contribution to the understanding of the requirements of threatened native species.

3.2 Methods

3.2.1 Study site

The study was conducted along a freeflowing reach of the San Pedro River between Lake Riñihue and a section of rapids 2 km downstream of the lake outlet (Figure 3.1). Located in the Valdivia region of Chile, the San Pedro River is part of a fluvial system draining a chain of eight lakes in the Andean mountains. Flow in this part of the system is not currently regulated, resulting in a seasonally variable hydrograph with a mean summer flow of 180 $m^3 s^{-1}$ and a mean winter flow of 652 $m^3 s^{-1}$ (E. Habit, unpublished data). The river here is deeply incised, with flow depths of up to 25 m. Bank morphology along the reach is varied and provides a range of shoreline habitats, from low gradient zones with submerged bedrock shelves to steeper areas with no shallow shoreline habitat (Figure 3.2). The substrate is made up mainly of bedrock and clay. Boulders, woody debris, overhanging vegetation and deep cracks and striations in the bedrock provide habitat complexity (*i.e.* cover).

A rich and complex biogeographical history in the region (Ruzzante *et al*., 2006; Zemlak *et al*., 2010) has resulted in the occurrence of distinctive fish communities and high levels of endemism (Habit & Victoriano, 2012). Despite their high conservation value, these communities are threatened by human development. The major anthropogenic impacts on this reach of the San Pedro River are currently leisure boating and game fishing. The latter of these human activities has been accompanied by the introduction of non-native species (*Oncorhynchus mykiss*, *Salmo trutta*) which have been shown to impact the behaviour and fitness of native taxa such as galaxiids (Sobenes, 2005; Milano *et al*., 2010), leading to declines in the abundance and contraction in the distributions of such species (Arismendi *et al*., 2009; Habit *et al*., 2010). HEP construction and operation has been shown to negatively impact the abundance and community composition of native communities in other Chilean rivers (Habit *et al*., 2007; García *et al*., 2011) so the planned construction of the *Central Hidroeléctrica San Pedro* HEP plant on the San Pedro River is expected to further affect the fish community here by transforming 12.5 km of the river into a reservoir (Habit & Parra, 2012).

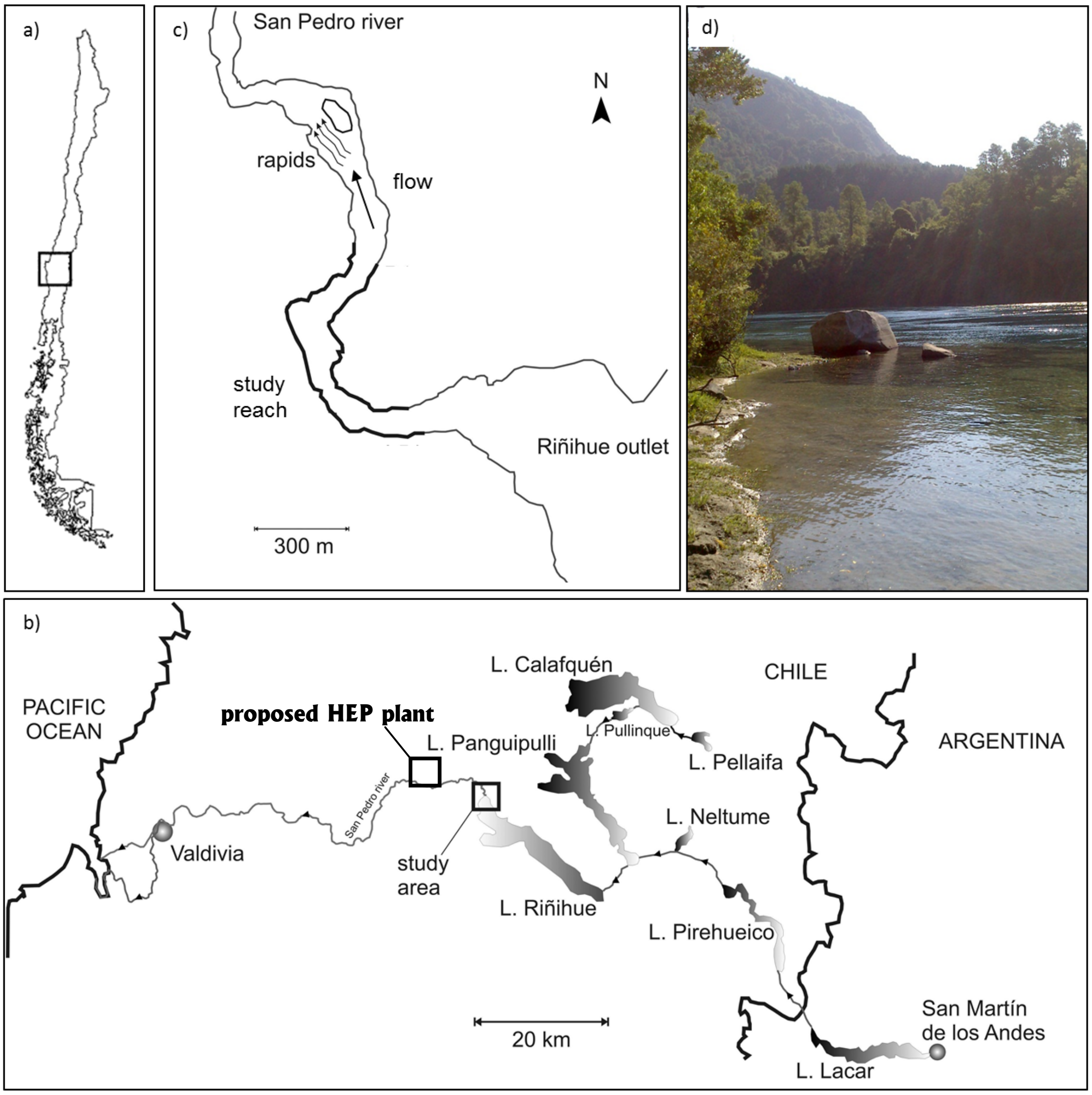


Figure 3.1 – Location of the study area including outline of Chile (a), an overview of the San Pedro River (b), the site layout (c) and an image of part of the reach (d).

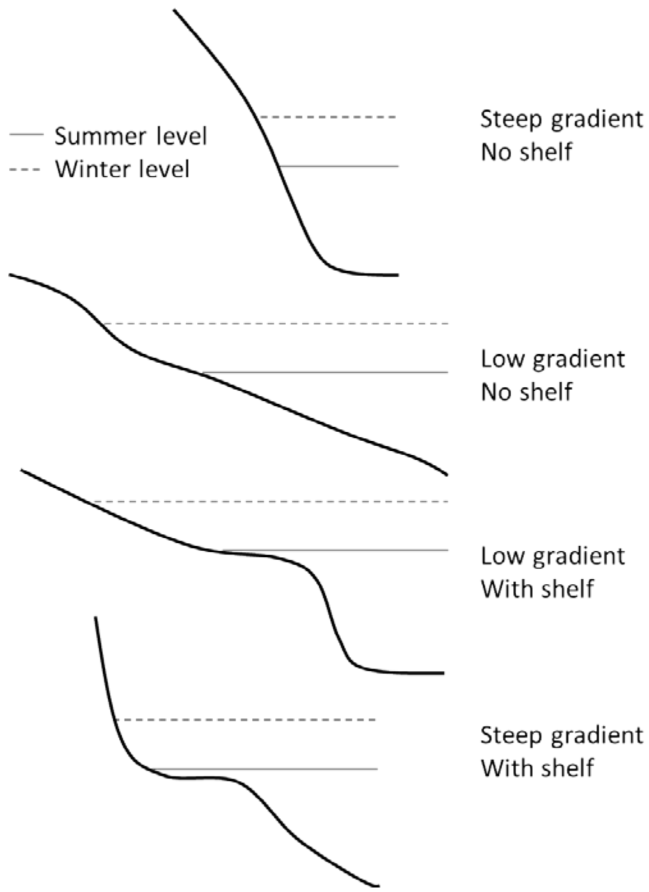


Figure 3.2 – Idealised cross-sections of banks typifying the morphology of shoreline habitats along the study reach.

3.2.2 Mesohabitat mapping

Distinct units of shoreline habitat (mesohabitats) along each bank were mapped using a Trimble GeoXT mapping grade GPS (sub-metre accuracy) and characterised by a mixture of visual assessment and direct measurement from a boat, traversing within close proximity to the shoreline. A number of environmental characteristics were recorded to describe below water, water's edge and above water features of each habitat (Table 3.1). These sets of variables refer to submerged, emergent and water's edge zones at the time fieldwork was undertaken. Individual mesohabitats and, therefore, divisions between them were identified where there was a change in one or more of the habitat features. At the end of a submerged bedrock shelf, for example, or at a break in the slope angle of the bank. Above water features were assessed because they are inundated during the high flow season and become important as spawning and nursery habitat for some species (illustrated in Figure 3.2). Other features such as overhanging cover provided by trees may also have been important for fish at the time of sampling. Characteristics of the water's edge also reflect important cover features (*e.g.* shoreline complexity, woody debris). Below water features reflect the available

Table 3.1 - A list of environmental variables recorded in each habitat along with their associated codes and levels. Above water refers to emergent features at the flow present during fieldwork.

Feature	Name	Code	Levels
Above Water	Gradient	AWGradient	Low, steep
	Dominant substrate Subdominant substrate Present substrate	AWDomSub AWSubdomSub AWPresSub	Bedrock fractured, bedrock smooth, boulders, clay, cobbles, gravel, mud, sand
	Number of substrate sizes	AWNumSubSizes	0-8
	Woody debris 1	AWWD1	Simple, complex, simple+complex, none
	Woody debris 2	AWWD2	Single, many, complex+many, none
	Dominant vegetation Subdominant vegetation Present vegetation	AWDomVeg AWSubdomVeg AWPresVeg	Bryophytes, forest, grass, shrubs
	Cover	AWCover	Overhanging out of water, overhanging into water, both, absent
Water's edge	Bank length (m)	BankLength	(Quantitative)
	Woody debris1	WEWD1	Simple, complex, simple+complex, none
	Woody debris 2	WEWD2	Single, many, complex+many, none
	Edge shape	WEShape	Simple, complex
	Lower layer substrate Middle layer substrate Upper layer substrate	WELowLay WEMidLay WEUpLay	Bedrock fractured, bedrock smooth, boulders, bryophytes, clay, cobbles, forest, grass, gravel, mud, none, roots, shrubs, sand
	Lower layer width (m) Middle layer width (m) Upper layer width (m)	WELowWidth WEMidWidth WEUpWidth	(Quantitative)
Below water	Water depth (m)	Depth	(Quantitative)
	Shelf presence	Shelf	None, shelf
	Shelf width (m)	ShelfWidth	(Quantitative)
	Dominant subsrate Subdominant subsrate Present substrate	BWDomSub BWSubdomSub BWPresSub	Bedrock fractured, bedrock smooth, boulders, clay, cobbles, gravel, macrophytes, mud, sand
	Number of substrate sizes	BWNumSubSizes	0-9
	Woody debris 1	BWWD1	Simple, complex, simple+complex, none
	Woody debris 2	BWWD2	Single, many, complex+many, none
	Living vegetation	BWVeg	Absent, simple, complex, simple+complex

aquatic habitat at the time of sampling. The set of environmental variables recorded was based on the ecologically relevant features typically assessed as part of mesoscale habitat mapping assessment protocols, such as the RHS (Raven *et al*., 1997) and the Rapid Bioassessment Protocol (Plafkin *et al*., 1989), and knowledge of the features that are likely to provide important physical habitat for the fish communities.

Representative mesohabitats within which to sample fish communities were selected by estimating the dispersion of groups defined by combinations of the factors AWGradient and Shelf. This is because there was an expectation that these factors would be important to the fish communities through their influence on local hydraulics and the availability of feeding, spawning, nursery and refuge habitats across a range of flow stages. Dispersion was estimated using the multivariate dispersion (MVDISP) algorithm in PRIMER (v6). This part of the analysis was performed separately for each bank as it is possible that the deep central portion of the channel acts as a dispersal barrier for some species, potentially creating differences in the community-environment relationship between banks. It was, therefore, deemed necessary to select a representative proportion of mesohabitats from each bank. A minimum of 30% of sites were selected from each group, with a higher proportion where the dispersion of the group was greater.

3.2.3 Fish sampling

In order to gain a complete representation of the abundance of each species five fish sampling techniques were used to sample the representative selection of mesohabitats. For each selected mesohabitat one or more fishing methods was used, depending on flow velocity and depth, which determine the relative efficiencies of the fishing methods (García *et al.* 2011; 2012a). In shallow (< 1.2 m depth) mesohabitats with slow current velocities (<0.3 m s^{-1}) a Halltech backpack electro-shocker was used. In addition to this seine netting was performed in areas without woody debris or living vegetation. In deeper (> 1.2 m) mesohabitats with low velocities (<0.3 m s^{-1}) multiple panelled gillnets (10, 15, 20, 30, 50, 60, 70 and 120 mm mesh sizes) were placed at the surface and on the bottom during night. This was achieved by weighting the nets and attaching buoys at the surface. In deeper (> 1.2 m) mesohabitats with faster velocity (>0.3 m s^{-1}) or abundant woody debris hook lines were set during night. Finally, underwater observations were made in each mesohabitat by two divers. Each individual fish was identified to species level and its standard length and weight measured. Species with a clear age structure were classified as juveniles or adults depending on size (Cifuentes *et al.*, 2012). Data collection was undertaken in January and February 2013.

3.2.4 Data analysis

Species data were transformed into relative abundance within each mesohabitat in order to reduce the effects of biases associated with different fishing methods (Clarke & Gorley, 2005; Smith *et al.*, 2013). MRTs were then produced for several scenarios (Table 3.2). Due to the relative ease with which sets of variables describing above water and water's edge features can be collected, it was decided that MRTs would be produced using subsets of the environmental data in addition to considering all environmental factors as predictor variables. MRTs for each bank were also produced separately to examine differences in the community-environment relationships of each bank.

Table 3.2 – Scenarios modelled using MRTs.

Explanatory variables	**Bank**
All	Both
Above water	Both
Water's edge	Both
Below water	Both
All	Left
All	Right

There are a number of statistics which are involved in the construction, selection and comparison of MRTs. These are described in detail by De'ath (2002). Within-group sum of squares (WSS) is the sum of squared distances to the group mean and describes the overall error associated with the terminal nodes (leaves) of the tree. The relative error (RE) is the ratio of the sum of WSS over all leaves to the overall sum of squared errors in the biological data. RE can be seen as 'explanatory error' (Borcard *et al.*, 2011). The MRT procedure is designed to minimise RE but this often leads to a tree with many leaves which is overfitted to the data and so some level of pruning is required. For this reason cross-validation is performed to find the optimum tree size based on the cross-validated relative error (CVRE). The CVRE is the ratio between the dispersion unexplained by the tree (summed over all iterations in the cross-validation procedure) and the overall dispersion of the response data. CVRE tends to reach a minimum for a certain tree size before increasing and can, therefore, be seen as predictive error (Borcard *et al*., 2011). There is no single accepted way of selecting the final tree. The tree retained may be selected as the one with the smallest CVRE, the next smallest tree within 1 standard error of this CVRE, or simply the one with a chosen number of leaves.

For the purposes of this study, a tree with the minimum CVRE was selected. As this method of tree selection resulted in two-leaf solutions for every scenario, trees with more leaves were also considered in order to aid understanding of community characteristics. It was decided to produce trees with four to six leaves as there were not always solutions available for a single arbitrary number of leaves. Furthermore, any trees with more leaves became progressively over-fitted to the data. After tree selection a PCA was performed to visualise the distances between groups and the species driving the splits between groups (species variance). This part of the procedure reports the interset correlation which describes the strength of the community-environment relationship for ordination axes (Borcard *et al*., 2011). Results for each leaf of the tree were submitted to IndVal (Dufrêne and Legendre, 1997) to search for indicator species. Finally, as a check on the proportion of overall species variance explained by explanatory variables included in MRTs, results were compared with unconstrained (k-means) cluster analysis (Ward's method) on the species data (Legendre & Legendre, 1998). All data analysis was undertaken using R (2.15.2) (R Core Team, 2013).

3.3 Results

3.3.1 Mesohabitat characteristics and the selection of sites for fish sampling

A total of 95 distinct mesohabitats were mapped, 41 on the right bank and 54 on the left bank (Figure 3.3). The environmental characteristics of these mesohabitats covered the range of levels classified at the time of mapping (Table 3.1). Field data sheets are provided in Appendix A (Figure A1). The NMDS procedure revealed that sites were particularly well grouped according to the presence or absence of a shelf and that there was also a degree of grouping with gradient (Figure 3.4a). Sites did not cluster according to bank side (Figure 3.4b), showing that the environmental characteristics of mesohabitats on each bank were similar. Table 3.3 summarises the selection of representative mesohabitat units for fish sampling. The selected units were well distributed throughout the NMDS plot and, therefore, representative of the range of mesohabitats present along the reach (Figure 3.4b).

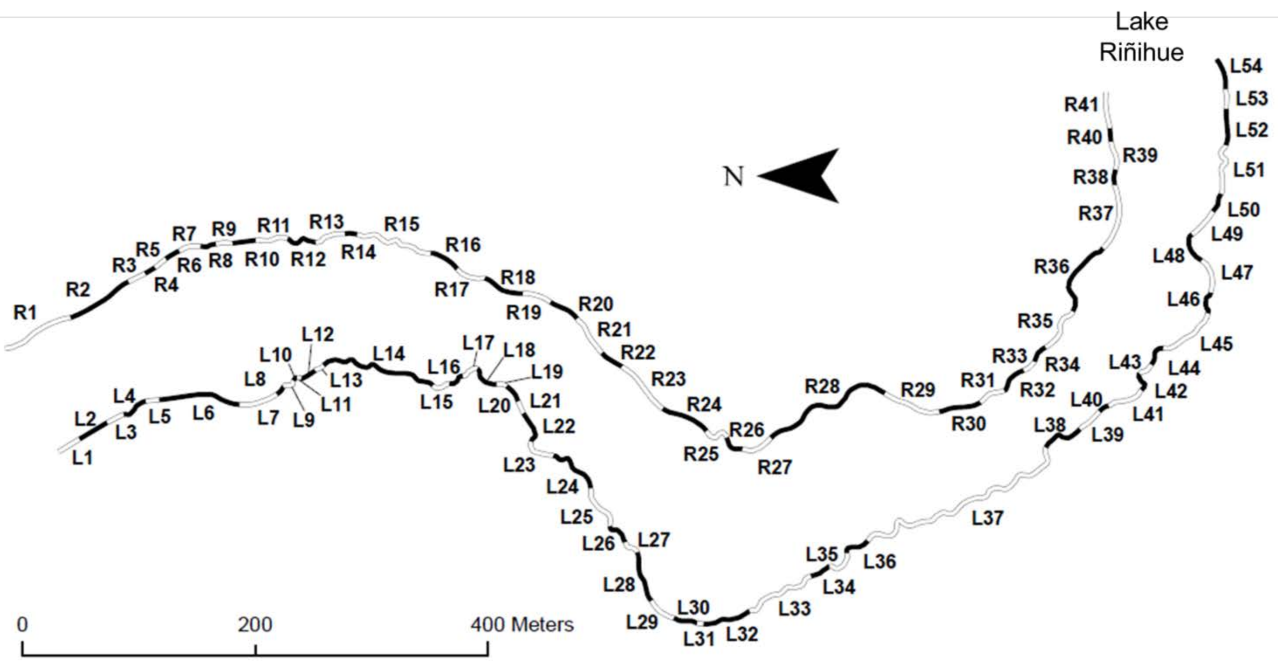


Figure 3.3 – Mesohabitats mapped along the study reach. Flow is from right to left.

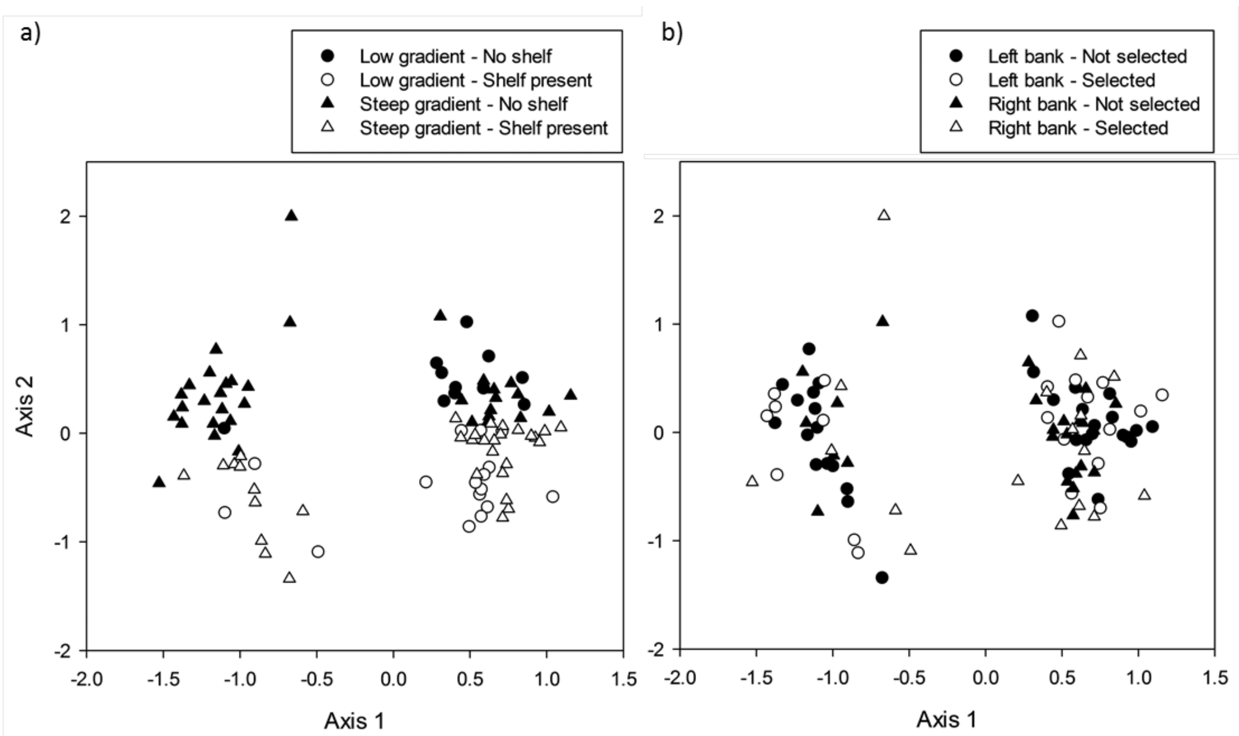


Figure 3.4 – NMDS results grouped by gradient and shelf (a) and by bank and selection for fish sampling (b). 2D stress 0.16.

Table 3.3 – Summary of representative mesohabitat selection for fish sampling.

Bank	Gradient	Shelf	No. units	Dispersion	No. selected
Right	Steep	Present	8	0.64	3
Right	Steep	Absent	12	1.31	5
Right	Low	Present	15	0.90	6
Right	Low	Absent	6	1.03	3
Left	Steep	Present	25	0.82	8
Left	Steep	Absent	23	1.24	8
Left	Low	Present	1	N/A	1
Left	Low	Absent	5	0.39	2
				Total	**39**

3.3.2 Multivariate regression trees

A total of 10 native and two non-native species were caught, some of which could be separated into juvenile (J) and adult (A) specimens (Table 3.4). Of these, three infrequent species (*Aplochiton zebra*, *Cheirodon australe*, *S. trutta*) were exclusively found on the left bank. The infrequently found juveniles of *Percilia gillissi* and the more common *Basilichthys australis* (adult and juveniles) were only caught in mesohabitats of the right bank. Three common taxa (*Galaxias maculatus*, *P.gillissi* and juveniles of *Galaxias sp.*) were found in similar abundances in every habitat and were, therefore, excluded from the analyses as they dominated gradients in the data, drowning out the signal from the rest of the community. Two of the representative habitats contained only these common species, reducing the number of sites to 37. Raw species data are provided in Appendix A (Table A1).

3.3.2.1 All variables, both banks

Based on the minimum CVRE rule, Figure 3.5 shows that the two-leaf tree was the best solution for this scenario. This tree selected water depth as the top discriminatory variable (Figure 3.6) and had an R^2 of 0.2. Many species were present in both leaves, although juveniles of *B. australis*, adults of *O. mykiss* (an indicator species), *S. trutta* and *A. zebra* were only found in leaf 1. Other indicator species for the two-leaf solution were *Percichthys trucha*, which had a much higher abundance in leaf 1, and *Galaxias platei*, which dominated leaf 2 indicating a preference for more shallow habitats where piscivorous salmonids were not found. Adults of *B. australis* were another indicator for leaf 2, being absent from leaf 1. A four-leaf solution gave a much higher R^2 (0.33) and depth was again the main split, distinguishing between deep (>0.78 m) and shallow habitats (Figure 3.7). The PCA biplot shows that many species were involved in the clustering of groups and that a strong community-environment relationship exists on the first axis, with an interset correlation of 0.87 (Figure 3.8). A closer examination of the four-leaf tree shows that one significant indicator species was found in each of the leaves. These included *O. mykiss* in the deep habitats of leaf 1 and *G. platei* in the relatively shallow habitats of leaf 4 with woody debris at the water's edge. Leaves in the lowest split of the tree were indicated by *B. australis* in leaf 2 (shallow habitats with WEMidLay = clay, grass or shrubs) and *P. trucha* in leaf 3 (WEMidLay = bryophytes, forest or none). Although not indicator species, two other taxa (*Ch. australe* and juveniles of *P. gilissi*) contributed a significant proportion of the explained variance due to their absence from leaves 2 and 3 (Table 3.5). The main split in both trees was caused by the specificity and fidelity of *O. mykiss* to deeper habitats and *G.platei* to more shallow areas.

Table 3.4 – A summary of the species caught along with short names used in the MRT analyses. *denotes non-native species

Species name	**Common name**	**Order**	**Short names**	**Total no.**
Aplochiton zebra	Galaxiid	Galaxiformes	Az	3
Basilichthys australis	Silverside	Atheriniformes	BaA	58
			BaJ	39
Cheirodon australe	Tetra	Characiformes	Ca	8
Diplomystes camposensis	Catfish	Siluriformes	Dc	24
Geotria australis	Lamprey	Petromyzontiformes	Ga	6
Galaxias maculatus	Galaxiid	Galaxiformes	Gm	2192 (adults)
Galaxias platei	Galaxiid	Galaxiformes	Gp	396 (adults)
Galaxias sp. (juveniles)	Galaxiid	Galaxiformes	GJ	2071
*Oncorhynchus mykiss**	Rainbow trout	Salmoniformes	OmA	44
			OmJ	10
Percilia gillissi	Darter	Perciformes	PgA	1443
			PgJ	20
Percichthys trucha	Darter	Perciformes	Pt	78
*Salmo trutta**	Brown trout	Salmoniformes	St	4
Trichomycterus areolatus	Catfish	Siluriformes	Ta	26

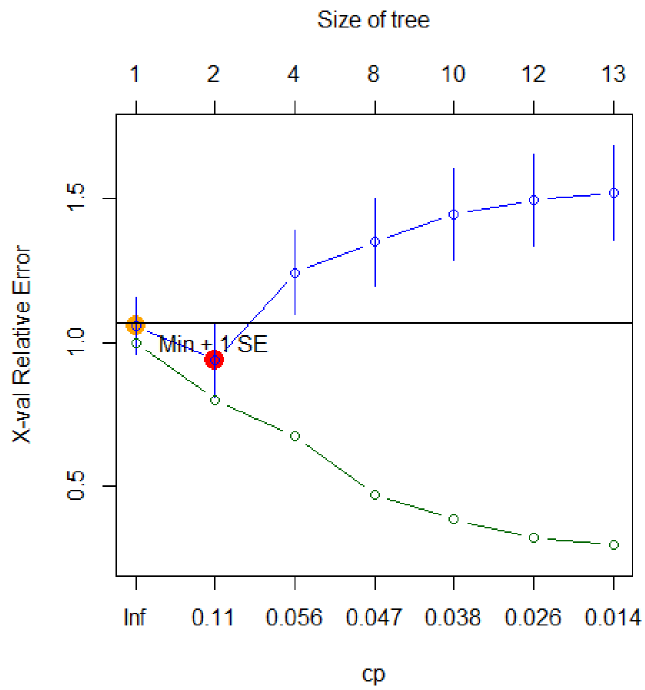


Figure 3.5 – Cross-validation results showing RE (dark green) and CVRE (blue) for the all variables and both banks scenario. 'cp' refers to the complexity parameter associated with a given tree size.

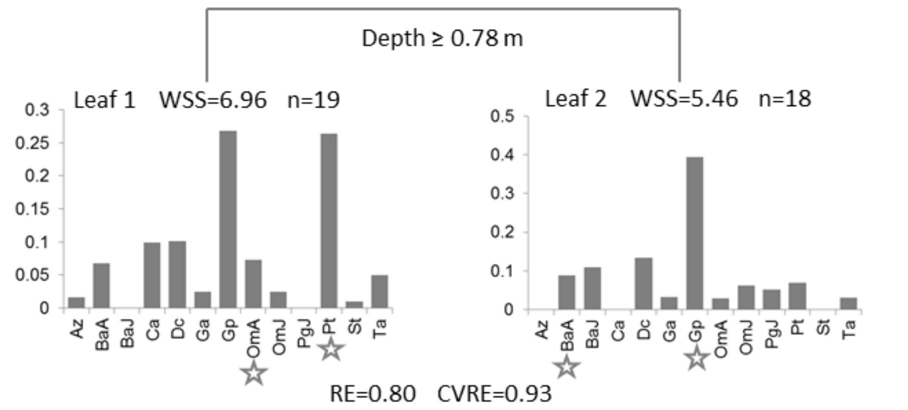


Figure 3.6 – Two-leaf MRT for all variables and both banks, including species composition (relative abundance) of leaves. Where a condition at a node is met move left down the tree. Figures above terminal leaves refer to the within-group sum of squared errors (WSS) and number of mesohabitats (n) within the group. Figures below the tree indicate relative error (RE) and cross-validated relative error (CVRE). Stars denote significant indicator species. NOTE different vertical axis scales.

3.3.2.2 Trees using subsets of environmental data

For variables describing above water features, cross-validation indicated that the two-leaf solution had the smallest CVRE, as was the case for all scenarios (Figure A2). This tree had relatively poor explanatory power (R^2=0.12) and split the data into two groups on the basis of AWDomSub. Leaf 1

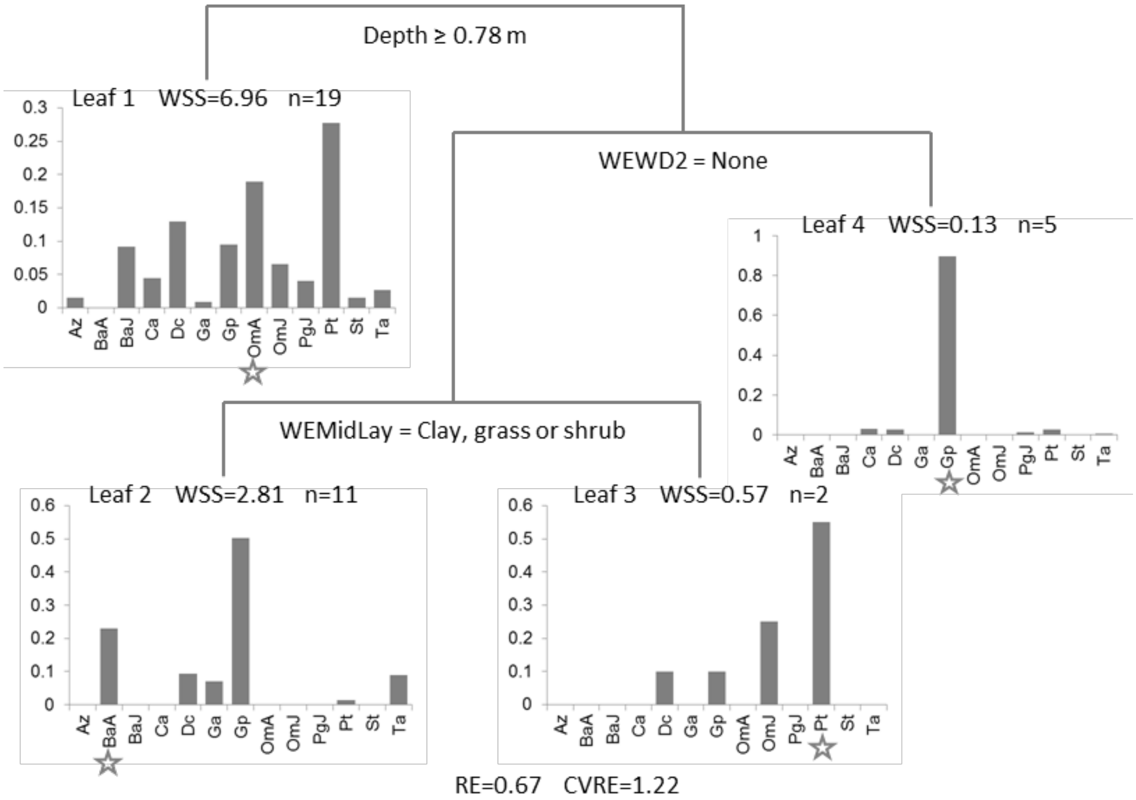


Figure 3.7 - Four-leaf MRT for all variables and both banks. See Figure 3.6 for an explanation of MRT presentation.

(non-bedrock substrate) was indicated by *G. platei* and *Trichomycterus areolatus*, whilst the indicator species of leaf 2 (bedrock substrate) were *O. mykiss* and *P. trucha*. With the exception of *T. areolatus*, a benthic species which is known to prefer shallow habitats (García *et al*., 2011; 2012), the presence of these indicator species suggests that the variable AWDomSub may be acting as a proxy for water depth, as these are the same species driving the split based on depth shown in Figure 3.6. A six-leaf solution (Figure 3.9) included variables describing above water cover and substrate diversity (AWNumSubSizes) and improved the fit markedly (R^2=0.28), although this tree had a larger error than the tree for all variables (Figure 3.7) despite having more leaves. Furthermore, with an interset correlation of 0.65 shown in the PCA biplot (Figure A3), the strength of the community-environment relationship was much weaker than the all variables scenario. The first split retained the same sites in leaf 1 as the two-leaf solution, with *G. platei* as the sole indicator species, but the remaining sites were split mainly on the basis of AWCover. Juveniles of *O. mykiss* were only found in

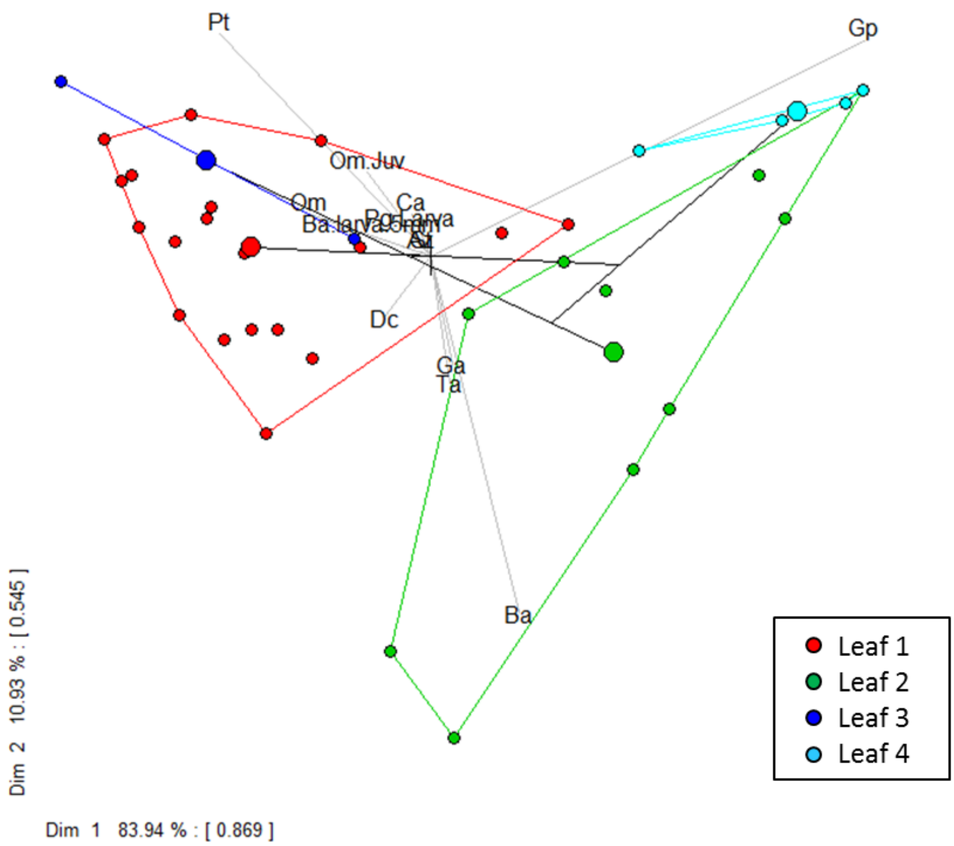


Figure 3.8 – PCA biplot of the first two axes from the four-leaf solution for all variables and both banks. Figures in square brackets denote the interset correlation for each dimension.

leaves 2 and 3 (indicator species) where cover was hanging into the water. Another salmonid, *S. trutta*, was also found in habitats rich in overhead cover and was an indicator species for leaf 2. Other notable species involved in the splits included juveniles of *P. gillissi*, only found in leaf 5 where it was an indicator species, and juveniles of *B. australis*, also an indicator of leaf 5, which contained three sites with uniform fractured bedrock substrate. This suggests the possibility that areas associated with fractured bedrock banks are important nursery habitat for these species. The only other indicator was *Diplomystes camposensis* in leaf 6, which contained two sites with uniformly smooth bedrock banks, but this species was found in all leaves. Finally, another noteworthy species in both the two- and six-leaf tress is *B. australis* (adults), who were only found in habitats to the left of the first split (AWDomSub=boulder, clay, gravel or mud). These points are supported by species variances (Table A2) for the six-leaf tree.

The two-leaf solution using water's edge variables produced a very similar tree to that generated using above water variables and had the same R^2 (0.12). This time the split was made on the basis of

WELowLay but described the same habitat characteristics as AWDomSub. The composition of the leaves was also identical. The six-leaf tree further grouped the habitats using bank length, WEMidLay and WEWD2 (Figure 3.10). The leaves of this tree separated more speciose and even communities (*e.g.* leaf 6) from less diverse ones dominated by one or a few species (*e.g.* leaf 5). Indicator species included *B. australis* in leaf 3 (WEMidLay = grass), which was the only leaf where this species was found, and *D. camposensis* in leaf 6, which contained sites poor in woody debris. Once again, *O. mykiss* and *G. platei* were also indicator species (Table A4). With an R^2 of 0.38, this water's edge tree was a substantial improvement on the equivalent tree based on above water variables (Figure 3.9) but provided only a marginally better fit that the 'all variables' tree (Figure 3.7) despite having two more leaves. The PCA biplot (Figure A4) illustrates the species driving the splits in the tree and shows that the community-environment relationship was strong, with an interset correlation of 0.85.

Table 3.5 – Species and tree variance for the four-leaf tree (all variables, both banks). Figures in bold denote significant discriminator species at each split.

Species code	**Depth**	**WEWD2**	**WEMidLay**	**Tree total**	**Species total**
Az	0.01	0	0	**0.01**	**0.22**
BaA	**1.18**	0.88	0.58	**2.64**	**8.75**
BaJ	0.5	0	0	**0.50**	**6.44**
Ca	0.08	0.02	**0**	**0.10**	**3.64**
Dc	0.17	0.11	0	**0.28**	**10.37**
Ga	0.07	0.08	0.05	**0.21**	**2.06**
Gp	**13.28**	**4.87**	**1.76**	**19.92**	**29.45**
OmA	**2.14**	**0**	**0**	**2.14**	**8.29**
OmJ	0.09	0.03	0.68	**0.80**	**7.91**
PgJ	0.08	0	**0**	**0.08**	**2.39**
Pt	**2.41**	0.11	**3.14**	**5.66**	**17.66**
St	0.01	0	0	**0.01**	**0.12**
Ta	0.05	0.11	0.09	**0.25**	**2.69**
Total	**20.08**	**6.23**	**6.3**	**32.61**	**100**

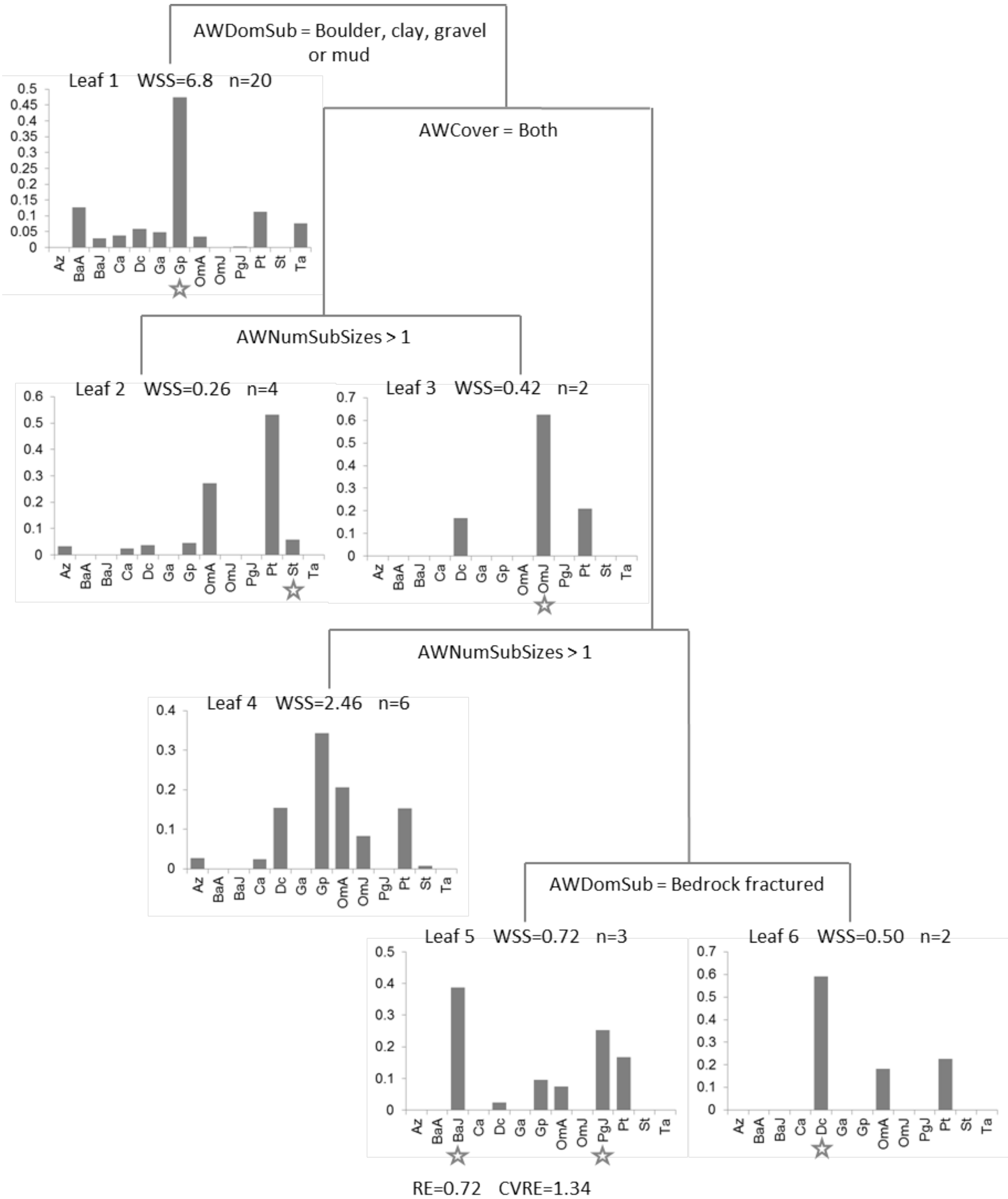


Figure 3.9 - Six-leaf MRT excluding common taxa, including only above water variables and both banks. See Figure 3.6 for an explanation of MRT presentation.

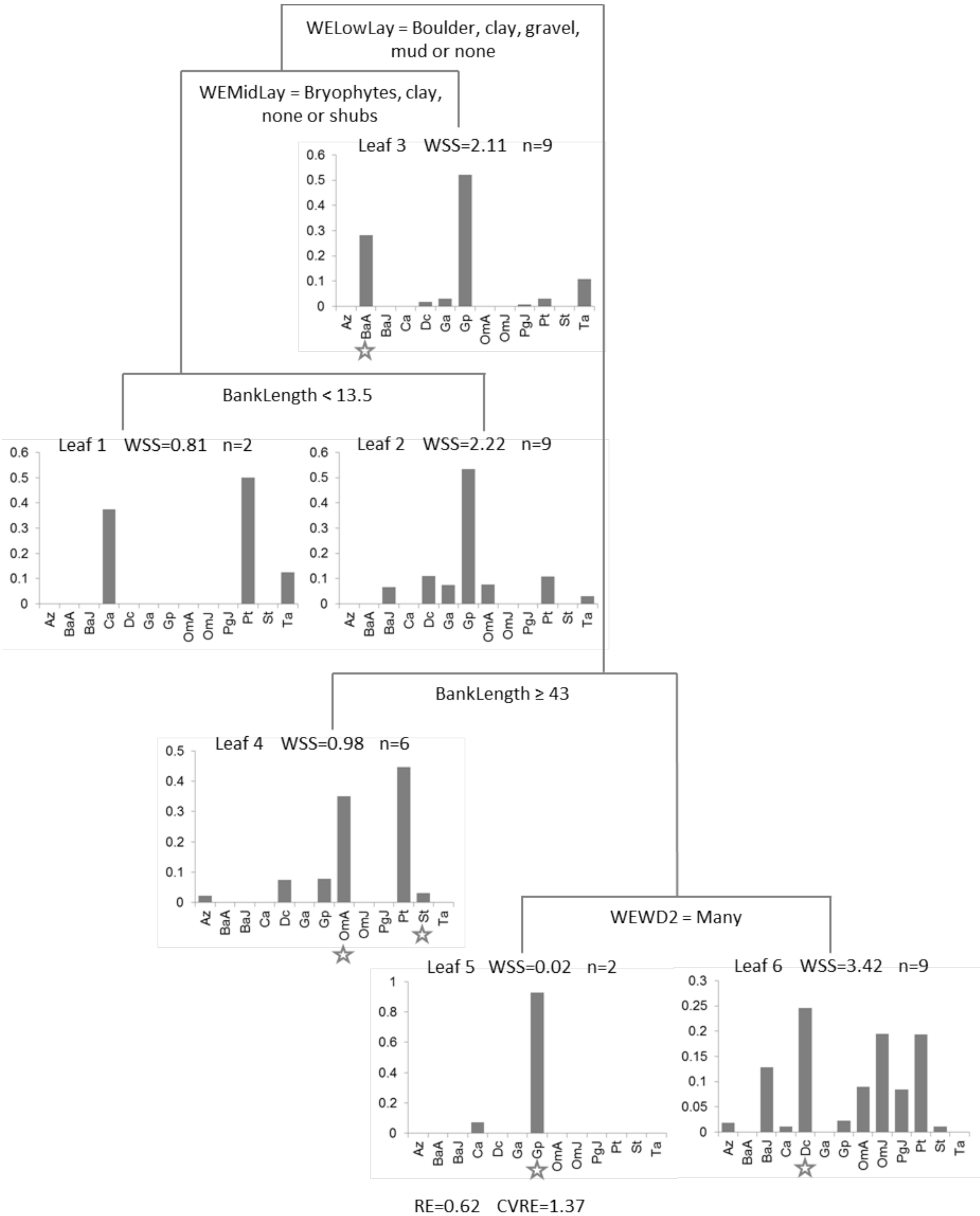


Figure 3.10 - Six-leaf MRT excluding common taxa, including only water's edge variables and both banks. See Figure 3.6 for an explanation of MRT presentation.

The two-leaf solution using below water variables was identical to the tree produced using all environmental variables (Figure 3.6), providing a better fit (R^2=0.2) than the above water or water's edge trees. A six-leaf tree was also produced as there were no four- or five- leaf solutions available. This added ShelfWidth and BWWD1 as explanatory variables along with further splits based on depth which separated habitats into very deep (leaf 1, >1.35 m), deep (leaf 2, 0.78-1.35 m), intermediate (leaves 5 and 6, 0.38-0.78 m) and shallow (leaves 3 and 4, <0.38 m) (Figure 3.11). This tree provided the same fit as the equivalent water's edge tree (R^2=0.38). Only one significant indicator species was found among the terminal leaves, namely *G. platei* in the moderately deep (0.38-0.78 m) mesohabitats of leaf 5, although several other species contributed a significant proportion of variance at the first split (Table 3.6). These were *B. australis* and *P. trucha* and *O. mykiss*, as illustrated by the PCA biplot for this scenario (Figure A5) which also shows a strong community-environment relationship (interset correlation=0.85).

Table 3.6 – Species and tree variance for the six-leaf tree (below water variables, both banks). Figures in bold denote significant discriminator species at each split.

	Depth (0.78)	**Depth (1.35)**	**ShelfWidth**	**Depth (0.38)**	**BWWD1**	**Tree total**	**Species total**
Az	0.01	0	0	0	0	**0.02**	**0.22**
BaA	**1.18**	0	2.09	0.02	0.48	**3.77**	**8.75**
BaJ	0.5	0.17	0	0	0	**0.67**	**6.44**
Ca	0.08	1.57	0	0	0	**1.65**	**3.64**
Dc	0.17	0.24	0.19	0.09	0.21	**0.90**	**10.37**
Ga	0.07	0	0.03	0.48	0.01	**0.59**	**2.06**
Gp	**13.28**	0.13	0.89	**2.94**	2.78	**20.02**	**29.45**
OmA	**2.14**	0.52	0	0	0	**2.65**	**8.29**
OmJ	0.09	0.06	0.02	0.05	0	**0.22**	**7.91**
PgJ	0.08	0.97	0	0	0	**1.05**	**2.39**
Pt	**2.41**	1.11	0.14	0.57	1.93	**6.15**	**17.66**
St	0.01	0	0	0	0	**0.02**	**0.12**
Ta	0.05	0.14	0.05	0.03	0.03	**0.30**	**2.69**
Total	**20.08**	**4.92**	**3.4**	**4.18**	**5.45**	**38.01**	**100**

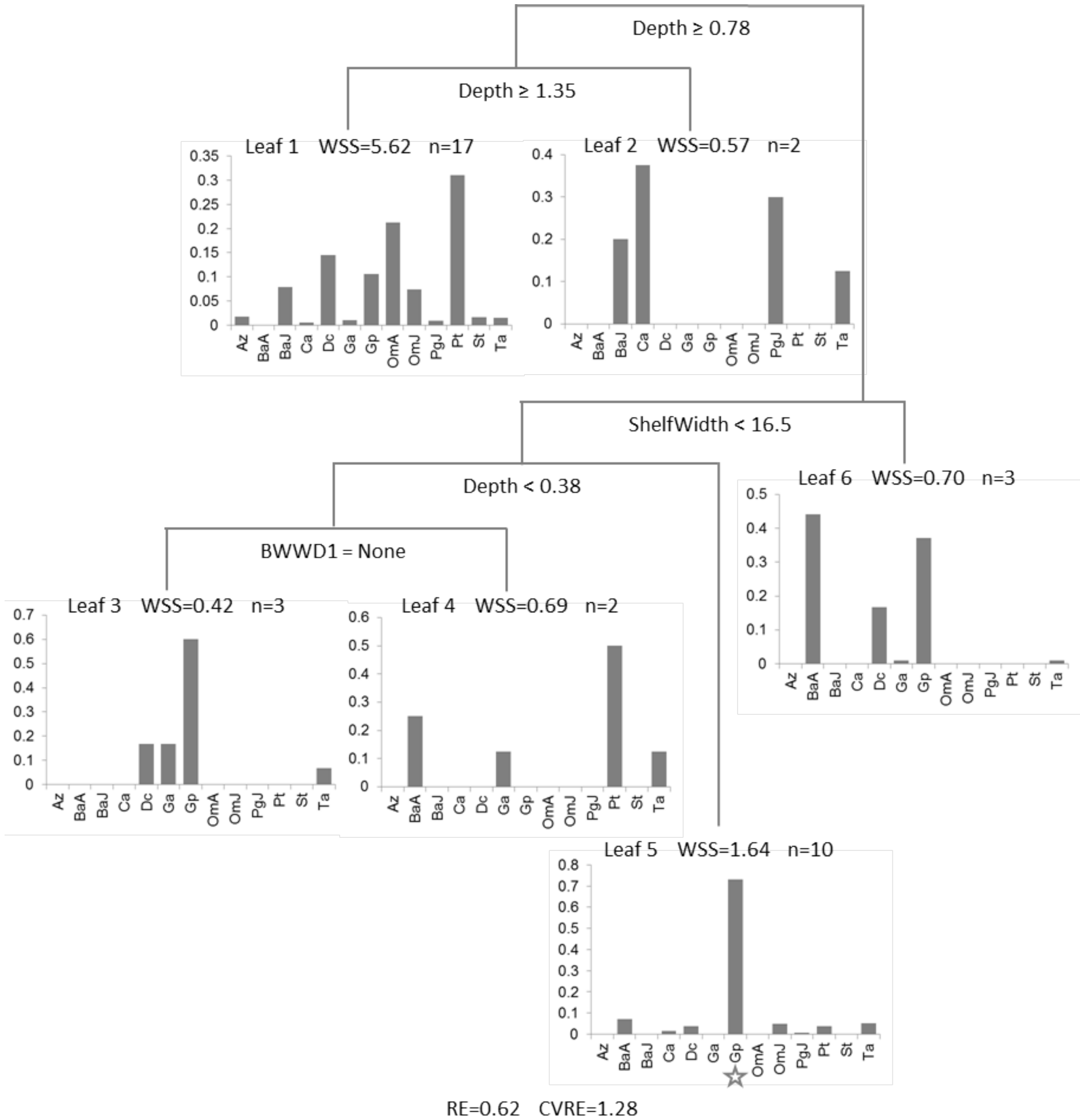


Figure 3.11 - Six-leaf MRT excluding common taxa, including only below water variables and both banks. See Figure 3.6 for an explanation of MRT presentation.

3.3.2.3 Trees for separate banks

Two- and four-leaved trees were produced for left bank mesohabitats as no five- or six-leaved solutions were available. The two-leaf solution selected the same split for depth as the both banks scenario (Figure 3.6). Despite having only one split this tree had a relatively high R^2 (0.44), higher than that of other trees with six leaves. The number of sites classified, however, was much smaller than for both bank scenarios. The indicator species were again *O. mykiss* and *P. trucha* in deeper habitats and *G. platei* in more shallow areas. The four-leaf tree improved the fit (R^2=0.6) by combining depth with variables describing the substrate composition at the water's edge and above the water (Figure 3.12). The PCA biplot shows that sites were well separated and that there was a very strong community-environment relationship, with an interset correlation of 0.98 (Figure A6). *G. platei* was found in much higher relative abundances in the relatively shallow habitats of leaves 1 and 2, being an indicator species for the latter. These first two leaves were comprised of relatively deep (>0.78 m) mesohabitats distinguished by the distribution of two species, with *Geotria australis* found exclusively in leaf 1 and *D. camposensis* found in leaf 1 in much higher relative abundances than elsewhere. *Trichomycterus areolatus* was the sole indicator species for leaf 2, where *Ch. australe* was also found in relatively high abundances. A number of taxa were exclusive to leaf 4, which contained relatively shallow sites with smooth or fractured bedrock or clay banks. These were *P. trucha* (an indicator species), *S. trutta*, *A. zebra* and juveniles of *O. mykiss*. These points are supported by the species variance matrix (Table A4).

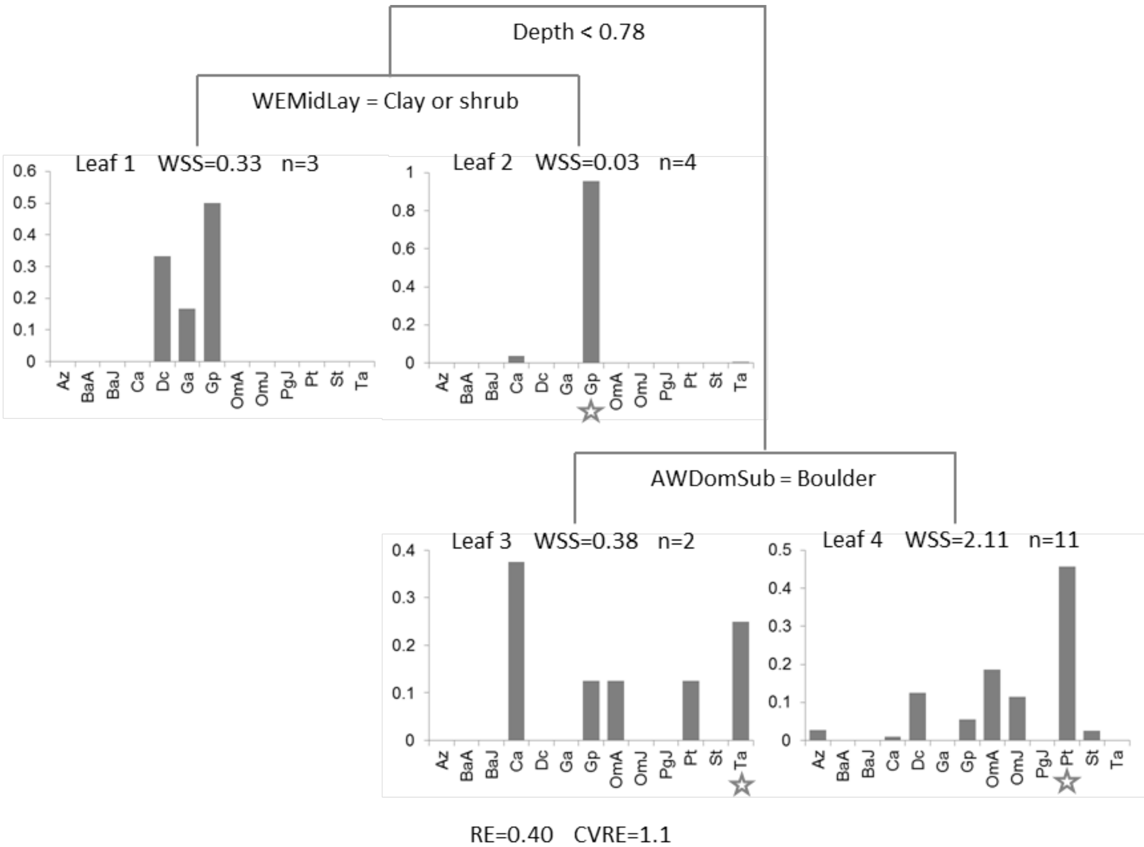


Figure 3.12 - Four-leaf MRT including all variables, left bank. See Figure 3.6 for an explanation of MRT presentation.

Two- and five-leaved trees were produced for right bank mesohabitats as no six-leaf solution was available. In contrast to other solutions including below water variables, the two-leaf tree did not include depth and provided a relatively poor fit to the data (R^2=0.19). Instead the split was provided by WELowLay. To the left of this split (WELowLay=none, fractured or smooth bedrock), leaf 1 contained juveniles of *B. australis*, an indicator species not found in leaf 2. In contrast, adults of this species were exclusively found in leaf 2 (WELowLay=boulder, clay, gravel or mud) in which *G. platei* was the only significant indicator species. The five-leaf solution (Figure 3.13) added AWCover, WEShape and BWWD1 to the set of predictor variables and fitted the data relatively well (R^2=0.51). The PCA biplot (Figure A7) shows a clear separation between sites and a relatively high interset correlation (0.9). Indicator species were identified in leaf 2 (juveniles of *B. australis* in bedrock habitats without cover overhanging out of water), leaf 4 (*G. platei* in non-bedrock habitats with a complex WEShape and simple, complex or no woody debris) and leaf 5 (*B. australis* in non-bedrock habitats with a simple WEShape) (Table A5). These tenuous relationships, however, are indicative of an overfitted tree, which is to be expected given such few sites (n=17).

3.4 Discussion

The use of MRTs to classify fish assemblages at the mesoscale produced meaningful results, explaining up to 60% of the variation in assemblage structure and supporting the use of the mesohabitat concept in this geographical context. **Two-leaf trees represented the best solutions based on the minimum CVRE rule**. The key explanatory variable was water depth, for which *O. mykiss* and *P. trucha* (deep) and *G. platei* (shallow) were the main indicator species. Other variables commonly selected were those describing woody debris (BWWD1, WEWD2) and characteristics of the water's edge (WELowLay, WEMidLay). AWCover, AWDomSub, AWNumSubSizes, BankLength, ShelfWidth and WEShape were also selected by at least one tree (Table 3.7). Surprisingly, the factors AWGradient and Shelf were not selected by any tree. This is likely to be because other factors (*e.g.* depth, cover) are of more direct relevance to the during the summer when this research was conducted.

A two-leaf tree based on below water variables provided a better fit than those using water's edge (R^2=0.2) or above water variables (both R^2=0.12), whereas the fit for six-leaf trees using water's edge and below water variables was the same (R^2=0.38) (Table 3.8). Interset correlations show that the community-environment relationship was very weak for the above water tree, suggesting that **river**

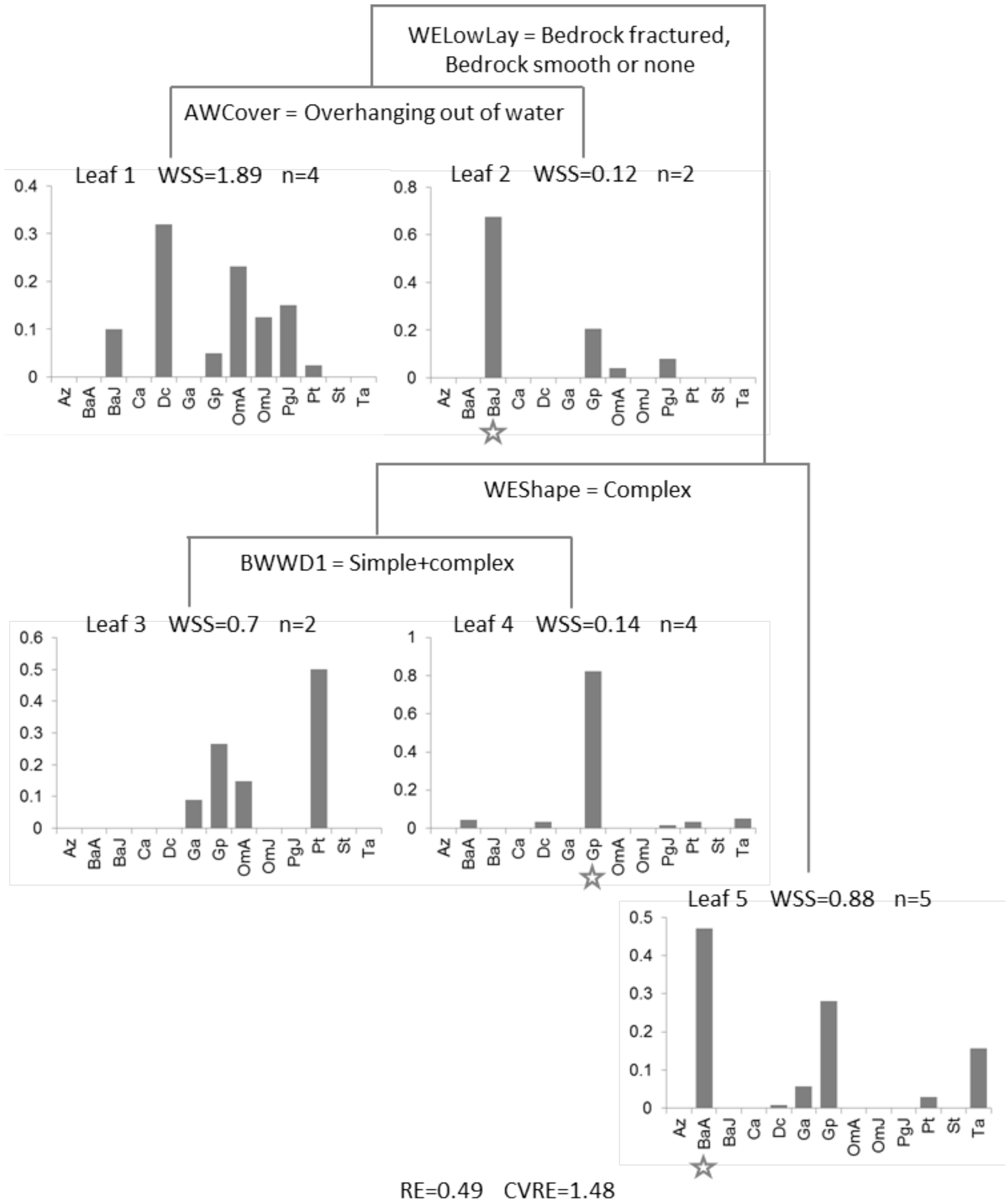


Figure 3.13 - Five-leaf MRT including all variables, only right bank habitats. See Figure 3.6 for an explanation of MRT presentation.

managers may not benefit from rapid reconnaissance methods which limit observations to the riparian zone in relatively pristine systems such as the San Pedro River. Trees produced for separate banks fitted the data better, particularly in the case of the left bank where a two-leaf solution explained 44 % of the variation in the communities. Trees for the right bank were the only ones that did not select water depth for the first split when it was available as an explanatory variable. The two trees with the best fit were the four- and five- leaf solutions for the left and right banks respectively but these were based on fewer sites than other trees, increasing the risk of overfitting to the data at the expense of predictive power. A comparison of MRTs with results of cluster analyses show that there is a substantial portion of species variance unexplained by the environmental variables collected, although this portion is smaller when each bank is classified separately (Figure 3.14). Nevertheless, all of **the MRTs presented here have the potential to provide insights into community-environment relationships, local spatial distribution patterns of resident species and the implications for river research and management**.

Table 3.7 – Explanatory variables selected by trees for each scenario.

Explanatory variables	**Bank**	**Tree size**	
		2	**4-6**
All	Both	Depth	Depth, WEWD2, WEMidLay
Above water	Both	AWDomSub	AWDomSub, AWCover, AWNumSubSizes
Water's edge	Both	WELowLay	WELowLay, WEMidLay, BankLength, WEWD2
Below water	Both	Depth	Depth, ShelfWidth, BWWD1
All	Left	Depth	Depth, WEMidLay, AWDomSub
All	Right	WELowLay	WELowLay, AWCover, WEShape, BWWD1

Depth explained up to 20% of the variation in fish communities when it was offered as a predictor variable for MRTs. These trees show that the native *G. platei* was found in highest relative abundances in relatively shallow habitats (<0.78 m) where piscivorous adult salmonids were not found (Figures 3.6, 3.7, 3.11 and 3.12). *Galaxias platei* is endemic to this region of South America, being found mainly in littoral zones of lakes (Barriga *et al*., 2002; Belk *et al*., 2013). It can tolerate a wide range of habitat conditions but its low metabolic rate and relatively poor swimming capacity make it vulnerable to predation by salmonids (Cussac *et al*., 2004; Macchi *et al*., 2007). In addition to lethal effects, changes in foraging behaviour and shifts in microhabitat use in the presence of salmonids may reduce the fitness of individuals (Sobenes, 2005). Salmonid density in Patagonian lakes has been found to be negatively correlated to trophic level in *G. platei* of piscivorous body length (Correa *et al*., 2012) but no specimens of this size were caught in the San Pedro River. Laboratory studies have concluded that native galaxiids show some tendencies towards anti-predatory behaviour (Sobenes *et al*., 2013), including increased swimming activity and reduced oxygen consumption but not including enhanced use of refugia in the presence of non-native predators (Milano *et al*., 2010; Sobenes, 2005). It is, therefore, unclear how much of the apparent segregation shown in the MRTs is as a result of predation, interference, predator avoidance or simply divergent habitat preferences. Nevertheless, **this example highlights the ability of MRTs to integrate biological interactions in a way that species-by-species approaches cannot**. This is important because introduced species have been found to negatively impact on a number of native taxa besides galaxiids (Arismendi *et al*., 2009; Pardo *et al*., 2009; Habit *et al*., 2010).

Table 3.8 – Goodness-of-fit (R^2) of trees for each scenario. Figures in parentheses show interset correlations.

Explanatory variables	**Bank**	**Tree size**	
		2	**4-6**
All	Both	0.20	0.33 (0.87)
Above water	Both	0.12	0.28 (0.65)
Water's edge	Both	0.12	0.38 (0.85)
Below water	Both	0.20	0.38 (0.85)
All	Left	0.44	0.60 (0.98)
All	Right	0.19	0.51 (0.9)

Another endemic species of high conservation value, *D. camposensis*, drove splits based on bank substrate (AWDomSub, WELowLay) and habitat complexity (AWCover, AWNumSubSizes, WEWD2) in the above water (Figure 3.9) and water's edge (Figure 3.10) trees, preferring relatively simple

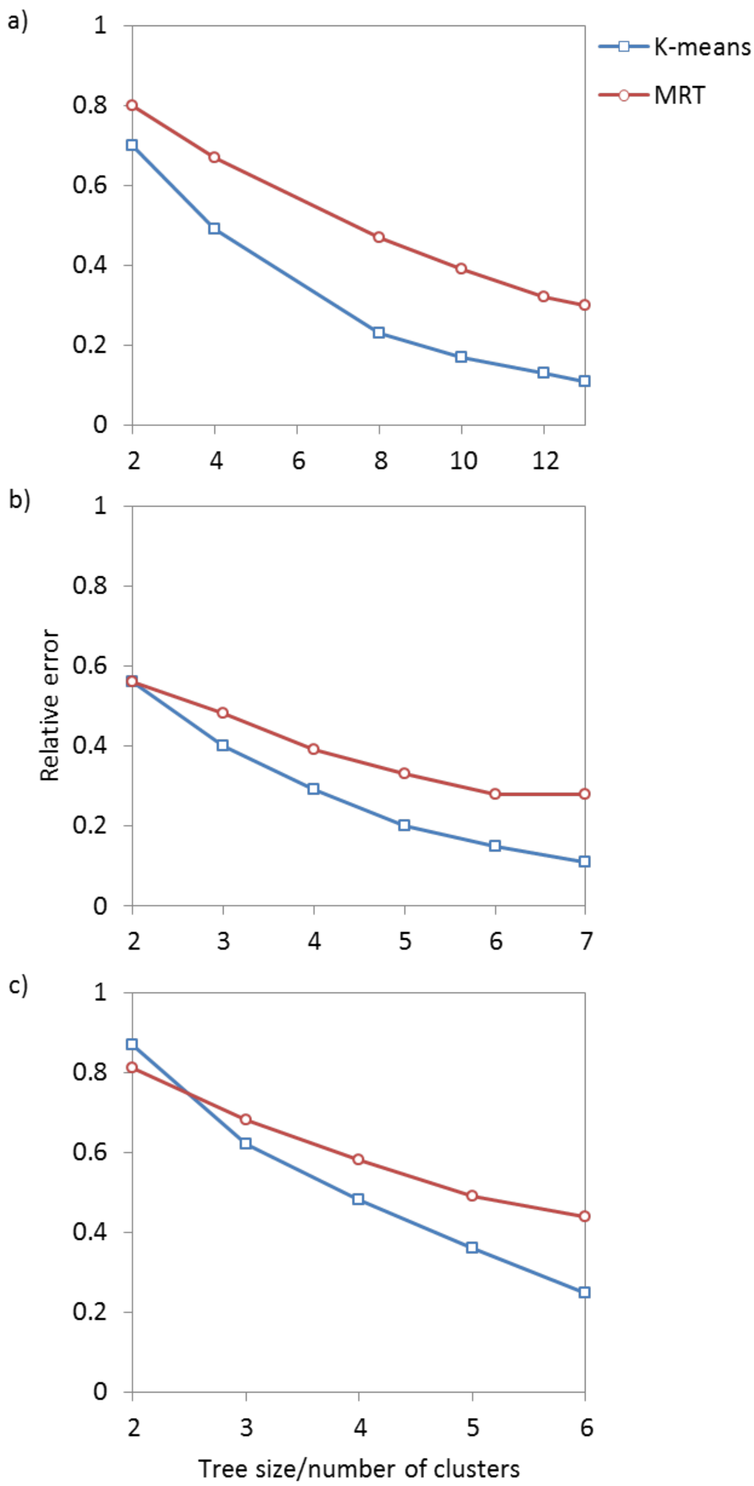


Figure 3.14 – A comparison of k-means cluster analyses against MRTs for the all variables scenarios for both banks (a), the left bank only (b) and the right bank only (c).

shoreline habitats with smooth bedrock or clay banks. This is valuable information since little is known about the preferences of this species except that it is highly mobile and inhabits a range of habitat types at the mesoscale (*e.g.* pools, riffles) and reach scale (Garcia *et al*., 2012a; Valdovinos *et* *al*., 2012). *Trichomycterus areolatus* was also strong indicator species, being found in deeper (≥0.78 m) left bank mesohabitats with banks made up of boulders (Figure 3.12). This supports previous work suggesting that this species prefers intermediate depths and relatively coarse substrata (Garcia *et al*., 2011; Habit & Link, unpublished data). The other indicator species of note was *P. trucha*, a native predator of galaxiids (Macchi *et al*., 2007) which was highly specific and faithful to deeper (≥0.78 m) mesohabitats (Figures 3.6 and 3.12). Again, this supports the fuzzy rules for depth used in the species-by-species model of Garcia *et al*. (2011) and **strengthens the foundation for modelling the habitat of these native species**.

The two-leaf tree for the all variables both banks scenario indicated that the spatial distribution of *B. australis* age-classes was dependent on water depth, with juveniles preferring relatively shallow (<0.78 m) mesohabitats (Figure 3.6). This is unsurprising given that adults of this species are known to use deeper habitats than juveniles (García *et al*., 2011; 2012a). In the equivalent five-leaf tree, however, this relationship appeared to be reversed (Figure 3.7). This inability to classify *B. australis* age-classes consistently likely stems from the fact that this species was only found in mesohabitats of the right bank. The right bank scenario produced the only tree that did not select depth as a predictor variable (Figure 3.13). Instead this tree suggests that juveniles of *B. australis* require refuges in the form of fractured bedrock or overhanging cover, whilst adults occupy mesohabitats with non-bedrock banks and a simple shoreline. In addition, adults of this species were indicative of mesohabitats where WEMidLay=grass (Figure 3.10). This could be important as *B. australis* is known to lay eggs around flooded terrestrial vegetation (Montoya *et al*., 2012). Another taxon exclusive to the right bank, Juveniles of *P. gillissi*, were also strong indicators of mesohabitats with fractured bedrock banks, showing that these sites are important as nursery habitat for native species. Other types of cover (overhanging, woody debris) were found to be favoured by salmonids (*e.g.* Figure 3.13), raising the possibility that mitigating the impact of these invasive species could be achieved through the manipulation of cover elements. **The protection of shallow shoreline habitats is crucial for the conservation of *G. platei* in water bodies affected by salmonid invasions**.

The fact that three species were exclusive to each bank suggests that either: (i) environmental conditions in mesohabitats differ substantially between banks; or (ii) that the deep central portion of the channel acts as a dispersal barrier to some species. Ordination showed that the mesohabitats of each bank had similar environmental characteristics, supporting the latter hypothesis. Furthermore, the low swimming capacity of many native species would render them vulnerable to isolation due to the width of the channel and the higher velocities found along the thalweg (Garcia *et al*., 2012b;

Sobenes *et al*., 2013). More research into the swimming capacity and dispersal behaviour of these species is required in order to evaluate these hypotheses. This could be important given that the planned HEP plant will result in reduced velocities along the study reach and greater variability in hydraulic conditions downstream, factors that have been found to affect endangered native species in other Chilean river systems (Habit *et al*., 2007). Further work should include hydraulic parameters such as mean velocity and turbulence intensity, as these have been found to play a role in the swimming stability and energetics of fish (Wilkes *et al*., 2013; Chapter 5).

The MRTs presented here can be used to predict the fish community structure of any mesohabitat along the study reach, and possibly other reaches in this system, by classifying just a small number of environmental variables. In light of the possibility that a dispersal barrier results in distinctive community-environment relationships, the best approach may be to use trees developed for mesohabitats of each bank separately. Further work is required to test the suitability of these models for predictive mapping. Particular difficulties are likely to result from the exclusion of common species, the static nature of the biological data and the habitat- and species-specific biases of the fishing methods used. Without excluding common species the signal from other species of high conservation value would have been undetectable. Though Habit *et al*. (2007) and Valdovinos *et al*. (2012) found seasonal variation in abundance at the reach scale, the variability was muted for many of the species encountered in this study. Nevertheless, seasonal variability at the mesoscale is likely to be more important as species move between spawning, nursery, feeding and resting habitats (Schlosser, 1987) (Figure 1.6), meaning that these models should only be used to predict community structure in the summer. Though the fishing methods used are known to have different efficiencies depending on the habitat, species and life-stage being targeted (Heggenes *et al*., 1990; Bozek & Rahel, 1991; Growns *et al*., 1996), the use of mixed methods is reported to be the best way to quantify fish assemblages for community-level analyses (Smith *et al*., 2013). Alhough modelling at the community-level brings a number of obvious benefits (Ferrier & Guisan, 2006) the use of mixed fishing methods limits predictions to the relative abundances of species making up the community, rather than their absolute abundance.

3.5 Conclusions

By **strengthening the ecological basis for the mesohabitat concept**, this work supports its use in relatively large, near-pristine systems such as the San Pedro River and represents a novel approach to analysing the habitat associations of riverine fishes at the community-level. It shows that **fish**

assemblages are structured at the mesoscale and provides a foundation for assessing the impact of any future HEP plant construction and operation by defining the expected structure of reference communities of mesohabitats in summer. Of the environmental variables considered, **flow depth, bank materials, the availability of cover and the abundance and complexity of woody debris were the main variables** driving differences between communities at the mesoscale. Together with the identification of these important environmental variables, the establishment of indicator species, among which were the endemic species *G. platei* and *D. camposensis*, and the integration of biological interactions (*e.g.* predation and interference) are the major advantages of the approach taken. A priority for future research is to extend these models to include the full range of habitats available in the San Pedro River and to test its ability to predictively map fish communities.

4

A hydrodynamic classification of mesohabitats

Chapter overview

This chapter aims to construct a new hydrodynamic classification of mesohabitats by mapping physical biotopes along reaches of two contrasting lowland rivers and selecting representative habitat units of four commonly found types (pool, glide, run, riffle) for detailed hydrodynamic characterisation at three flow stages. Separate classifications are presented based on within-biotope variability and the absolute magnitude of turbulent flow properties describing the intensity, periodicity, orientation and scale of turbulence. Some hydrodynamic variables provided clearer discrimination between physical biotopes than others but no single descriptor of the turbulence alone was capable of classifying the habitats. The results did not fit an existing, variability-based classification of physical biotopes. Instead, a quantitative classification using combinations of hydrodynamic properties was suggested as a more effective, transferable and practical solution. A set of variables describing turbulent kinetic energy, integral time scales, Reynolds stress and average eddy length, as well as the 'standard hydraulic variables' of mean velocity and flow depth were able to describe up to 82.9% of the variation between physical biotopes. The results support the idea that physical biotopes have distinctive turbulent flow but the strength and direction of the relationship between turbulence and key biota, such as Atlantic salmon, is uncertain.

4.1 Introduction

Turbulence is ubiquitous in river ecosystems and, as such, it **pervades all aspects of the lives of riverine biota**, from primary producers (*e.g.* Stoecker *et al*., 2006; Labiod *et al*., 2007) to predators (*e.g.* Liao *et al*., 2003a; Enders *et al*., 2003; Cotel *et al*., 2006; Smith *et al*., 2006). Complimentary approaches to studying turbulence, namely the statistical framework and coherent flow structures (CFSs), are both crucial to understanding the interaction between hydromorphology and hydrodynamics. It is this interaction which is expected to result in distinctive turbulent flow properties within morphologically distinct mesohabitats. **The establishment of a strong hydrodynamic calibration of such mesohabitats, however, has been limited by a lack of data and the use of measurement devices incapable of resolving the smallest and largest scales of turbulent motion**.

4.1.1 The hydrodynamics of mesohabitats

Wilkes *et al*. (2013) have established the link between channel morphology at a range of scales (e.g. pebble clusters, pool-riffle sequences, meander bends) and velocity fluctuations in three dimensions (Appendix C). In particular, **h and h/k represent fundamental controls on the occurrence and nature of CFSs** (Roy *et al*., 2004; Legleiter *et al*., 2007). Due to their association with CGUs (Figure 2.1), **PBs differ fundamentally in terms of their morphological attributes (h, k, microbedforms) and would, therefore, be expected to have contrasting turbulent flow characteristics**. Indeed, river research applications have already made a qualitative link between turbulence and the identification of CGUs (Table 2.2), leading to **calls for the inclusion of turbulent flow properties as quantitative variables in habitat assessment and classification protocols** (Crowder & Diplas, 2002; Lacey *et al*., 2007). As the most morphologically contrasting PBs in the above respects (Sear, 1996), pools and riffles provide an initial indication of how turbulent flow varies at the mesoscale. Clifford and French (1993b) presented early evidence that the structure of turbulent flow may differ between these PBs in gravel bed rivers. Though their analysis was based on just a single time series from only one pool and one riffle, and the sampling frequency (10 Hz) used was unlikely to have been sufficient to resolve the smallest flow structures, their results suggested that flow in the pool was characterised by lower frequency fluctuations than in the riffle (Figure 4.1). Smith and Brannon (2007) also used a sampling frequency of 10 Hz and found that *TKE* values in riffles were around twice that of pools in four salmon streams in Idaho.

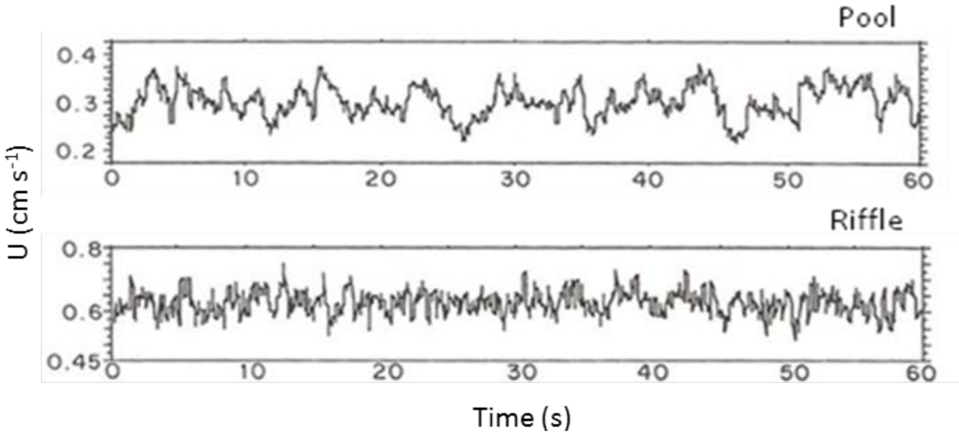


Figure 4.1 – Streamwise velocity (u) time series at riffle and pool locations in a gravel-bed river. From Clifford & French (1993b).

A more robust investigation of turbulent flow in pools and riffles at low discharge was undertaken by Roy *et al*. (2010). They took a number of 80 s time series at 25 Hz using an Acoustic Doppler Velocimeter (ADV) based on a high resolution grid (16 points m^{-2}) at 10 cm above the beds of two riffles and two pools in a gravel-bed river in Canada. They applied a method of spatial partitioning, known as principle components of neighbour matrices (PCNM), to the data. PCNM can be used in conjunction with multiple or multivariate regression to quantify the spatial structure of environmental variables at a range of scales (Borcard & Legendre, 2002). Based on the resolution and extent of their sampling grid, they classified the spatial structuring of a range of turbulent flow properties according to six arbitrarily defined spatial scales. These were very fine (VF, 0.25-0.5 m), fine (F, 0.5 -1 m), medium (M, 1-1.5 m), large (L, 1.5-2.5 m), extra large (XL, 2.5-3m), and +extra large (XXL, 3-4 m). Results suggested that flow in the pools was spatially structured in a more orderly way, as illustrated by the fact that the PCNM model was able to explain a greater proportion of the total variance in turbulent flow properties in the pools (Figure 4.2). *RMS* values and *TKE* were consistently the most spatially structured variables and individual multiple regressions revealed that the organisation of turbulent flow properties tended to be explained at larger scales in pools than in riffles. Of the so called 'standard fluvial habitat variables' (h, U, k), the single best predictor of turbulent flow characteristics across all PBs was U, with combinations of these variables explaining most of the variation. The 'standard' variables were generally poor predictors of turbulent flow structure at all scales, **suggesting that turbulence can be considered as a distinct ecological variable**.

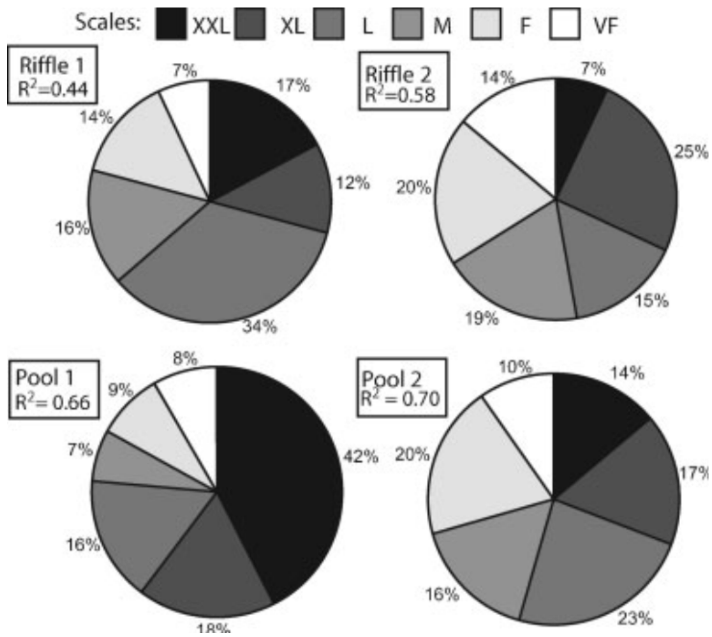


Figure 4.2 – Total variation (adjusted R^2) in turbulent flow properties explained by six spatial scales (see text). From Roy *et al*. (2010).

Harvey & Clifford (2009) noted that there had been no previous attempts to explicitly link turbulence with the problem of mesohabitat classification. Working at two sites on the River Tern, a third- to fourth-order mixed-bed river in Shropshire, UK, they took several two-dimensional (u, v) velocity time series from two pairs of PBs: glide-pool (Oakley Hall site); and riffle-pool (Napeley Lodge Farm site). They took measurements at y/h=0.2 and 0.8 at 1 m intervals along a 5 m transect following the channel centreline and along a cross-sectional transect across the middle of each PB. Data were collected on two occasions to represent low (Q_{96}, Q_{91}) and intermediate (Q_{39}, Q_{57}) discharges. Example time series for the streamwise component are presented in Figure 4.3. An initial inspection of these plots suggests that results for the pools and riffle are in agreement with conclusions drawn by Clifford and French (1993b) and Roy *et al*. (2010). Fluctuations in the pools appear to be ordered at a larger scale than in the riffle, with the glide exhibiting intermediate behavior. Results for mean velocities (U, V), standard deviations ($SD_{u,v,}$), average intensity ($AvInt$), average eddy lengths (L_u) and event structure ($T_{Q2}T_{H:2}$, $\tau_{uv\ Q2}T_{H:2}$) are presented in Figures B1 to B4. Of particular note are the spectral characteristics of each PB. Typical wavenumber spectra (a spatial analogue of the frequency spectra) for both u' and v' components (Figure 4.4) show that the riffle had the largest (least frequent) flow structures, illustrated by a peak at low K, but also had spectral peaks at the highest K (smaller eddies). This suggests that **the riffle had the most complex turbulent flow whereas the pools were most simple**, although the time series record length (30 s) may have been too short to capture the largest flow structures in the pools.

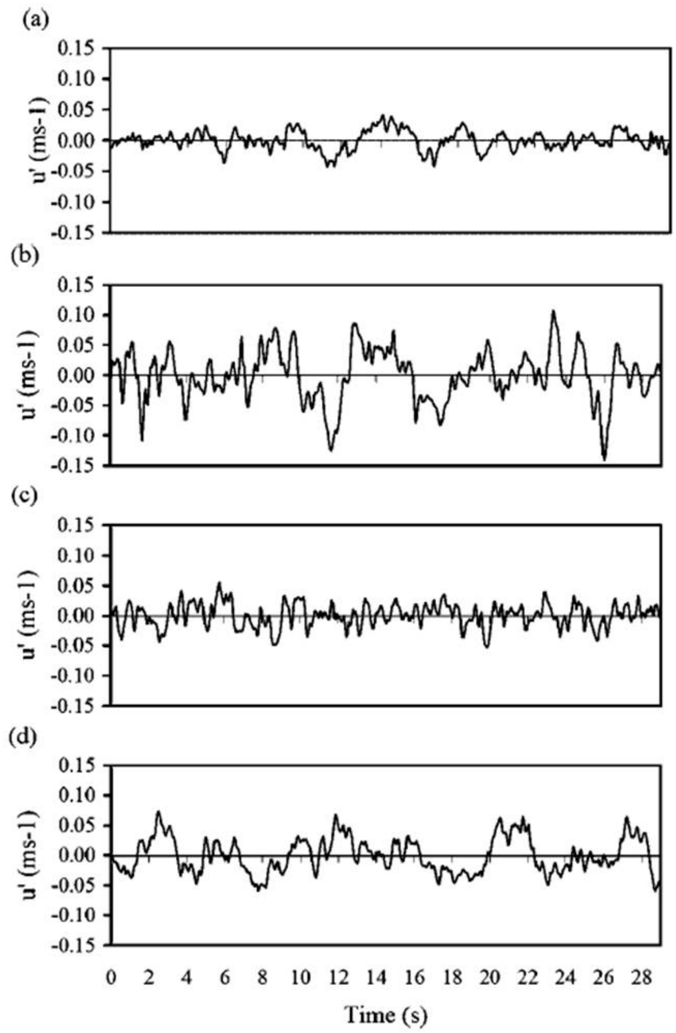


Figure 4.3 - Example time plots for streamwise turbulent residuals (u') from channel centreline locations within each Physical Biotope (PB) under low flow conditions. (a) Glide (Oakley Hall), (b) Pool (Oakley Hall), (c) Riffle (Napely Lodge Farm), (d) Pool (Napely Lodge Farm). From Harvey & Clifford (2009).

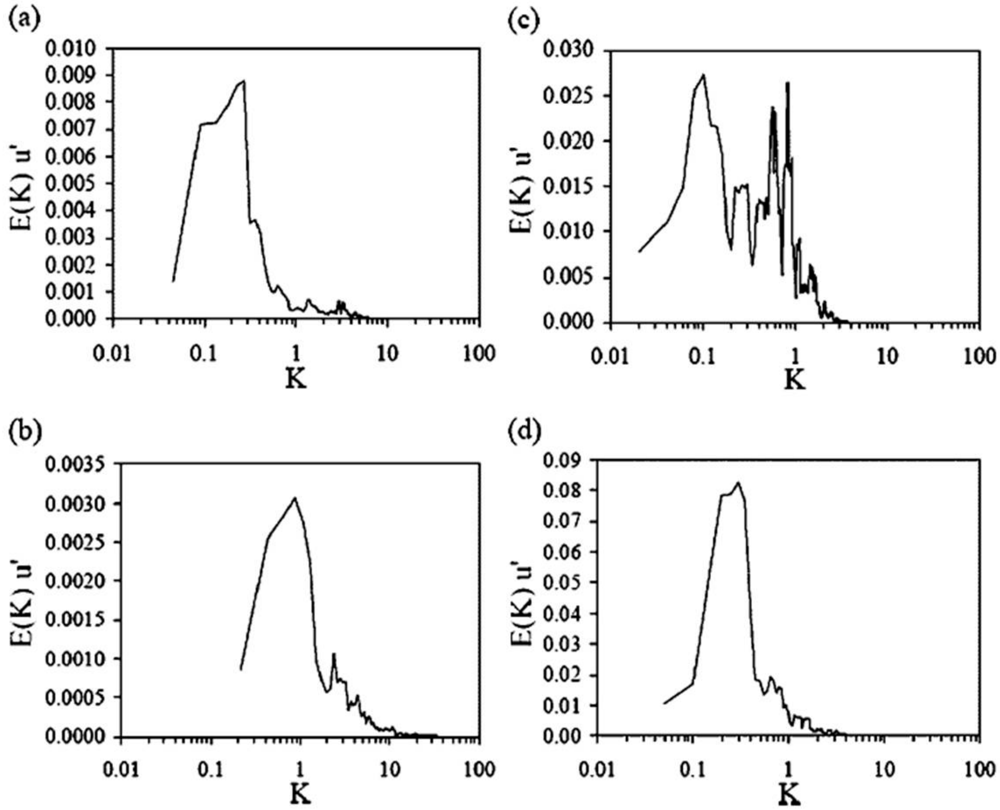


Figure 4.4 - Sample velocity wavenumber spectra for each Physical Biotope (PB). (a) Glide (Oakley Hall), (b) Pool (Oakley Hall), (c) Riffle (Napely Lodge Farm), (d) Pool (Napely Lodge Farm). From Harvey & Clifford (2009).

Whilst some turbulent flow properties provided clear separation for a given y/h and discharge between certain pairs of PBs (*e.g.* overall turbulence intensity for the glide-pool, L_u for the riffle-pool) it was concluded that the range of a combination of flow statistics, rather than their absolute values or central tendencies, provided the best level of discrimination between the limited sample of PBs studied. Thus, **Harvey and Clifford (2009) proposed a conceptual model** which classifies PBs according to their levels of heterogeneity in space, with relative depth (y/h) and between discharges (Figure 4.5). This tentative framework, known as '**within-biotope hydrodynamic heterogeneity'**, plots pools as the most variable and glides as the most uniform, with riffles characterised by intermediate levels of heterogeneity. **The validity of the model, however, remains to be tested**. This is especially important given that there **are several**

potential methodological problems with the approach taken by Harvey & Clifford (2009). Firstly, the **frequency** (16 Hz) and **length** (30 s) of velocity time series was insufficient to resolve the smallest and largest flow structures respectively. Secondly, **Harvey and Clifford (2009) used an ECM which, among other potential issues, are known to disturb the flow and bias hydraulic measurements**. Thirdly, **the model was based on a limited number of two-dimensional velocity time series from four PBs of only three types on just one river**, which may not have been sufficient to adequately describe the typical turbulent flow characteristics of PBs. Harvey & Clifford's (2009) pools did not fit the conventional model of relatively slow, quiescent flow. Furthermore, **no data were collected at relatively high discharges**. Despite these issues, there is much emerging evidence suggesting that such a classificatory framework could have important ecological applications, particularly in the case of juvenile Atlantic salmon and other river-dwelling salmonids (Chapter 5).

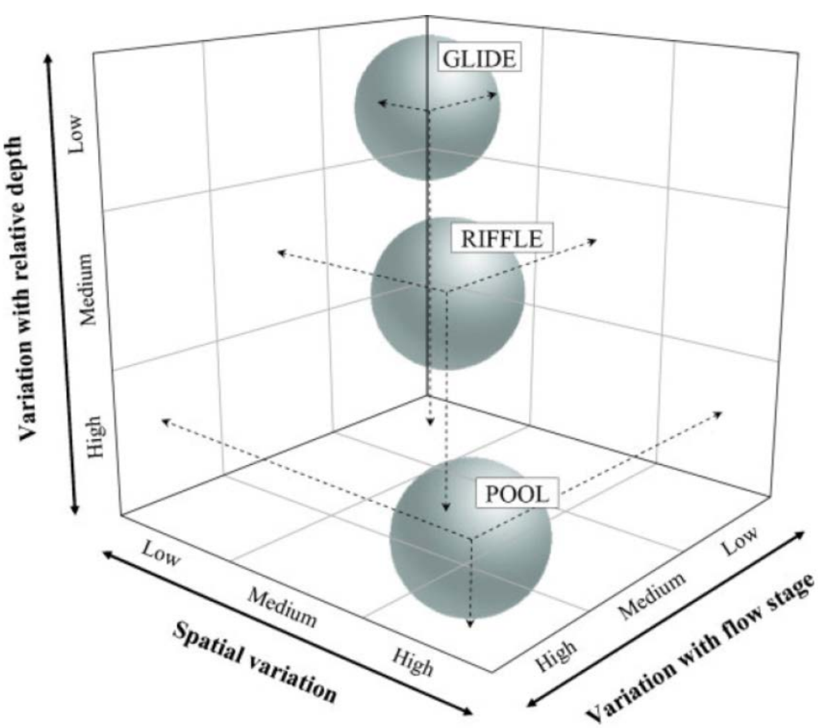


Figure 4.5 - Conceptual diagram illustrating levels of internal (within-biotope) heterogeneity identified for the glide, riffle and pool Physical Biotopes (PBs) on the River Tern in terms of heterogeneity in hydraulic parameters spatially, with relative depth of the measurement and with flow stage. From Harvey & Clifford (2009).

4.1.2 Aims and hypotheses

The primary aim of this chapter is to construct a hydrodynamic classification of mesohabitats. This will be achieved through the following objectives.

1. Map PBs along reaches of two rivers
2. Select representative PBs of each of four common types (pool, riffle, run, glide) for more detailed study
3. Measure turbulence at high spatial and temporal resolution in representative PBs at three flow stages (low $Q_{90\text{-}98}$, intermediate $Q_{50\text{-}60}$, and high $Q_{25\text{-}35}$)
4. Assess the magnitude and variability (within-biotope heterogeneity) of ecologically relevant turbulent flow properties (*i.e.* that describe turbulence phenomena that may affect the fitness of individuals and/or the structure of populations and communities).

Lacey *et al.* (2012) have emphasised the need to consider **four ecologically relevant aspects of turbulence - namely intensity, periodicity, orientation and scale (IPOS)** - in a framework which draws together the turbulent flow properties discussed by Wilkes *et al*. (2013) (Table 4.1). Results will be presented within this framework and with reference to the axes of Harvey & Clifford's (2009) model (Figure 4.5). Particular emphasis will be placed on the key variables highlighted in Table 4.1, which were selected to represent each aspect of turbulence. Due to the strong dependence of turbulence on morphology at different scales (Wilkes *et al*., 2013; Appendix C) and the morphological differences between PBs (S 2.2), **it was hypothesised that PBs could be classified based on the magnitude and/or variability of turbulence**.

4.2 Methods

4.2.1 Site descriptions

Two sites were selected to represent the spectrum of small to medium (third- to fourth- order) streams of the British lowlands. These are the types of river for which the mesohabitat concept is relatively well established but the hydraulic calibration is weak (S 2.4). The characteristics of these sites are summarised in Table 4.2. The Leigh Brook is a third-order stream draining an area to the north-west of the Malvern Hills on the border of Herefordshire and Worcestershire (Figure 4.6). A study reach of the stream was selected in a National Nature Reserve close to the confluence with the River Teme. The River Arrow at Studley is a fourth-order tributary of the River Avon and drains parts of north Worcestershire and Warwickshire (Figure 4.7). In comparison with the River Arrow, the Leigh Brook is smaller, has a relatively stable flow regime (Figure 4.8) and is less affected by urbanisation and abstraction. Morphologically, the River Arrow is less steep, more sinuous and has a higher bedform amplitude with finer substrate than the Leigh Brook (Table 4.2). With a HMS of 1, Maddock and Hill (2007) classified the Leigh Brook at 'pristine'. The River Arrow, on the other hand, was relatively heavily modified with a HMS of 29 (see S 1.5.1 for explanation). Thus, the study sites differ in terms of hydrology, geomorphology and levels of human impact, representing a gradient within small lowland streams between relatively steep, straight and pristine sites to low gradient, sinuous and heavily impacted sites. If it is to be useful, therefore, any new classification must be capable of incorporating PBs from this range of sites.

Table 4.1 – The IPOS framework for studying biota-turbulence links. Modified from Lacey *et al*. (2012). *Denotes key variables.

Relevant turbulent flow properties	
Intensity	Turbulence intensity ($SD_{u, v, w}$)
	Relative turbulence intensity (TI_u)
	Turbulent kinetic energy (TKE*)
Periodicity/ Predictability	Average eddy frequency ($f_u*_{, v, w}$)
	Integral time scale ($ITS_u*_{,v ,w}$)
	Kurtosis ($Kurt_{u, v, w}$)
	Spectral peaks and flatness
Orientation	Dominant axis of eddy rotation (x, y, z)
	Reynolds stresses (τ_{uv}*, τ_{uw}*)
	Skewness ($Skew_{u, v, w}$)
	Event structure ($T_{Q2}T_{H:2}$, $\tau_{uvQ2}T_{H:2}$)
Scale	Average eddy dimensions ($L_u*_{, v, w}$)
	Integral length scale ($ILS_u*_{, v, w}$)

Figure 4.6 – Leigh Brook location map. Study site indicated by red polygon.

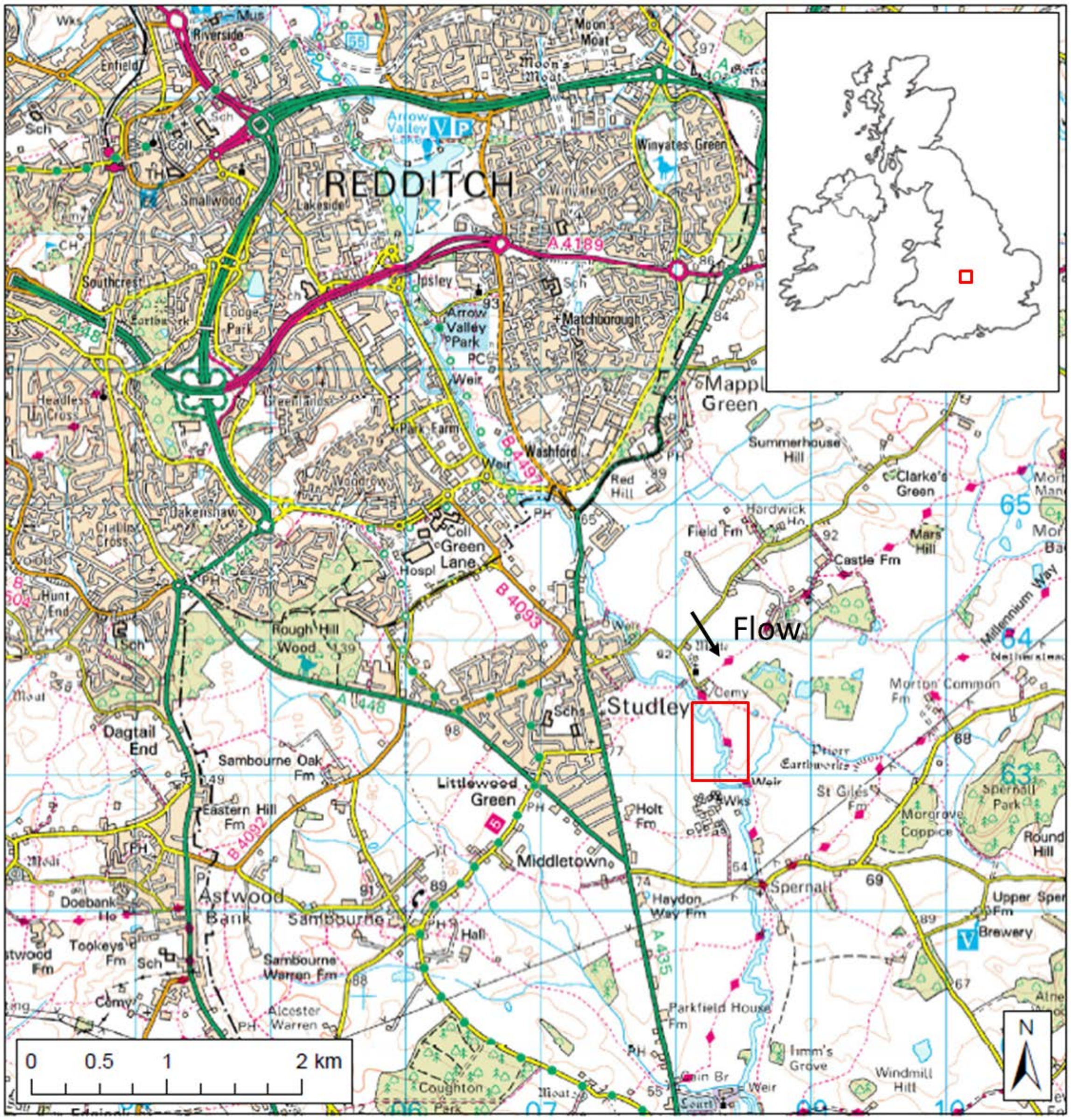


Figure 4.7 – River Arrow location map. Study site indicated by red polygon.

Table 4.2 – Summary site characteristics. *From Flood Estimation Handbook (Centre for Ecology & Hydrology, 2007). †From Maddock & Hill (2007).

Characteristic	Leigh Brook	River Arrow
Catchment area (km^2)*	77.5	91.95
Stream order (Strahler)	3	4
Mean annual discharge ($m^3\ s^{-1}$)	0.51	0.55
Baseflow index*	0.537	0.424
Flow variability (Q_{10}/Q_{95})	10.19	11.17
Urban and suburban extent (%)*	1.1	10.8
Slope ($m\ m^{-1}$)	0.005	0.002
Sinuosity index	1.02	1.33
Dominant substrata	Cobbles	Sand and gravel
RHS Habitat Modification Score (HMS)†	1 (Pristine)	29 (Heavily modified)

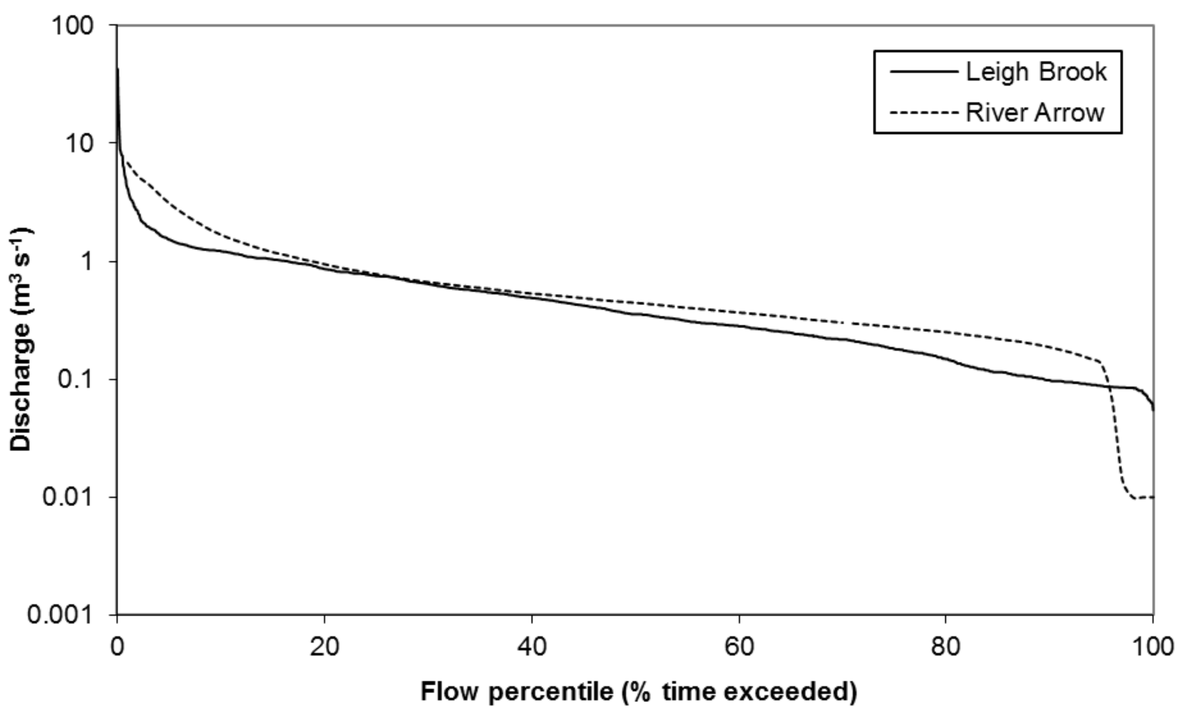


Figure 4.8 – Flow duration curves for the study sites.

4.2.2 Habitat mapping and selection of representative physical biotopes

In order to ensure, as far as possible, that PBs selected for study at each site were representative of the range of PBs present, a semi-objective habitat mapping and clustering procedure was carried out at approximately median flow (Q_{50}). This involved mapping units of habitat with relatively homogenous characteristics in terms of *h*, dominant SFT, dominant substrate and coherent bed and bank morphology. Mapping began at the upstream extent of a 300m reach (over 15-21 x channel width) in order to capture at least three pool-riffle sequences. The location and boundary of each discrete habitat unit was mapped and photographed. For the Leigh Brook this was done using a 1:2500 map and the width and length of habitat units measured using a laser distance measurer or tape measure. The River Arrow site was more open allowing for the use of a survey-grade GPS (Trimble R8). The habitat units mapped can be considered as PBs but they were not named (*e.g.* pool, riffle, run, glide) at this time to avoid subjective judgement. The percentage areal cover of dominant, subdominant and present SFTs within each unit was estimated as this is one of the primary criteria for classifying PBs (S 2.2). Substrate characteristics were recorded for each unit by estimating the percentage cover of bed-surface particles falling into one of four categories (fine [<2 mm], gravel [2-64 mm], cobble [64-256 mm], boulder/bedrock [>256 mm]). Percentage cover of macrophytes, woody debris, trailing vegetation and roots was also estimated in order to characterise habitat complexity. Within each unit, five *h* measurements were taken based on a cruciform design, with three samples along the channel centreline at 20%, 50% and 80% of the length of the unit, and two samples adjacent to the centre of the unit at 20% of the channel width in from the water's edge at each bank. These locations were chosen to minimise the influence of transitions between habitat units whilst still providing information on the gross morphology of the unit.

Means and ranges of *h* were calculated for each sampled unit and the data analysis began with an inspection of a scatter plot of mean *h* versus the *h* range for each unit. This was designed to reflect the morphological contrasts between habitat units and provided an indication of the number of clusters discernible in the data set. K-means cluster analysis using Ward's method (Legendre & Legendre, 1998) was then performed on a set of variables describing the morphological, surface flow and substrate characteristics of each unit (Table 4.3) with values of k (number of clusters) ranging from two to 15. The categorical data dominant SFT and substrate were converted to integers before performing the analysis. The cluster analysis was based on Euclidean distance with a maximum of 10 iterations and 100 random starting points. The final solution retained was selected according to the variation in the sum of squared distances of habitat units from the centre of their respective clusters (within-groups sum of squared errors, WSS) (Legendre & Legendre, 1998). The optimum solution (number of clusters) was defined as the point at which WSS began to level-off and remain stable. The selection of one representative PB from each cluster which most closely represented one of the four common PBs (pool, riffle, run, glide) for further study then progressed by assessing the proximity of each unit to the cluster centre in multi-dimensional space. Practical considerations were also factored into the decision based on the size and accessibility of the units, time resources and habitat complexity. Mapping was undertaken at approximately median flow (Q_{50}) to characterise the central tendency of hydromorphological conditions. SFTs were also mapped within representative PBs at three survey discharges (see S 4.2.3) in order to analyse changes in dominant SFT with flow, as this is the main criteria by which PBs are identified (S 2.2).

4.2.3 ADV data collection and processing

At low and intermediate flows a three-dimensional Nortek acoustic Doppler velocimeter (ADV) was used to collect a number of time series within representative PBs at 25 Hz for 90 s. Time series were collected at the nodes of a grid covering each representative PB designed to result in approximately 25 vertical sampling locations per PB. At each of these locations where y>20 cm, measurements were taken at a maximum of two points in the water column: near-bed (h=6 cm); and point-six depth (y/h=0.4). At locations where 12<y<20 cm only near-bed measurements were taken and where y>95 cm only point-six measurements were taken due to the amount of drag placed on the sensor and mounting apparatus (Figure 4.15). Where y<12 cm the ADV could not be deployed and only mean streamwise velocity was measured using a one-dimensional ECM at point-six depth. Near bed time series were taken to reflect, as close as possible, the flow conditions at the focal point of benthic or benthopelagic fish and invertebrates. Point-six measurements were taken to describe conditions for pelagic fish, to aide comparison with previous studies and to allow for the evaluation of turbulence variability through the water column. Particle size distributions were also calculated based on pebble counts (random walk, 100 particles; Gordon *et al*., 2004) within PBs to augment the analyses.

Table 4.3 – Variables used in the habitat clustering procedure. Figures in parentheses indicate codes used in the analysis.

Variable	**Units/levels**
Mean h	m
h range	m
Dominant SFT	Free fall, FF (7)
	Broken standing waves, BW (6)
	Unbroken standing waves, UW (5)
	Rippled, RP (4)
	Upwelling, UP (3)
	Smooth/Smooth boundary turbulent, SM (2)
	No/scarcely perceptible flow, NP (1)
Dominant substrate	Fine substrate (<2 mm) (1)
	Gravel (2-64 mm) (2)
	Cobble (64-256 mm) (3)
	Boulder (bedrock) (>256 mm) (4)

Due to the environmental sensitivity and relative fragility of the high-frequency NDV, at high flow a more robust two-dimensional ADV (Sontek Flowtracker) was used to collect time series at 1 Hz for 180 s. Data could not be collect at higher flows than $Q_{25\text{-}35}$ due to safety issues and the drag forces placed on the ADV sensor. Due to the intermittency and ephemerality of high flow events, high flow data were collected based on the cruciform layout used for habitat mapping (S 4.2.2). As with the NDV, measurements were taken at near-bed and point-six locations where y>20 cm but, due to the characteristics of the Flowtracker probe, the minimum depth at which measurements could be taken at high flow was 2 cm (Figure 4.9). Thus, the criteria for ADV data quality outlined in Appendix C were met to different extents at low-intermediate and high flows. Table 4.4 shows that the NDV meets the criteria for dimensionality, f_D and RL but neither probe is capable of resolving the smallest eddies. Nevertheless, most of the turbulent energy is contained at larger scales and 6< D_s<9 mm is sufficient to capture this (Pope, 2000).

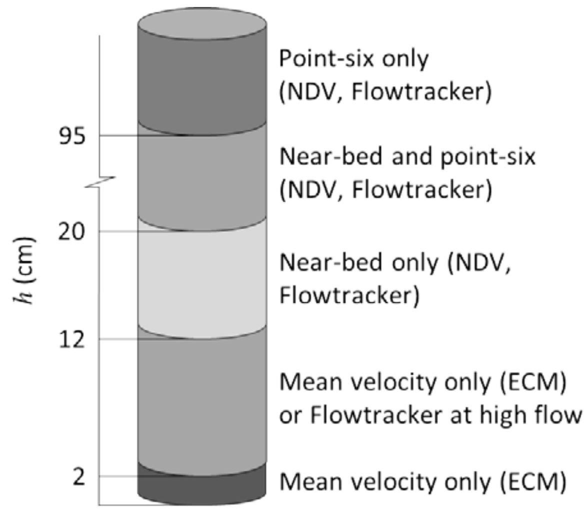


Figure 4.9 – Sampled locations in the water column depending on flow depth.

Table 4.4 – Characteristics of the ADV sensors used compared to those recommended based on the literature (Wilkes *et al*., 2013).

Criterion	**Recommended**	**Low and int. flow (NDV)**	**High flow (Flowtracker)**
Dimensionality	3D	3D	2D
f_D (Hz)	>25	25	1
f_N (Hz)	>12.5	12.5	0.5
RL	1300	2250	180
D_s (mm)	3	6	9

Field data collection involved careful positioning of the ADV so that the primary axis was parallel with the banks and the vertical axis was normal to the bed. Quality control was performed during data collection through visual inspection of time series plots and adherence to recommended data quality thresholds (Figure 4.10), including the criterion established by Garcia *et al*. (2005) (Eqn. 4.20). Postprocessing involved rotating the velocity data into the primary flow vector by matrix multiplication so that $V = W = 0$. Since some aspects of the un-rotated velocity signal may be of interest, the original data were also retained. Spikes were detected using the phase-space thresholding (PST) filter of Goring and Nikora (2002) modified (mPST) by Parsheh *et al*. (2010) and replaced using a third-order polynomial through 12 points on either side of the spike, as recommended by the original authors of the filter. A reverse arrangement test (Bendat & Piersol, 2000) was performed to test the null hypothesis that the first- and second- order moments of each time series were stationary. Any time series found to describe non-stationary processes were detrended using linear or second- to third- order regressions. Finally, mean and turbulent flow properties were calculated. Data processing was performed in WinADV (version 2.030) (US Bureau of Reclamation, 2013), MATLAB (version 2013a) (The Mathworks, 2013) and R (version 2.15.2) (R Core Team, 2013).

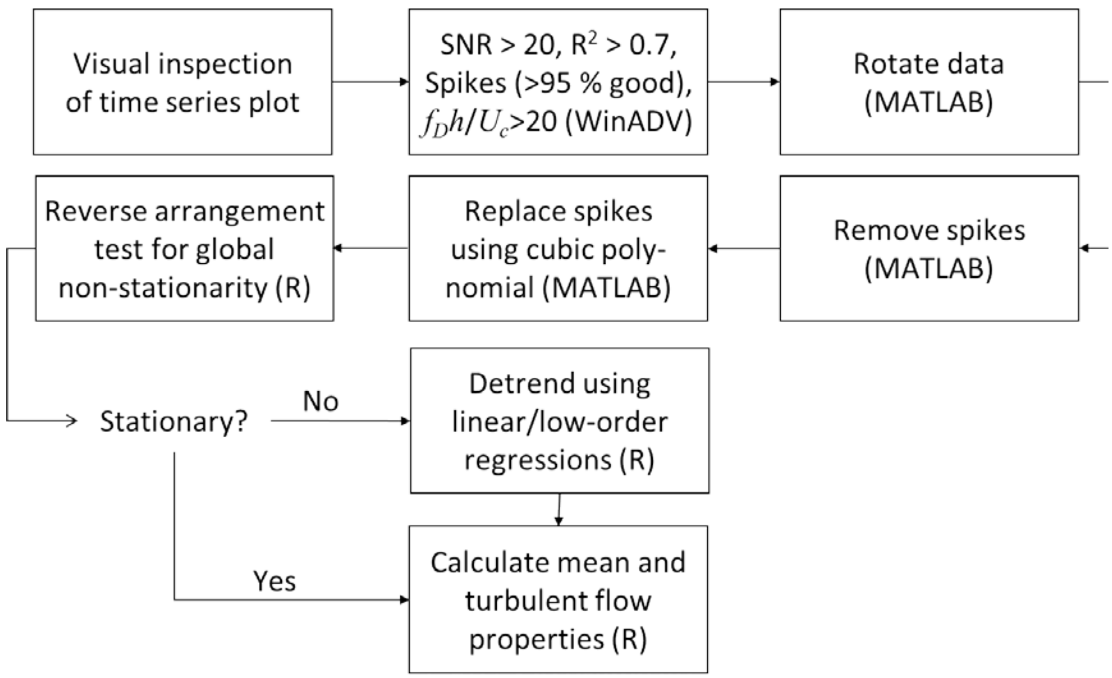


Figure 4.10 – Data processing procedure for ADV measurements. Software used for each stage shown in parentheses.

4.2.4 Data analysis

Data were plotted using box and whisker plots showing mean, inter-quartile range (IQR) and complete ranges to aide comparison of the magnitude and within-biotope heterogeneity of turbulence. Recursive partitioning methods (classification trees, random forests) were used to classify the PB membership of near-bed and point-six samples separately using a selection of hydrodynamic properties (Table 4.1). At each node of a classification tree, the computation procedure finds the best variable and the optimum threshold value of that variable with which to split the data into two groups in a way which minimises within-group variability (Breiman *et al*., 1984). This process continues, adding nodes until all objects (*i.e.* time series) are correctly classified and the tree is perfectly fitted to the data. For most applications, however, it is more useful to have a tree with high predictive power, rather than mere explanatory power. For this reason cross-validation is performed to find the level at which to 'prune' the tree (see S 3.2.4 for explanation).

A type of machine-learning method known as random forests (RF) was used to classify PBs and rank the importance of predictor variables for near-bed and point-six samples separately. As a classification method, RF has been shown to outperform other similar techniques, such as linear discriminant analysis and logistic regression (Cutler *et al*., 2007), and provides a more robust indication of the importance of predictor variables than classification trees. RF fits a large number of classification trees (*i.e.* 500) to a dataset and then combines predictions from them. At each stage RF selects a bootstrap sample (60%) of the data and fits a classification tree using a subset of available predictor variables. The tree is then used to predict out-of-bag samples (test set). To assess the importance of a predictor variable, the values of the variable are permuted for the out-of-bag samples and new modified predictions obtained and compared to the original predictions. A measure of variable importance (I) was defined based on the Gini index (G):

$$G_{i,x} = 1 - p_j^2 - p_0^2 \tag{5.1}$$

where p_j is the fraction of samples from class j out of the total samples p_0 at node i for variable x. Thus, the Gini index is a measure of node impurity and I is its standardised form summed over all iterations:

$$I_x = \left[\sum_{k=500}^{n} G_{i,x} \right] - G_{\max} \tag{5.2}$$

This index was used to rank the average importance of predictor variables across all trees, with more important variables causing a greater decrease in the index. The RF procedure was performed on scenarios stratified by site and flow stage. RF was also performed for all sites and all flows scenarios and, in these cases, values of the predictor variables were first standardised (z-scores) for each site-flow combination. Classification trees were then produced for the best predictive scenarios using the most important variables to visualize the RF results and provide a useable classification.

4.3 Results

This data set contains 584 time series constituting more than 3.4 million individual data points (time steps x velocity components). Although Roy *et al*. (2010) published a greater number of data points overall, by investigating a wider range of mesohabitat types in two rivers **this study represents the most comprehensive study of turbulence in river habitats to date** (Table 4.5). 70.4% of time series met data quality thresholds and a further 26.8% met the relaxed signal-to-noise ratio (SNR) threshold (>15) recommended by Wahl (2000). Only 16 out of 584 time series (2.7%) were rejected (Table B1). All time series were stationary according to reverse arrangement tests. Results are presented below for each study site separately (S 4.3.1, S 4.3.2) before a classification is developed (S 4.3.3). Since velocity measurements at high flow were taken using a sensor less suited to turbulence measurements, these data are presented with a note of caution. All turbulence data presented refer to rotated, near-bed measurements unless otherwise stated.

5.3.1 Leigh Brook

4.3.1.1 Habitat mapping and selection of representative physical biotopes

A total of 28 individual habitats were mapped along the study reach (Figure 4.11). Of these, 24 were sufficiently accessible to collect data. Mean *h* ranged from 0.08 to 0.56 m and the within-habitat *h* range varied between 0.05 and 0.56 m, reflecting a gradient from shallow habitats with a uniform profile to deep habitats with concave cross- and/or long-sections. Habitats fell into one of four different dominant SFT categories and all four dominant substrate classifications. The full data set on which the cluster analysis was based is provided in Appendix B (Table B2) alongside photographs of the habitat units mapped (Figure B5). A summary of the cluster analysis results is provided in Table 4.6. Examination of the WSS for solutions with varying numbers of clusters indicated that the five cluster (k=5) solution was most suitable. Beyond this the relative error increased and solutions with k>6 were unstable (Figure 4.12). Figure 4.13 summarises the cluster analysis results in the case of the first two discriminator variables and suggests that dominant SFT and substrate played an important part in the classification as clusters are not clearly separated according to mean h and h range alone.

Table 4.5 – Volume of data collected for studies of turbulence in river habitats.

Reference	**Habitat types**	**Total number of habitats**	**Number of flow stages**	**Number of time series**	**Total number of data points**
Clifford & French (1993b)	Pool, riffle	2	1	2	64,400
Harvey & Clifford (2009)	Pool, riffle, glide	4	2	124	119,040
Smith & Brannon (2007)	Pool, riffle	4	1	20	180,000
Roy *et al*. (2010)	Pool, riffle	4	1	1932	11,592,000
This thesis	Pool, riffle, run, glide	8	3	584	3,402,480

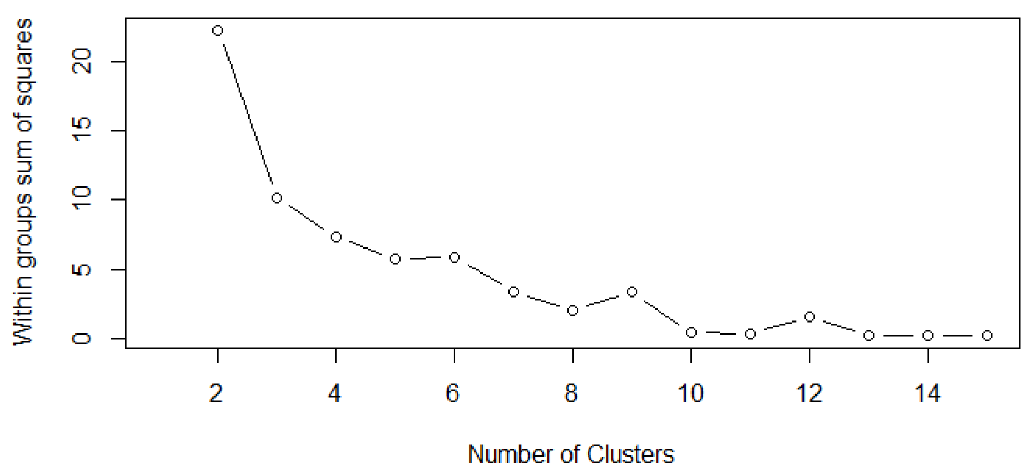


Figure 4.12 –Within-groups sum of squares (WSS) for alternative cluster solutions for habitat units along a reach of the Leigh Brook.

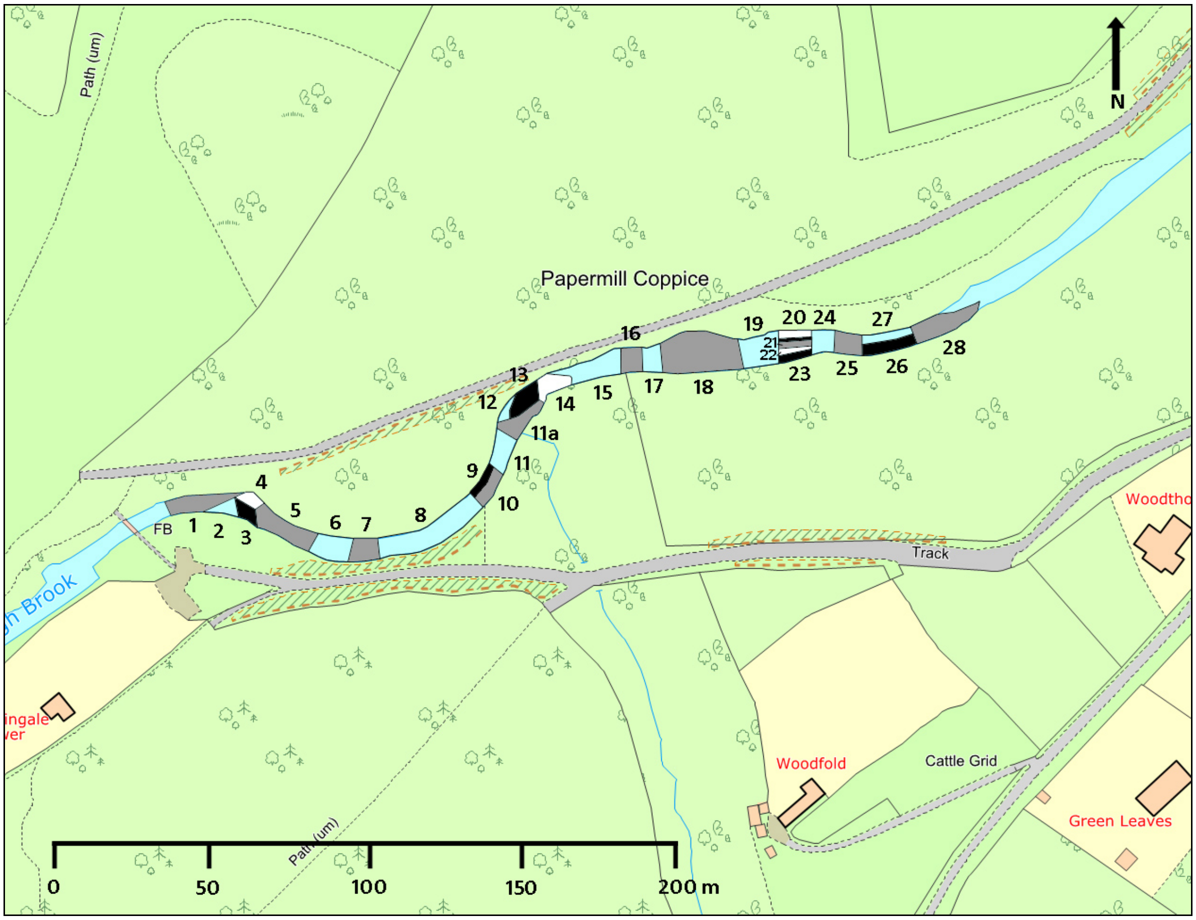


Figure 4.11 – Distinct units of habitat mapped along a reach of the Leigh Brook. Note: shading is only included for contrast between neighbouring habitats and does not reflect cluster membership.

Table 4.7 shows that cluster 4 had only one member, namely habitat number 4. This habitat was intermediate in mean h and h range and had a unique dominant SFT-substrate combination (RP-fine) (Table 4.6). As a rare feature, therefore, this unit was not considered for further study and cluster 4 was disregarded. Of the remaining clusters, habitat number 11 was selected from cluster 1 as it was closest to the cluster centroid for three out of four discriminator variables (Table 4.7). This habitat was deep in comparison to others, had a relatively high h range with smooth SFT and fine substrate, and most closely resembled a pool. Cluster 2 was characterised by shallow habitats with low h variation, coarse substrate and high-energy SFTs (*e.g.* UW, BW), fitting the description of riffles. Although only joint closest to the cluster 2 centroid for

Table 4.6 – Summary data for habitat units mapped along a reach of the Leigh Brook. NA entries refer to units inaccessible for depth measurements.

Habitat number	Mean depth (m)	Depth range (m)	Dominant SFT	Dominant substrate
1	0.474	0.27	UW	Cobble
2	0.224	0.26	SM	Fine
3	0.268	0.33	RP	Cobble
4	0.32	0.3	RP	Fine
5	NA	NA	NA	NA
6	0.148	0.07	UW	Boulder
7	0.322	0.32	RP	Boulder
8	0.48	0.56	SM	Cobble
9	0.256	0.15	UW	Cobble
10	0.242	0.29	UW	Cobble
11	0.48	0.26	SM	Fine
12	0.154	0.19	UW	Cobble
13	NA	NA	NA	NA
14	0.14	0.1	RP	Boulder
15	0.476	0.2	SM	Boulder
16	0.12	0.05	BW	Cobble
17	0.256	0.18	RP	Cobble
18	0.562	0.37	SM	Fine
19	0.214	0.14	SM	Boulder
20	0.144	0.1	UW	Cobble
21	NA	NA	NA	NA
22	0.296	0.18	UW	Boulder
23	0.552	0.48	SM	Cobble
24	0.33	0.21	SM	Cobble
25	NA	NA	NA	NA
26	0.336	0.11	RP	Boulder
27	0.076	0.05	SM	Gravel
28	0.148	0.17	RP	Cobble

substrate, habitat number 16 was selected for further study as other units within this cluster had relatively high cover of trailing vegetation, roots and macrophytes and/or did not span the full width of the channel. Similar considerations were made in the case of cluster 3, which contained relatively deep habitats with generally smooth SFT. Habitat number 19 was chosen from this cluster and this unit most closely resembled a glide. Finally, cluster 5 contained relatively shallow habitats (though not as shallow as cluster 2) with uniform morphology, rippled

SFT and coarse substrate, resembling a run. Habitat number 17 was closest to the cluster 2 centroid but habitat 26 was selected for further study as it contained less trailing vegetation and organic detritus, factors which can hinder the collection of ADV data and confound results due to seasonal and discharge-related variation.

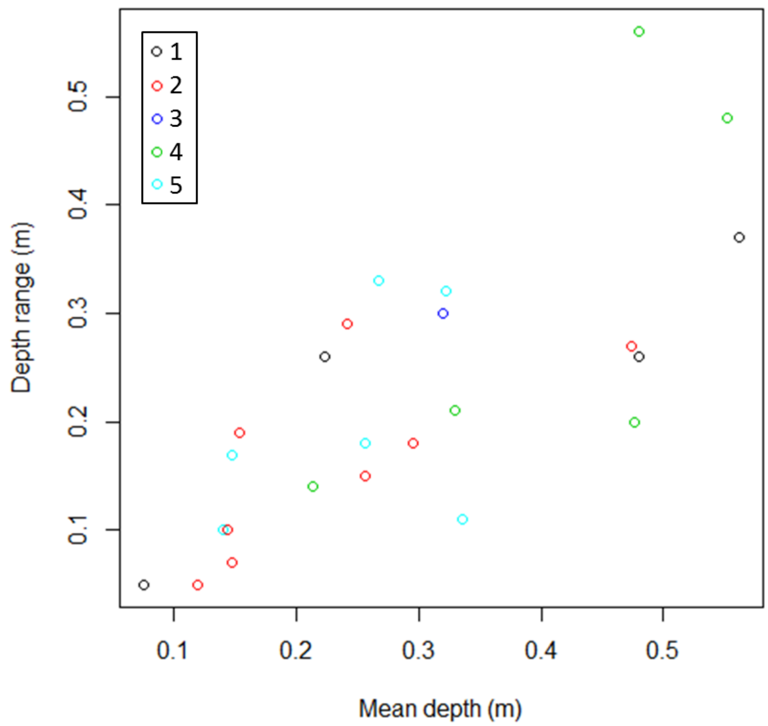


Figure 4.13 – Cluster membership for habitat units along a reach of the Leigh Brook.

4.3.1.2 Standard hydraulic variables

An examination of standard hydraulic variables within representative PBs of the Leigh Brook provides an initial indication of the magnitude and variability of prevailing hydraulic conditions. Figure 4.14 plots the joint h-U distributions of PBs at three flow stages, where U represents the mean, un-rotated streamwise velocity component at point-six depth in order to replicate the traditional approach to mesohabitat classification (Chapter 2). In terms of central tendency this illustrates the expected differences between PBs at low and intermediate flows; there was a clear contrast between the deep, slow pool through to the relatively shallow, fast riffle, with the glide and run completing the gradient. At high flow this relationship broke down as the pool became faster than the glide and the run substantially faster than the riffle. U was more sensitive than h to discharge in the run and riffle, whilst h responded more strongly to flow stage in the pool and glide.

Table 4.7 – Cluster membership and distance to cluster centroids for each discriminator variable in the k-means cluster analysis for the Leigh Brook. Figures in bold show closest habitat to cluster centroid for each variable. *denotes habitat units selected for further study.

		Distance to cluster centroid			
Habitat number	**Cluster (k=5)**	**Mean depth**	**Depth range**	**SFT**	**Substrate**
2	1	**0.11**	**0.03**	**0.00**	**0.25**
11* (pool)	1	0.14	**0.03**	**0.00**	**0.25**
18	1	0.23	0.14	**0.00**	**0.25**
27	1	0.26	0.19	**0.00**	0.75
1	2	0.24	0.11	**0.13**	**0.25**
6	2	0.08	0.09	**0.13**	0.75
9	2	0.03	**0.01**	**0.13**	**0.25**
10	2	**0.01**	0.13	**0.13**	**0.25**
12	2	0.08	0.03	**0.13**	**0.25**
16* (riffle)	2	0.11	0.11	0.88	**0.25**
20	2	0.09	0.06	**0.13**	**0.25**
22	2	0.07	0.02	**0.13**	0.75
8	3	**0.07**	0.24	**0.00**	**0.40**
15	3	**0.07**	0.12	**0.00**	0.60
19* (glide)	3	0.20	0.18	**0.00**	0.60
23	3	0.14	0.16	**0.00**	**0.40**
24	3	0.08	**0.11**	**0.00**	**0.40**
4	4	**0.00**	**0.00**	**0.00**	**0.00**
3	5	0.02	0.13	**0.00**	**0.50**
7	5	0.08	0.12	**0.00**	**0.50**
14	5	0.11	0.10	**0.00**	**0.50**
17	5	**0.01**	**0.02**	**0.00**	**0.50**
26* (run)	5	0.09	0.09	**0.00**	**0.50**
28	5	0.10	0.03	**0.00**	**0.50**

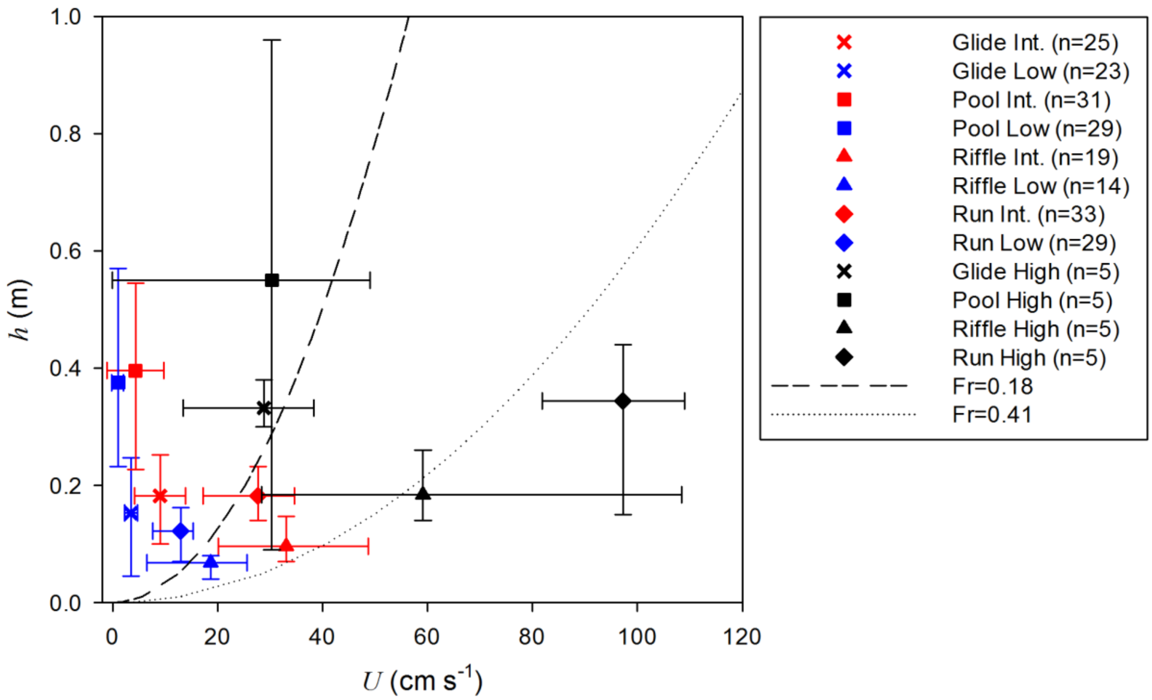


Figure 4.14 – Mean (symbols) and distribution (whiskers, interquartile range for low and intermediate flow, range for high flow) of standard hydraulic variables at point-six depth within PBs of the Leigh Brook at three flow stages. Froude numbers from Jowett's (1993) classification shown with dotted and dashed lines. Note: U refers to the un-rotated mean streamwise velocity component.

A comparison of IQRs (or complete range at high flow) shows a large degree of overlap (Figure 4.14). The pool was the most distinctive PB at low and intermediate flows but even here there was overlap with the glide for both h and U. At high flow there was even a large amount of overlap between the pool and riffle. Indeed, the riffle's U range overlapped all other PBs at high flow. When the streamwise velocity component was rotated to reflect local variations in the primary velocity vector (U_{res}), which is possible with 2D (horizontal) or 3D flow measurements, much of this overlap between habitats remained (Figure B6). This illustrates the problem with using h and U to classify mesohabitats and explains why previous researchers have attempted to use other hydraulic variables, such as Fr, to distinguish between them (*e.g.* Kemp *et al.*, 2000). The Fr classes of Jowett (1993), where pools are found at Fr <0.18, runs at 0.18-0.41 and riffles at <0.41 (Figure 2.9), however, do not consistently fit the hydraulic characteristics of these PBs (Figure 4.14). The pool conformed to this classification at all flows but, apart from this, only the run at intermediate flow and the riffle at high flow plotted in the expected range. It can be seen from Figure B6 that, at any given flow, the run was most spatially variable followed by the riffle, glide and pool, suggesting that a classification based on within-PB variability could be valid.

4.3.1.3 Turbulence intensity

Mean streamwise turbulence intensity (SD_u) within PBs at any given flow followed the order pool<glide<run<riffle but there was some overlap in the IQRs (or complete data ranges) of the pool and glide at intermediate and high flows and between the run and riffle at all flows (Figure B7). Levels of spatial and discharge related variability within PBs also generally followed this order, although the limited number of samples for the riffle mean that results for this PB must be interpreted with caution. These points are exemplified by the selected streamwise velocity time series shown in Figure 4.15 (note the varying y axis scales between flows). Both the mean velocity and the turbulence intensity increased with flow stage. These same patterns were evident for vertical (Figure B8) and spanwise (Figure B9) turbulence intensities, although the magnitude of the fluctuations in these components were lower than that of the streamwise component. As an overall summary of turbulence, therefore, TKE (or $AvInt$ at high flow) also followed this general pattern (Figure 4.16). An opposite and less consistent pattern was found in the case of relative turbulence intensity (TI_u), which was highest in the pool (Figure B10). There was much overlap in the TI_u distributions between PBs and even between flows. In terms of variability through the water column, Figure B11 and B12 plot the rate of change in U and TKE respectively with height above the bed (y) for locations where there was sufficient depth to collect both near bed and point-six samples. These plots show that the order pool<glide<run holds for water column variability at any given flow. This is exemplified by the time series plots in Figure B13. Interestingly, for many flow-PB combinations, negative rates of change were found for both U and TKE. There was not enough data from the riffle to make any firm conclusions as to the rate of vertical variability for this PB and TKE could not be calculated for high flow data.

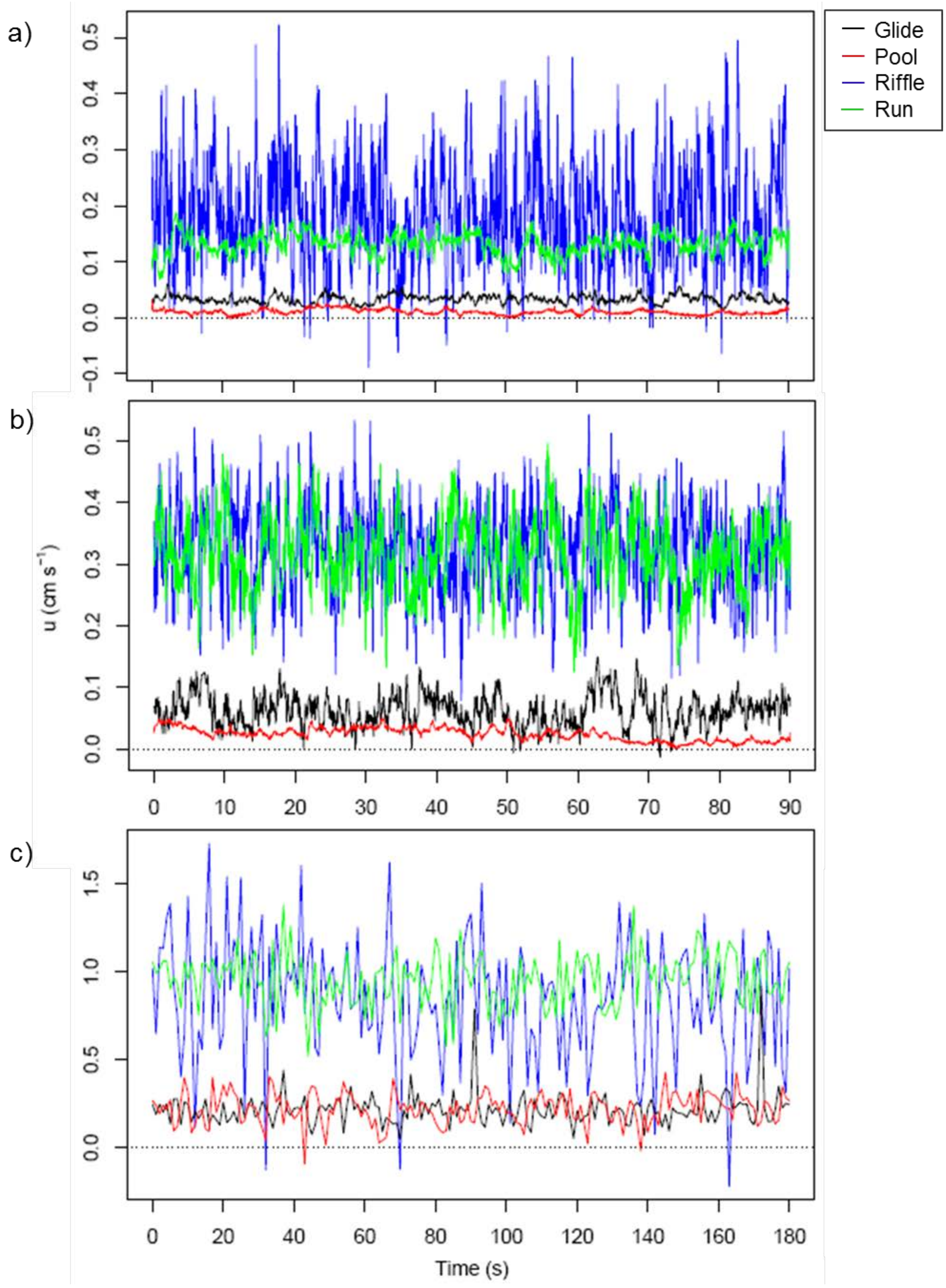


Figure 4.15 – Selected time series typifying the streamwise component for PBs of the Leigh Brook at low (a), intermediate (b) and high (c) flow.

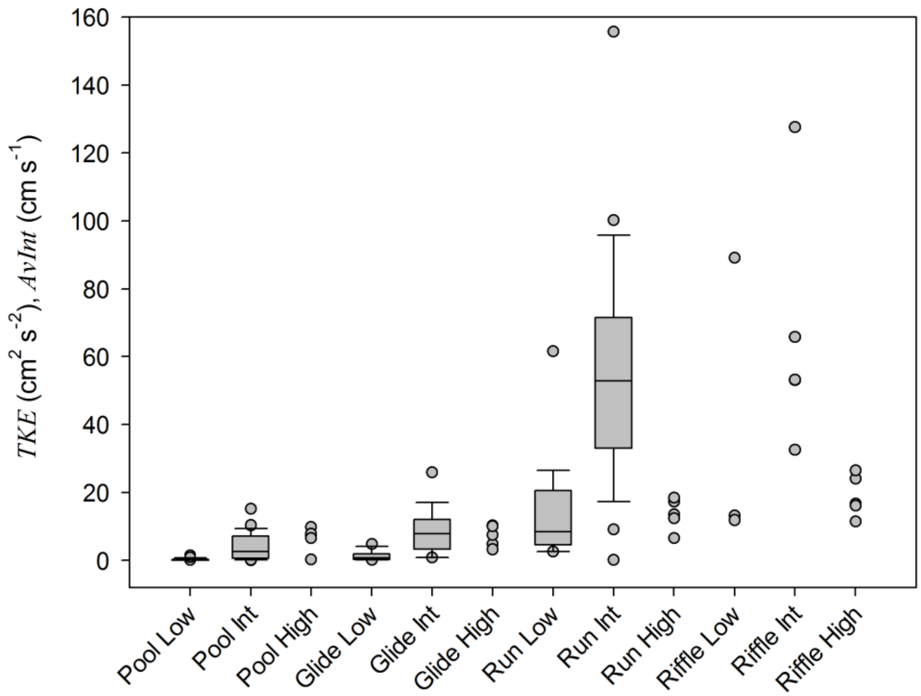


Figure 4.16 – Turbulent kinetic energy (low and intermediate flow) or average intensity (high flow) for PBs of the Leigh Brook.

4.3.1.4 Periodicity and predictability

For time series meeting the criteria for pseudo-periodicity (98% of samples) (Clifford & French, 1993a) Figure 4.17 shows average eddy frequency for the streamwise component (f_u) calculated from second-order auto-regressive modelling (see Appendix C for explanation). Overall, f_u was between 0.1 and 1 Hz, equating to passage times through the sampling volume of between 10 and 1 s respectively. There was much overlap in the IQRs (or complete range for riffle and high flow comparisons) of f_u in PBs but some interesting discharge-related patterns were evident. Between low and intermediate flows the average eddy within each PB became less frequent. This change was most marked for the pool and glide. In contrast, at high flow f_u was found to increase and mean f_u was higher in the run and riffle than in the pool. A similar pattern was evident in the spanwise component (f_w; Figure B14). As stated previously, however, high flow results must be interpreted with caution. In the case of the average vertical eddy (f_v), the opposite discharge-related pattern was evident; mean f_v in the pool and glide increased with flow stage, whereas it decreased in the run and riffle (Figure B15). No data were available for the vertical component at high flow. In terms of variability through the water column, Figure B16 shows that f_u either increased or decreased with y and was most variable in the pool, then the glide and run at low flow. With only one data point from the riffle, no conclusion can be drawn regarding water column variability for this PB.

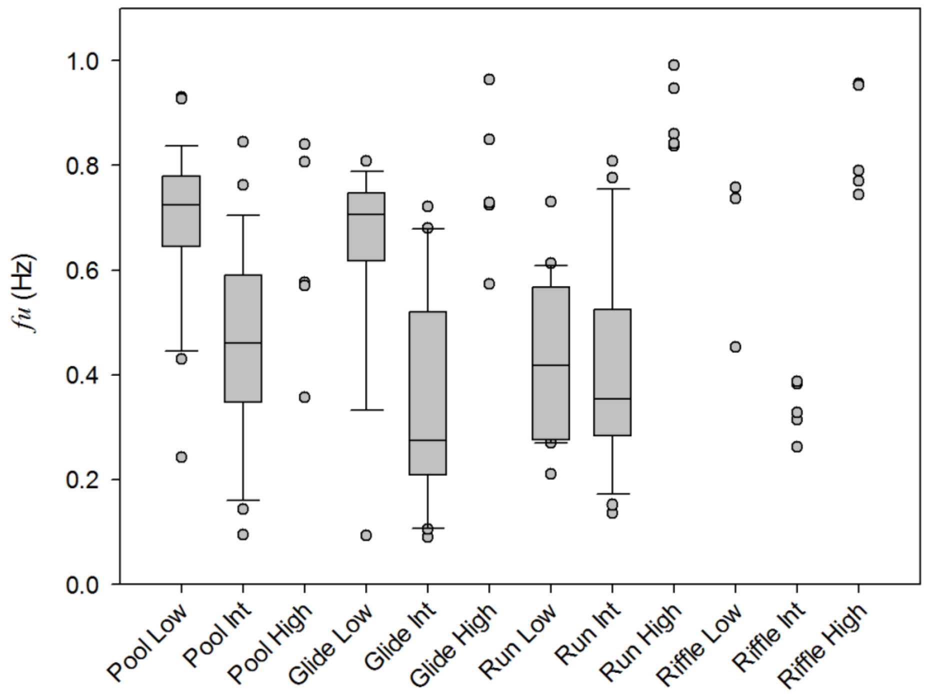


Figure 4.17 – Average eddy frequency of the streamwise component for PBs of the Leigh Brook.

Integral time scale, a measure of the passage time of the largest productive eddies, is an alternative description of eddy frequency. In the streamwise component (ITS_u), this metric showed similar distributions to f_u but the spatial and discharge-related patterns of variability were more consistent (Figure 4.18). Levels of spatial variability followed the order riffle<run<glide<pool and there was a clear tendency for the frequency of productive eddies to increase with flow stage (*i.e.* for the passage time to decrease). This change with flow was most marked for the pool and glide. Again, there was overlap between the within-PB distributions. The same patterns were evident in the vertical (ITS_v; Figure B17) and spanwise (ITS_w; Figure B18) data, although there was less overlap between PBs at a given flow in these cases. Example autocorrelation functions (ACFs) from which ITSs were calculated are shown in Figures B19 and

B20. That the largest productive eddies were of lower frequency in the pool is also illustrated by the typical streamwise power spectra at low flow shown in Figure 4.19, where there is a substantial peak at 0.02-0.03 Hz and a sharp slope down to the noise floor at around 5 Hz in the pool (see Appendix C for explanation). The much flatter power spectrum of the riffle shows that flow in this PB was made up of a wider range of eddies, ranging in frequency from 0.03-1 Hz. The glide and run were intermediate in terms of both dominant eddy frequencies (0.05-0.15 Hz) and spectral flatness. These same differences were also evident in the vertical (Figure B21) and spanwise (Figure B22) components. A comparison of Figure 4.19 with the example streamwise power spectra at intermediate flow (Figure B23) shows that the lowest frequency peaks decreased in frequency in the pool and riffle, at 0.01 and 0.02 Hz respectively, but increased in the glide (0.04 Hz) and run (0.05-0.08 Hz). Water column variability in ITS_u showed similar patterns to f_u, although there was a clearer gradient of variability in the order glide<run<pool (Figure B24).

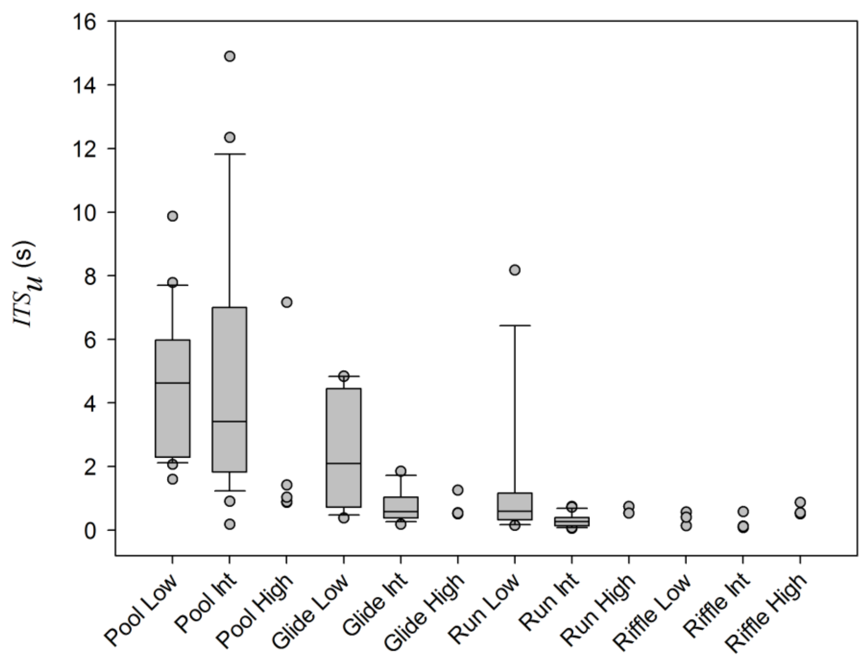


Figure 4.18 – Integral time scale of the streamwise component for PBs of the Leigh Brook.

The kurtosis of the instantaneous velocities can be seen as a description of the 'predictability' of the velocity at a point, with positive values indicating a more peaked distribution and, therefore, more predictable velocities. Mean kurtosis in the streamwise component ($Kurt_u$) was slightly negative at low and intermediate flows and there was a great deal of overlap in the PB distributions (Figure B25). At high flow, $Kurt_u$ was much more variable and often strongly positive, although again high flow data must be treated with caution. There was, however, also a slight tendency for $Kurt_u$ to increase between low and intermediate flows, suggesting that higher flows may indeed lead to more predictable velocities. In terms of levels of spatial variability, this followed the order riffle<run<glide<pool. These same patterns were evident in the vertical (Figure B26) and spanwise (Figure B27) components.

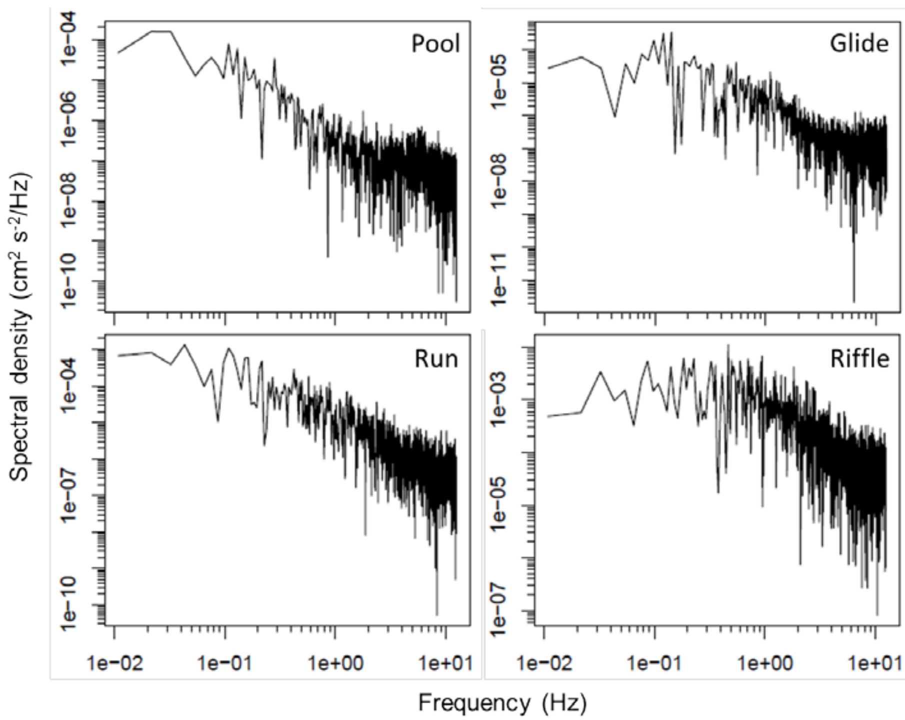


Figure 4.19 – Selected velocity power spectra typifying the streamwise component for PBs of the Leigh Brook at low flow.

4.3.1.5 Orientation

Plots of the primary horizontal velocity vector show that the flow direction in the pool was less likely to be in the streamwise direction than in other PBs (Figure B28). Flow direction was also more variable between flow stages in the pool; the primary flow vector in other PBs was relatively uniform across flow stages. The primary vertical velocity vector tended to be close to 0° at both low and intermediate flows, although there was noticeable upward flow at the tail of the glide at intermediate flow (Figure B29). These points are further illustrated by example three-dimensional time series plots at low (Figure B30) and intermediate (Figure B31) flows and two-dimensional plots at high flow (Figure B32). Figure 4.20 summarises the orientation of turbulent eddies within each PB and shows that most dominant eddies at all flows were rotating on a spanwise axis. There was more variability between flows in the pool and glide, where eddies were more likely to be rotating on a vertical axis than in the run and riffle. A small contribution from eddies rotating on a streamwise axis shows that the flow in parts of the riffle (at intermediate flow), glide and pool was particularly complex.

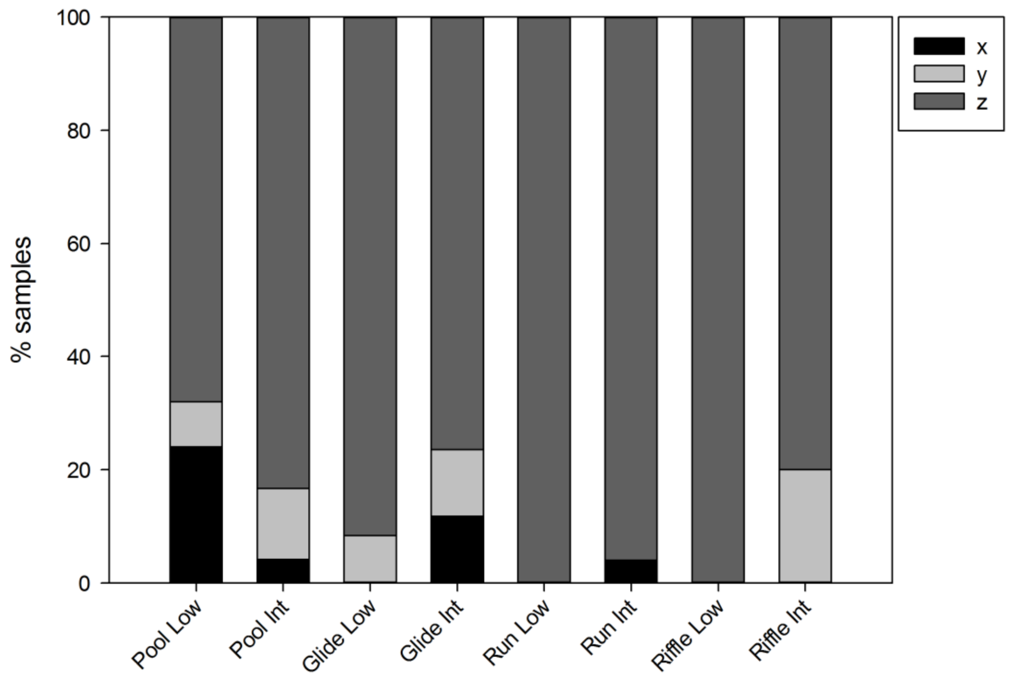


Figure 4.20 – Dominant axis of eddy rotation for PBs of the Leigh Brook, including streamwise (x), vertical (y) and spanwise (z) axes.

Reynolds shear stress on the streamwise-vertical plane (τ_{uv}) tended to be positive in all PBs, indicating a net flux of turbulent momentum away from the bed (Figure 4.21). τ_{uv} in the pool was close to zero and, in terms of magnitude and levels of spatial and discharge-related variability, the order pool<glide<run=riffle was apparent. Reynolds stress on the streamwise-spanwise plane (τ_{uw}) was higher than τ_{uv} but the same patterns of magnitude and variability were evident (Figure 4.22). Absolute values of τ_{uw} are reported here as the direction of stresses on this plane is of less interest than the magnitude (Chapter 5). In the case of both τ_{uv} and τ_{uw},

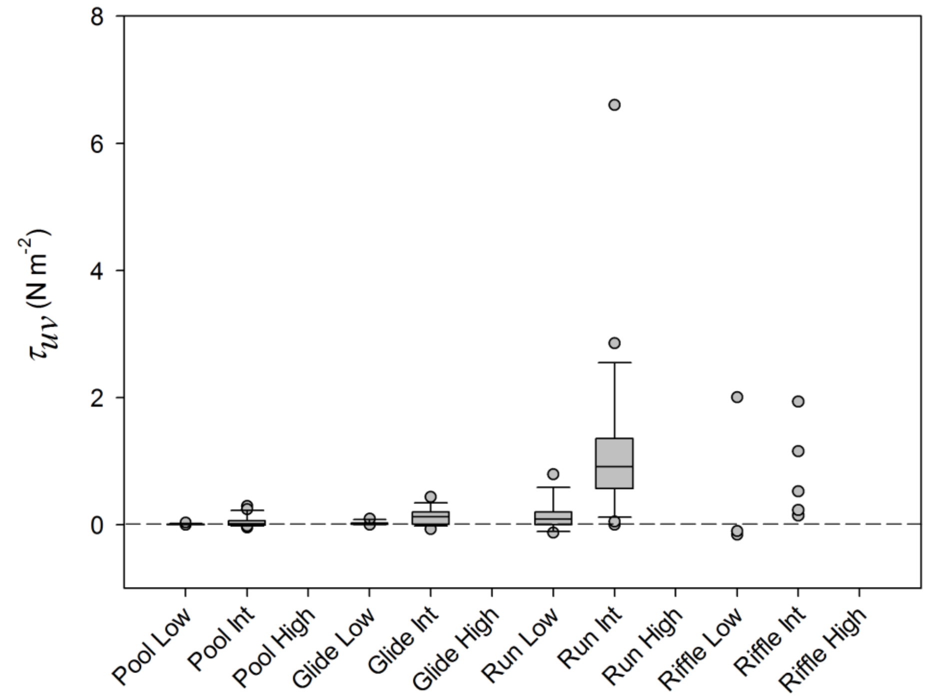


Figure 4.21 – Reynolds shear stress on the streamwise-vertical plane for PBs of the Leigh Brook.

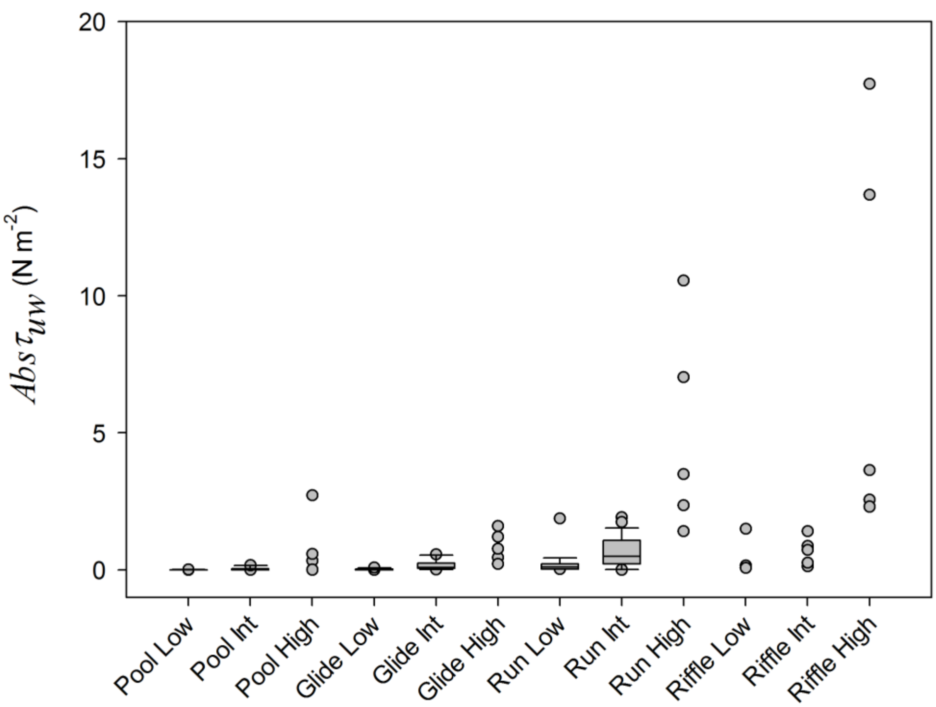


Figure 4.22 – Absolute Reynolds stress on the streamwise-spanwise plane for PBs of the Leigh Brook.

Reynolds stresses consistently increased with flow stage and, at any given flow, there was some overlap in the IQRs (or complete ranges) of PBs. The variability of τ_{uv} through the water column tended to increase in the order pool<glide<run, with a dramatic increase in rates of change with y for the run at intermediate flow (Figure B33). A similar conclusion can be drawn for water column variability in τ_{uw}, where a substantial amount of variability in the riffle at high flow was found (Figure B34). Again, this interpretation is made only tentatively due to a lack of samples from the riffle, and the limitations of the Flowtracker used at high flow.

An analysis of event structure shows that the cumulative duration of strong ejections ($T_{Q2}T_{H:2}$) was lowest in the pool and riffle but there was a great deal of overlap between PBs and no consistent patterns of spatial or discharge-related variability were evident (Figure B35). In the case of strong sweeps ($T_{Q4}T_{H:2}$) there was a clear tendency for an increase in the cumulative duration of this event for every PB-flow combination, although there was still a large amount of overlap and a lack of any clear patterns of spatial variability (Figure B36). These events contributed up to 50% to τ_{uv} (Figure B37 and B38). These contributions tended to be highest in the pool and run at low flow but, again, no clear patterns in terms of magnitude, spatial or discharge-related variability were evident. An alternative, more simplistic analysis of extreme velocity events is provided by skewness coefficients for the streamwise (Figure B39) and vertical (Figure B40) components. $Skew_u$ distributions show that slow events tended to predominate ($Skew_u$ <0) except in the pool at low and intermediate flow, where mean $Skew_u$ was positive. At high flow two outliers are apparent: a large positive skewness coefficient in the glide; and a large negative value for the riffle. These outliers may be the product of residual spikes in the high flow time series. $Skew_w$ distributions were similar to $Skew_u$ (Figure B41). In terms of $Skew_v$, positive values indicate suitable conditions for sediment entrainment and transport and Figure B40 shows that such conditions were found in every PB-flow combination. The pool was most likely to have downward flow events ($Skew_v$<0) and the glide at low flow had the highest positive $Skew_v$.

4.3.1.6 Scale

Average eddy dimensions calculated using average eddy frequency and Taylor's frozen turbulence hypothesis (Appendix C) show that, in the streamwise component (L_u), the length of the average eddy grew with flow stage (Figure 4.23). Eddies grew to almost 4 m long in the run at intermediate flow. There was a clear and consistent order of pool<glide<run=riffle in terms of magnitude and spatial and discharge related variability. Figure B42 shows that the height of the average eddy, as well as the spatial variability of L_v, was also greatest in the run and riffle but the same clear discharge related patterns of variability were not evident. Contrasts between PBs in terms of water column variability were only clear at intermediate flow, where the order pool<glide<run was again found (Figure B43). As the largest productive eddies have been reported to scale with flow depth (Appendix C), one would expect a steady increase in integral length scales (ILS) as discharge, and therefore depth, increases. ILS for the streamwise (ILS_u) and vertical (ILS_v) components shown in Figure 4.24 and B44 respectively, however, do not show a clear increase with flow stage. There was some tendency for ILS_u to increase with discharge, especially between intermediate and high flows, but no such pattern is evident at all in the ILS_v data, where productive eddies were calculated to be as small as <1 mm. Neither were there any consistent contrasts in the spatial variability of ILS_u or ILS_v between PBs, although ILS_v tended to be greater in the pool. The water column variability of ILS_u would be expected to be very small as these productive eddies should occupy the whole flow depth Appendix C). Figure B45, however, shows that ILS_u changed by over 20 cm cm^{-1} in the pool, although this high flow observation may again be affected by poor data quality. Levels of variability with y at a given flow were similar for all PBs, excluding the riffle for which insufficient data were available.

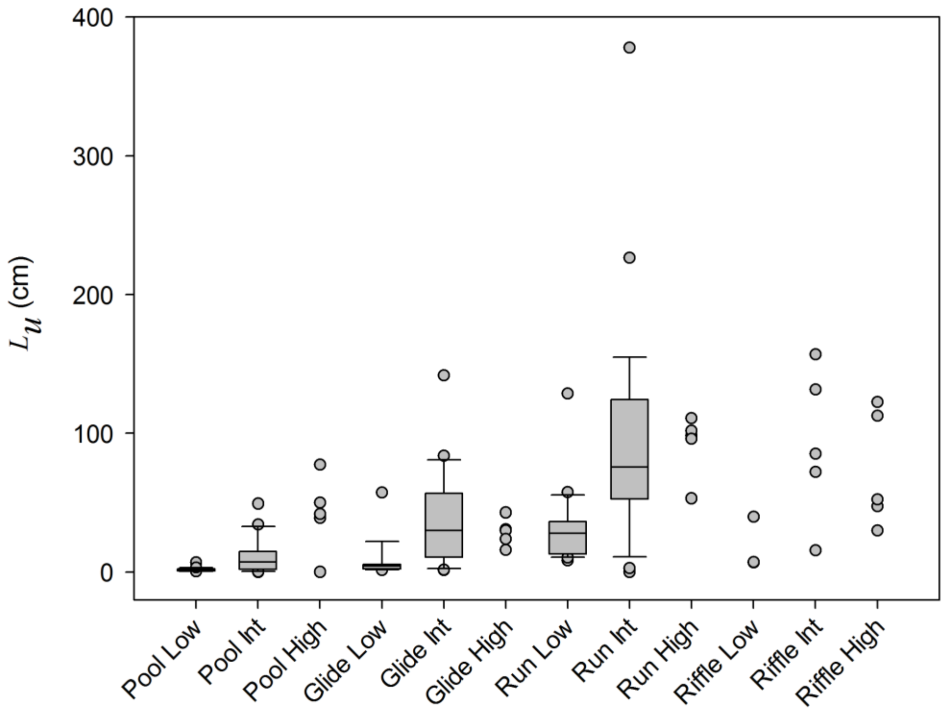


Figure 4.23 – Average eddy length for PBs of the Leigh Brook.

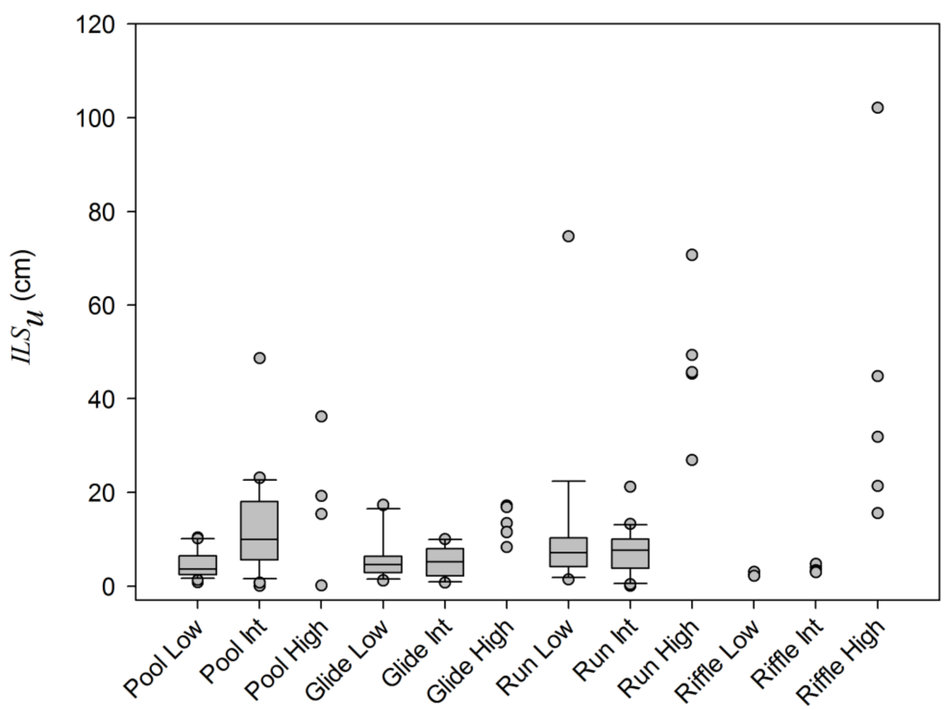


Figure 4.24 – Integral length scale of the streamwise component for PBs of the Leigh Brook.

4.3.2 River Arrow

4.3.2.1 Habitat mapping and selection of representative physical biotopes

At the River Arrow site a total of 22 distinct habitat units were and remain stable' ped (Figure 4.25). Of these, 17 were sufficiently accessible to collect data. Mean *h* (0.07-0.83 m) and *h* range (0.04-0.73 m) were more variable than at the Leigh Brook, reflecting the greater bedform amplitude of the River Arrow (Table 4.8). Four different dominant SFTs were recorded and these were at the lower energy end of the spectrum (NP-UW) than the Leigh Brook. Only two dominant substrate categories were found and most habitats had gravel beds. The full data set on which the cluster analysis was based is provided in Appendix B (Table B3) alongside photographs of the habitat units mapped (Figure B46). Variation in WSS with increasing numbers of clusters again indicated that k=5 was the best solution. Beyond this WSS increased and solutions with k>6 were unstable (Figure 4.26). Figure 4.27 summarises the cluster analysis results in the case of the first two discriminator variables and shows that mean *h* and *h* range were important variables in the clustering procedure, with cluster 1 characterised by shallow flow and uniform morphology and cluster 3 deep with variable bed elevation.

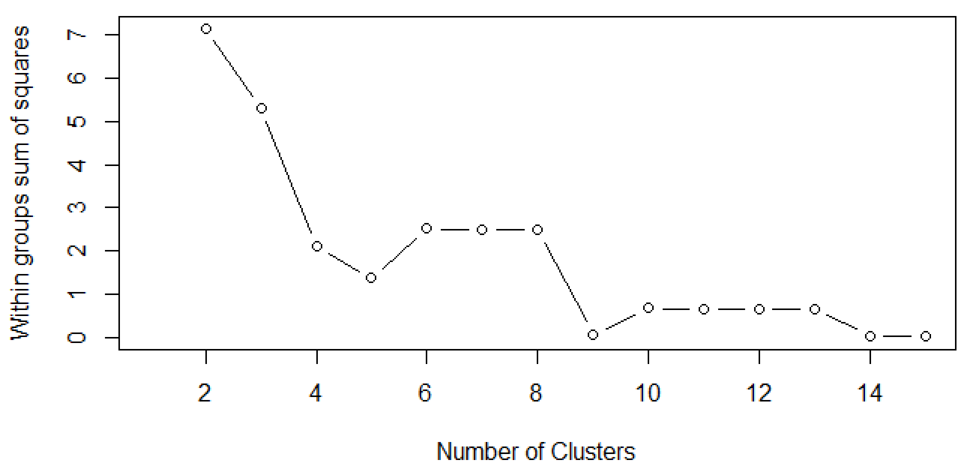


Figure 4.26 – Within-groups sum of squares (WSS) for alternative cluster solutions for habitat units along a reach of the River Arrow.

Figure 4.25 - Distinct units of habitat mapped along a reach of the River Arrow. Note: shading is only included for contrast between neighbouring habitats and does not reflect cluster membership. Aerial photographs from A. Woodget (unpublished data).

Table 4.8 - Summary data for habitat units mapped along a reach of the River Arrow. NA entries refer to units inaccessible for depth measurements.

Habitat number	Mean depth (m)	Depth range (m)	Dominant SFT	Dominant substrate
1	0.08	0.07	UW	Gravel
2	NA	NA	NA	NA
3	NA	NA	NA	NA
4	0.114	0.11	SM	Gravel
5	0.224	0.34	SM	Gravel
6	0.092	0.06	UW	Gravel
7	0.468	0.52	NP	Gravel
8	NA	NA	NA	NA
8a	0.13	0.09	SM	Gravel
9	0.316	0.17	NP	Cobble
10	0.39	0.27	SM	Gravel
11	0.462	0.35	NP	Cobble
12	0.12	0.08	SM	Gravel
13	0.07	0.04	UW	Gravel
14	0.658	0.17	RP	Gravel
15	NA	NA	NA	NA
16	0.294	0.15	SM	Gravel
17	0.17	0.15	RP	Cobble
18	NA	NA	NA	NA
19	0.15	0.21	SM	Gravel
20	0.108	0.13	UW	Gravel
21	0.828	0.73	SM	Gravel

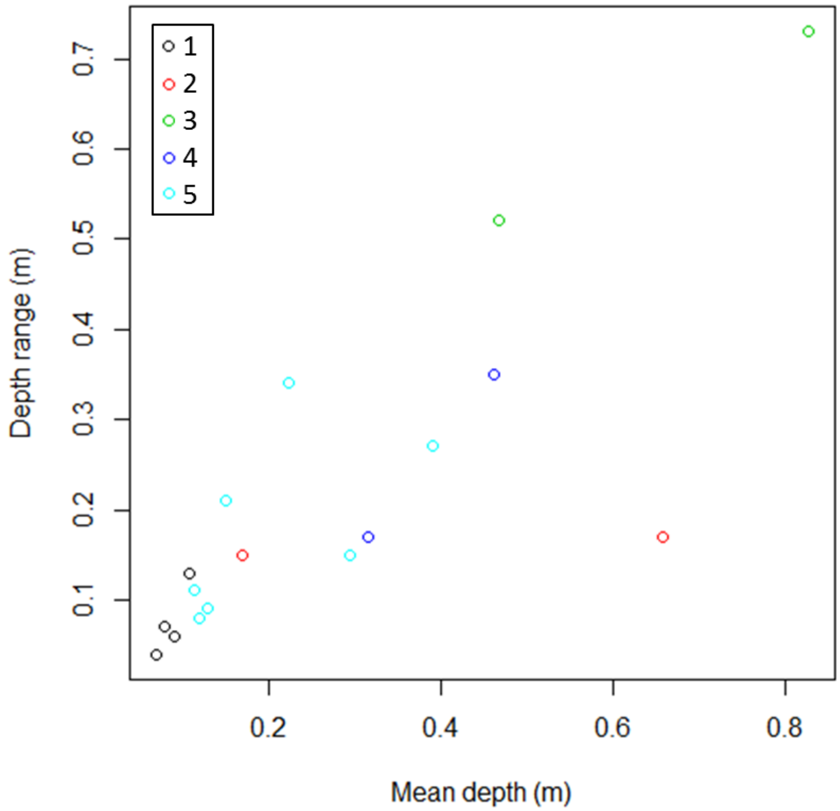


Figure 4.27 – Cluster membership for habitat units along a reach of the River Arrow.

Table 4.9 shows cluster membership and distance to respective cluster centroids for the purposes of selecting habitat units for further study. Habitat number 20 was selected from cluster 1 as, although other habitat units were closer to the cluster centroid, this was the only member with sufficient flow depth to capture turbulence data using the NDV. Dominated by unbroken standing waves and underlain by gravel and cobble, this habitat can be classified as a riffle. Cluster 2 contained only two habitats which were both equal distances from the cluster centroid. Of these, habitat number 17 was selected as it was more easily accessible. This habitat was relatively shallow with rippled SFT and coarse substrate, closely resembling a run. Cluster 3 smilarly had only two members and, of these deep, concave, pool-like habitats, habitat number 21 was selected for further study. Cluster 4 also contained only two members and, with intermediate depths and depth ranges, these habitats did not fit the description of any of the four common PBs (Chapter 2). Habitats from this cluster, therefore, were exlcuded from further study. Finally, habitat number 10 was selected from cluster 5 and this unit resembled a glide.

Despite being further from the cluster centroid than other habitats, this unit was selected for its accessibility. In any case, cluster 5 was a well defined group with all members relatively close to the centroid.

Table 4.9 – Cluster membership and distance to cluster centroids for each discriminator variable in the k-means cluster analysis for the River Arrow. Figures in bold show closest habitat to cluster centroid for each variable. *denotes habitat units selected for further study.

		Distance to cluster centroid			
Habitat number	**Cluster (k=5)**	**Mean depth**	**Depth range**	**SFT**	**Substrate**
1	1	0.01	**0.00**	**0**	**0**
6	1	**0.00**	0.02	**0**	**0**
13	1	0.02	0.04	**0**	**0**
20*(riffle)	1	0.02	0.06	**0**	**0**
14	2	**0.24**	**0.01**	**0**	**0.5**
17*(run)	2	**0.24**	**0.01**	**0**	**0.5**
7	3	**0.18**	**0.11**	**0.5**	**0**
21*(pool)	3	**0.18**	**0.11**	**0.5**	**0**
9	4	**0.07**	**0.09**	**0**	**0**
11	4	**0.07**	**0.09**	**0**	**0**
4	5	0.09	0.07	**0**	**0**
5	5	**0.02**	0.16	**0**	**0**
8a	5	0.07	0.09	**0**	**0**
10*(glide)	5	0.09	0.09	**0**	**0**
12	5	0.08	0.10	**0**	**0**
16	5	0.09	**0.03**	**0**	**0**
19	5	0.05	**0.03**	**0**	**0**

4.3.2.2 Standard hydraulic variables

Patterns of h and U (mean, un-rotated velocity at point-six depth) in representative PBs of the River Arrow (Figure 4.28) were similar to those exhibited by PBs at the Leigh Brook (Figure 4.14) except that discharge related variability was less consistent. The central tendency and IQR of h in the pool, for example, did not change between low and intermediate flows. Other PBs did generally exhibit the expected changes in h and U with flow, although the transition from intermediate to high discharge in the run resulted in a slight decrease in h. A comparison of bivariate IQRs (or complete range at high flow) shows a large amount of overlap at any given flow. The glide and pool overlaped in terms of both h and U, whilst there was also overlap in U between the run and pool and the run and riffle. At intermediate and high flows there was more overlap, even in the U distributions of the pool and riffle, the latter of which plots within the run's U distribution at intermediate flow. Once again, the Fr distributions plotted in Figure 4.28 show that Jowett's (1993) classification (Figure 2.9) rarely fits the data. Spatial variability varied according to the PB and hydraulic parameter (h or U) considered, with the pool and glide most variable in h (except high flow in the pool) and the run and riffle more variable in U at a given flow. These same velocity patterns remain when the data are rotated to reflect the resultant velocity vector (Figure B47).

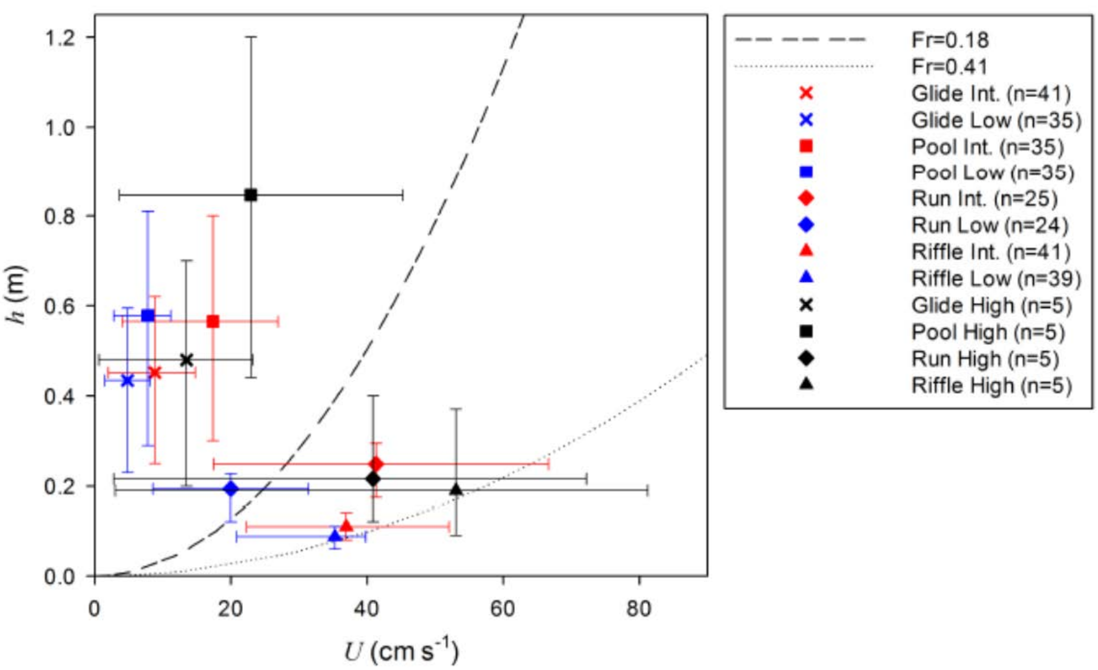


Figure 4.28 – Mean (symbols) and distribution (whiskers, interquartile range for low and intermediate flow, range for high flow) of standard hydraulic variables at point-six depth within PBs of the River Arrow at three flow stages. Froude numbers from Jowett's (1993) classification shown with dotted and dashed lines.

4.3.2.3 Turbulence intensity

Both the magnitude and levels of spatial variability in SD_u distributions of PBs at the River Arrow followed the order glide<pool<run=riffle (Figure B48). The glide was relatively distinctive based on SD_u but the IQR (or range for high flow) of the pool overlapped the run and the run overlapped the riffle at low and intermediate flows. Levels of discharge related variability, illustrated by the change in mean SD_u with flow stage, followed the order glide=riffle<pool=run. Example time series at each flow shown in Figure 4.29 reinforce these general patterns, with mean velocity and turbulence in the pool exceeding that in the glide at each flow. At high flow, velocities in the pool even exceeded those in the run (Figure 4.29c). Similar conclusions can be drawn from SD_v (Figure B49) and SD_w (Figure B50) distributions, except that there was less overlap between the pool and other PBs in these cases. This is summarised by the TKE (or $AvInt$ at high flow) distributions which, apart from the run and riffle and intermediate flow, generally show good discrimination between PBs based on IQRs (Figure 4.30). A relative measure of turbulence intensity, TI_u, however, was a poor discriminator of PBs, with overlap in the IQRs (or ranges) of all habitat-flow combinations (Figure B51). Figure B52 and B53 depict the water column variability of PBs for U and TKE respectively and show that the run was the most variable, followed by the pool then the glide. These plots also show that U and TKE could either increase or decrease with y. Example time series shown in Figure B54, where velocities in the pool actually decrease between near bed and point-six locations, illustrate these points. With only one sample available for the riffle no firm interpretations can be made regarding water column variability for this PB.

4.3.2.4 Periodicity and predictability

All records met the criteria for pseudo-periodicity (Clifford & French, 1993a) allowing for the calculation of average eddy frequencies from autoregressive models. f_u varied from 0.02 Hz in the run at intermediate flow to almost 1 Hz for other PB-flow combinations (Figure 4.31). These frequencies equate to eddy passage times of between 50 and 1 s. The glide had the highest mean f_u at low flow but, beyond this, there were few clear and consistent patterns of either magnitude or spatial variability. In terms of discharge related variability, there was a tendency

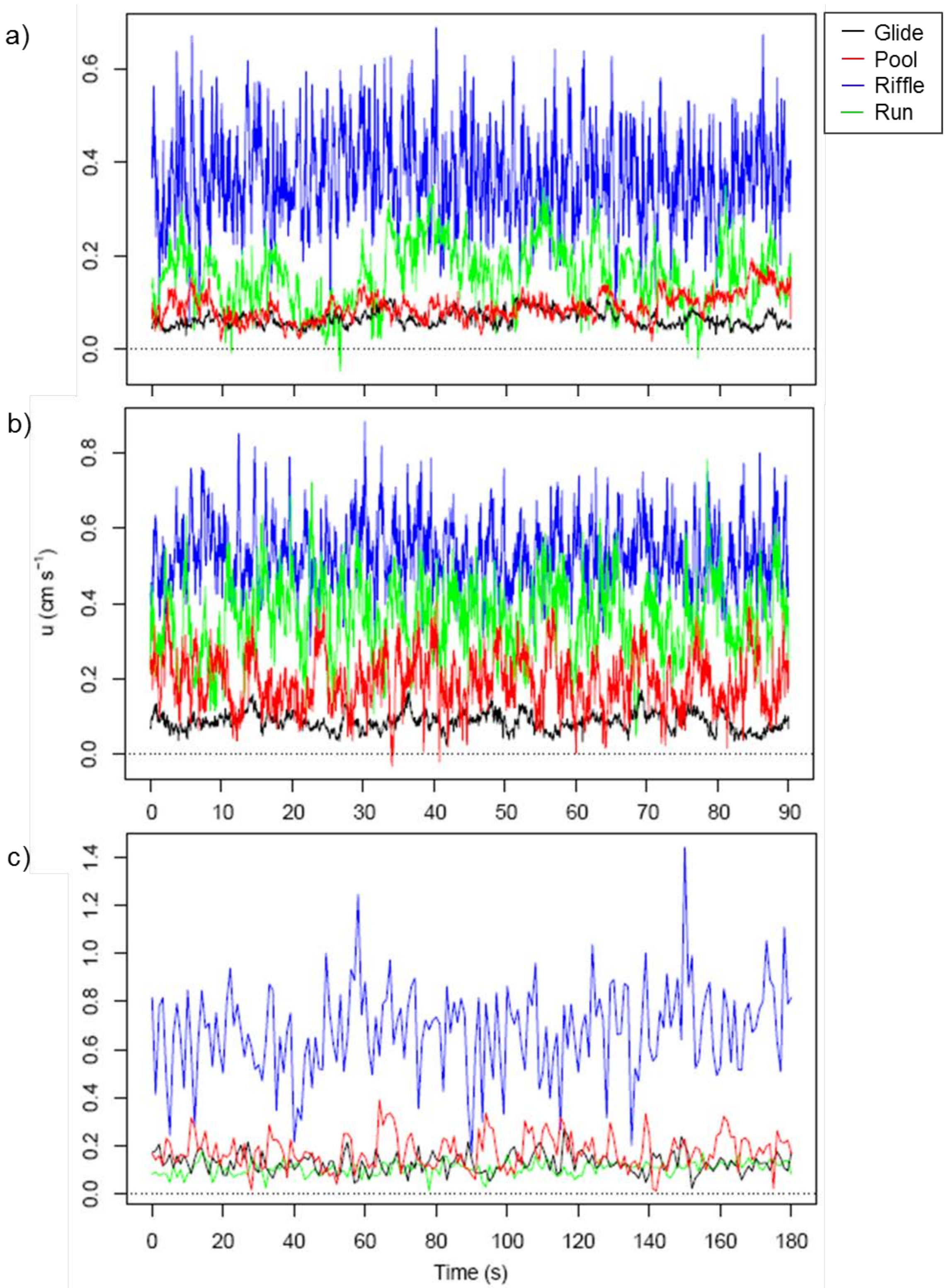


Figure 4.29 – Selected time series typifying the streamwise component for PBs of the River Arrow at low (a), intermediate (b) and high (c) flow.

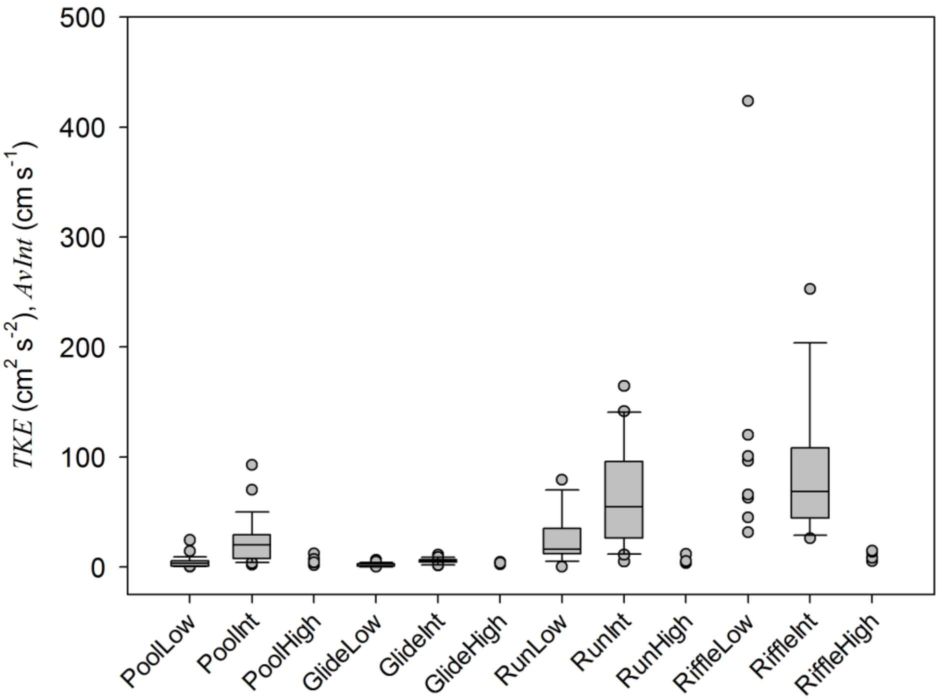


Figure 4.30 – Turbulent kinetic energy (low and intermediate flow) or average intensity (high flow) for PBs of the River Arrow.

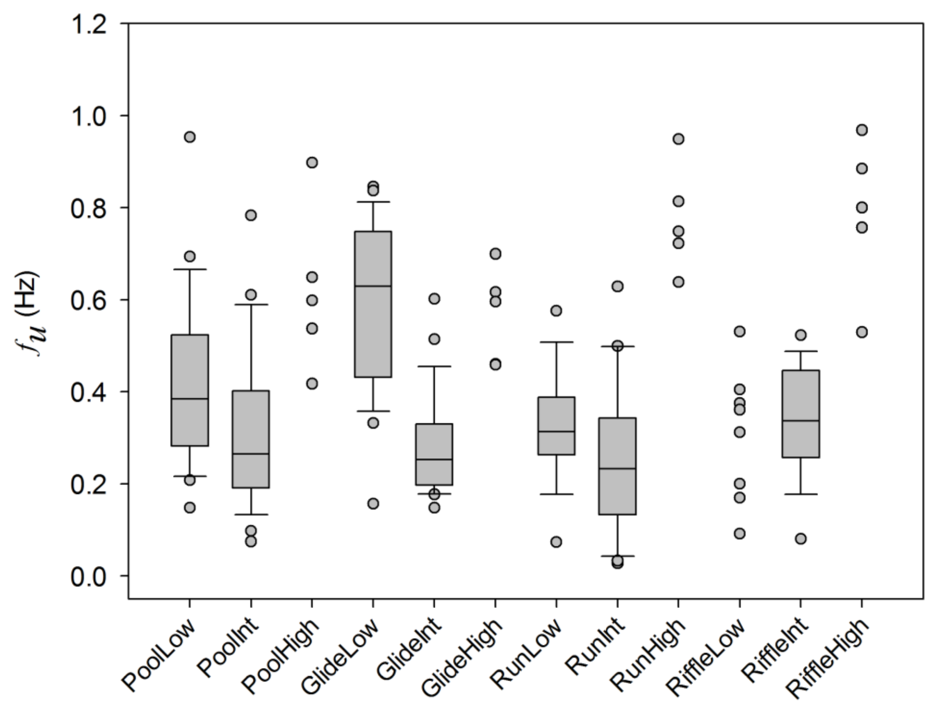


Figure 4.31 – Average eddy frequency of the streamwise component for PBs of the River Arrow.

for f_u to decrease between low and intermediate flows and then increase up to high flow. Because of the lower f_D of the ADV used at high flow, however, it is unclear whether this increase is real or a result of the different method used. Figure B55 shows that f_v spanned a similar overall range to f_u and again the glide had the highest frequency eddies, this time at both low and intermediate flows. Levels of spatial and discharge related variability in both f_u and f_v were not strong and there was much overlap between PBs. f_w distributions followed a similar pattern (Figure B56), although changes with flow stage were more muted than for f_u. In terms of water column variability in f_u, Figure B57 shows that eddies were just as likely to become less frequent as more frequent with y, with the order of variability following glide<pool=run.

ITS_u was relatively invariant with flow stage, apart from the glide where there was a discernible decrease between low and intermediate flows (Figure 4.32). The riffle had the shortest ITS_u (around 0.1 s) at all but the highest flow, followed by run<pool=glide. The IQRs of the glide, run and riffle were well separated at low and intermediate flows but the high amount of spatial variability in the pool meant that this PB overlapped the glide and run at both flows. In the riffle at high flow there was a strong outlier at around 15 s but, excluding this, levels of spatial variability followed the order riffle<run=glide<pool at any given flow. Figure B58 shows that levels of water column variability also followed this general pattern and once again indicates that eddies could either increase or decrease in frequency with y. ITS_v (Figure B59) and ITS_w (Figure B60) showed similar patterns to ITS_u. These time scales were calculated from ACFs, examples of which can be found in Figures B61 and B62.

An examination of example streamwise velocity spectra at low (Figure 4.33) and intermediate (Figure B63) flows shows that the riffle had a flatter spectrum in the productive range and, therefore, a wider range of eddies with different frequencies. At low flow the riffle has spectral peaks between 0.025 and 1 Hz, whilst peaks in the other PBs extend to a maximum frequency of around 0.1 Hz. This contrast is still apparent at intermediate flow although it is muted by the flattening of spectra in the pool, glide and run. Similar differences between PBs can be seen in example spectra for vertical (Figure B64) and spanwise (Figure B65) components. In terms of predictability, Figure B66 illustrates the close similarity in $Kurt_u$ between PBs. There was a lack of any spatial or discharge related patterns of variability except for the tendency for $Kurt_u$ to

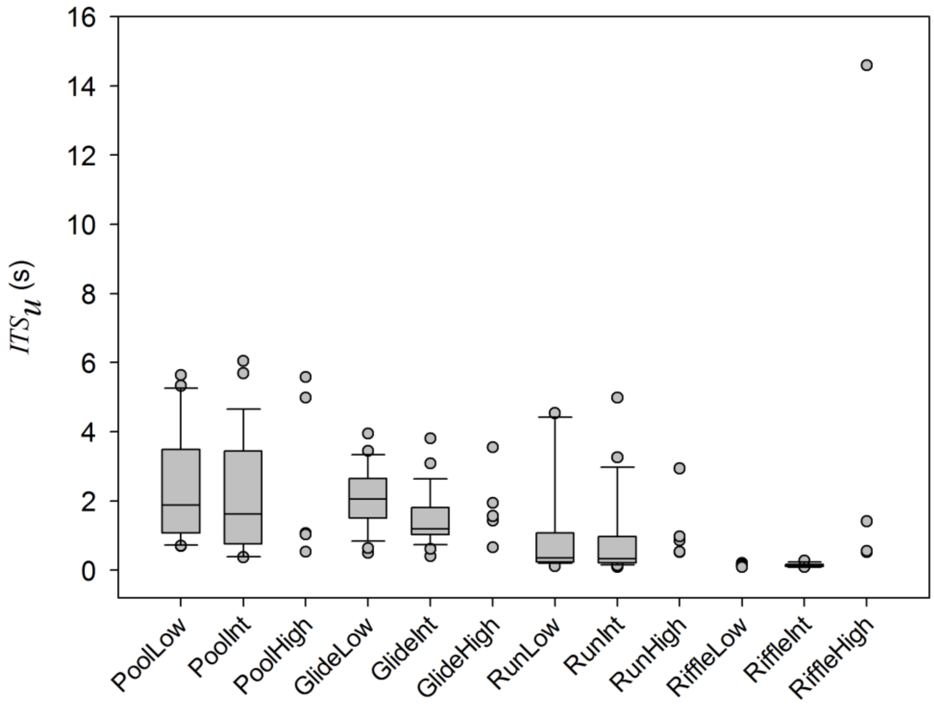


Figure 4.32 – Integral time scale of the streamwise component for PBs of the River Arrow.

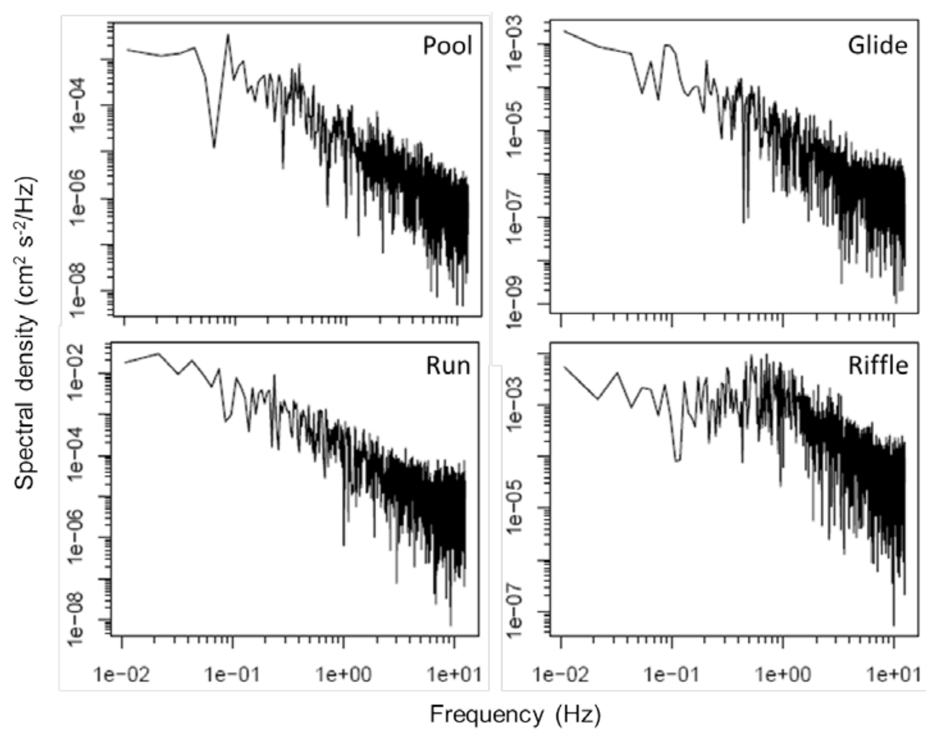


Figure 4.33 – Selected velocity power spectra typifying the streamwise component for PBs of the River Arrow at low flow.

increase at the highest flow, thus leading to more predictable instantaneous velocities. $Kurt_v$ (Figure B67) and $Kurt_w$ (Figure B68) distributions similarly had few discernible and consistent patterns of magnitude or variability between PBs.

4.3.2.5 Orientation

Vector plots of the resultant velocity on the horizontal plane shown in Figure B69 and B70 illustrate that flow in the pool was most likely to be in a direction other than streamwise, with a tendency for reverse flow to occur near the pool head and along the channel margins. The glide was most likely to exhibit uniform, downstream flow. Flow direction in the glide and riffle was relatively invariant with discharge, whereas the resultant velocity vectors at several points in the pool and run changed noticeably with flow stage. On the vertical plane the riffle had the most variable flow direction, although there was a point of substantial downward flow near the pool head (Figure B71). Selected un-rotated, two- and three-dimensional time series plots for low (Figure B72), intermediate (Figure B73) and high (Figure B74) flows illustrate these points. Figure 4.34 shows that flow in all PBs was dominated by eddies rotating on a spanwise axis. This was true of 100% of the samples from the pool, whilst there was some variability in other PBs. Small areas of the glide had streamwise-rotating and vertical-rotating eddies at low and intermediate flow respectively. Eddy rotation axes were most variable in the riffle, where a 20% contribution from vertical eddies at low flow was replaced by a 10% share of streamwise-rotating eddies at intermediate flow, reflecting complex and variable patterns of three-dimensional flow here.

τ_{uv} was generally positive in all PBs, although several samples from the run and riffle indicated points in these habitats where there was a net flux of turbulent momentum towards the bed (Figure 4.35). There was a tendency for τ_{uv} to increase with flow stage and PBs followed the order glide<pool<riffle≤run in terms of magnitude and spatial, discharge related and water column variability, although this conclusion can only be tentative in the case of water column variability in the riffle (Figure B75). Absolute τ_{uw} distributions (Figure 4.36) and the variation of τ_{uw} with y (Figure B76) exhibited the same patterns as τ_{uv}. In terms of event structure, $T_{Q2}TH{:}2$ (Figure B77) and $T_{Q4}TH{:}2$ (Figure B78) distributions were generally similar between PBs,

although sweeps (Q4) were more dominant in the glide than in other habitats. The cumulative duration of both event types tended to increase slightly with flow stage. This increase was clearer for sweeps. The contribution of ejections and sweeps to τ_{uv} is shown in Figure B79 and B80 respectively. These plots illustrate few discernible differences between PBs, although it can be seen that the IQR of the pool tended to be more variable than other PBs. $Skew_u$ distributions show that slow events ($Skew_u$<0) predominated throughout most PBs (Figure B81), whilst most mean $Skew_v$ coefficients were positive (Figure B82). Areas of negative $Skew_v$, however, were found in all PBs. There was much overlap in skewness values between PBs and no discernible patterns of spatial or discharge related variability, except for a substantial decrease in $Skew_u$ at high flow in the riffle. Similar conclusions can be drawn from an examination of $Skew_w$ (Figure B83).

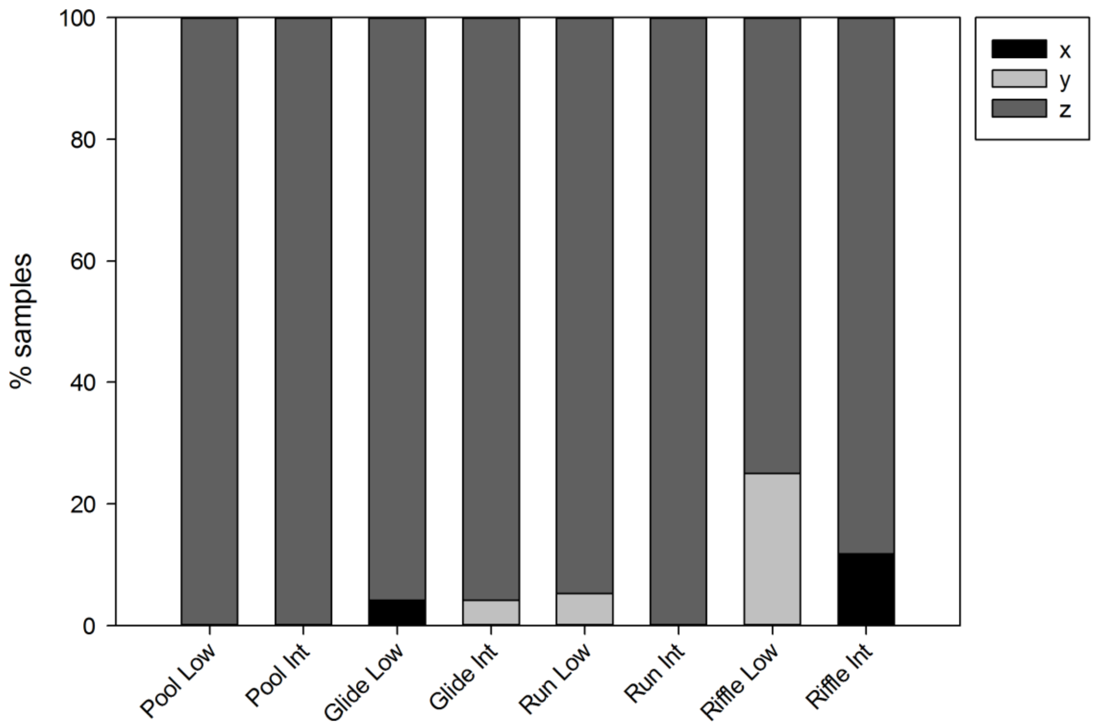


Figure 4.34 – Dominant axis of eddy rotation for PBs of the River Arrow, including streamwise (x), vertical (y) and spanwise (z) axes.

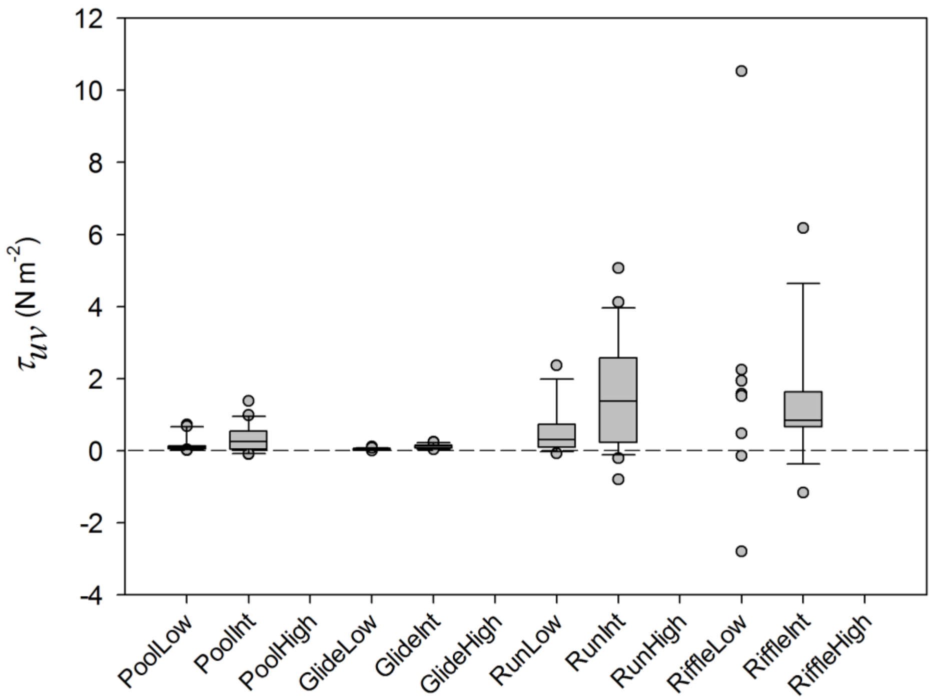


Figure 4.35 – Reynolds shear stress on the streamwise-vertical plane for PBs of the River Arrow.

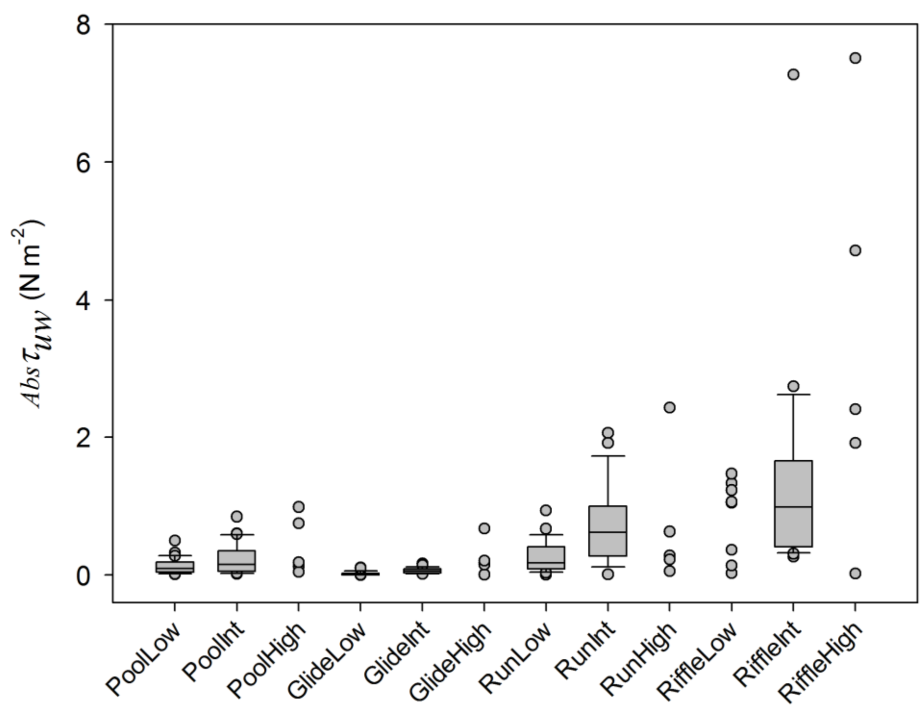


Figure 4.36 – Absolute Reynolds stress on the streamwise-spanwise plane for PBs of the River Arrow.

4.3.2.6 Scale

L_u generally ranged from 0.02 m to 3 m, though it reached 23 m in the run at intermediate flow (Figure 4.37). Levels of magnitude and spatial variability followed the order glide<pool<run=riffle, although there was overlap in the IQRs of each PB at a given flow. The same order of habitats was apparent for water column variability (except for the riffle), where the average eddy was as likely to decrease in length as to increase (Figure B84). In all cases L_u increased slightly from low to intermediate flow and then appeared to decrease again up to high flow (Figure 4.37). L_v showed the same order of PBs in terms of magnitude and spatial variability but was relatively invariant with flow (Figure B85). There was a slight tendency for L_v to decrease in the pool and glide and increase in the run and riffle. ILS_u ranged from near zero up to 1.17 m in the riffle at high flow (Figure 4.38). On average, the pool had slightly longer ILS_u than other PBs at low and intermediate flows. There was a slight tendency for ILS_u to increase with flow stage. This was most clearly evident in the pool and in the transitions of PBs from intermediate to high flow. Water column variability in ILS_u showed that the length of these productive eddies could either increase or decrease with y and that levels of variability were

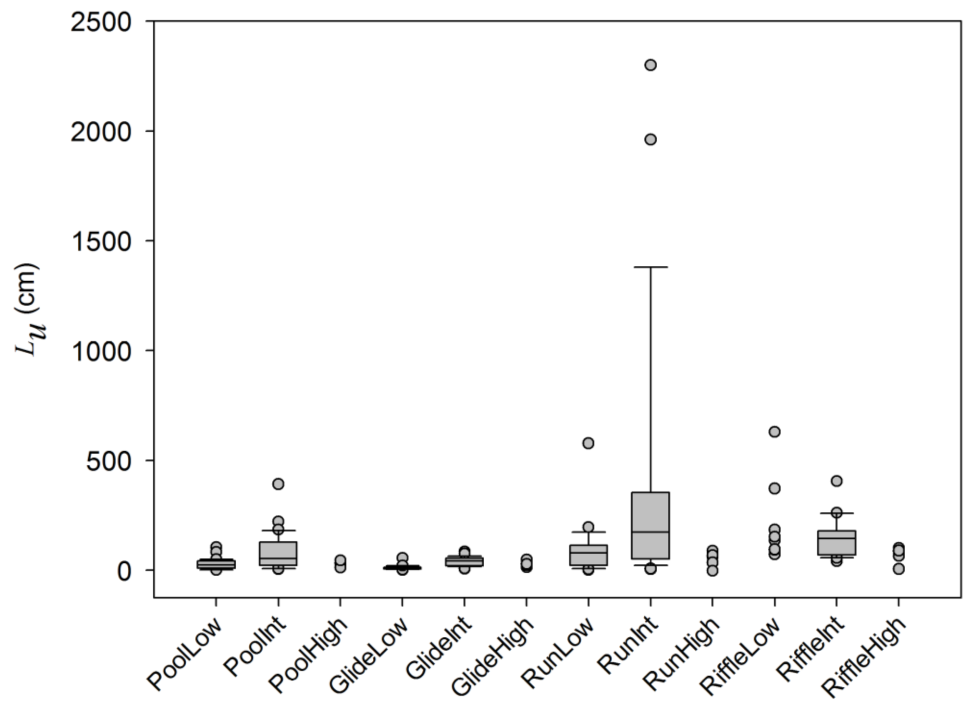


Figure 4.37 – Average eddy length for PBs of the River Arrow.

similar between PBs (Figure B86). In the case of productive eddy height, ILS_v distributions were similar across all PB-flow combinations and few spatial or discharge related patterns of variability were evident, although the pool was clearly the most spatially variable and there was a clear tendency for ILS_v to increase with flow stage in the run (Figure B87).

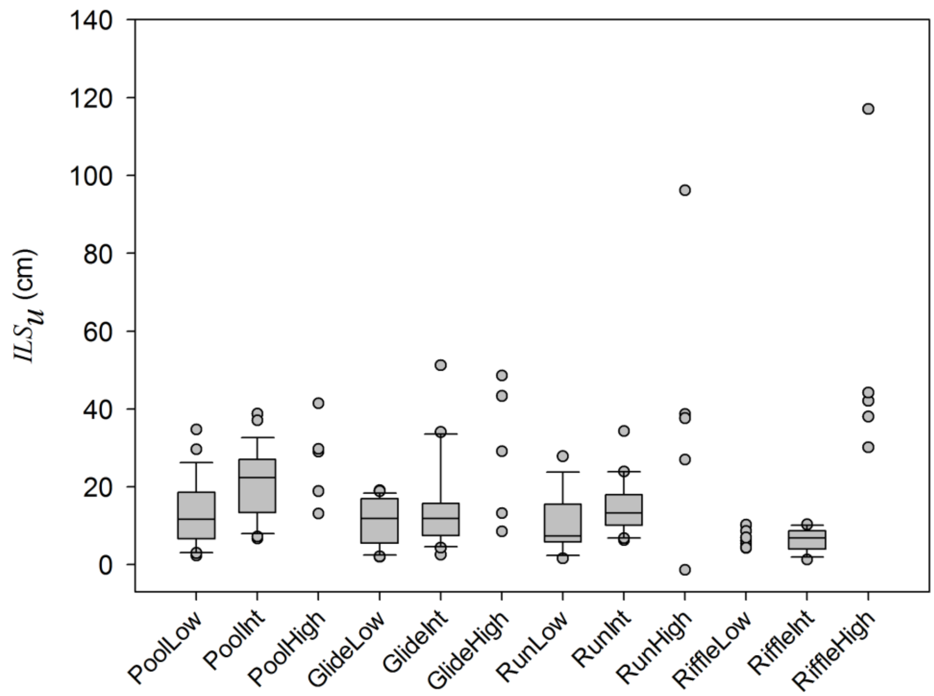


Figure 4.38 – Integral length scale of the streamwise component for PBs of the River Arrow.

4.3.3 Hydrodynamic classification

S 4.3.1 and S 4.32 presented results suggesting that a number of hydrodynamic variables could consistently describe the contrasts between PBs, in terms of both magnitude and levels of within-PB variability, at two sites. TKE, for example, exhibited relatively distinctive distributions between PBs at a given flow and contrasting levels of discharge related variability, increasing at different rates in PBs (Figure 4.16 and 4.30). Variables describing periodicity (f_u, ITS_u) provided less discrimination between PBs but were associated with complex and distinctive temporal dynamics. The average eddy, for instance, became less frequent between low and intermediate flows (Figure 4.17 and 4.31) yet ITS_u, a description of the passage time of large productive eddies, became more frequent (*i.e.* lower timescale) (Figure 4.18 and 4.32). Calculation of Reynolds stresses showed that the direction and magnitude of turbulence related forces on the vertical (Figure 4.21and 4.35) and horizontal (Figure 4.22 and 4.36) planes differed consistently between PBs at a given site. Finally, descriptions of eddy size (*e.g.* L_u) also provided discrimination between PBs in terms of both central tendency and heterogeneity, although as with many variables, the difference between the runs and riffles were muted (*e.g.* Figure 4.23 and 4.37). No single variable alone, however, would be capable of providing an adequate calibration for every PB-flow stage combination (*e.g.* non-overlapping IQRs). Any new classification based on hydrodynamics, therefore, must be multivariate. It should also consider levels of within-PB variability (S 4.3.3.1) as well as absolute magnitude (S 4.3.3.2).

4.3.3.1 Variability

Table 4.10 lists the levels of spatial, discharge related and water column variability of core hydrodynamic variables identified for PBs of each study site across low and intermediate flows. High flow data were not explicitly considered here due to the sparse number of locations sampled at this discharge. In addition to core hydrodynamic variables, h and U_{res} were also included as these are currently key hydraulic variables with which mesohabitats are calibrated (S 2.4). It can be seen from this analysis that several hydrodynamic variables yielded consistent patterns (*i.e.* ranking of PBs) at both sites. The exceptions to this in the case of certain variables are the differences in the spatial variability of pools and the discharge related variability of riffles between sites. For the riffles, the source of this exception could potentially be the inclusion of samples (time series) at intermediate flow in locations that were too shallow to access with the ADV at low flow. Table 4.10, therefore, also shows data where only sampling locations accessible to the ADV at both flows were included (eqv). The discharge related patterns, however, remain, suggesting that there is a flow dependent process occurring over the riffle at the River Arrow that was not detected elsewhere. Contrasting levels of spatial variability in the pools could be the result of differences in the identity of the adjacent upstream PB, which was a pool-like habitat at the Leigh Brook (Table 4.7) but a riffle at the River Arrow (Table 4.9). Despite this, the consistent and distinctive patterns exhibited by TKE, τ_{uv}, τ_{uw}, L_u and ILS_u lend themselves to a classification based on variability when pools from each site are plotted separately. Figure 4.39 presents this classification. In this case spatial variability includes water column variability as these followed the same trends in Table 4.10.

Figure 4.39 shows that riffles exhibited the highest spatial (including water column) variability in hydrodynamic variables describing the overall magnitude (TKE) and orientation (τ_{uv}, τ_{uw}) of turbulent fluctuations. The run was the most heterogeneous on the temporal (discharge related) axis for these variables, whilst the pool at the Leigh Brook was the least variable on both axes. The pool at the River Arrow, however, plotted as intermediate on both the spatial and temporal axes, as did the glides. A different pattern was evident for variables describing the scale of turbulence. This was particularly true for ILS_u, the only key variable for which pools at both sites plotted together. Here the order was reversed; pools had the highest levels of spatial and temporal variability and the riffles the least. Bubbles scaled to the mean magnitude of each variable in Figure 4.39 suggest that a classification based on magnitude could be appropriate. The often large differences in magnitude between sites (*e.g.* TKE in riffles), however, means that any general classification would need to be produced using standardised data.

4.3.3.1 Magnitude

Due to the multivariate and possibly nonlinear temporal dynamics identified in S 4.3.1 and S 4.3.2 (*e.g.* the increase in TKE coupled with a decrease in f_u), and the differences in the magnitude and spatial variability of hydrodynamic variables between sites (Figure 4.39), RF was performed on scenarios stratified by site and flow stage. In addition, results are presented based on standardised data for all sites and all flows scenarios, as stated in S 4.2.4. In these cases the method is predicting the PB membership of each time series relative to all other time series (at near bed and point-six locations separately) at a given site and flow stage. Results for these scenarios are presented in Table 4.11. The variability classification presented above suggests that pools at the Leigh Brook and River Arrow should be classified separately. Results of a further set of scenarios were, therefore, produced to predict the membership of time series from the pools of each site independently (Table 4.12). Overall errors (OOB errors), however, indicated that there was no need to classify pools separately as the scenarios presented in Table

Table 4.10 – Summary of the internal heterogeneity of PBs for selected variables. Spatial variation is described as the standard deviation within each PB averaged over low and intermediate flows. Discharge related variation is calculated as the change between low and intermediate flows. Water column variation is described as the average rate of change per cm above the bed. Equivalent (eqv) data also shown for riffle (see text).

		Leigh Brook				River Arrow				
		Pool	**Glide**	**Run**	**Riffle**	**Pool**	**Glide**	**Run**	**Riffle**	**(eqv)**
h (cm)	Spatial	0.21	0.10	0.07	0.04	0.21	0.19	0.12	0.02	0.02
	Discharge	0.01	0.02	0.06	0.03	0.04	0.06	0.04	0.00	0.01
U_{res} (cm s-1)	Spatial	1.97	2.75	11.02	11.05	9.09	2.60	20.96	19.30	20.97
	Discharge	2.51	2.75	16.29	19.99	8.18	3.96	19.66	-3.58	-1.85
	Water column	0.22	0.71	1.74	NA	0.44	0.28	0.92	NA	NA
TKE (cm2 s-2)	Spatial	2.19	3.87	23.23	40.21	12.93	1.93	34.78	93.36	100.8
	Discharge	3.80	7.02	40.94	28.40	18.63	3.69	40.51	-33.5	-4.86
	Water column	0.11	0.28	2.91	NA	0.41	0.10	2.19	NA	NA
f_u (Hz)	Spatial	0.18	0.20	0.17	0.11	0.17	0.14	0.14	0.13	0.15
	Discharge	-0.23	-0.23	-0.03	-0.31	-0.10	-0.30	-0.06	0.03	0.00
	Water column	0.02	0.02	0.03	NA	0.02	0.01	0.03	NA	NA
ITS_u (s)	Spatial	3.08	2.67	1.19	0.21	1.59	0.82	1.34	0.05	0.05
	Discharge	0.29	0.66	-1.13	-0.17	-0.22	-0.63	-0.25	0.01	0.03
	Water column	0.28	0.13	0.12	NA	0.10	0.10	0.09	NA	NA
τ_{uv} (N m-2)	Spatial	0.05	0.07	0.78	0.99	0.29	0.04	1.13	2.75	3.13
	Discharge	0.04	0.06	1.08	0.22	0.19	0.09	0.96	-0.61	-0.19
	Water column	0.36	1.08	9.16	NA	0.02	0.00	0.08	NA	NA
$Abs\tau_{uw}$ (N m-2)	Spatial	0.03	0.08	0.48	0.66	0.17	0.03	0.42	1.13	1.44
	Discharge	0.03	0.07	0.39	0.10	0.10	0.04	0.45	0.54	1.12
	Water column	1.06	3.45	19.54	NA	0.02	0.00	0.09	NA	NA
L_u (cm)	Spatial	6.55	22.37	53.85	36.85	55.96	15.83	368.3	142.2	154.8
	Discharge	10.79	15.39	60.84	74.22	53.32	27.52	294.7	-68.0	-36.6
	Water column	0.84	4.68	13.81	NA	4.33	0.76	33.14	NA	NA
ILS_u (cm)	Spatial	6.59	6.88	10.55	0.56	8.93	8.55	66.71	2.45	2.46
	Discharge	8.04	3.51	-4.26	1.06	7.25	3.13	4.17	0.00	0.94
	Water column	0.56	1.02	1.16	NA	1.53	1.09	2.13	NA	NA

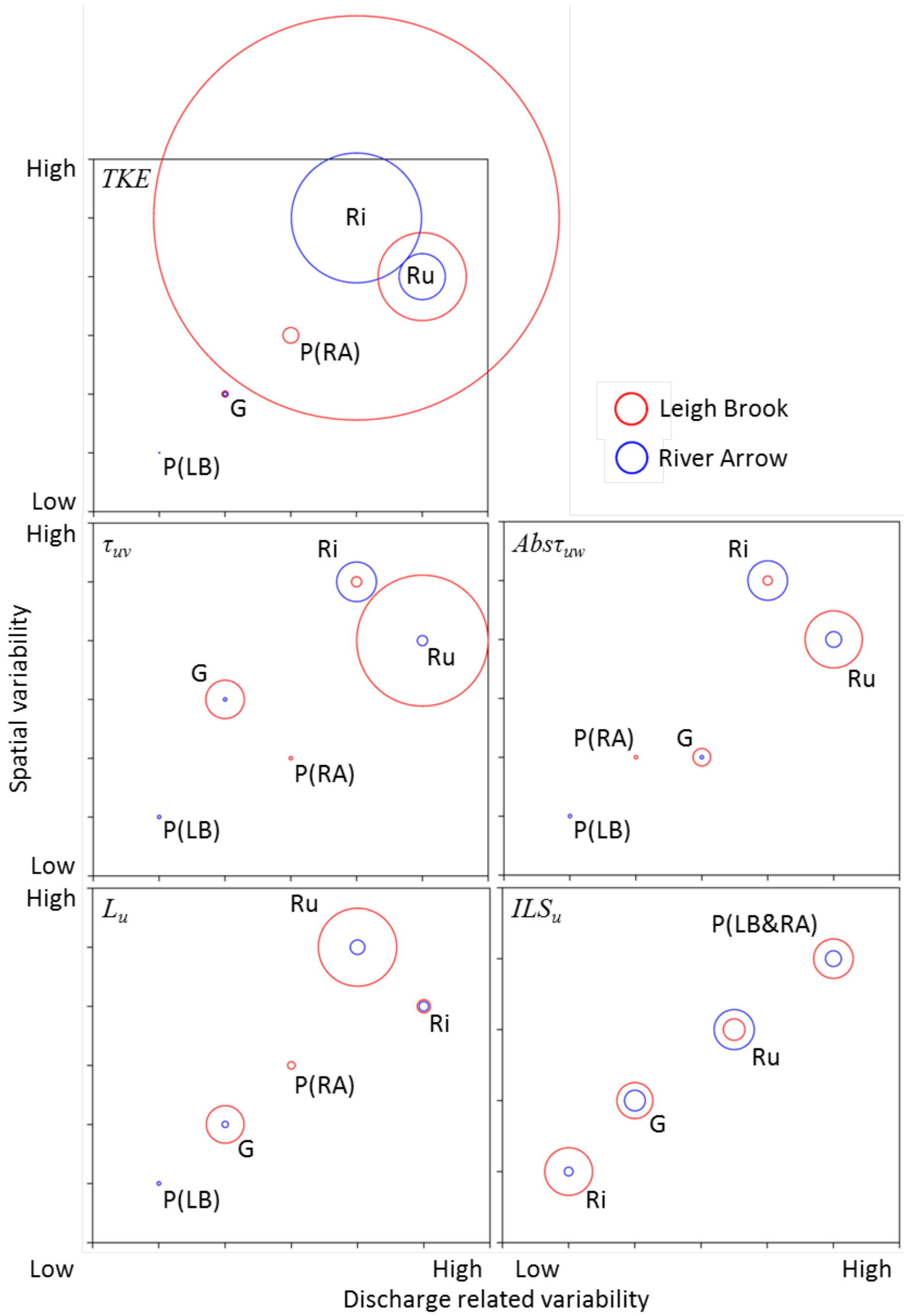


Figure 4.39 – Relative levels of internal heterogeneity found for the riffles (Ri), runs (Ru) and glides (G) at both sites and the pools at the Leigh Brook, P(LB), and River Arrow, P(RA), separately. Physical biotopes are ranked in terms of spatial (including water column) and temporal (discharge related) variability for each variable. Bubbles scaled to mean magnitude (across low and intermediate flows) for each variable.

4.12 only produce a better classification in one case ('Both NB All'), and even in this case the pools had a lower error rate for the combined classification (Table 4.11).

Table 4.11 – Error rates (% misclassified time series) of random forests scenarios for the Leigh Brook (LB), River Arrow (RA) and both sites combined. Classifications based on near bed (NB) and point-six (P6) time series at three flow stages (low, intermediate, high) and all flow stages together. OOB error describes the error rate when out-of-bag samples are classified using the tree for each iteration of the procedure.

Scenario	**OOB error**	**Glide**	**Pool**	**Riffle**	**Run**
LB NB Low	20.3	50.0	8.0	66.7	10.5
LB P6 Low	18.6	50.0	4.0	100.0	5.3
LB NB Int	23.9	23.5	16.7	100.0	16.0
LB P6 Int	20.5	22.2	12.5	100.0	11.5
LB NB High	60.0	40.0	80.0	60.0	60.0
LB P6 High	45.0	20.0	80.0	60.0	20.0
LB NB All	22.0	29.4	7.4	92.3	14.3
LB P6 All	17.1	17.1	5.6	92.3	10.0
RA NB Low	17.9	4.2	18.5	25.0	31.6
RA P6 Low	18.3	10.0	17.1	25.0	26.3
RA NB Int	23.3	4.2	30.8	17.6	39.1
RA P6 Int	17.9	12.5	12.9	23.5	26.1
RA NB High	65.0	20.0	80.0	80.0	80.0
RA P6 High	65.0	40.0	80.0	60.0	80.0
RA NB All	20.2	5.7	17.2	30.0	34.0
RA P6 All	20.3	14.3	12.7	33.3	29.8
Both NB Low	20.4	27.8	9.6	54.5	18.4
Both P6 Low	22.7	40.6	8.3	45.5	23.7
Both NB Int	24.2	14.6	24.0	31.8	29.2
Both P6 Int	18.4	19.0	14.5	36.4	14.3
Both NB High	37.5	20.0	50.0	40.0	40.0
Both P6 High	40.0	30.0	60.0	40.0	30.0
Both NB All	29.0	29.9	19.6	55.8	27.1
Both P6 All	19.2	21.4	10.4	51.2	14.4

Classifications using time series collected at point-six depth often performed better than those for equivalent scenarios using near bed samples. 'LB P6 All' and 'Both P6 All' scenarios, as examples, had almost 5 and 10 % lower OOB error rates than their near bed equivalents. For the River Arrow classifications at all flows the near bed version performed better than the point-six scenario but the difference was only marginal (0.1%). High flow scenarios provided the poorest classifications, with error rates of 37.5-65%. Time series from riffles were most often misclassified and the error rate for this PB was as much as 100% for some Leigh Brook scenarios. Confusion matrices for point-six, all flows scenarios presented in Tables 4.13 to 4.15 show that riffle time series were most often misclassified as runs. Apart from this, the most common misclassification was between pool and glide samples.

Figure 4.40, 5.87 and 5.88 show the relative importance (I/I_{max}) of variables for RF scenarios at the Leigh Brook, River Arrow and both sites respectively. ITS_w was the best predictor of PB membership overall and the top ten classificatory variables also included ITS_u, ITS_v, measures of

turbulence intensity in all three components, TKE and the standard hydraulic variables of Fr, U_{res} and h. These variables were clearly most important (*i.e.* associated with greater reduction in node impurity) for most scenarios. Other variables were ranked as among the most important for high flow scenarios (*e.g.* $Kurt_u$ for the River Arrow). h and Fr were less important at the River Arrow (Figure 4.41) and for low flow scenarios in the both sites classification (Figure 4.42). These top ten variables, however, did not include any descriptions of the orientation or scale of the turbulence. If the next two most important variables, namely (absolute) τ_{uw} and L_u, are included then these 12 variables cover all aspects of turbulence listed in Table 4.1.

Table 4.12 – Error rates (% misclassified time series) of random forests scenarios for scenarios where pools from each site are classified separately.

Scenario	**OOB error**	**Glide**	**Pool(LB)**	**Pool(RA)**	**Riffle**	**Run**
Both NB Low	20.4	22.2	12.0	14.8	45.5	21.1
Both P6 Low	20.6	18.8	20.0	17.1	45.5	18.4
Both NB Int	27.3	12.2	25.0	38.5	31.8	33.3
Both P6 Int	18.5	7.1	25.0	22.6	36.4	14.3
Both NB High	40.0	10.0	100.0	80.0	30.0	30.0
Both P6 High	45.0	20.0	80.0	100.0	30.0	40.0
Both NB All	26.3	17.2	24.1	34.5	44.2	22.9
Both P6 All	23.8	16.7	27.8	23.9	53.5	14.4

Table 4.13 – Random forests confusion matrix showing the number of time series correctly and incorrectly classified for the Leigh Brook, point-six, all flows (LB P6 All) scenario.

		Predicted				Error
		Glide	Pool	Riffle	Run	rate (%)
Observed	Glide	29	4	0	2	17.1
	Pool	3	51	0	0	5.6
	Riffle	1	0	1	11	92.3
	Run	1	0	4	45	10.0

Table 4.14 – Random forests confusion matrix showing the number of time series correctly and incorrectly classified for the River Arrow, point-six, all flows (RA P6 All) scenario.

		Predicted				Error
		Glide	Pool	Riffle	Run	rate (%)
Observed	Glide	42	7	0	0	14.3
	Pool	7	62	0	2	12.7
	Riffle	0	2	20	8	33.3
	Run	1	9	4	33	29.8

Table 4.15 – Random forests confusion matrix showing the number of time series correctly and incorrectly classified for the both sites, point-six, all flows (Both P6 All) scenario.

		Predicted				Error
		Glide	Pool	Riffle	Run	rate (%)
Observed	Glide	66	15	0	3	21.4
	Pool	10	112	0	3	10.4
	Riffle	3	1	21	18	51.2
	Run	3	7	4	83	14.4

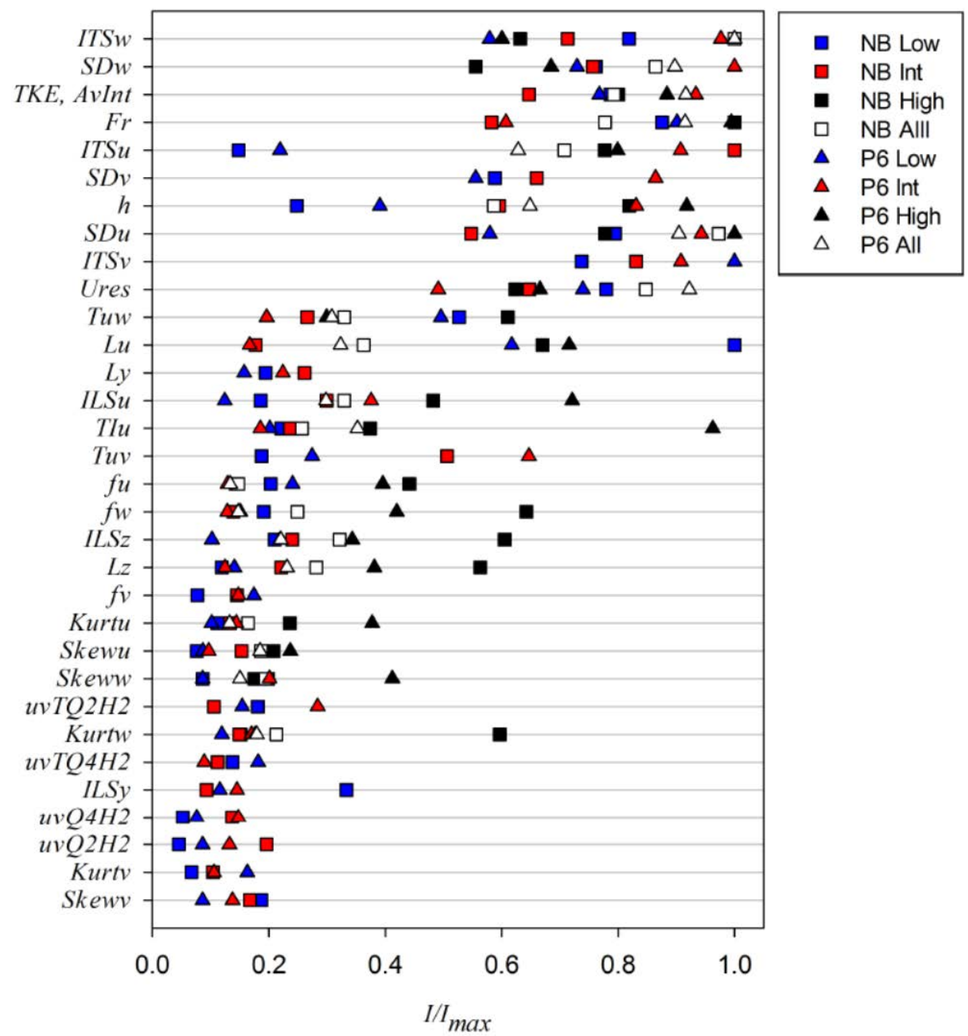


Figure 4.40 – Relative importance (I/I_{max}) of hydrodynamic variables in classifying physical biotopes of the Leigh Brook. Variables on the y axis sorted by average I for the whole dataset.

Overall, the classifications with the lowest error rates were those for the 'LB P6 All', 'RA NB Low' and 'RA P6 Int' scenarios. The most useful and transferable classification, however, would encapsulate both sites at all flows. The 'Both P6 All' scenario meets this condition and, with an error rate of less than 20%, provides an acceptable level of discrimination between PBs. Yet, as many aquatic biota live in close association with the bed (*e.g.* juvenile Atlantic salmon; Armstrong *et al*., 2003), an ecologically relevant classification would be based on near bed conditions. As the 'LB NB All' and 'RA NB All' scenarios provided classifications with error rates that were among the lowest reported, it was decided to look at these cases in closer detail with the use of classification trees to visualise the results of the RF analyses. A classification tree was also produced for the best 'Both P6 All' scenario and it is suggested that this classification would be relevant to pelagic biota.

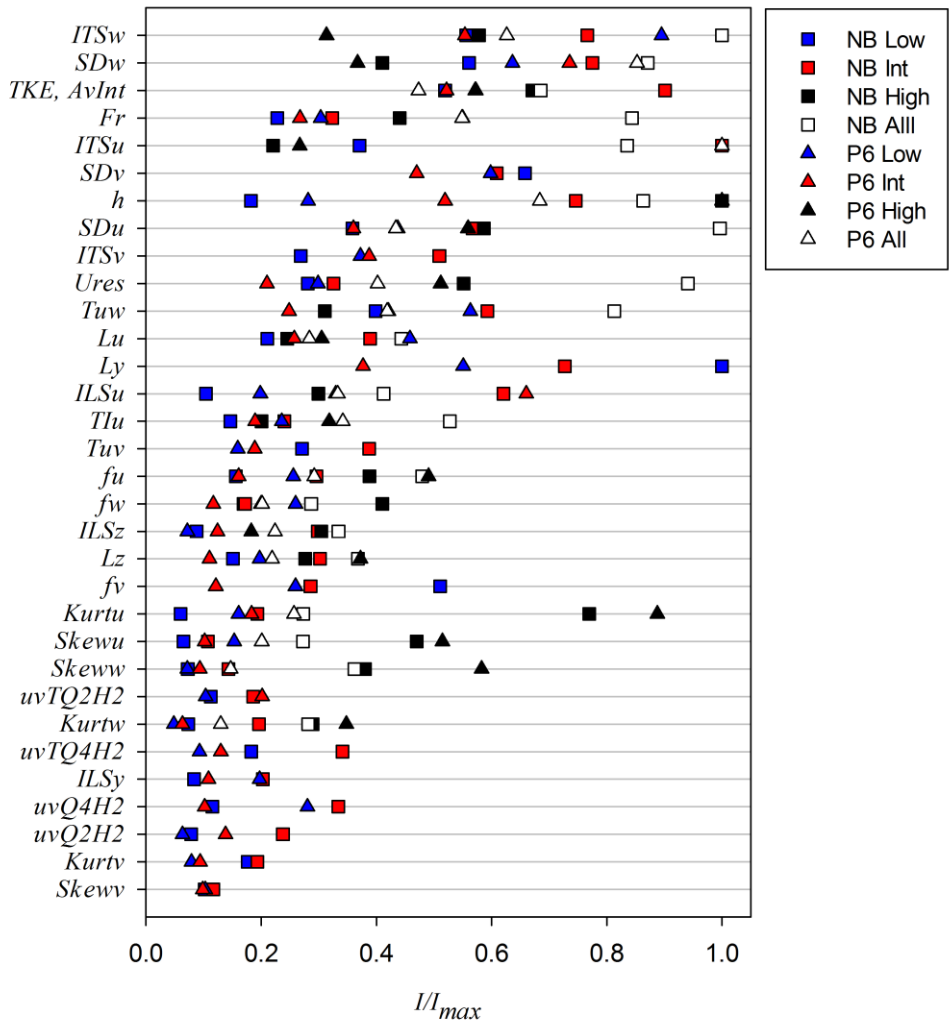


Figure 4.41 – Relative importance (I/I_{max}) of hydrodynamic variables in classifying physical biotopes of the River Arrow. Variables on the y axis sorted by average I for the whole dataset.

RF deals well with multicollinearity and complex interactions between predictor variables but for classification trees highly correlated variables should be deleted (Legendre & Legendre, 1998). Figure 4.43 shows the relationship between variables selected in the RF process where r>0.7. This illustrates a very close linear relationship between Fr and U_{res} and strong correlations (r>0.9) between descriptions of turbulence intensity ($SD_{u,\ v,\ w}$ and TKE). Although Fr was ranked higher overall in the RF analyses it was deleted in favour of U_{res} as the ecological relevance of Fr is uncertain (Allan, 1995). TKE was retained in preference to separate measures of turbulence intensity for each component as these were intercorrelated. The complete list of variables entered as candidate predictors in the classification tree analyses, therefore, was ITS_w, TKE ($AvInt$), ITS_u, h, ITS_v, $Ures$, τ_{uw} and L_u.

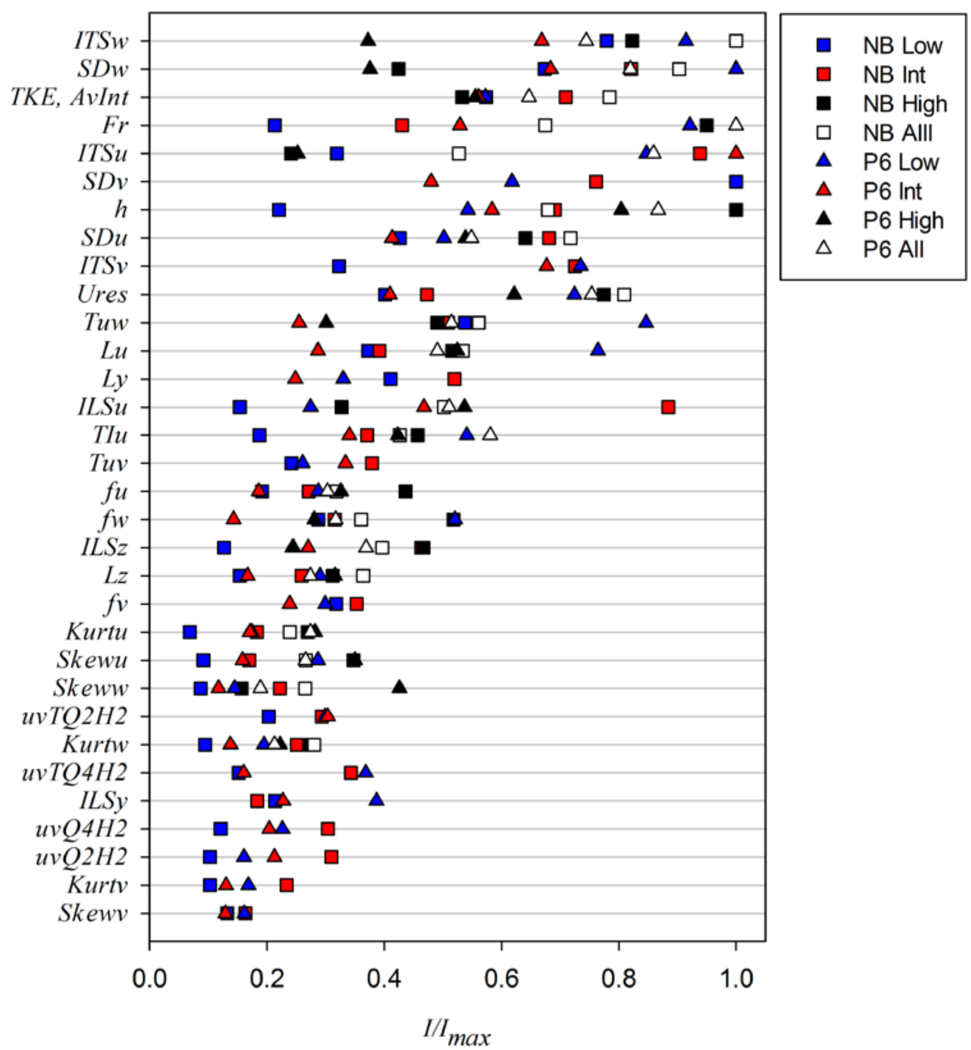


Figure 4.42 – Relative importance (I/I_{max}) of hydrodynamic variables in classifying physical biotopes of both study sites. Variables on the y axis sorted by average I for the whole dataset.

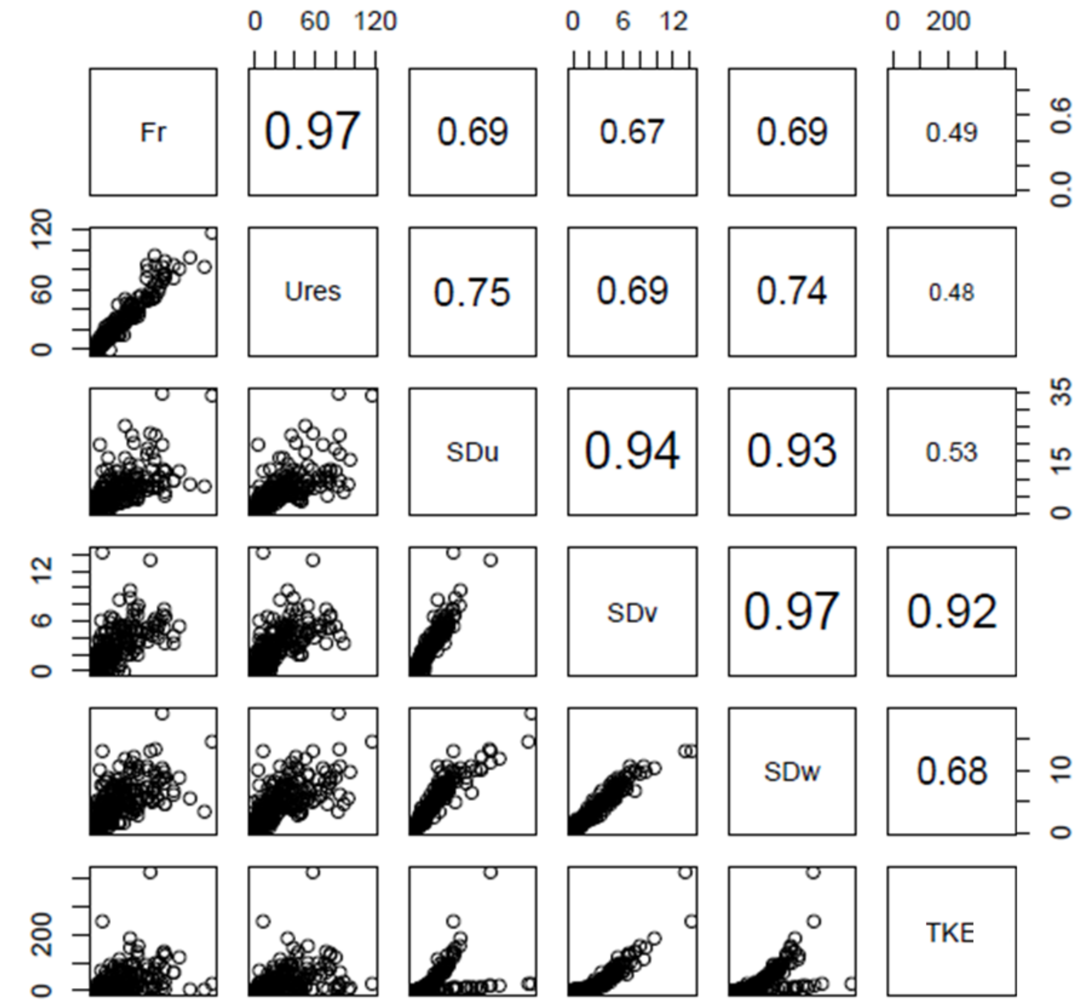


Figure 4.43 – Relationships between variables where r>0.7. Upper panels show absolute correlations with text size scaled to Pearson's r.

The cross-validation procedure indicated that the optimum classification tree for the 'LB NB All' scenario had four terminal nodes (Figure B88). For the 'RA NB All' and 'Both P6 All' scenarios the optimum trees had five (Figure B89) and seven (Figure B90) terminal nodes respectively. The 'LB NB All' tree's first split was predicated by U_{res} and separated the run from other PBs (Figure 4.44). The pool was classified at the second split on the basis of it exhibiting relatively high ITS_w. Finally, the glide was split from the riffle due to the higher turbulence intensities (TKE or $AvInt$) found in the latter. The confusion matrix in Table 4.16 shows that this tree was poor at classifying riffle samples, with over half of time series incorrectly assigned run membership. Only relatively few samples, however, were available for the riffle (n=13). Table 4.16 also shows that the first split in the tree correctly separated all pool and glide samples from other PBs. In the run, three samples were misclassified as glide and three as riffle. The spatial distributions of misclassifications shown in Figure 4.45 indicate that samples near the run-head were misclassified as riffle, whilst those of the run-tail were misclassified as glide. Errors in the glide were only found at the channel margins except at high flow. No such clear spatial patterns were evident in the pool and riffle errors for the Leigh Brook tree, particularly given the limited number of samples available for the riffle. This tree had an overall error rate of 18%.

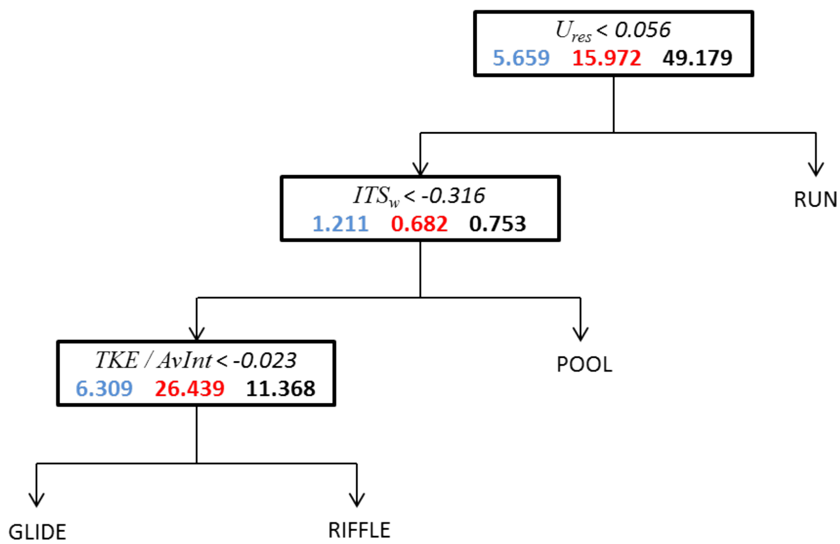


Figure 4.44 – Classification tree for the Leigh Brook, near bed, all flows (LB NB All) scenario. Standardised (z scores) thresholds at each node of the tree shown in italics. Equivalent raw scores at low (blue), intermediate (red) and high (black) flows also shown. Where a statement is true move left down the tree.

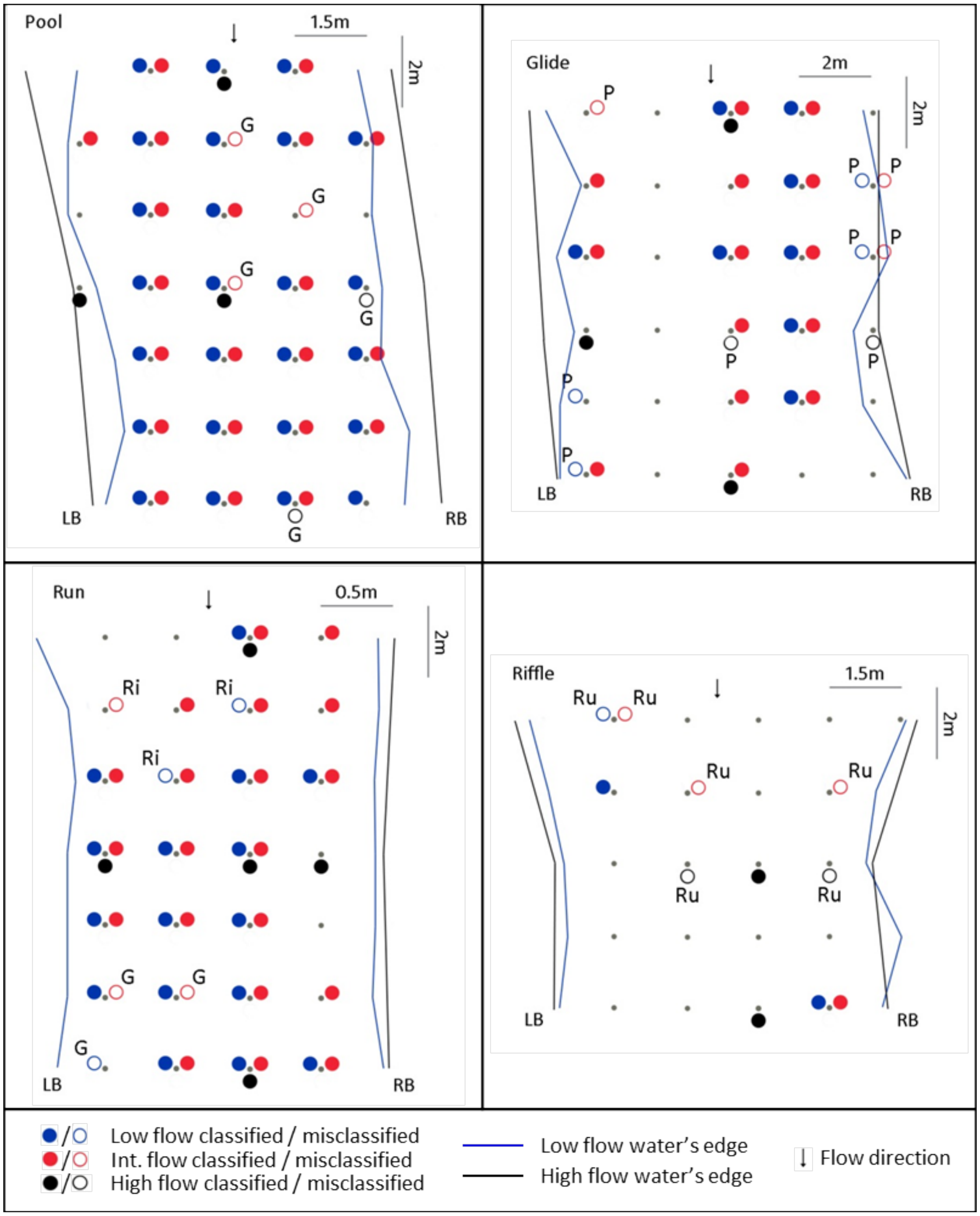


Figure 4.45 – Spatial distribution of errors in the classification of PBs at the Leigh Brook for the near bed, all flows (LB NB All) scenario. Time series misclassified as pool (P), glide (G), run (Ru) or riffle (Ri).

Table 4.16 – Classification tree confusion matrix showing the number of time series correctly and incorrectly classified for the Leigh Brook, near bed, all flows (LB NB All) scenario. Total error rate=18%.

		Expected				Error
		Glide	Pool	Riffle	Run	rate (%)
Observed	Glide	25	9	0	0	26.5
	Pool	5	49	0	0	9.3
	Riffle	0	0	6	7	53.8
	Run	3	0	3	43	12.2

For the 'RA NB All' scenario, ITS_w provided the first split, separating the pool and glide from the run and riffle on the basis of lower ITS_w in the latter pair of PBs (Figure 4.46). Riffle samples were further discriminated from run time series by virtue of the greater depths in the run. Surprisingly raw scores for this h threshold did not increase with flow and actually decreased at the highest flow. The error rate for run and riffle samples was relatively high (Table 4.17) and they were misclassified as a range of other PBs, with no spatial or temporal (discharge related) patterns evident in the errors (Figure 4.47). To the left of the first split was a node with a τ_{uw} threshold, to the right of which were placed most of the pool samples at all flows. The final split was based on U_{res} and separated the relatively slow glide samples from the remaining pool time series. The tree successfully classified most of the glide samples at low and intermediate flows, with only two samples at the head and one sample at the tail misclassified as pool (Figure 4.47). At high flow, however, classification of the glide was poor, with four out of five samples misclassified as run or pool. Pool samples were most often misclassified as glide and, at low and intermediate flows, these errors were associated with the pool margins (Figure 4.47). The tree was generally poor at predicting PB membership at high flow, with 12 out of 20 samples misclassified. Overall, with an error rate of 28.7%, this tree was less successful than the equivalent tree for the Leigh Brook.

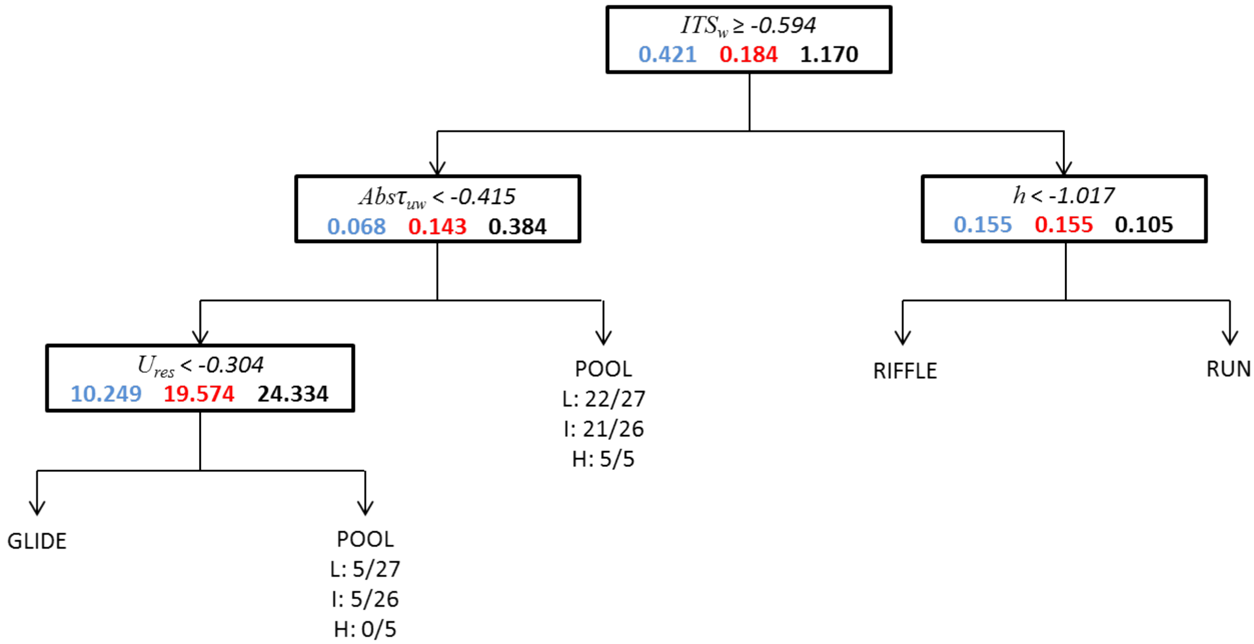


Figure 4.46 – Classification tree for the River Arrow, near bed, all flows (RA NB All) scenario. Standardised (z scores) thresholds at each node of the tree shown in italics. Equivalent raw scores at low (blue), intermediate (red) and high (black) flows also shown. Where a statement is true move left down the tree. Number of samples classified (out of those available) shown where PB classification split across terminal nodes.

Table 4.17 – Classification tree confusion matrix showing the number of time series correctly and incorrectly classified for the River Arrow, near bed, all flows (RA NB All) scenario. Total error rate=28.7%.

		Expected				Error
		Glide	Pool	Riffle	Run	rate (%)
Observed	Glide	46	4	0	3	13.2
	Pool	12	45	1	0	22.4
	Riffle	0	4	18	8	40.0
	Run	3	14	5	25	46.8

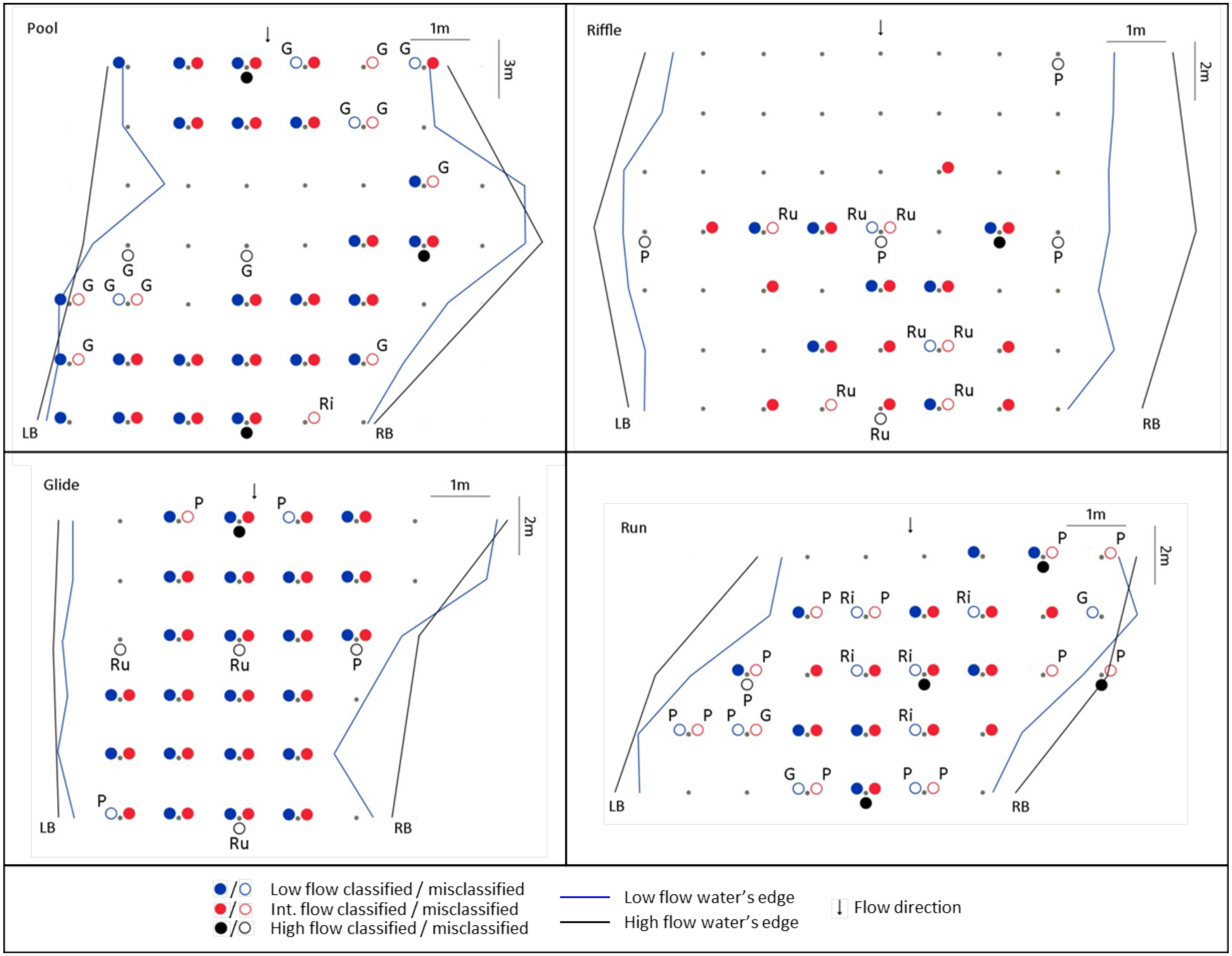


Figure 4.47 – Spatial distribution of errors in the classification of PBs at the River Arrow for the near bed, all flows (RA NB All) scenario. Time series misclassified as pool (P), glide (G), run (Ru) or riffle (Ri).

ITS_u played a key role in the classification of PBs under the 'Both P6 All' scenario, providing the first split to separate pools and glides from runs and riffles (Figure 4.48). To the right of this was a split based on h which separated-out deeper run samples. At the Leigh Brook, this run class contained most samples at all flows. The remaining time series from the run were discriminated from riffle samples at lower levels of the tree. This was achieved by first splitting off riffle samples with relative short L_u and then classifying the remaining riffle time series by virtue of their greater τ_{uw}. Glides and pools were classified to the left of the first split. The minority of pool samples were classified at the second level of the tree with an ITS_w threshold. Finally, most pool time series were separated from glide samples because they exhibited higher τ_{uw}. This tree had an overall error rate of 27.2%. Table 4.18, however, shows that it was disproportionately good at classifying pool and run samples but relatively poor at glide and riffle time series. Glide samples were misclassified as either pool or run, pool samples as glide or run, and runs and riffles as any of the other PBs (Table 4.18). The tree was especially poor at classifying glide samples from the Leigh Brook (Figure 4.49). Apart from riffles, for which little data were available, most misclassifications at both sites were associated with the margins of PBs (Figure 4.49).

Table 4.18 – Classification tree confusion matrix showing the number of time series correctly and incorrectly classified for the both sites, point-six, all flows (Both P6 All) scenario. Total error rate=27.2%.

		Expected				Error
		Glide	Pool	Riffle	Run	rate (%)
Observed	Glide	41	31	2	10	51.2
	Pool	8	110	1	6	12.0
	Riffle	1	6	27	9	37.2
	Run	4	11	6	76	21.6

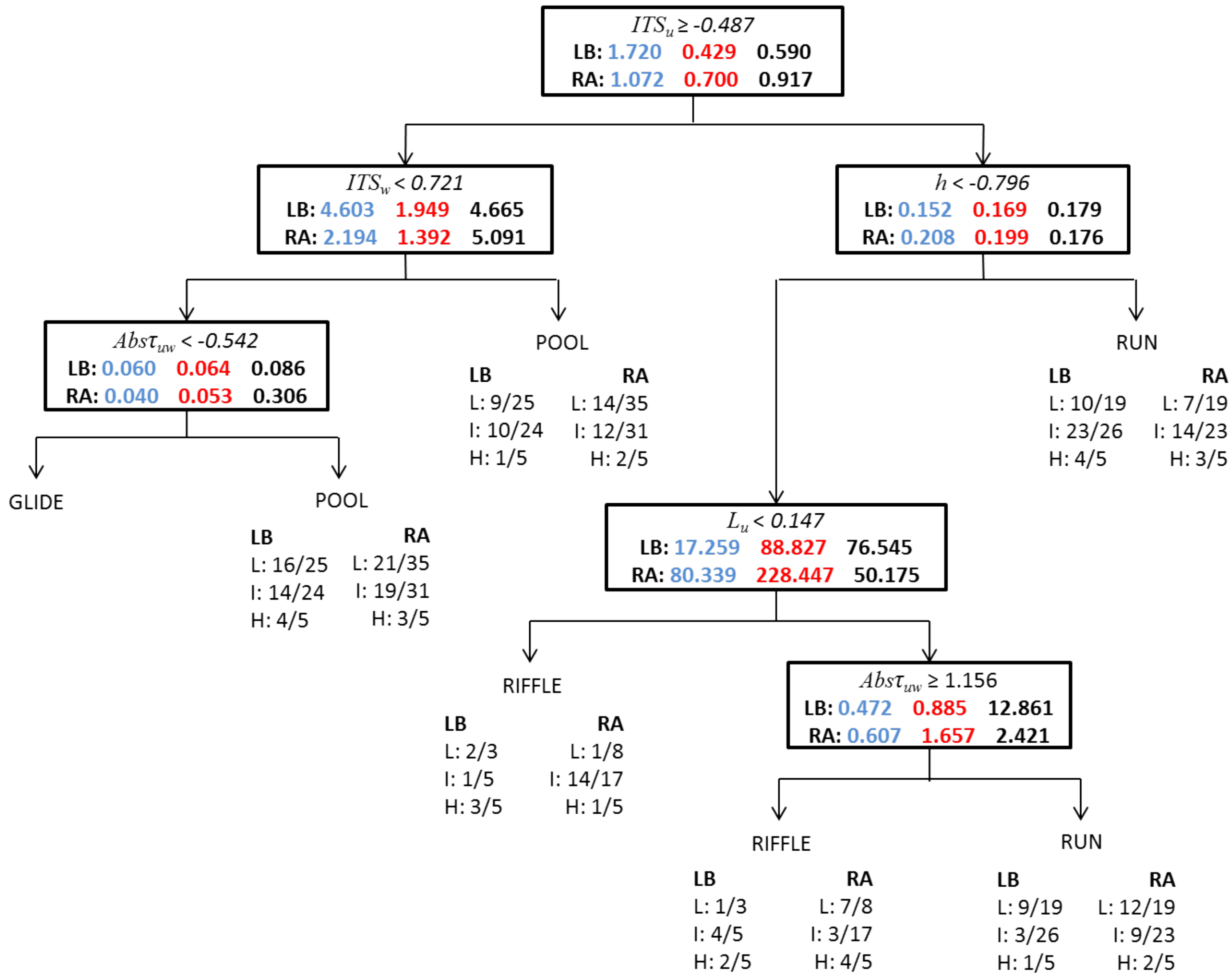


Figure 4.48 – Classification tree for the both sites, point-six, all flows (Both P6 All) scenario. Standardised (z scores) thresholds at each node of the tree shown in italics. Equivalent raw scores at low (blue), intermediate (red) and high (black) flows also shown. Where a statement is true move left down the tree. Number of samples classified (out of those available) shown where PB classification split across terminal nodes.

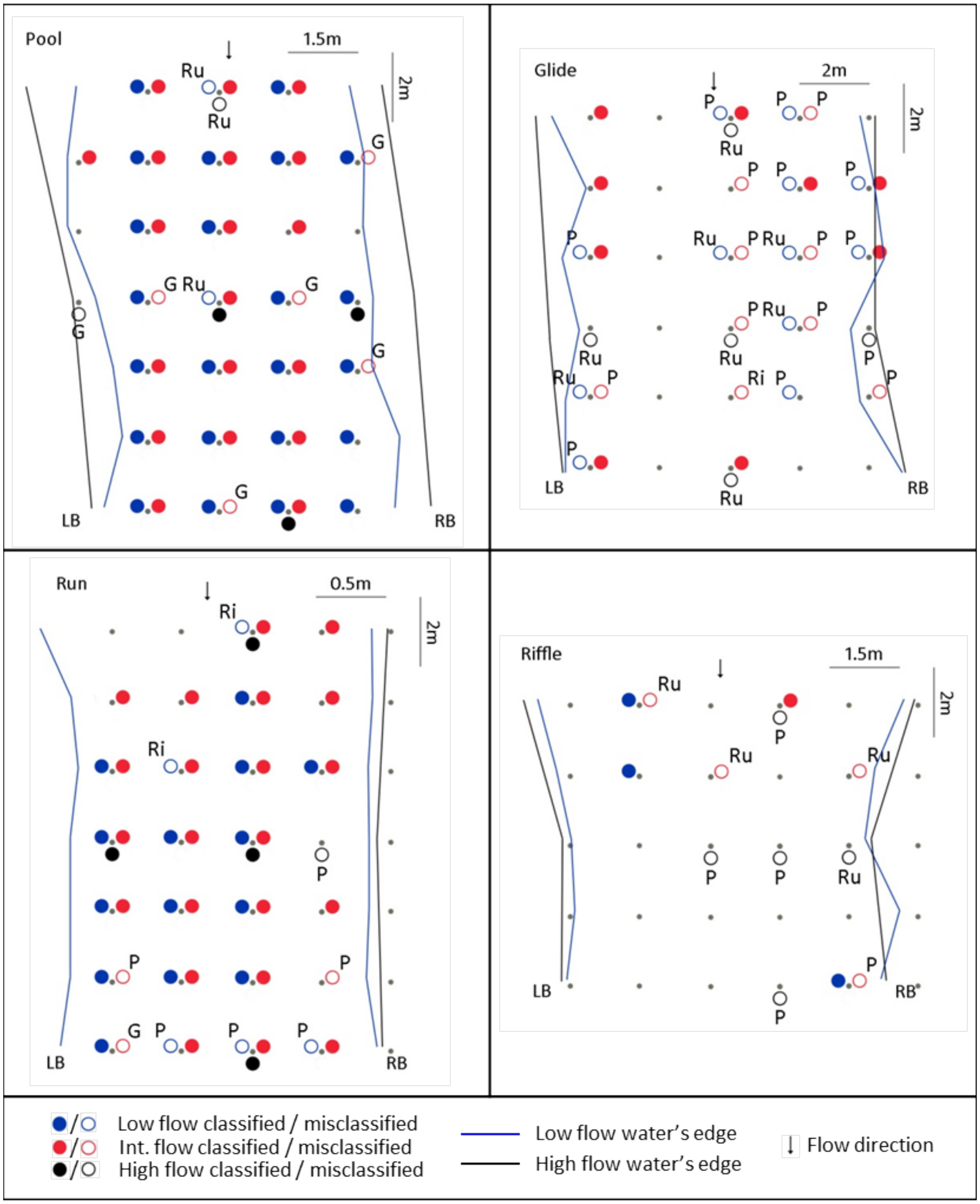


Figure 4.49 (a) – Spatial distribution of errors in the classification of PBs at the Leigh Brook for the point-six, all flows (Both P6 All) scenario. Time series misclassified as pool (P), glide (G), run (Ru) or riffle (Ri).

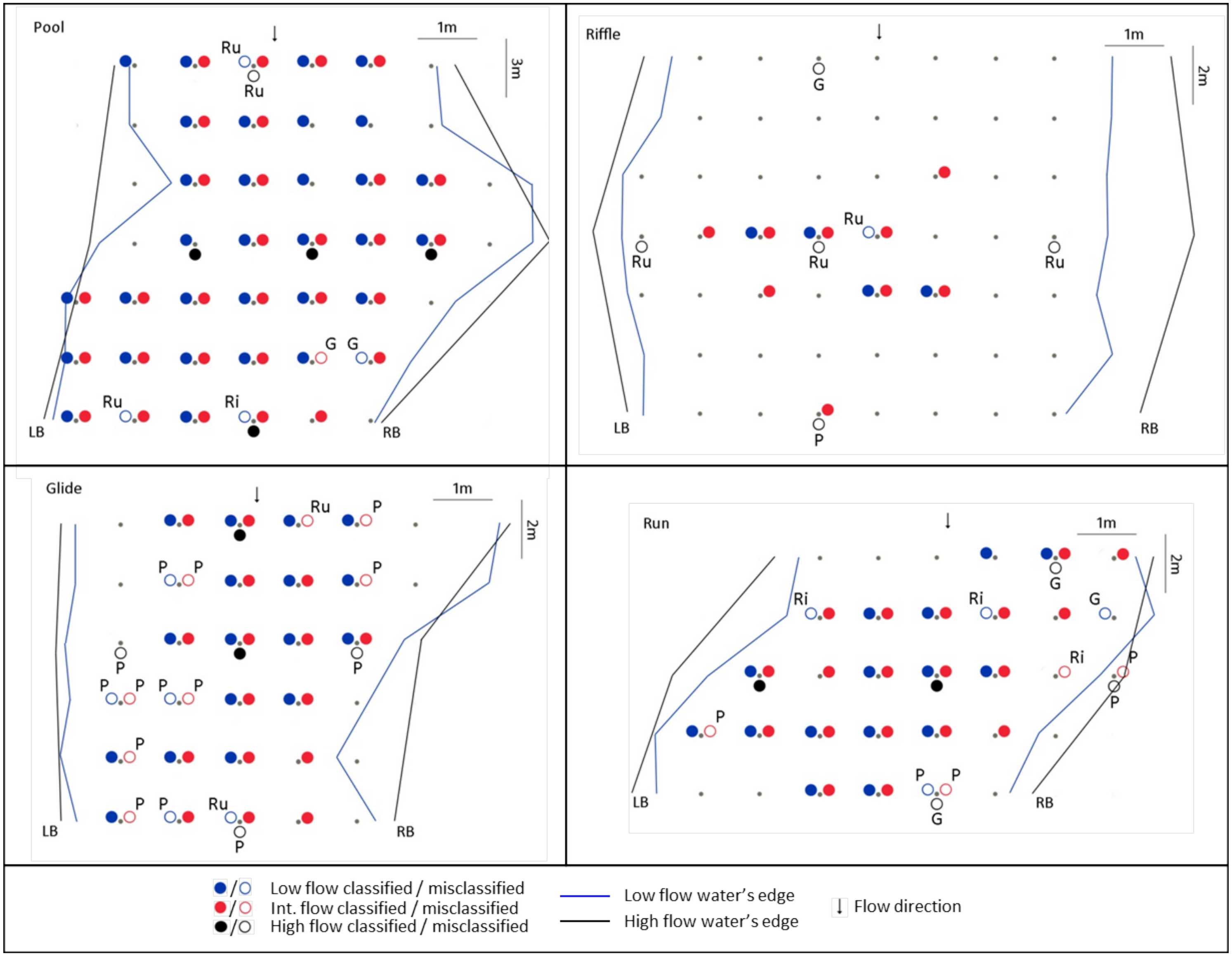


Figure 4.49 (b) – Spatial distribution of errors in the classification of PBs at the River Arrow for the point-six, all flows (Both P6 All) scenario. Time series misclassified as pool (P), glide (G), run (Ru) or riffle (Ri).

4.4 Discussion

The within-PB variability classification presented in Figure 4.39 suggests that **the Harvey and Clifford (2009) model (Figure 4.18) is too simplistic**. In particular, **pools are poorly characterised by such a classification**, with the four pools (including those of Harvey and Clifford, 2009) exhibiting different levels of variability. Furthermore, the order of PBs along axes describing spatial and temporal variability depends on the hydrodynamic variable considered. The general order of PBs on axes shown for most variables in Figure 4.39, for example, is reversed for ILS_u. **Instead, more effective and practical classifications based on the magnitude of hydrodynamic variables are proposed** (Figures 4.44, 4.46 and 4.48). These classification trees, along with their RF equivalents, suggest that the **PB membership of samples can be classified with an overall success rate as high as 70.3-82.9%** using a combination of h, U_{res}, $TKE/AvInt$, ITS_u, ITS_w, τ_{uw} and L_u. The merits of these classifications include their flexibility as, being based on standardised data, they integrate variability and **could be applied at a range of flow stages and/or sites**. No single classification, however, was consistently able to correctly assign membership to every PB at a rate of >40% (Tables 4.16, 4.17 and 4.18). The spatial distributions of errors for most PB-flow combinations (Figures 4.45, 4.47 and 4.49) suggest that this may be due to the inclusion of samples from PB transitions and those close to channel margins. Before considering the detail of these classifications further, it must be verified that the hydrodynamic data used in the calibrations are reliable and realistic (S 4.4.1). The discussion subsequently compares the results with those reported by a limited number of studies investigating the hydrodynamics of PBs. It then attempts to establish links between hydromorphology at different scales and the results of the classification analyses (S 4.4.3). Finally, the potential limitations of the study are identified and further research requirements suggested (S 4.4.4).

4.4.1 Data reliability

An initial indication of the reliability of the hydrodynamic data reported here is given by a comparison with values reported in the literature (Table 4.19). All mean values for variables describing turbulence phenomena that were included in the classification were within an order of magnitude of those reported by previous studies. Furthermore, mean values often fell within ranges reported previously. Distributions of hydrodynamic variables reported herein, however, often spanned a wider range, with lower minima and/or higher maxima. This could indicate that the data are unreliable. Alternatively, it is more likely to be the result of reporting from a diversity of flow (discharge) conditions, river types and microhabitats within those types. Roy *et al*. (2010), Lacey *et al*. (2007), Buffin-Bélanger and Roy (1998) and Lacey and Roy (2008), for example, reported turbulence statistics from a relatively large (Q=1.2-2.5 $m^3 s^{-1}$) and steep (slope=0.2-3%) river, with the latter two investigating flow around pebble clusters. Pebble clusters are associated with distinct zones of turbulent flow conditions (Appendix C) and this may explain the higher TKE and τ_{uw} and lower ITSs reported by these studies. Tritico and Hotchkiss (2005) found high TKE and τ_{uw} maxima in comparison to this study but their data was from a relatively large river (Q=5.4-12.7 $m^3 s^{-1}$) and included many time series in the turbulent wake of emergent boulders. The TKE values reported by Smith & Brannon (2007) are closest to those reported herein and these are from pools and riffles of similar sized streams as investigated here. Clifford and French (1993b) and MacVicar *et al*. (2007) reported narrower ranges of TKE than found here but these ranges were produced from just two and 28 time series respectively.

Table 4.19 – Mean values (range in italics) for they key hydrodynamic variables involved in the classification reported from rivers. Data from various flow stages and heights above the bed.

TKE (cm^2 s^{-2})	ITS_u (s)	ITS_w (s)	τ_w (N m^{-2})	L_u (cm)	Author(s)
19.9 *0.02-423.6*	2.0 *0.05-14.9*	1.6 *0.03-15.2*	0.4 *0-33.9*	73.3 *3.1-2300*	This thesis
0-800	*0.1->0.3*		*0-15*		Lacey & Roy (2008)
106.5 *4-306*	0.5 *0.14-1.6*	0.3 *0.1-0.9*			Roy *et al*. (2010)
50->800			*0->300*		Tritico & Hotchkiss (2005)
56-90					Clifford & French (1993b)
	<0.6-1.9				Buffin-Bélanger & Roy (1998)
70->200					Lacey & Roy (2007)
	0.8				Lacey *et al*. (2007)
5-150					MacVicar *et al*. (2007)
36.1 *0.6-173*					Smith & Brannon (2007)
<50->650					Thompson (2007)
6-1000					Wilcox & Wohl (2007)

Wilcox and Wohl (2007) observed values of TKE up to 1000 cm^2 s^{-2}, more than double the maximum reported here. Their data, however, was collected in a very steep step-pool reach, explaining the elevated turbulence levels. Harvey and Clifford (2009) is the only study listed which reported L_u calculated from autoregressive models. They found a similar minimum and average but a much lower maximum L_u in a river of similar size to those studied here. The maximum L_u reported here, however, was from a run at the Leigh Brook, a PB type not investigated by Harvey & Clifford (2009). **This discussion provides an empirical indication that the data used in the calibrations are reliable**. A more robust assessment of data reliability, however, should include a comparison with turbulence theory.

Turbulence theory developed from laboratory studies states that the ratios SD_w:SD_u and SD_v:SD_u should be 0.71-0.75 and 0.5-0.55 respectively (Appendix C). Mean ratios found herein were 0.88 for SD_w:SD_u and 0.68 for SD_v:SD_u. A comparison of these ratios may suggest elevated noise in the v and w components. Alternatively, the higher mean ratios could reflect the increased complexity and dimensionality of natural river flows in comparison to those over smooth boundaries (Nezu & Nakagawa, 1993) or beds with a relatively simple structure constructed in the laboratory (*e.g.* Dancey *et al*., 2000; Song & Chiew, 2001). Ratios reported from natural rivers by Lacey *et al*. (2007), Smith and Brannon (2007) and Roy *et al*. (2010), for instance, vary between 0.73 and 0.94 for SD_w:SD_u and 0.51 and 0.8 for SD_v:SD_u, ranges which encompass those reported here.

The variability of turbulence intensity through the water column also deviated from that expected based on turbulence theory in some cases. Results presented in S 4.3.1 and S 4.3.2 illustrate how TKE could either increase or decrease between near bed and point-six locations yet turbulence theory (Appendix C) suggests that TKE should decrease with y. Once again, however, this equation was based on data from studies of flow in artificial open channels and ducts (Nezu & Nakagawa, 1993). The roughness characteristics and depth-limited nature of gravel bed rivers, together with their relatively high Re in comparison to most laboratory flows, could explain this deviation (Buffin-Bélanger & Roy, 1998; Lacey & Roy, 2007). An alternative explanation is that noise associated with ADV measurements was elevated at point-six depth in locations where TKE was found to increase with y, though this is unlikely given that noise in ADV signals is expected to increase with proximity to a solid boundary due to the effects of greater velocity shear in the sampling volume and side-lobe interference (McLelland & Nicholas, 2000). ADV noise was still apparent in the data even after careful filtering and processing (S 4.2.3). This can be seen in the levelling-off of velocity spectra in the inertial subrange in the streamwise and other components where well established turbulence theory states that Kolmogorov's -5/3 power law should be evident (Appendix C). Because turbulence is generated in the production range, and this range is unaffected by the Doppler noise that causes flattening of velocity spectra, this noise is expected to have a negligible effect on turbulence statistics calculated from carefully processed time series (Appendix C).

4.4.2 Comparing results with the literature on PB hydrodynamics

The above discussion suggests that the hydrodynamic data upon which the classifications were based can be treated as reliable. Section 5.3.3 presented evidence that classification using the magnitude of hydrodynamic variables was more practical and quantitative than a scheme based on within-PB variability. Classifications using the RF procedure coupled with a correlation analysis indicated that a set of key hydrodynamic variables, which included descriptions of the intensity (TKE, $AvInt$), periodicity (ITS_u, ITS_w), orientation (τ_{uw}) and scale (L_u) of turbulence, as well as the standard hydraulic variables of U_{res} and h, provided the best calibration. Decision trees produced using these variables as predictors of the PB membership of each time series provided classifications based on near bed and point-six measurements that achieved acceptable overall goodness-of-fit (>70% correct). RF scenarios consistently showed that point-six measurements were slightly more suitable for classification of PBs than near bed samples. The analysis did not select any measures of average eddy frequency, predictability (kurtosis), event structure, τ_{uv} or skewness, suggesting that PBs do not differ substantially along axes based on these variables. That the top ten variables in the RF analyses did include Fr lends credence to the approaches to mesohabitat classification taken by Wadeson and Rowntree (1998), Padmore (1997a, b, 1998), Kemp *et al*. (1999, 2000) and Jowett (1993), although it has already been shown that the Fr classes of the latter do not fit the data presented here (Figures 4.14 and 4.28). Furthermore, **it has been shown that 97% of the variability in Fr can be explained by**

U_{res} **(Figure 4.43), casting further doubt on the usefulness of** Fr **for calibrating an ecologically relevant classification of habitats**. In any case, the aim of this chapter is to classify PBs using a range of variables describing turbulent flow. A check on the generality or transferability of these classifications involves comparing the magnitude of hydrodynamic variables found with those reported from PBs by previous studies (Table 4.20). Due to the limited number of studies explicitly linking hydrodynamics with the PB concept, and the even more limited selection of hydrodynamic variables reported, Table 4.20 lists SD_u, τ_{uv} and ILS_u in addition to the key hydrodynamic variables for which data is available from the literature.

The studies listed in Table 4.20 were based on time series collected from gravel and mixed bed rivers of a range of sizes and slopes and taken at various heights above the bed, either a relative (y/h) or an absolute height. Roy *et al*. (2010), for instance, collected data at 15 cm from the bed, whereas Harvey and Clifford (2009) took measurements at y/h=0.2 and 0.8. This confounds any attempt to make direct comparisons. Nevertheless, as the classifications are based on standardised data, it is the *relative* differences between PBs and across flow stages that are of utmost importance. The first point to note about the comparison presented in Table 4.20 is that no previous studies have investigated turbulence in runs and that most have only considered pools and riffles. Another noteworthy point to be reiterated is that the magnitude of variables listed for this study varied depending on site. PBs at the River Arrow had higher SD_u, TKE and τ_{uv} and lower ITSs than those at the Leigh Brook, suggesting that the gross morphological characteristics of reaches have a large influence on turbulent flow, as reported by Lamarre and Roy (2005) and Legleiter *et al*. (2007). Levels of turbulence intensity within PBs did not always match those expected based on previous work**. In most cases the relative differences between PBs are preserved but, as noted previously, the hydrodynamic characteristics of pools appear to be particularly variable between sites**. Clifford and French (1993b) and Harvey and Clifford (2009), for example, found that turbulence intensity (TKE and SD_u respectively) in pools was much higher than reported herein and exceeded turbulence intensity in riffles. **Turbulence intensities previously reported in riffles and glides, on the other hand, were remarkably similar to those found at the Leigh Brook and River Arrow**.

Table 4.20 - Mean values (or range in italics) for key hydrodynamic variables in PBs reported by previous studies. Data from the Leigh Brook (LB) and River Arrow (RA) at low and intermediate flows shown for comparison. Data reported from various heights above the bed.

		LB Low	**LB Int**	**RA Low**	**RA Int**	**Previous studies***				
						a	**b**	**c**	**d (low†)**	**d (int†)**
SD_u	Pool	0.5	1.8	2.4	4.6				*2-15*	*2-11*
	Riffle	5.2	7.3	10.1	8.3				*2-3*	*4-12*
	Glide	0.9	2.5	1.2	2.2				*0.5-3*	*1-3*
	Run	3.0	6.7	4.4	7.2					
TKE	Pool	0.3	4.7	6.7	26.7	67.1	12.1	90		
	Riffle	38.0	66.4	118.3	84.8	145.9	60.2	85		
	Glide	1.2	8.1	1.8	5.6					
	Run	12.5	52.9	25.1	62.5					
τ_{uv}	Pool	0.01	0.01	0.1	0.2	9.7				
	Riffle	0.6	0.8	1.9	1.3	30.7				
	Glide	0.01	0.1	0.01	0.1					
	Run	0.1	1.1	0.5	1.4					
ITS_u	Pool	4.7	4.1	2.3	2.2	0.69				
	Riffle	0.4	0.2	0.1	0.1	0.33				
	Glide	2.6	0.9	2.3	1.7					
	Run	1.6	0.3	1.0	0.7					
ITS_w	Pool	4.4	2.8	2.2	1.5	0.35				
	Riffle	0.2	0.1	0.1	0.1	0.25				
	Glide	1.2	0.5	1.3	0.9					
	Run	0.5	0.1	0.4	0.4					
L_u	Pool	2.2	20.4	33.1	126.1				*5-70*	*1-40*
	Riffle	18.1	92.3	216.9	148.9				*75-105*	*50-80*
	Glide	7.2	59.7	12.1	45.8				*1-37*	*1-30*
	Run	31.6	109.5	88.8	313.7					

* (a) Roy *et al*. (2010); (b) Smith & Brannon (2007); (c) Clifford & French (1993b); (d) Harvey & Clifford (2009). † Low flow (Q_{91}-Q_{96}); Intermediate flow (Q_{39}-Q_{57}).

Only one previous study, Roy *et al*. (2010), reported τ_{uv} and ITSs from PBs. Mean τ_{uv} was up to three orders of magnitude greater than reported herein, suggesting either a problem with the data or, alternatively, that unique characteristics of the study site (*e.g.* river size, slope, substrate size, microbedforms) have a large influence on Reynolds shear stress. In any case, τ_{uv} was not included in the classifications developed in S 4.3.3.1. Reynolds stress on the horizontal plane (τ_{uw}), which was included in the classifications, has never been reported by any of the previous studies. ITS_u and ITS_w levels reported by Roy *et al*. (2010) were very similar to those found in riffles in this study. ITSs in the pools, however, were much higher at the Leigh Brook and River Arrow than in the relatively large gravel bed river used by the aforementioned study, again suggesting high between-pool variability. Finally, ranges of L_u reported by Harvey and Clifford (2009) were similar to those found herein but their PBs exhibited different temporal (discharge related) dynamics, with the average eddy tending to decrease in length as flow stage rose rather than to increase between low and intermediate flows, as found at the Leigh Brook and River Arrow sites.

The idea that pools are highly variable between sites is supported by the findings of Alcaraz-Hernández *et al*. (2011), who classified PBs in four streams using morphological measures (*e.g.* length, width, substrate size). They found that morphology varied from pool to pool to a greater degree than it did for a range of other mesohabitat types. Given the links between morphology and hydrodynamics established by Wilkes *et al*. (2013) (Appendix C), it is reasonable to suspect that such morphological variability would be manifested in high levels of between-pool hydrodynamic heterogeneity. This is unsurprising given the range of pool types included in classifications such as those of Bisson *et al*. (1982), Frissell *et al*. (1986) and Poole *et al*. (1997) (*e.g.* Figure 2.4). The differences between pool types are given by the dominant process active in their formation (*e.g.* lateral scour pool), and this gives rise to high morphological and, therefore, hydrodynamic variability between pools. Furthermore, Figure 2.4 suggests that morphological contrasts are generally associated with pool-head (*e.g.* plunge pool) and/or pool-tail (*e.g.* dammed pool) areas, locations where most pool misclassifications were found (Figures 4.45, 4.47 and 4.49). An alternative explanation for the high degree of between-pool variability could be that pools are ‘passive’ habitats, with pool hydrodynamics highly dependent on the identity of the habitat immediately upstream. At the Leigh Brook, where the pool exhibited lower spatial and temporal variability, the upstream PB was another pool-like habitat, whilst at the River Arrow the pool was downstream of a riffle. In terms of the internal variability of pools, the classification presented in Figure 4.39 suggests that the pools investigated were among the least internally variable PBs. This is surprising given the findings of Rosenfeld *et al*. (2011), whose results indicated that pools should contain a relatively wide variety of microscale hydraulic conditions (S 2.4).

4.4.3 Relating the classification to hydromorphology

Pools were not the only PB type to exhibit errors in the classification that were associated with locations near the margins of the habitat. The run at the Leigh Brook and glides at both sites also had a high proportion of errors either at the head and tail of the habitat or at locations close to the banks. This suggests three pertinent points. Firstly, that PBs are, to a certain extent, situated along habitat gradients. This was most evident for the run at the Leigh Brook where locations at the head were misclassified as riffle and samples at the tail as glide. Secondly, hydrodynamic differences between PBs are muted at near bank locations. These first two points suggest that **classification of PBs may be best achieved through the collection of hydrodynamic data from the core of the habitat**. A third and related point is that PBs are composed of patches of smaller scale habitat. These habitats may be considered analogous to SFTs and FHs (Newson & Newson, 2000) (Figure 2.2). Indeed, the idea that **habitats are spatially nested and made up from a common suite of SFTs and FHs** has already been propounded by Harvey *et al*. (2008) (Figure 2.6). Figures 4.50 and 4.51 show that this is true of the PBs investigated here.

Pools were made up of 'lower energy' SFTs (NP, SM) and riffles of 'higher energy' SFTs (RP, UW), with glides and runs completing the gradient. As flow stage increased the makeup of SFTs within PBs predictably switched from lower to higher energy SFTs. Clear patterns in FH (dominant substrate) proportions were less evident and more site-specific. Nevertheless, Figure 4.51 still supports the idea that PBs are composed from a common set of habitat elements. To summarise, errors in the classification may be partially attributable to this nesting of similar, smaller scale habitats within PBs (S 4.4.3). If this is true then one would expect to see that errors in the classifications were disproportionately attributable to samples associated with SFTs and FHs that were rare in a given PB. Table 4.21 shows that, in the case of the 'Both P6 All' classification tree, relatively rare SFTs were associated with a disproportionate number of errors (ratio>1). In particular, at the Leigh Brook rippled flow contributed disproportionately to errors in the pool, smooth in the run and unbroken and broken standing waves in the riffle. In the run at the River Arrow, non-perceptible flow, an SFT usually associated with pools, contributed over five times more than expected if errors were distributed evenly across SFTs. FH categories were more likely to be associated with disproportionately high error rates than SFTs. At the Leigh Brook, bedrock (pool and run) and boulder (glide) FHs had ratios>>1. At the River Arrow, boulder and fine substrate (pool), gravel (glide) and cobble (run and riffle) also had disproportionately high error rates.

Table 4.21 – Ratios between the proportion of errors associated with samples of a given SFT or FH and the proportion of that SFT or FH found within the PB. Figures shown for the 'Both P6 All' scenario.

	Leigh Brook				**River Arrow**			
	Pool	**Glide**	**Run**	**Riffle**	**Pool**	**Glide**	**Run**	**Riffle**
SFTs								
Non-perceptible	0.9	0.9	-	-	0.8	-	5.2	-
Smooth	1.0	1.0	1.8	-	1.0	1.0	0.9	1.3
Rippled	1.7	-	0.9	1.0	1.1	-	1.0	0.8
Unbroken waves	-	-	-	1.7	-	-	-	1.3
Broken waves	-	-	-	1.7	-	-	-	-
FHs								
Boulder	-	2.7	-	-	2.9	-	-	-
Cobble	0.4	0.9	0.9	1.0	0.8	0.4	1.7	1.1
Gravel	0.7	0.7	0.4	-	0.8	1.4	0.9	0.7
Bedrock	2.0	-	3.8	-	-	-	-	-
Sand/silt/clay	-	-	-	-	1.9	-	-	-

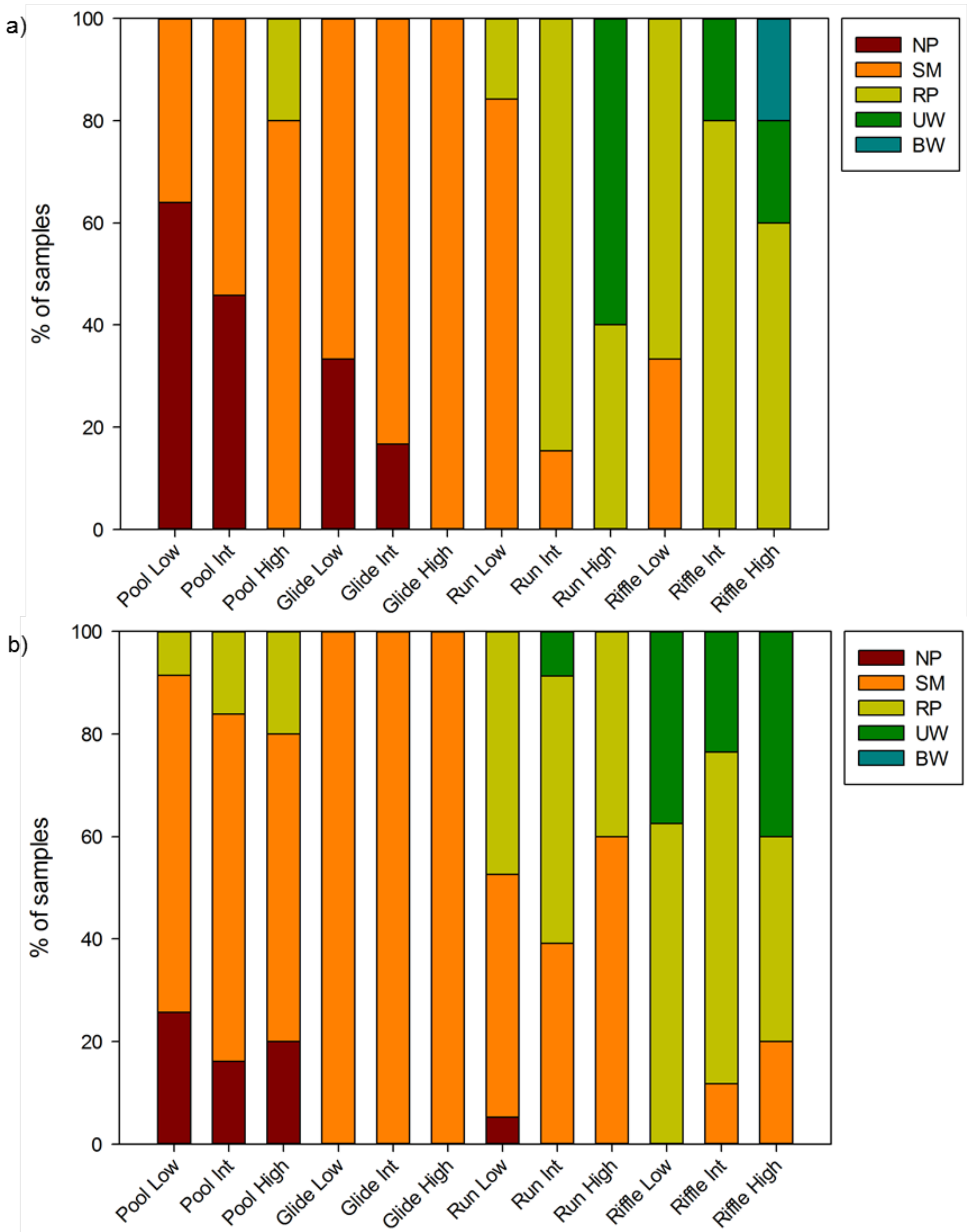


Figure 4.50 – Surface flow type (SFT) proportions found in PBs at the Leigh Brook (a) and River Arrow (b), including non-perceptible (NP), smooth (SM), rippled (RP), unbroken standing waves (UW) and broken standing waves (BW).

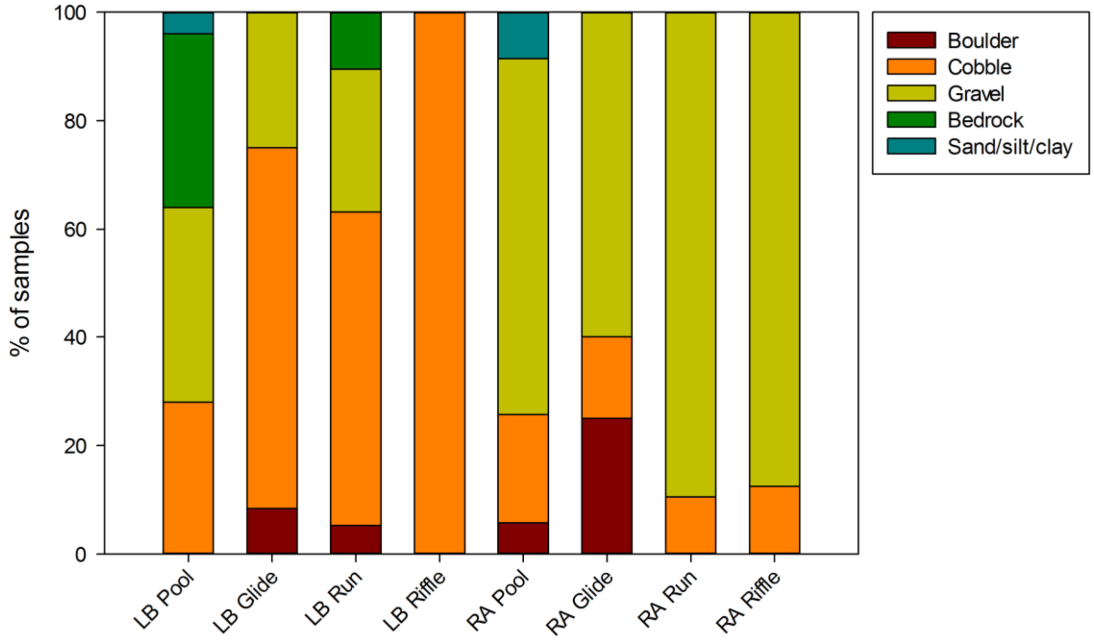


Figure 4.51 – Functional habitat (FH) proportions (dominant substrate) found in PBs at the Leigh Brook (LB) and River Arrow (RA).

Section 5.3.3 showed that classifications based on time series taken at point-six depth were often better (lower OOB error). This is good for data collection as point-six depth is where hydraulic measurements are traditionally taken (Gordon *et al*., 2004). Any application of the classification, therefore, would not require a change in tradition. Flow conditions at point-six depth, however, may be less relevant to biota as most aquatic fauna live in close association with the bed (Allan, 1995). That near bed classifications were generally less successful suggests that near bed hydrodynamics are more homogeneous between PBs than are equivalent mean column (point-six) conditions. Also, that high flow classifications performed poorly suggests reach scale homogenisation of hydraulic conditions occurs as flow stage approaches bankfull, a phenomenon observed by Padmore (1998), Emery *et al*. (2003) and Hill *et al*. (2008) and attributed to the diminishing effects of morphology on hydraulics as flow stage rises. The Strouhal (S) relationship (Eqn. 4.15) and the scaling of macroturbulent structures (Table 4.1) are suitable tools for examining the strength of morpho-hydrodynamic interactions.

Figure 4.52 shows that the estimated diameters of eddy shedding bodies (du), assuming S=0.2, were close to the representative particle sizes (D_{50}, D_{84}) calculated from pebble counts within PBs. There were few differences between near bed and point-six locations and du was close to D_{50} at low flow, whereas the average eddy became elongated at intermediate flow and du often exceeded that expected based on observed particle size distributions. This suggests a declining influence of substrate on turbulence as discharge increases. As discharge increased further, however, du decreased back to levels similar to low flow, although this may be due to the characteristics of the sensor used at high flow. Figure 4.52 provides only a crude indication of how the average eddy scaled with particle size as pebble counts were undertaken at the mesoscale and do not describe local variations in substrate.

In Figure 4.53 the relationship between the size of macroturbulent structures, represented by ILS_u, and h is compared to that expected given Roy *et al*'s (2004) scalings from a gravel bed river, where $3<ILS_u/h<5$. Results were similar at both sites and, again, there were few differences between near bed and point-six locations, although the latter was often associated with slightly higher ILS_u/h. Contrary to expectations, $ILS_u/h<1$ in all but two cases, namely runs and riffles at high flow where the ratio approached 3, suggesting that the scaling of macroturbulent structures is dependent on both flow stage and PB type. Both of these analyses indicate that, although there may be some expansion of macroturbulent structures with y, turbulent flow structures occupy the whole water column, as reported by Schvidenko and Pender (2001), Roy *et al*. (2004) and Lacey and Roy (2007). This makes a morpho-hydrodynamic explanation of the differences in the performance of near bed and point-six classifications difficult. The analyses do, however, suggest that flow-dependent processes are occurring to varying extents in different PBs, helping to explain why classifications performed less well at high flow. Such morpho-hydrodynamic linkages show that measures of turbulence can integrate hydromorphological factors (*i.e.* effective roughness, depth variation) which may be difficult to measure directly. This could be useful for habitat assessment (S 1.5.1) and the monitoring of river rehabilitation projects (S 1.5.3) (Chapter 7).

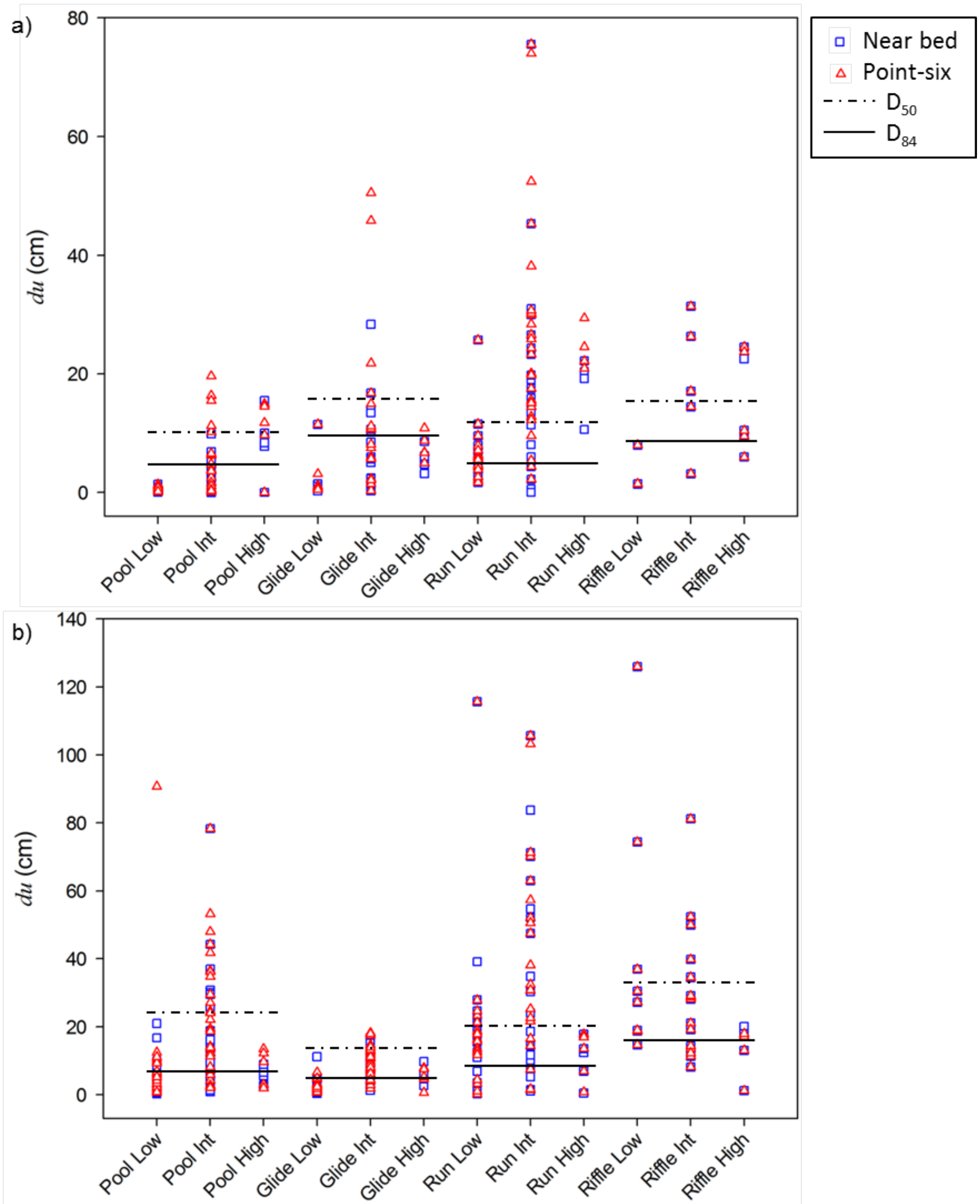


Figure 4.52 – Estimated diameter of eddy shedding body (du) calculated from autoregressive models and the Strouhal relationship (assuming S=0.2) compared to particle size (D) percentiles from pebble counts. Data shown for the Leigh Brook (a) and River Arrow (b).

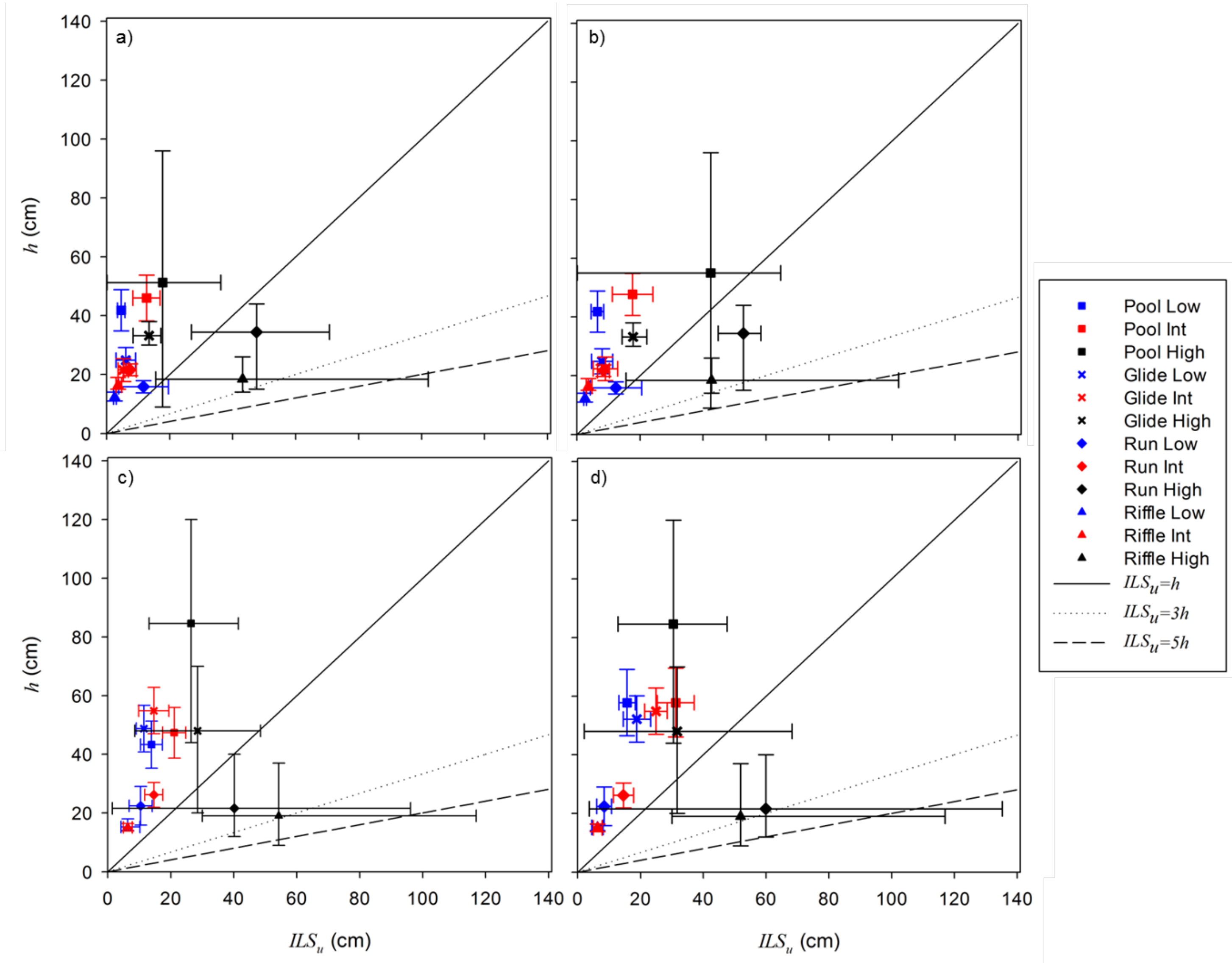


Figure 4.53 – Observed integral length scale (ILS_u) and that expected given the scalings of Roy *et al*. (2004). Symbols represent means and whiskers show 95% confidence intervals (or complete range at high flow). Data shown for the Leigh Brook near-bed (a) and point-six (b) and River Arrow (c, d).

4.4.4 Limitations of the study and further research

The potential limitations of this study fall into two categories. Firstly, there are several possible sources of error associated with ADV data collection and processing. Secondly, a number of confounding factors may have arisen from the way that the study was designed. Each of these is discussed below before future research priorities are identified, with the emphasis on applications of the findings and the assessment of their ecological relevance.

Although great care was taken to satisfy criteria outlined by Wilkes *et al*. (2013) (Appendix C), with the exception of high flow data (Table 4.4), there remain several potential sources of error in the ADV data upon which these classifications are based. Table 4.22 shows that, according to Nezu and Nakagawa's (1993) approximation of minimum f_D, the highest frequency fluctuations were not resolved in riffles and that the Flowtracker ADV was inadequate at high flow. This is likely to have affected results whereby riffle and high flow turbulence intensities would be biased low and measures of eddy size biased high. These results are in contrast to the suggestions made by Clifford & French (1993b) and Harvey & Clifford (2009) that f_D=20 Hz and 16 Hz respectively was adequate to capture the smallest turbulent flow structures. Instead, ADV sensors may need to be capable of digitisation rates of up to 70 Hz to capture the highest frequency fluctuations in riffles. Table 4.22, however, shows that the highest minimum f_D was often found to be at high flow and the capabilities of second-generation ADV sensors capable of up to 200 Hz (Nortek, 2013) have not been tested in these conditions. For the description of the largest flow structures, where RL is the critical parameter, it has been shown that the ADV protocol used at low and intermediate flows (RL=2250) was more than adequate according to empirical evidence (Buffin-Bélanger & Roy, 2005) but the high flow ADV protocol was inadequate by a substantial margin (Figure 4.7, Table 4.4). In addition to these drawbacks, another important limiting characteristic of the ADVs used is their geometrical design. In particular, the ADV used at low and intermediate flows could only be used where h>12 cm and this led to a situation where shallow habitats (*e.g.* riffles) were relatively poorly characterised. To summarise, objective 3 was not fully met for the riffle and for all PBs at high flow.

Table 4.22 – Average minimum digitisation rates (f_D, Hz) required to capture the highest frequency turbulent fluctuations based on turbulence theory (see equation 4.17) in PBs of the Leigh Brook (LB) and River Arrow (RA). Figures in bold denote situations where the f_D was insufficient to resolve the highest frequencies. At high flow this is based on the Flowtracker ADV.

PB (site)	**Low**	**Intermediate**	**High**
Pool (LB)	0.5	1.9	**8.7**
Pool (RA)	2.0	4.6	**4.3**
Glide (LB)	3.5	8.4	**13.5**
Glide (RA)	1.6	3.2	**4.4**
Run (LB)	16.1	23.3	**43.9**
Run (RA)	16.1	**26.1**	**29.5**
Riffle (LB)	**42.7**	**53.7**	**49.2**
Riffle (RA)	**70.0**	**53.4**	**42.3**

In terms of study design, there are several ways in which the statistical power and/or ease of interpretation could have been improved. Firstly, the study was not balanced; the sample size varied for different PBs, sites and flow stages, potentially causing bias in the classifications whereby some PB-site-flow combinations were better characterised than others. This was due to the depth limitations of the ADV but the study could have been designed to account for this by collecting random samples until a given number of time series had been taken from locations with sufficient depth. Another way in which the spatial sampling strategy could have been different is by taking time series at consistent sampling intervals for each PB-site-flow combination. Sampling intervals varied between 2 and 3 m in the longitudinal direction and 0.5 and 1.5 m in the lateral direction. The study was designed in this way so as to result in a consistent number of samples for each PB-site-flow combination but, as stated above, this was not possible because of ADV deployment limitations. An alternative design would have located samples at the same spatial intervals in each PB yet this would have led to vastly different sample sizes due to the varying spatial extent of each PB-site combination. Furthermore, the ephemeral nature of high flow events would not have allowed for the same relatively high resolution sampling during these conditions. After considering these issues, the resulting sampling strategy was a compromise based on time resources, ADV deployment and environmental conditions.

It has already been noted that samples at the margins of PBs were most often where misclassifications occurred. Whilst environmental gradients would be expected to exist within any unit of habitat (Forman, 1995), these misclassifications may have been due to poor delineation of PBs at the habitat mapping stage. An alternative approach would have been to collect time series on a reach scale grid and then to classify each sample separately. Even in this alternative sampling strategy, however, there would have needed to be an *a priori* classification of the PB membership of each time series. In other words, any sampling strategy would have been associated with its own set of confounding factors. Instead, these issues may be best addressed in the application of the classifications. If the classification was applied to a new site, for example, there would be two options. Given that the core of habitats for most PB-site-flow combinations were correctly classified, application could be based on a visual delineation of PBs (as undertaken herein) and then collection of hydrodynamic data from the core of the PB (excluding marginal locations). This approach would be similar to those taken by Schneider *et al*. (2005) (MesoCASIMIR) and Parasiewicz (2001, 2007) (MesoHABSIM), though these methods are based on standard hydraulic variables. Alternatively, a more traditional, microscale approach would be to collect time series at the nodes of a reach scale grid followed by classification by passing samples through the classification tree (*e.g.* the 'Both P6 All' tree) without any prior delineation of PBs.

In addition to exploring issues surrounding the application of these classifications, there are a number of other future research priorities relating to the elucidation of turbulent flow structures and the ecological relevance of a range of hydrodynamic variables. A major research priority is the improvement of field techniques capable of making direct observations of eddy dimensions. The method used to estimate eddy length scales (*i.e.* $L_{u, v, w}$, $ILS_{u, v, w}$) herein relied on the assumptions of Taylor's frozen turbulence hypothesis (Eqn. 4.10), in particular its assumption that the convective velocity (U_c) of eddies is equal to the mean velocity. Whilst Roy *et al* (2004) showed that the U_c of macroturbulent eddies was close to U, there remains a need to compare results derived from point measurements of turbulence with those calculated from particle imaging velocimetry (PIV) (*e.g.* Tritico & Cotel, 2010) and/or space-time correlations using multiple syncrhonised sensors (*e.g.* Lacey & Roy, 2007). PIV approaches provide the best direct characterisation of eddy scales but these systems are sensitive to environmental variation and models capable of field deployment are only in the early stages of development (Tritico *et al*., 2007; Liao *et al*., 2009). The improved characterization of eddy scales may be particularly important in shedding light on the links between aquatic biota and turbulence. Eddy dimensions and the orientation of flow perturbations, for instance, have been shown to be particularly important in determining swimming stability for fish and, therefore, the energetic costs of swimming (Pavlov, 2000; Webb, 2004; Lupandin, 2005; Liao, 2007; Tritico & Cotel, 2010). There is a rich body of literature pertaining to the hydrodynamics of rivers and the swimming capabilities of key fish species (*e.g. S. salar*) but these lines of research have, for the most part, proceeded separately and there is a need to establish links between the two subjects. Chapter 6 attempts to establish these links by testing the ecological relevance of a habitat classification based on turbulence.

4.5 Conclusions

The primary aim of this chapter was to construct a hydrodynamic classification of mesohabitats. In order to achieve this aim PBs were mapped along reaches of two small (third- to fourth-order) lowland streams. The mapping approach used was similar to other well established mesoscale methods. The benefits of this approach are that it minimises observer bias and its outcomes are readily interpretable. There are, however, still subjective judgements which must be made when deciding where to place habitat boundaries. Habitats at each site fell into one of five distinct clusters and four of these clusters closely matched each of four PB types commonly found in lowland rivers (glide, pool, riffle, run). One PB from each of these four clusters was selected for more detailed study of their hydrodynamic characteristics upon which the classifications were based. These ‘representative’ habitats were to be chosen based on the data produced by the cluster analysis but practical considerations (*e.g.* access, vegetation) meant that this was not always possible. Overall, therefore, the habitat mapping and selection procedure can be said to be ‘semi-objective’.

Results of the hydrodynamic characterisation of PBs along reaches of two rivers that differed on the basis of hydrology, geomorphology and human impact were broadly similar in that, although there were differences in the magnitude and variability of turbulent flow properties between similar PBs of each river, the relative differences between PB-flow combinations were the same between sites. Standard hydraulic variables (h, U, Fr) showed a gradient between habitats of pool<glide<run<riffle at low flow. This gradient was clearer at the Leigh Brook and became less obvious as flow increased. At any given flow stage, however, there was much overlap in the distributions of PBs. Measures of absolute turbulence intensity (SD_u, SD_v, SD_w, TKE) showed the same gradient between habitats but relative measures of turbulence (*e.g.* TI_u) showed an opposite and much less clear gradient. Turbulence intensity didn't always decrease away from the bed as expected based on theory (Appendix C). It is suggested that environmental complexity is the cause of this deviation from theory, which is generally based on observations of flow over smooth or very simple boundaries.

In terms of periodicity and predictability, dominant and average eddy frequencies were found to be between 0.01 and 1 Hz, whereas the largest eddies (ITS_u) had passage times of between 0.1 and 15 s. Interestingly, f_u and f_v exhibited opposite curvilinear responses to flow stage, with the former having minima at intermediate flow and the latter having maxima at this flow stage. The analysis of velocity spectra showed that the riffles had the most complex flow made up of a range of eddy sizes, as evidenced by their flatter spectra. Variables describing the orientation of the turbulent flow provided additional information. Pools often had primary flow vectors that deviated from streamwise. All site-PB-flow combinations were dominated by eddies rotating on spanwise axes, suggesting that the macroturbulent structures discussed by Wilkes *et al*. (2013) (Appendix C) can be detected. The net flux of turbulent momentum on the streamwise-vertical plane (τ_{uv}) was generally positive for all site-PB-flow combinations, in agreement with theory suggesting that turbulence is exported from the bed towards the surface (Appendix C). TKE, however, often increased away from the bed, raising doubts over the established theory. Conditional sampling showed that event structure was similar across PBs and flows, limiting the utility of related variables (*e.g.* $T_{Q2}T_{H:2}$) for classification purposes. Skewness coefficients, however, indicated that slow events ($Skew_u$<0) tended to dominate in all situations and that conditions for sediment transport ($Skew_v$>0) were found in all PBs at all flows. The average eddy was found to range from 0.02 to 4 m in length, with runs and riffles having larger eddies (L_u and L_v) than pools and glides. Eddies grew larger as flow stage increased.

The classification analyses considered solutions based on within-PB variability (*sensu* Harvey & Clifford, 2009) and the magnitude of hydrodynamic variables at individual sampling points within PBs. **It was proposed that the contrasts between PBs can be classified in a more quantitative and readily applicable way using the latter approach (classification trees) as PBs did not exhibit consistent patterns in terms of internal heterogeneity**. Errors in the classification trees were most likely to occur at the edges of PBs. Any attempts to classify new PBs with these models, therefore, would be better if measurements are limited to the core of the habitat (i.e. by omitting a 20% margin). Classifications based on near bed hydrodynamics were less transferable than those based on point-six measurements. The choice of which to use in future applications should be directed by the purpose of its application. For a relatively straight, steep stream (*e.g.* Leigh Brook) in which the habitat of benthic biota is of interest, then the 'LB NB All' tree could be used, whereas for a more sinuous and less steep river (*e.g.* River Arrow) the 'RA NB All' tree may be preferable. For pelagic biota the generalised 'Both P6 All' tree would be more appropriate. To summarise**, a combination of variables describing the intensity (TKE, $AvInt$), periodicity (ITS_u, ITS_w), orientation (τ_{uw}) and scale (L_u) of turbulence, as well as the standard hydraulic variables of U_{res} and h, were found to provide the best calibration of PBs leading to classifications which were able to predict up to 82.9% of individual samples correctly** ('LB P6 All' RF classification) **but further work is required to assess their ecological relevance** (Chapter 6).

5

Hydrodynamic habitat selection by Atlantic salmon parr

Chapter overview

The aim of this chapter is to test the ecological relevance of a habitat classification based on turbulence using Atlantic salmon as a model organism. Turbulence is expected to influence habitat selection in fish through its effects on swimming performance but the evidence on the strength and direction of the relationship is equivocal, even for a well-research species, Atlantic salmon. Some bioenergetic models do not include the costs of swimming, others do model swimming costs but only in relation to mean velocity. In order to improve understanding in this area the habitat selection of 42 parr was analysed with respect to turbulence within an artificial habitat constructed in the laboratory. The ability of two existing swimming costs models to predict habitat selection was tested - one based on mean velocity (forced model) and one including turbulence (turbulent model). A bespoke model using a combination of hydrodynamic variables was also produced to describe the relationship between position choice and turbulent flow. A permutation-based test showed that most parr chose locations associated with low swimming costs predicted by the turbulent model, whereas the relationship was not as clear for the forced model. Regressions (generalised linear models) showed that, of the two swimming costs models, the turbulent model was better able to predict position choice. The bespoke model included mean velocity, spatial velocity gradient and Reynolds stresses and showed that parr preferred locations with low velocities and a net flux of turbulent momentum towards the bed, presumably because this aided station-holding behaviour.

5.1 Introduction

Chapter 1 established the growing importance of the mesohabitat concept, bioenergetic modelling and hydrodynamics to river research and management activities and identified Atlantic salmon as a model organism for research (Aas *et al*., 2011). Limited evidence for the ecological relevance of mesohabitats was presented in Chapter 2. This evidence was strengthened in Chapter 3 using a holistic, community-level approach to examining the links between biota and physical habitat at the mesoscale. Wilkes *et al*. (2013) outlined the structure and complexity of turbulent flow in rivers (Appendix C) and Chapter 4 discussed the implications for the hydraulic calibration of mesohabitats, which Chapter 2 had already identified as weak. Chapter 4 went on to present the most detailed evidence to date that mesohabitats are distinct when a combination of hydrodynamic variables are considered. A new generalised, quantitative classification of the habitats investigated was proposed. **The current chapter seeks to link the evidence for ecological relevance and hydrodynamic distinctiveness by examining the habitat selection of the model organism, Atlantic salmon** (S 1.4.3)**, in relation to turbulent flow within an artificial habitat constructed in the laboratory**.

Turbulence is expected to influence habitat selection in stream-dwelling fish through its effects on swimming performance (Wilkes *et al*., 2013). This is likely to be especially true of Atlantic salmon parr due to their possession of a lateral line, which allows them to detect small pressure differences in the surrounding fluid, and their close association with shear zones characterised by a highly dynamic flow environment (Cunjak, 1988; Buffin-Bélanger & Roy, 1998). The evidence on the strength and direction of the relationship between turbulence and swimming performance, however, is equivocal and much of the existing knowledge is based on work with coarse species. In considering the relationship between fish behaviour and turbulence, Lacey *et al*. (2012) emphasise the need to consider four aspects of turbulence: intensity, periodicity, orientation and scale (Table 4.1). These aspects will be considered below; first with respect to swimming performance and second in relation to habitat selection.

5.1.1 Swimming performance

Early work on the relationship between turbulence and fish swimming performance, reviewed by Pavlov *et al*. (2000), suggested that the critical mechanism responsible for destabilising fish in turbulent flow was related to eddy length. Working with gudgeon (*Gobio gobio*), perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) they reported a significant ($p<0.002$) relationship between L_u and the critical swimming speed at which fish were unable to maintain position. Specifically, when L_u>0.66bl, where bl is fish body length, the moments of the forces acting on the body of the fish were unevenly distributed, destabilising fish and requiring corrective movements using pectoral fins. This was assumed to result in increased energy expenditure. Lupandin (2005), who also worked with perch, concurred with these findings. Juvenile salmonids are also known to use pectoral fins to perform corrective movements (McLaughlin & Noakes, 1998; Drucker & Lauder, 2003) and, especially in the case of Atlantic salmon parr, to hold station near the bed (Arnold *et al*., 1991).

Eddy orientation has been cited as an important factor in determining the potential for turbulent flow to destabilise fish (Webb, 2004; Liao, 2007). Using PIV in a flume, Tritico and Cotel (2010) found that creek chub (*Semotilus atromaculatus*), a laterally compressed fish, were not destabilised until the 95th percentile of L_u exceeded 0.75bl. The frequency of destabilising events doubled and their duration increased by 24% when eddies were rotating on a horizontal axis, rather than a vertical axis, presumably resulting in increased swimming costs. Lacey *et al*. (2012) have suggested that laterally compressed fish are more susceptible to destabilisation by horizontal eddies, whereas dorso-ventrally flattened species are more sensitive to vertical eddies. Not only are the orientation and scale of eddies important, but also their intensity. Specifically, the ratio of eddy momentum (Π_e) to fish momentum has been suggested as the critical factor (Webb *et al*., 2010; Webb & Cotel, 2010). Tritico and Cotel (2010) found that challenges to creek chub swimming stability increased dramatically when Π_e>30 000 g cm^2 s^{-1}.

Juvenile salmonids tend to hold position downstream of home rocks (Cunjak, 1988; Guay *et al*., 2000) in the Kármán vortex street characterised by eddies rotating on a vertical axis (Wilkes *et al*., 2013), a zone which may be associated with energetic benefits. Liao *et al*. (2003b) found that rainbow trout matched their body kinematics (amplitude, tail-beat frequency) to the more or less predictable shedding of vertical eddies from a cylinder in a laboratory flume, where the size of eddies was $0.25<L_u/bl<0.5$, in a distinctive swimming style termed 'Kármán gaiting'. When given a choice of where to swim in proximity to the cylinder, Liao (2006) reported that four rainbow trout spent most time in an areas where this swimming style could be employed (Figure 5.1). Liao *et al*. (2003a) and Liao (2004) measured red axial muscle activity using electromyography to show that rainbow trout Kármán gaiting downstream of a cylinder were saving energy in comparison to fish swimming in the free stream (Figure 5.2). This work was carried out at approximately $7500<Re<14000$ (Liao *et al*., 2003b) raising doubts as to the realism of the findings, as Re may be orders of magnitude greater in natural habitats. In such hydraulically rough conditions, the structure and predictability of the Kármán vortex street is diminished (Davidson, 2004).

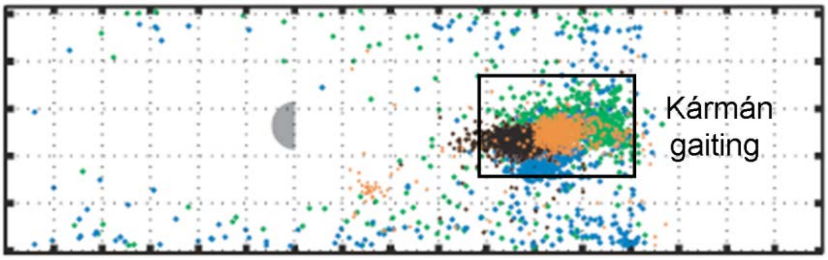


Figure 5.1 – Head locations of four rainbow trout (*Oncorhynchus mykiss*) in a flume in relation to the area with suitable conditions for Kármán gaiting. Individual fish illustrated by four different colours. Locations tracked every 5 s for 1 h. Modified from Liao (2006), Wilkes *et al*. (2013).

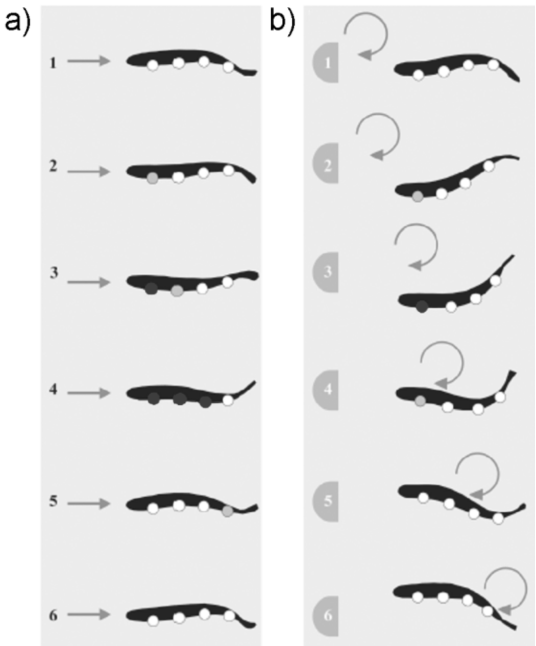


Figure 5.2 – Time series (1-6) illustrating that red axial muscle activity measured in a flume using electromyography differed between rainbow trout (*Oncorhynchus mykiss*) swimming in the free stream (a) and behind a cylinder (b). Circles denote electrode positions with no (open), intermediate (grey) or high (closed) muscle activity. From Liao *et al*. (2003a), Wilkes *et al*. (2013).

By measuring the oxygen consumption of Atlantic salmon parr in a respirometer, Enders *et al*. (2003) found a negative relationship between turbulence and swimming costs (SC). For any U, the rate of oxygen consumption increased significantly ($p<0.05$) with SD_u (Figure 5.3). Enders *et al*. (2005a) later reported that SD_u explained 14% of the variation in SC in a model also including U (46% of variation), fish body mass (31%) and temperature (2%). An existing model used to predict SC based on forcing fish to swim at a constant mean velocity without considering turbulence (Boisclair & Tang, 1993) severely underestimated SC. Studies on other species have found no relationship between swimming performance and turbulence (*e.g.* Nikora *et al*., 2003), underlining to equivocality of the evidence. The often stark contrasts between findings from such studies, however, may be due to the way that turbulence is generated. Respirometry studies often use pumps (*e.g.*Enders *et al*., 2003; 2005a) which create a different turbulent flow structure (eddy intensity, orientation, scale) compared to other work on swimming performance in proximity to artificial structures designed to mimic natural habitats (*e.g.* Liao *et al*., 2003a, b). Observing where fish choose to swim in relation to hydrodynamics in more naturalised habitats may provide an opportunity to evaluate such apparent contradictions.

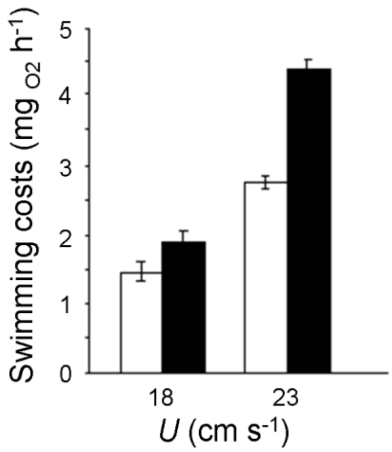


Figure 5.3 - Swimming costs of Atlantic salmon parr for four experimental treatments. Low turbulence conditions (*SDu*=5 cm s^{-1}) are represented by open bars and high turbulent conditions (*SDu*=8 cm s^{-1}) are represented by solid bars. Vertical lines represent 95% confidence intervals. From Enders *et al*. (2003), Wilkes *et al*. (2013).

5.1.2 Habitat selection

The evidence on fish responses to turbulence in terms of habitat selection is equally as antithetical as that on swimming performance, and few studies into the response of juvenile salmonids exist. In the laboratory, Smith *et al*. (2005) observed the habitat selection of juvenile rainbow trout in an artificial habitat with cover provided in the form of bricks. Of a range of hydrodynamic variables, they found that fish preferred significantly lower V (p=0.01) and L_x (p<0.01) in a low discharge treatment and lower U (p<0.01), τ_{uv} (p<0.01) and L_x (p=0.03) at higher discharge. Later Smith *et al*. (2006) placed 30 fish in the same artificial habitat in a series of four replicate trials where fish were able to exit the test section voluntarily. After 24 hours they counted the remaining fish and found that TKE was better at predicting their density than U (Figure 5.4) because turbulence was more sensitive to combinations of cover and discharge used in the trials. This idea was supported by Smith and Brannon (2007) who found that turbulence intensities were better at detecting the proximity of cover (*e.g.* boulders, scour holes, woody debris) than mean velocities in gravel-bed rivers.

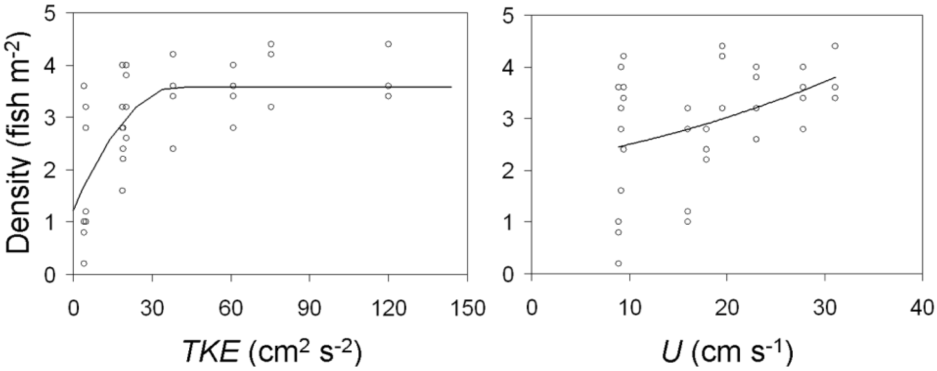


Figure 5.4 – Comparison of models to predict volitional rainbow trout density in response to experimental treatments in a flume. From Smith *et al*. (2006), Wilkes *et al*. (2013).

Field studies into the link between juvenile salmonid habitat selection and turbulence are limited to just two examples. Working in a sand-bed river, Cotel *et al*. (2006) recorded the microscale position choices of brown trout during three consecutive summers and took hydrodynamic measurements in these locations as well as similar locations (h, U, cover) not occupied by fish. Brown trout tended to select locations with lower TI_u than unoccupied locations (Figure 5.5a). Working at the reach scale, Enders *et al*. (2009) tracked the habitat use of four Atlantic salmon parr over two summer periods. They also took hydrodynamic measurements at the nodes of a 2 m x 2 m grid throughout the 80 m reach. They found no consistent relationship between SD_u and position choice at the reach scale (Figure 5.5b). There are three possible explanations for the equivocal nature of these findings. First, the relationship between habitat selection and turbulence in juvenile salmonids may be scale-dependent. Alternatively, the relationship may be highly species-specific so that even closely related species exhibit distinctive responses to turbulence, as suggested by Wilkes *et al*. (2013). A final, possibly confounding explanation, is that these studies reported different measures of turbulence. Cotel *et al*. (2006) defined turbulence intensity relative to mean velocity (TI_u), whereas Enders *et al*.

(2009) used an absolute measure (SD_u). The former definition assumes that fish are able to maintain greater swimming stability for a given SD_u when U is higher, and assumption that later commentators have not supported (Smith *et al*., 2005; Webb, 2006).

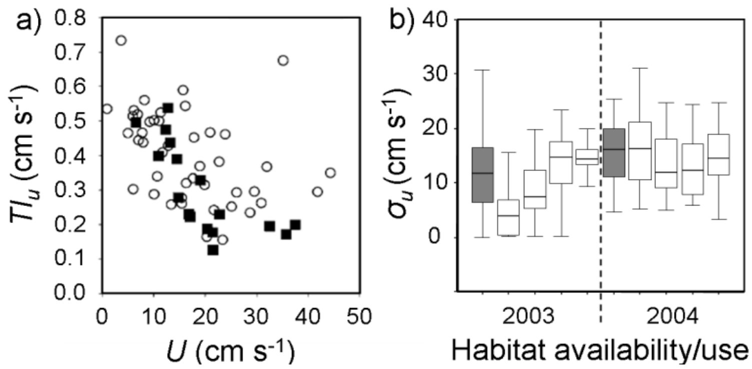


Figure 5.5 - Relationships between turbulence and salmonids in rivers. (a) Turbulence intensity (TI_u) and nose velocity (U) for various locations with brown trout (closed symbols) and similar locations with no fish (open symbols). From Cotel *et al*. (2006). (b) Reach-scale habitat availability (grey boxes) and locations of four tagged Atlantic salmon parr (open boxes) in relation to SD_u (σ_u)over two years. Vertical bars represent upper and lower 5th percentiles. From Enders *et al*. (2009), Wilkes *et al*. (2013).

5.1.3 Aim and hypothesis

If hydrodynamics is to be integrated into bioenergetic models then key knowledge gaps need to be addressed. Some bioenergetic models assume that swimming performance does not play a role in the habitat selection of salmonids (*e.g.* Nislow *et al*., 1999) but there is little evidence for this assumption. Others predict habitat quality using an estimation of SC based on mean velocity (*e.g.* Booker *et al*., 2004), yet laboratory studies are revealing a more complex relationship between turbulent flow and swimming performance (Lacey *et al*., 2012). **The aim of this chapter is to test the ecological relevance of a habitat classification based on turbulence**, such as that presented in Chapter 4. The objectives are to (i) **compare the ability of two empirical equations**, the 'forced' (Boisclair and Tang, 1993) and 'turbulent' (Enders *et al*., 2005) SC models, **to predict habitat selection in Atlantic salmon parr** and (ii) **assess whether their predictions may be improved upon by including other potentially important hydrodynamic properties**. **It was hypothesised that parr**

would occupy positions within an artificial habitat that were associated with energetically favourable hydrodynamic conditions.

5.2 Methods

5.2.1 Creating turbulent flow and predicting SC in an artificial habitat

A 2 m x 2 m section of a large flume was sectioned off using screens. A mesh size of 5 mm was used to minimise the effects of the screens on the flow structure, which are likely to be in the form of flow straightening and a reduction in turbulence scales (Nikora *et al*., 2003; Smith *et al*., 2005). A series of 50 and 100 mm diameter clear plastic hemispheres was fixed to the bed to create a range of hydrodynamic conditions. Water temperature and discharge were maintained at 15 °C (± 0.1 °C) and 0.056 $m^3 s^{-1}$ respectively. When the water temperature exceeded 15.1 °C the flume was shut down and the header tank refreshed with water from the mains supply. The flow depth throughout the test section was 165 mm, within the range reported to be used by Atlantic salmon parr in the literature (Symons and Heland, 1978; Kennedy and Strange, 1982; Morantz *et al*., 1987; Heggenes, 1990). A Nortek Vectrino II ADV was used to collect velocity time series (25 Hz for 90 s) at set locations around the hemispheres. Velocities were taken at 20-24 mm above the bed to approximate the focal point of the parr. All time series met recommended data quality thresholds (signal-to-noise ratio >25, velocity correlation >70) (Lane *et al*., 1998; McLelland and Nicholas, 2000) and were passed through an mPST filter (>95% good), with bad data points replaced using a third-order polynomial fitted to the data either side of the spike (Parsheh *et al*., 2010). The data were rotated into the primary velocity vector and the following hydrodynamic quantities were calculated: mean velocity (U) and turbulence intensity (standard deviation of velocity, SD_u) of the resultant vector; Reynolds stress on the streamwise-vertical (τ_{uv}) and streamwise-lateral (τ_{uw}) planes

$$\tau_{uv} = -\rho\overline{uv}, \quad \tau_{uw} = -\rho\overline{uw} \qquad 5.1$$

where ρ is fluid density and u, v and w are instantaneous velocities in the streamwise, vertical and spanwise components respectively; and average eddy length (L_u) calculated using a second-order autoregressive model of the form

$$u_t = a_1 u_{t-1} + a_2 u_{t-2} + e_t \qquad 5.2$$

where a_1 and a_2 are coefficients of the velocity at a given time lag and e_t is a random component (Clifford and French, 1993a). These quantities were interpolated to a grid (25 mm mesh size) using an Ordinary Kriging method (Oliver, 1990) in ArcGIS 10 (ESRI, 2011) and predicted SC calculated for each cell according to equations for the forced model ($FTSC$)

$$\log FTSC = 0.96\log M + 0.23\log U + 0.67\log T - 1.85 \qquad 5.3$$

(Boisclair and Tang, 1993, modified by Enders *et al*., 2005 to include standard metabolic rate) and turbulent model (CR)

$$\log CR = 0.23\log T + 0.64\log M + 2.43\log U + 0.67\log SDu - 4.06 \qquad 5.4$$

where M is fish body mass and T is temperature (Enders *et al*., 2005). These SC models were constructed based on the results of respirometry experiments. Predictions were made for the average mass of fish used in this study (9 g) at a temperature of 15 °C. In addition to the characteristics of turbulent flow outlined in S 5.1, spatial gradients in mean velocity have also been implicated in the habitat selection of juvenile salmonids due to their distinctive 'sit-and-wait' feeding behaviour (Hayes & Jowett, 1994; Booker *et al*., 2004). Velocity gradient (V_{grad}), therefore, was also calculated for each cell as the standard deviation of U in all neighbouring cells within a 200 mm radius. This is equal to roughly two body lengths in order to approximate the foraging radius of an Atlantic salmon parr (Fausch, 1984).

5.2.2 Experimental procedure

A total of 42 yearling parr measuring 86 to 105 mm (standard fork length) were electrofished from the River Frome, Dorset and transported to an experimental facility owned by the University of Southampton. Fish were fed and held in accordance with normal husbandry for one week before experimental trials began. Fish were starved for 24 hours prior to trials to standardise hunger, as fish may seek different hydraulic habitat conditions if they are satiated (Pavlov *et al*., 2000; Lupandin, 2005). Each trial began by adding an individual fish to the flume at randomly generated starting coordinates on the grid. Lights were switched off and, after 30 minutes to acclimatise to the flow and explore the habitat, each fish was recorded for 10 minutes using an infra-red camera. Tracking software (Kinovea 0.8.15) was then used to track the focal position of each fish to the nearest grid cell every 5 seconds, giving 121 observations per fish. A selection index (SI_{xy}) for each cell was calculated based on the number of times a fish was observed in that cell (cell occupancy, CO_{xy}), summed over all fish

$$CO_{xy} = \sum_{i=1}^{n} fish_{i,xy}$$

$$SI_{xy} = \frac{CO_{xy}}{CO_{\max}} \quad 5.5$$

where $fish_{i,xy}$ is the occupancy count for each fish in each cell and CO_{max} is the maximum cell occupancy or, in other words, the CO_{xy} associated with the most popular cell.

5.2.3 Statistical analyses

A permutation test was used to test the null hypothesis that fish chose cells at random with respect to mean predicted SC from each model. The null distributions of SC were constructed from 10000 bootstrap samples of 121 random cells (with replacement). For each fish, the probability (p) that the fish chose cells at random was calculated as

$$p = \frac{\sum_{i=1}^{n}(SC_{null} \geq SC_{fish})}{k} - 1 \quad 5.6$$

where k=10000, SC_{null} is the mean predicted SC associated with each bootstrap sample and SC_{fish} is the mean predicted SC of cells used by each fish. Generalised linear models were used to predict SI based on a linear combination of variables. Habitat selection followed a Poisson distribution but there were many zeros, necessitating the use of a zero-inflated model. Overdispersion was dealt with by using a zero-inflated negative binomial (ZINB) model of the form:

$$g(\mu_i) = \beta_0 + \mathrm{X}^T \beta, \quad g(\pi_i) = \beta_0 + \mathrm{X}^T \beta \quad 5.7$$

where g is a link function, β_0 is the intercept, X^T is a vector of m predictor variables and β is a vector of m regression coefficients. Thus the probability of finding false zeros (*i.e.* locations in which fish were not observed but nevertheless represent 'good' habitat) was modelled separately to the count data (see Zuur *et al*., 2009). This process is illustrated in Figure 5.6. A log link was used for the count model (μ) whilst the binomial (zero mass) model (π) was facilitated by a logit link function

$$g = \log\left[\frac{\pi_i}{1-\pi_i}\right] \quad 5.8$$

The Akaike information criterion (AIC), an inverse measure of goodness-of-fit, was used to compare results for the forced, turbulent and bespoke hydrodynamic models. AIC was also used for model selection along with likelihood ratio (LR) tests for nested models. All statistical procedures were carried out using R2.15.3 (R Core Team, 2013).

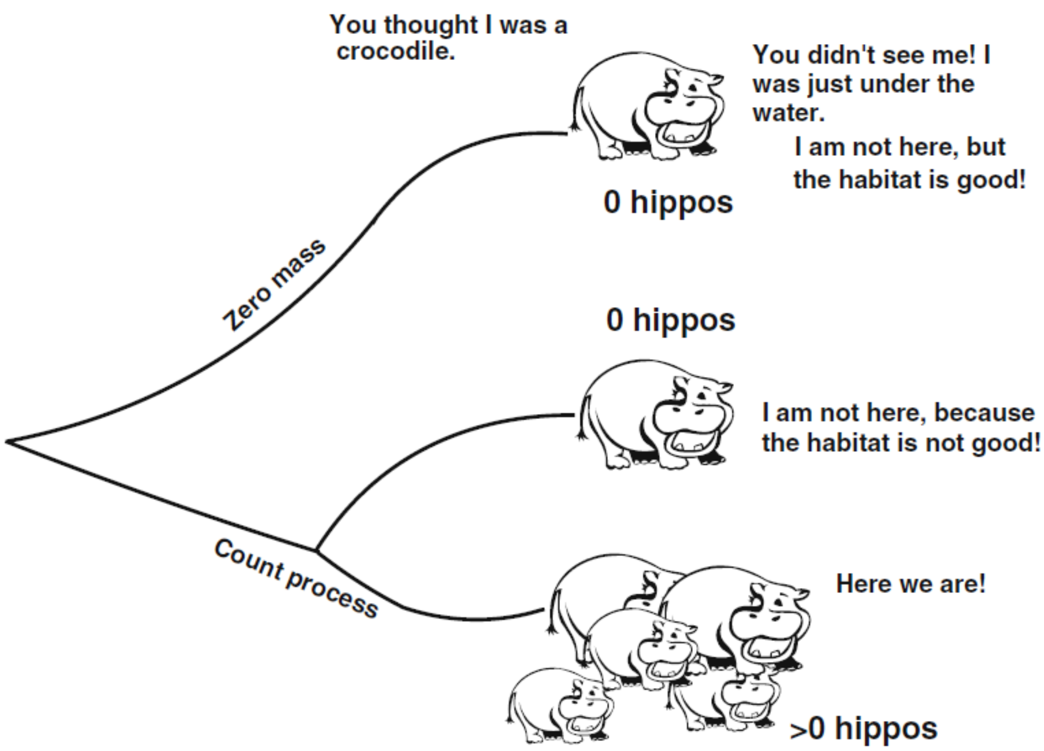


Figure 5.6 – Sketch of the underlying principle of mixed models (ZINB). In counting numbers of the study organism at sites, one can measure a zero because the habitat is not good, because of poor experimental design, because the study species are difficult to observe or simply because they happened to be absent at the time of sampling. From Zuur *et al*. (2009).

5.3 Results

Mean velocities (0.15 – 20 cm s^{-1}) (Figure 5.7a) and turbulence intensities (0.4 – 8 cm s^{-1}) (Figure 5.7b) were within the range used to construct the SC models (Boisclair and Tang, 1993; Enders *et al*., 2005) and, together with other hydrodynamic variables, were within an order of magnitude of those reported from natural rivers (Lacey *et al*., 2007; Smith and Brannon, 2007; Roy *et al*., 2010). Bulk Re ranged from 7244 to 45230 (mean Re = 26416). Primary flow vectors were variable, reflecting the turbulent flow regions and patterns of flow divergence and convergence (Wilkes *et al*., 2013; Appendix C) in the vicinity of obstacles on the bed (Figure 5.7C). Predicted SC for the forced model was between 0.46 and 1.43 mg O_2 hr^{-1} (Figure 5.8a). Predictions from the turbulent model were more widely distributed between 0.01 and 3.89 mg O_2 hr^{-1} (Figure 5.8b). Parr moved around the test section to varying degrees. Some fish remained in the same or neighbouring cells for the duration of observations, others used a wider range of predicted SC (Table 5.1). Fish most often selected cells close to hemispheres and the edges of the test section (Figure 5.8c). Figure 5.9 shows null distributions for the forced and turbulent SC models. The permutation tests revealed that 71% of parr chose cells with significantly lower mean SC than available at random for the forced model (p < 0.05). For the turbulent model this was higher at 86%.

Results of ZINB modelling for the SC equations showed that predicted SC was negatively related to habitat selection in both cases (Figure 5.10). Count model coefficients for both equations were highly significant (Table 5.2). Observed SI was more widely distributed for the forced compared to the turbulent equation. Observed SI for the turbulent equation was clustered around low predicted SC. The probability of finding a false zero (*i.e.* where the habitat is good but no fish were observed) was relatively high for low values of FTSC, whereas it was consistently low for the turbulent equation (Figure 5.10). Model coefficients for these binomial models, however, were non-significant (p>0.05). A comparison of AIC showed that the turbulent model fitted the data better than the forced model (6967.16 < 6971.97).

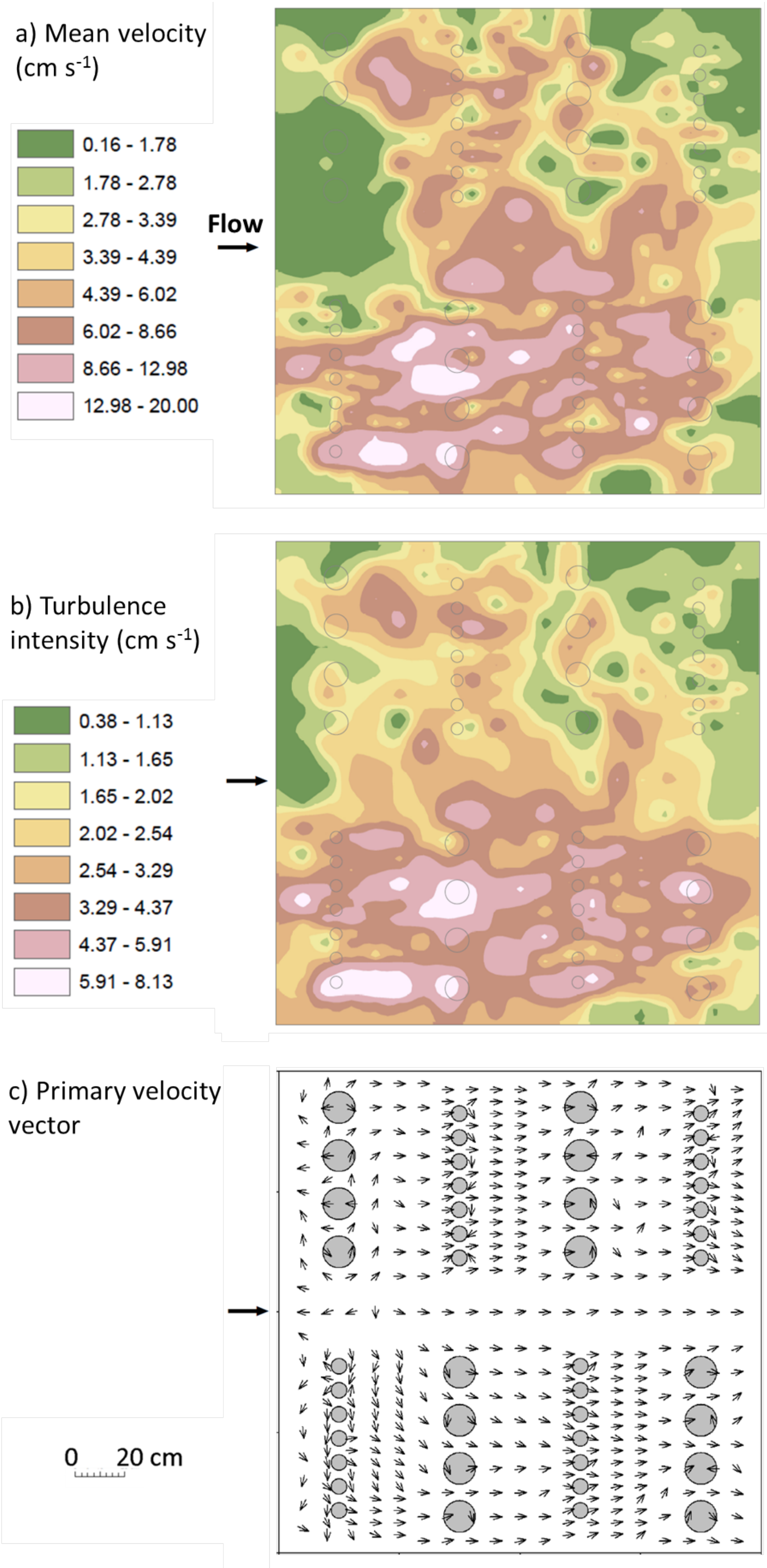


Figure 5.7 – Maps of interpolated mean velocity (a), turbulence intensity (b) and primary flow vector for each individual measurement location (c).

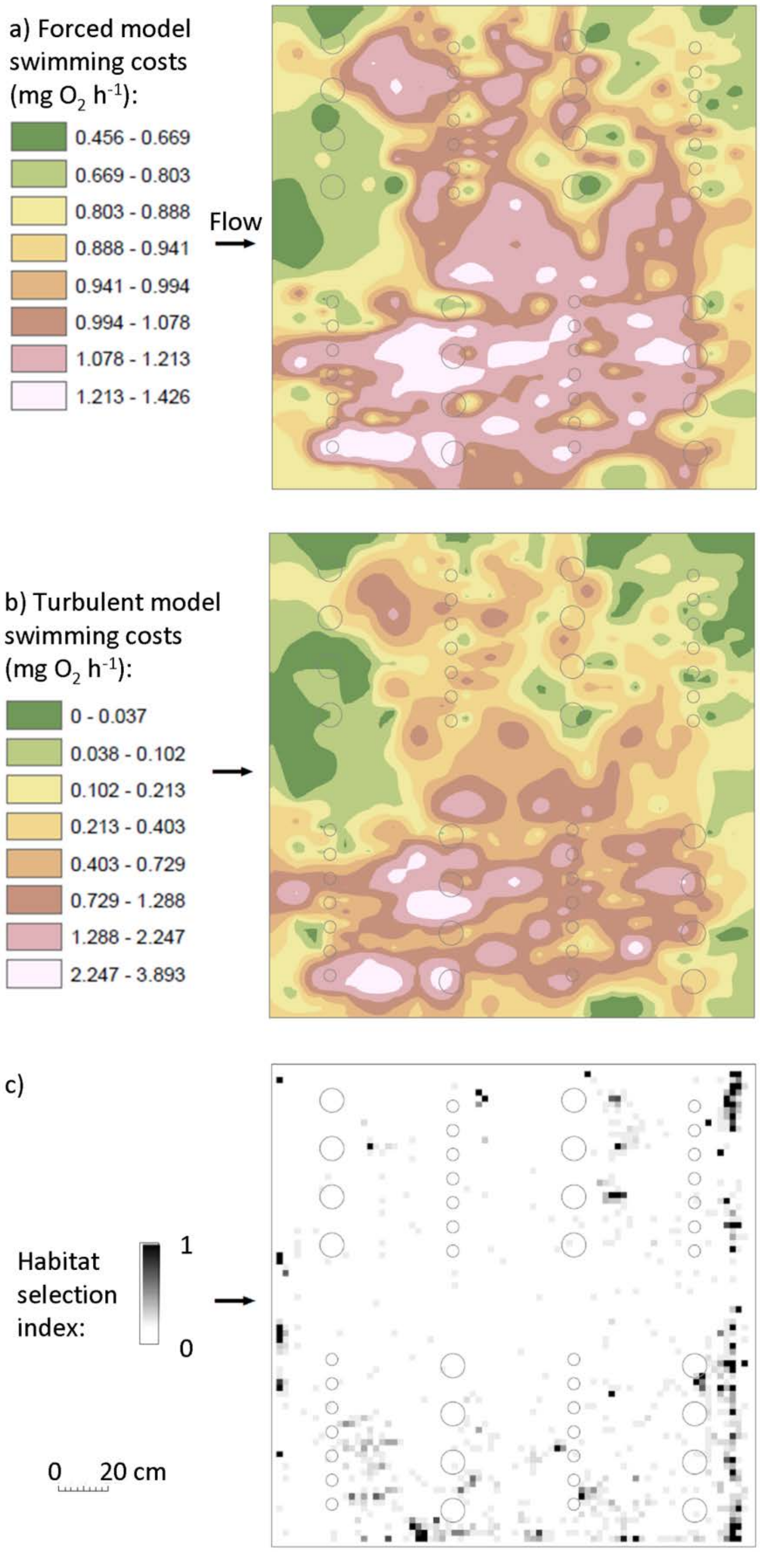


Figure 5.8 – Maps of SC predictions from the forced (a) and turbulent (b) equations and habitat selection index (c) on an interpolated grid.

Table 5.1 – Summary of mean (range) predicted swimming costs and permutation test results.

Fish	*FTSC* (mg O_2 h^{-1})*	*p*	*CR* (mg O_2 h^{-1})*	*p*
1	0.82 (0.82)	0	0.08 (0.08)	0
2	0.89 (0.61-1.14)	0	0.19 (0.013-0.83)	0
3	1 (0.61-1.27)	0.97	0.48 (0.01-2.06)	0.37
4	0.96 (0.93-1.04)	0.23	0.29 (0.18-0.67)	0
5	0.76 (0.70-0.81)	0	0.03 (0.02-0.06)	0
6	0.87 (0.63-1.19)	0	0.23 (0.01-1.44)	0
7	0.88 (0.88)	0	0.09 (0.09)	0
8	0.74 (0.70-0.92)	0	0.03 (0.01-0.15)	0
9	0.97 (0.70-1.36)	0.54	0.64 (0.05-3.42)	0.99
10	1.08 (0.75-1.23)	1	0.71 (0.04-1.63)	0.99
11	0.71 (0.70-0.82)	0	0.02 (0.02-0.07)	0
12	0.74 (0.69-0.96)	0	0.14 (0.05-0.23)	0
13	0.75 (0.68-0.88)	0	0.03 (0.01-0.08)	0
14	0.76 (0.70-0.94)	0	0.05 (0.02-0.22)	0
15	0.86 (0.71-0.98)	0	0.32 (0.13-0.70)	0
16	0.88 (0.87-1.01)	0	0.1 (0.08-0.38)	0
17	0.88 (0.57-1.22)	0	0.28 (0.01-1.68)	0
18	0.57 (0.57)	0	0.002 (0.002)	0
19	1.04 (0.86-1.20)	1	0.58 (0.27-1.47)	0.95
20	0.61 (0.61-0.62)	0	0.03 (0.03)	0
21	0.7 (0.7)	0	0.02 (0.02)	0
22	1.03 (1.01-1.04)	1	0.39 (0.35-0.41)	0.008
23	0.8 (0.74-0.83)	0	0.039 (0.02-0.05)	0
24	0.75 (0.64-0.89)	0	0.05 (0.001-0.25)	0
25	0.81 (0.74-1.17)	0	0.06 (0.00-1.07)	0
26	0.95 (0.71-1.19)	0.08	0.33 (0.02-1.28)	0
27	0.92 (0.68-1.21)	0.0001	0.33 (0.01-2.30)	0
29	0.99 (0.99)	0.89	0.41 (0.41)	0.04
30	0.89 (0.73-1.05)	0	0.11 (0.06-0.51)	0
31	0.99 (0.73-1.27)	0.9	0.46 (0.01-2.20)	0.24
32	1.11 (0.54-1.33)	1	1.38 (0.002-3.24)	1
33	0.96 (1.22)	0.25	0.3 (0.04-1.26)	0
35	0.7 (0.7)	0	0.02 (0.02)	0
36	0.86 (0.86)	0	0.36 (0.36)	0.0006
37	0.85 (0.85)	0	0.06 (0.06)	0
38	0.93 (0.93)	0.006	0.21 (0.21)	0
39	0.72 (0.72)	0	0.03 (0.03)	0
41	0.65 (0.65)	0	0.01 (0.01)	0
43	0.82 (0.82)	0	0.05 (0.05)	0
44	0.91 (0.91)	0	0.25 (0.25)	0
45	0.91 (0.91)	0.0001	0.13 (0.13)	0
46	0.97 (0.97)	0.51	0.29 (0.29)	0

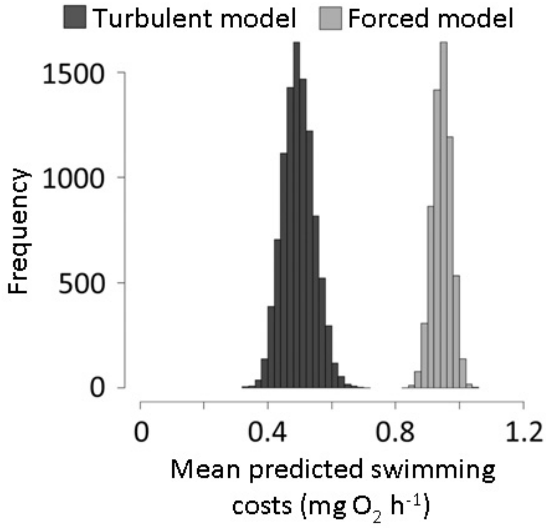


Figure 5.9 – Null distributions for the forced and turbulent SC equations taken from permutation tests.

Due to the correlation structure of hydrodynamic properties (U and L_u, for instance, were highly correlated; *r* = 0.96) (Figure 5.11) only U, τ_{uv}, τ_{uw} and V_{grad} were entered as explanatory variables for the bespoke model. In the case of τ_{uw}, the magnitude of turbulence-related disturbances on this horizontal plane, rather than the direction, is of most interest, thus absolute values were used ($Abs\tau_{uw}$). Model selection proceeded by dropping each explanatory variable in turn from the count and binomial models. Reynolds stresses were the weakest contributing variables to the model and, therefore, the effect of dropping both of these variables simultaneously was explored. The solution which dropped both τ_{uv} and $Abs\tau_{uw}$ from the count model was optimum as this was the most parsimonious model with a low AIC compared to the full model (Table 5.3). All coefficients for both the count and binomial components of this optimum model were significant (Table 5.4). Predicted SI was negatively related to U and V_{grad}, whilst the probability of finding false zeros was also negatively related to Reynolds stresses (Figure 5.12). The AIC of the hydrodynamic model was lower than either of the SC models (6925.55 < 6967.16 < 6971.97).

Table 5.2 – Results of ZINB modelling for the forced and turbulent SC models.

Term	**Estimate**	**SE**	**z value**	***p***
Forced equation	$g(\mu)$			
(Intercept)	3.80817	0.45578	8.355	$< 2 \times 10^{-16}$
FTSC	-4.40597	0.45379	-9.709	$< 2 \times 10^{-16}$
log (theta)	-3.14336	0.05596	-56.172	$< 2 \times 10^{-16}$
	$g(\pi)$			
(Intercept)	11.542	7.156	1.613	0.107
FTSC	-19.244	11.705	-1.644	0.100
			Log-lik = -3481 on 5 Df	
			AIC = 6971.97	
Turbulent equation	$g(\mu)$			
(Intercept)	0.1009	0.1521	0.664	0.507
CR	-0.8979	0.1129	-7949	1.87×10^{-15}
log (theta)	-3.1132	0.1287	-24.186	$< 2 \times 10^{-16}$
	$g(\pi)$			
(Intercept)	-1.829	1.127	-1.622	0.105
CR	-1.214	0.817	-1.486	0.137
			Log-lik = -3504 on 5 Df	
			AIC = 6967.16	

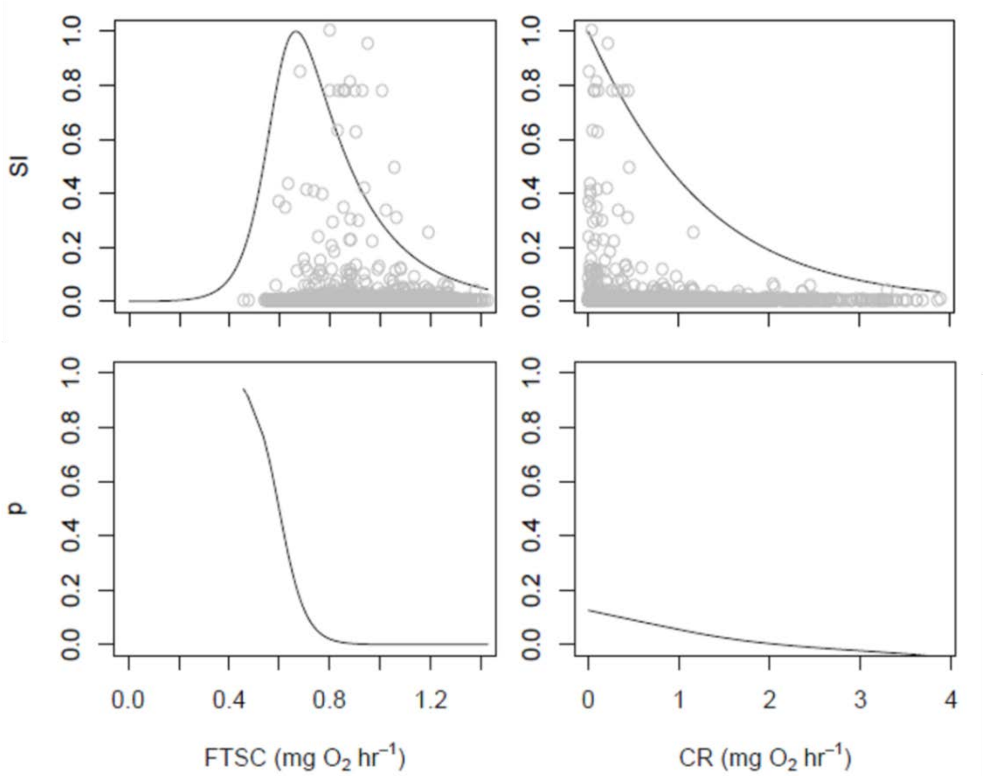


Figure 5.10 – Count (upper) and binomial (lower) model results for the forced ($FTSC$) and turbulent (CR) equations. Count model predictions standardised (μ_i / μ_{max}) to visualise results. Symbols denote observed selection index (SI) for each cell.

Table 5.3 – Summary of ZINB model selection for the bespoke hydrodynamic model.

Dropped term	**df**	**AIC**	**LR test**
None	11	6926.53	
U from count model	10	6938.33	X^2 = 13.8 (df = 1, p = 2.03 x 10^{-9})
V_{grad} from count model	10	6932.62	X^2 = 8.0965 (df = 1, p = 0.00444)
τ_{uv} from count model	10	6925.05	$X2$ = 0.5291 (df = 1, p = 0.467)
$Abs\tau_{uw}$ from count model	10	6927.45	X^2 = 2.92 (df = 1, p = 0.0875)
U from binomial model	10	6936.66	X^2 = 12.128 (df = 1, p = 4.97 x 10^{-4})
V_{grad} from binomial model	10	6938.52	X^2 = 13.989 (df = 1, p = 1.84 x 10^{-4})
τ_{uv} from binomial model	10	6945.09	X^2 = 20.567 (df = 1, p = 5.76 x 10^{-7})
$Abs\tau_{uw}$ from binomial model	10	6964.76	X^2 = 40.231 (df = 1, p = 2.26 x 10^{-10})
τ_{uv} and $Abs\tau_{uw}$ from count model	9	6925.55	X^2 = 3.0203 (df = 2, p = 0.221)
τ_{uv} and $Abs\tau_{uw}$ from binomial model	9	6964.11	X^2 = 41.584 (df = 2, p = 9.34 x 10^{-10})
τ_{uv} and $Abs\tau_{uw}$ from both models	7	6963.14	X^2 = 44.614 (df = 4, p = 4.78 x 10^{-9})

Table 5.4 – Results of ZINB modelling for the optimal bespoke hydrodynamic model.

Term	**Estimate**	**SE**	**z value**	p
	$g(\mu)$			
(Intercept)	1.31874	0.18825	7.005	2.47 x 10^{-12}
U	-0.14748	0.02827	-5.217	1.82 x 10^{-7}
V_{grad}	-0.29105	0.09463	-3.076	0.0021
log (theta)	-2.62764	0.099	-26.543	< 2 x 10^{-16}
	$g(\pi)$			
(Intercept)	0.47686	0.27764	1.718	0.08588
U	0.16404	0.05232	3.135	0.00172
V_{grad}	-0.60384	0.17324	-3.485	4.91 x 10^{-4}
τ_{uv}	-0.05798	0.01423	-4.074	4.62 x 10^{-5}
$Abs\tau_{uw}$	-0.09924	0.03010	-3.297	9.77 x 10^{-4}
			Log-lik = -3454 on 9 Df	
			AIC = 6925.55	

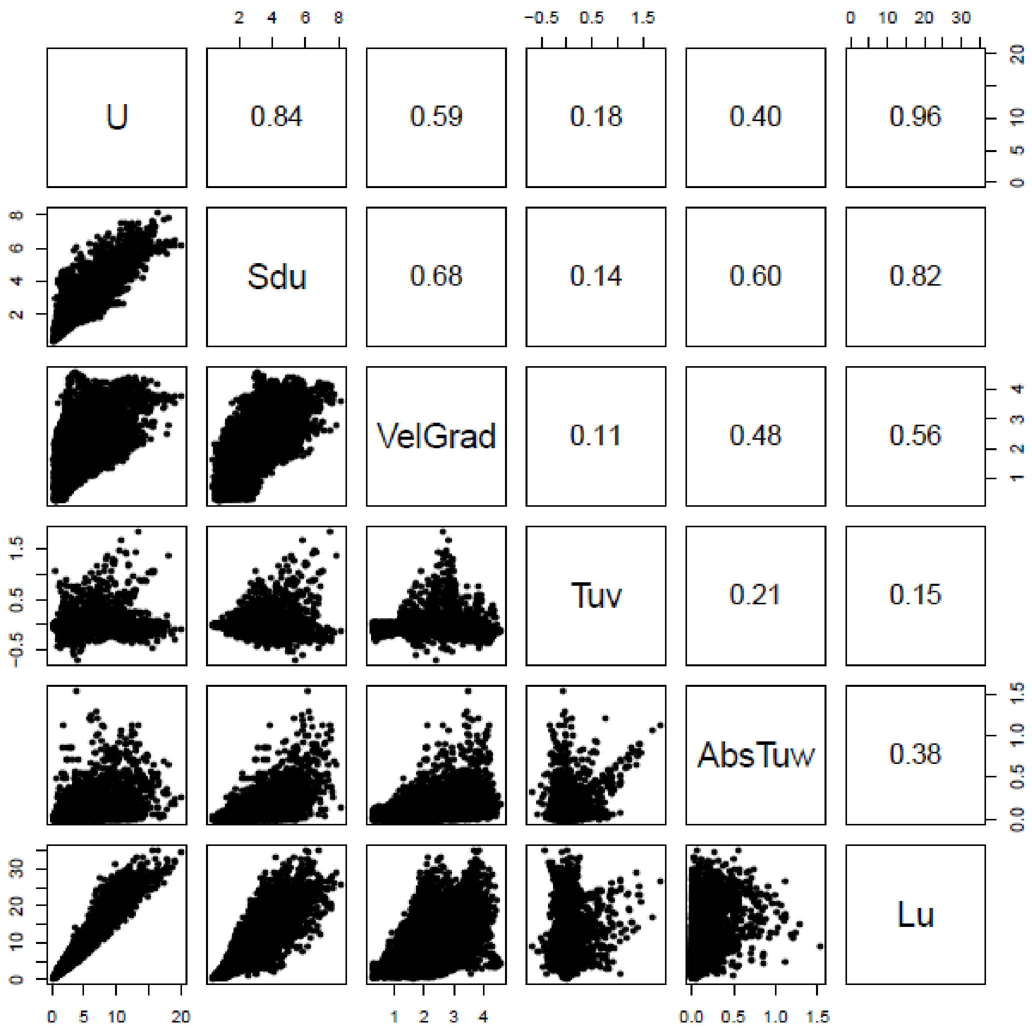


Figure 5.11 – Correlation structure of data considered for the bespoke hydrodynamic model. Upper-right panels show Pearson product-moment correlation coefficients (r).

5.4 Discussion

Though some bioenergetic models have assumed that energetic costs do not significantly influence habitat selection (*e.g.* Nislow *et al.*, 1999), many do include the costs of swimming based on empirical equations from laboratory experiments (*e.g.* Hughes and Dill, 1990; Hill and Grossman, 1993). **This chapter presents indirect evidence to suggest that swimming energetics does affect position choice in Atlantic salmon parr**. Furthermore, **the results support the use of turbulent flow properties in habitat modelling for this species and life-stage, lending credence to a mesohabitat classification based on hydrodynamics**.

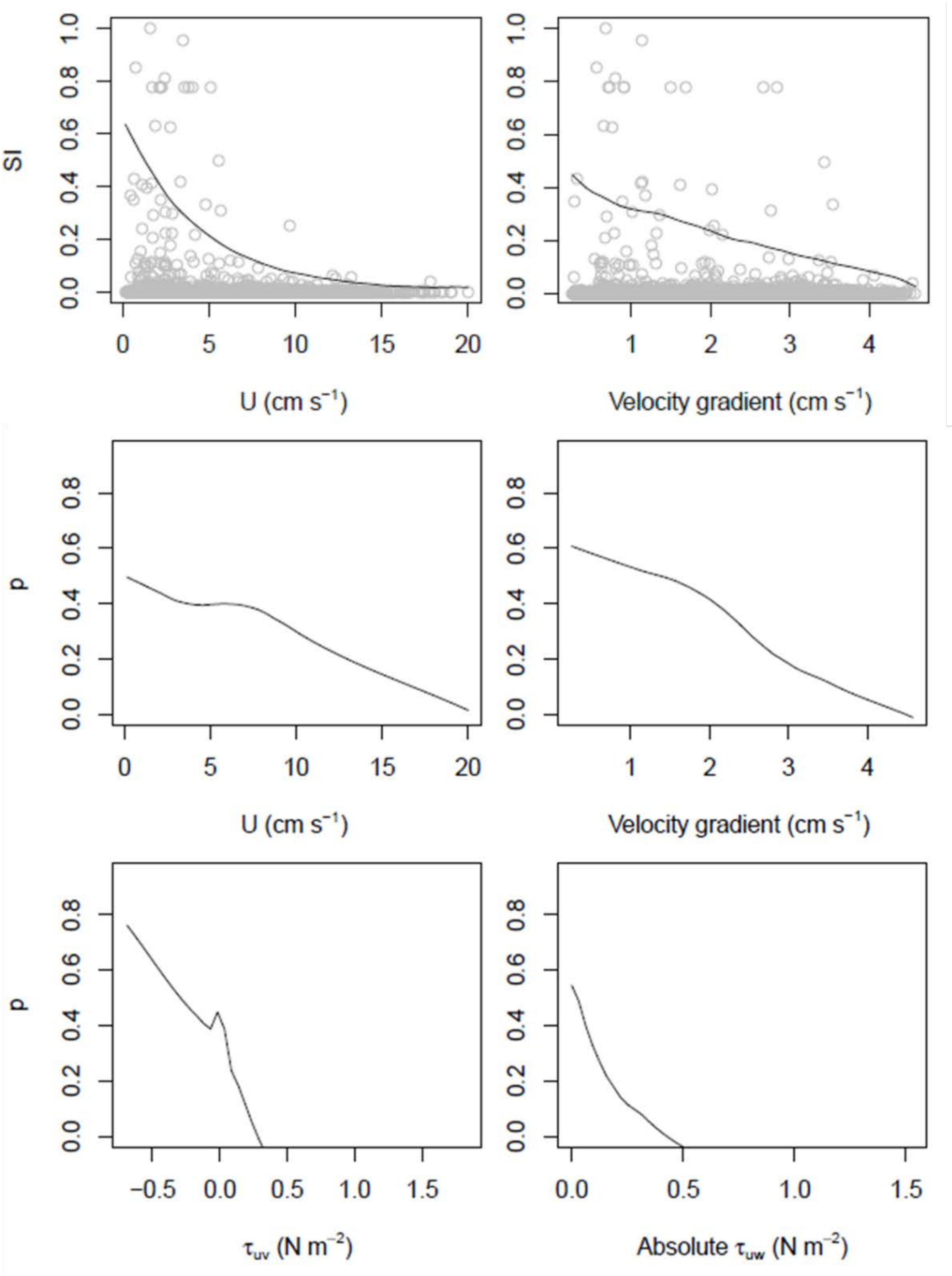


Figure 5.12 – Contributions of explanatory variables included in the count (upper) and binomial (lower) components of the optimal bespoke hydrodynamic model. Count model results standardised (μ_i / μ_{max}) and all model predictions smoothed using a loess smoother (span = 0.5) to visualise results. Symbols denote observed selection index (*SI*) for each cell.

The results of permutation tests and ZINB modelling using the SC equations both support the idea that **fish avoided areas associated with high SC**. This relationship was clearest for the turbulent SC model suggesting that, in high Re flows, **parr do not exploit zones of elevated turbulence behind obstacles to gain an energetic advantage**, as proposed by Liao *et al*. (2003a, b) and Liao (2004) in the case of rainbow trout. The structure of the turbulent SC equation (Enders *et al*., 2005), and the inclusion of a term to describe turbulence intensity, meant that it was better able to predict the habitat selection of 42 parr than a model based on forced swimming at mean velocity (Boisclair and Tang, 1993). This is surprising given that these equations are based on the results of respirometer studies where fish were forced to swim in the free-stream; Atlantic salmon parr are known to use large pectoral fins to 'anchor' themselves to the bed (Arnold *et al*., 1991), a behavioural trait observed in many fish used in this study. That the turbulent SC model fitted the response of parr better may, at least partially, be due to the fact that it is derived from studies on Atlantic salmon parr of a similar age and size as used in this study. The forced model, on the other hand, was developed using sockeye salmon (*Oncorhynchus nerka*) and rainbow trout (*O. mykiss*).

A bespoke hydrodynamic model which included mean velocity, velocity gradient and Reynolds stresses performed better than either SC equation, as evidenced by a substantially lower AIC despite the model being less parsimonious. Whilst a negative relationship between mean velocity and habitat selection was expected on an energetic basis, it was surprising that the velocity gradient was also negatively related to position choice given that the feeding behaviour of juvenile salmonids makes them better suited to focal positions with low mean velocity that are situated close to zones of high velocity (Hayes and Jowett, 1994; Booker *et al*., 2004). Previous work has indicated that turbulent flow properties are poorly correlated with mean velocity (Smith and Brannon, 2007; Roy *et al*., 2010). Data presented here shows that, in this case, there were strong correlations between mean and turbulent flow descriptors. This is particularly true of eddy length, making any evaluation of the ideas of Pavlov *et al*. (2000), Lupandin (2005) and Tritico and Cotel (2010) impossible. Future laboratory research should use reductionist techniques to examine the relative effects of mean velocity and eddy size on the swimming stability of parr.

Reynolds stresses, which describe the magnitude and direction of turbulence-related disturbances, were independent of mean velocity and were included in the binomial component of the optimum hydrodynamic model. Results presented in Figure 5.12 show that negative values of τ_{uv} were associated with 'good' habitat, whereas high positive values were not. This suggests that parr exhibited a preference for locations at which there was a net flux of turbulent momentum towards the bed, presumably because this aided station-holding. Results also indicated that areas of high absolute τ_{uw} did not represent 'good' habitat. That Reynolds stresses were not included in the optimum count model and did not, therefore, have a stronger effect on habitat selection is perhaps because maximal values were two orders of magnitude lower than previous laboratory experiments reporting a clear avoidance of high Reynolds stress zones (Silva *et al*., 2011; 2012).

There are several factors which could have confounded these results. Firstly, parr were assumed to be responding to hydraulics but, although trials were performed in darkness and the artificial habitat features (hemispheres) were transparent, the possibility that parr selected locations based on proximity to physical structures (*e.g.* hemispheres or netting) cannot be ruled out. Secondly, the data analysis methods used ignore the possibility of strong spatial intercorrelation in the response of individual fish. If it is assumed, as the results suggest, that parr chose energetically favourable locations then a third related factor is the possibility that parr chose local, rather than global, energetic minima (*i.e.* that they are only selecting the 'best' habitat from a small area). The use of random starting co-ordinates and the time allowed for acclimation and habitat exploration was an attempt to mitigate this. Furthermore, many fish were observed to be rapidly moving around the test arena, indicating that they were able to 'sample' the available habitat.

A further potential confounding factor relates to the realism of flume or 'mesocosm' experiments. In the specific case of studying relations of riverine biota to hydraulics in flumes, Rice *et al*. (2010) suggest that four factors should be considered. These factors are the subject's responses to the physico-chemical environment; the presence of measurement instruments; the physical environment; and the simplified biotic environment. During this experiment, physico-chemical parameters were monitored and kept to levels typical of the donor stream (*e.g.*. pH, temperature, ammonia) and parr were left in holding tanks supplied with the same water as the flume to acclimate for one week prior to experiments. It was assumed that the presence of measurement instruments would have no effect on the fish as the only device present in the arena was an infra-red camera suspended approximately 3 m above the water surface. The experimental arena used in this study was designed to maximise realism of the physical environment. The flume was setup to provide parr with a choice of habitats spanning the range that they are known to use in natural environments (Table 1.8). One of the greatest challenges of conducting mesocosm experiments is often related to scale. From a hydrodynamic perspective, this may be due to wall effects, blocking effects or the development of a fully developed boundary layer (Rice *et al*., 2010; Lacey *et al*., 2012) The relative scale of the study organism and the artificial environment created is also a critical consideration. In terms of flume width, Jonsson *et al*. (2006) recommend that this should exceed $2\delta+bl$ in order to avoid wall and blocking effects and to promote realism The maximum value of this threshold for this experiment is approximately 100 mm, far less than the width of the flume used (2 m). To ensure that the boundary layer is fully developed, Lacey *et al*. (2012) recommend that the flume length is >50h. Given an average depth in the flume of 165 mm, the flume length of over 50 m can be considered more than sufficient. One final problem related to scale is that of nesting. Several studies have found that position choice in fish is not only a function of the immediate environment but also the characteristics of adjacent habitat conditions (Inoue & Nakano, 1999; Schwartz & Herricks, 2008; Hauer *et al*. (2011). Indeed, conceptions of rivers as 'riverscapes' are highly suggestive that habitat selection occurs over multiple scales (Schlosser & Angermeier, 1995; Fausch *et al*., 2002; Wiens, 2002). Given the limited time and space available for this experiment, however, it was not possible to investigate position choice as a spatially nested phenomenon.

The realism of the biotic environment is more difficult to incorporate into flume studies. Three points are worth considering here in relation to the realism of this experiment: the absence of competitors; the absence of predators; and the lack of food resources. Atlantic salmon parr exhibit territorial behaviour and are prone to aggressive displays towards conspecific competitors. Mikheev *et al*. (1994) and Kemp *et al*. (2005; 2006) all found that social dominance influenced position choice, with dominant individuals occupying more favourable feeding and cover locations, which are likely to be associated with relatively high turbulence intensities (Wilkes *et al*., 2013). Furthermore, predator presence is known to increase cover use in salmonids (Jonsson, 1997; Reinhardt & Healey, 1997). The evaluation of these influences on position choice was outside of the scope of this chapter but future flume studies should consider incorporating them. The fact that no food resources were supplied is another factor that potentially compromises the realism of this study. However, as the fish were starved for 24 hours prior to trials, it is likely that they were searching for suitable feeding locations in much the same way that they would in nature, using their distinctive 'sit-and-wait' feeding strategy (Cunjak, 1988; Guay *et al*., 2000).

Although the bespoke hydrodynamic model presented here performed better than models based on SC equations, it is prone to the same criticism that has been directed at traditional hydraulic habitat models in that it is merely correlative (Lancaster and Downes, 2010). Bioenergetic models have been heralded as a solution yet their application has been limited due to their complexity and resource-intensiveness, leading to calls for the simplification of such process-based approaches (Dunbar *et al*., 2012). Instead, due to its mechanistic foundation, it is speculated that the model based on turbulent SC is suitable for inclusion as a habitat suitability criterion in hydraulic habitat models as it is a compromise between parsimony and causality. Future research should investigate the accuracy of predictions made using this model in field settings. A similar approach may be applicable to other river-dwelling life-stages of salmonid species, and possibly coarse fish species, but empirical relationships between flow and SC are likely to be species-specific. Further respirometer studies will be valuable in this respect.

5.5 Conclusions

This chapter sought to link the issues of ecological relevance (Chapter 3) and hydrodynamic distinctiveness (Chapter 4) associated with the mesohabitat concept. Through its effect on fish swimming performance, stability and energetics, turbulence was expected to influence position choice in Atlantic salmon parr. This is important because bioenergetic models currently either omit any parameters describing swimming energetics (*e.g.* Nislow *et al*., 1999) or predict SC using a model which has U as its only hydraulic parameter (*e.g.* Booker *et al*., 2004). Of two existing SC models developed for salmonids, a model including SD_u (turbulent model; Enders *et al*., 2005a) was better able to predict the position choice of 42 parr than a model that did not include any terms describing turbulence (forced model; Boisclair & Tang, 1993). Furthermore, the expected negative relationship between SC and habitat selection was observed for the turbulent model but not for the forced model. Although a bespoke hydrodynamic model including U, V_{grad} and Reynolds stresses performed better than either SC model, it is suggested that the turbulent SC model of Enders *et al*. (2005a) is most suitable for application in bioenergetic modelling due to its mechanistic foundations. **These results support the development of a hydrodynamic habitat classification in the case of Atlantic salmon, which is considered a model organism for ecohydraulic studies** (Aas *et al*., 2011).

6

Conclusions

Chapter overview

This thesis combined the mesohabitat concept with knowledge of turbulence in rivers and its effects on bioenergetics. Chapter 1 established the motivation for the research and identified the objectives associated with each chapter. Chapter 2 argued that the ecological and theoretical bases for the mesohabitat concept were weak and identified community-level analyses and hydrodynamic classification respectively as means with which to make progress. Chapter 3 used community-level modelling in order to strengthen the ecological basis. Based on a review of the literature on the hydrodynamics of river ecosystems and its interactions with biota and morphology (Wilkes *et al*., 2013; Appendix C), Chapter 4 sought to assess the characteristics of turbulence in physical biotopes and develop a new hydrodynamic classification of mesohabitats. In developing the classification, Chapter 4 strengthened the theoretical basis for the use of the mesohabitat concept. Chapter 5 linked the ideas of hydrodynamic classification and ecological relevance by showing that turbulence affects the habitat selection of Atlantic salmon parr. Each of these main findings has implications for river research and management activities. In particular, the results could lead to new approaches to river habitat assessment and modelling and help guide activities seeking to conserve aquatic biota and rehabilitate river environments but further work is required to test the validity and transferability of the results.

6.1 Introduction

The overall aim of this research was:

> *to strengthen the theoretical and ecological bases for mesoscale approaches to river habitat assessment, modelling and rehabilitation by developing a new, ecologically relevant and readily applicable hydrodynamic classification of mesohabitats*

This was met by combining three recent trends in approaches to river research, namely the **mesohabitat concept** (Newson & Newson, 2000), the **hydrodynamics of river ecosystems** (Nikora, 2010) and **bioenergetic modelling** (*e.g.* Dunbar *et al*., 2012), in order to drive progress in key river management applications (Figure 1.1). The main findings of the project are summarised below (S 6.2) before the implications for river research and management activities are discussed (S 6.3). Finally, the thesis concludes with recommendations for future research in related areas of river science (S 6.4).

6.2 Main findings

Chapter 1 established ecological degradation, modern environmental legislation and the **practicality and cost-effectiveness of mesoscale (10^0-10^2 m) approaches** to river research and management as the principal motivating factors for this thesis. It set the disciplinary context, identifying the **combination of holistic (Darwinian) and reductionist (Newtonian) philosophies** as a means of making progress within sub-disciplines of hydroecology, including ecohydraulics - the study of links between flow forces and aquatic biota. The thesis integrates Harte's (2002) 'elements of synthesis' and Newman *et al*'s (2006) idea of hierarchical scaling theory. Figure 6.1 conceptualises this in terms of this combination of philosophical approaches and illustrates the relationships between results chapters. Chapter 1 further recognised Atlantic salmon as a model organism in river ecology and bemoaned the **major knowledge gaps remaining in our understanding of ecohydraulic relationships**. It recommended key **priorities for the improvement of river management activities** associated with habitat assessment, modelling, rehabilitation and conservation. Finally, it outlined five research objectives around which the thesis is organised (Table 1.1). The main findings associated with each of these objectives are outlined below.

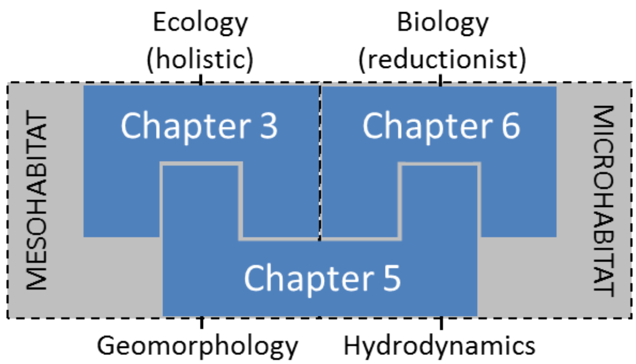


Figure 6.1 – The relationships between results chapters, disciplinary areas, conceptual frameworks (in parentheses) and habitat scale associated with this thesis.

6.2.1 Clarify the relationships between existing mesohabitat classifications and review their ecological and theoretical bases

Chapter 2 introduced the concept of mesohabitats and presented a new typology of mesohabitat classifications in order to combat confusion due to a lack of common terminology (Figure 2.1). It **identified the PB (*e.g.* pool, riffle, run, glide) as a practical mesohabitat classification** for hydroecological research and river management but noted that **associations between habitat types and single species, families or guilds are only loosely known**, particularly in large rivers where the mesohabitat concept is relatively poorly developed. **It proposed community-level analyses as a suitable approach** to test the ecological relevance of the mesohabitat concept.

6.2.2 Strengthen the ecological basis for mesohabitat classification

The idea of a community-level approach was taken up in **Chapter 3**, which modelled fish assemblage structure in the relatively large San Pedro River, Chile. This chapter reported that **up to 60% of variation in the relative abundance of fish making up communities within mesohabitats could be explained** using only a small set of environmental predictor variables describing *h*, bank materials, cover and woody debris (Table 3.7 and 3.8). Though the holistic approach taken was merely correlative, by showing that fish communities are structured at the mesoscale **the results presented in Chapter 3 support the application of the mesohabitat concept**.

6.2.3 Review the theory, structure and measurement of turbulence in rivers

Chapter 2 also reviewed the calibration of mesohabitat classifications, which has generally relied on the so called 'standard hydraulic variables' of h, U and Fr. It found **limitations in existing approaches to hydraulic calibration and proposed a new classification based on hydrodynamics** as a way to strengthen the theoretical basis for the mesohabitat concept and to aid the objective identification of habitat types. Wilkes *et al*. (2013) laid down **the prerequisite understanding of turbulent flow phenomena and their measurement** necessary for developing a new hydrodynamic classification (Appendix C). In particular, aspects of turbulence describing its intensity, periodicity, orientation and scale as potentially useful metric were outlined and the occurrence of coherent flow structures linked to morphological features at different scales. Finally, **the implications of turbulence theory, structure and measurement for the classification of Mesohabitats were discussed**, setting the context for Chapter 4.

6.2.4 Construct a hydrodynamic classification of mesohabitats

Based on the discussion presented in Wilkes *et al*. (2013) (Appendix C), **Chapter 4 hypothesised that PBs exhibit distinctive hydrodynamics due to their contrasting morphology**. Using a semi-objective mesohabitat mapping and clustering procedure, it focused on a representative sample of commonly found PBs from two lowland rivers representing a spectrum from relatively steep, pristine streams with coarse substrata to relatively sinuous, impacted rivers with finer bed materials. Through high resolution measurement of turbulent flow at three discharges it reported consistent differences between PB types across flow stages and between sites. **The gradient pool<glide<run<riffle was generally found to be associated with increasing turbulence intensity, Reynolds stresses and L_u and decreasing passage time of the largest, turbulence producing eddies**. It portrayed pools as relatively quiescent habitats with a simple flow structure compared to highly turbulent riffles characterised by a wide range of eddy sizes.

It found that an existing classification (Figure 4.5) based on the spatial and temporal (discharge related) variability of turbulent flow within PBs did not match the data well (Figure 4.39). Instead, using classification trees, it proposed **a new hydrodynamic classification based on the absolute magnitude of turbulent flow properties** as a more practical and effective solution (Figures 4.44, 4.46 and 4.48).

6.2.5 Test the ecological relevance of the hydrodynamic classification

Any habitat classification should have ecological relevance (*i.e.* do the model parameters affect the fitness of individuals and, therefore, the distribution of populations?) but **the strength and direction of the relationship between turbulence and biota is poorly understood**, even for a relatively well-researched species, Atlantic salmon. **Chapter 5 sought to fill this knowledge gap by analysing the habitat selection of Atlantic salmon parr in relation to turbulence** within an artificial habitat constructed in the laboratory. It outlined the possible mechanisms responsible for avoidance or attraction to locations within habitats associated with elevated levels of turbulence and **hypothesised that parr would occupy positions that minimised the energetic cost of swimming**. Of two competing models for the prediction of SC in juvenile salmonids (Boisclair & Tang, 1993; Enders *et al*., 2005a), it reported that a model including a parameter describing turbulence intensity was better able to predict position choice than a model with U as the only hydraulic term (Figure 5.10). **86% of parr chose areas with significantly lower turbulent SC** than expected if fish chose locations at random (Table 5.1, Figure 5.9). Locations with low U, low V_{grad}, low τ_{uw} and negative τ_{uv} were found to represent good habitat (Figure 5.12). The **results support the application of a hydrodynamic classification** of mesohabitats by illustrating that turbulence does affect the habitat selection of Atlantic salmon parr.

6.3 Implications for river research and management

6.3.1 Habitat assessment

Several commentators have clarified the theoretical bases for monitoring physical habitat conditions in rivers (Harper & Everard, 1998; Boulton, 1999; Maddock, 1999) and the assessment of hydromorphological quality is a requirement under the WFD (EC, 2000). Despite this, most current habitat assessment methods require expert geomorphological knowledge (Downs & Gregory, 2004) and lack ecological relevance (Vaughan *et al*., 2009). Furthermore, rapid techniques for habitat inventorying rely on highly subjective classifications of mesohabitat types (Roper & Scarnecchia, 1995; Poole *et al*., 1997; Roper *et al*., 2002). The hydrodynamic classification presented in Chapter 4 has the characteristics required to overcome these difficulties. Its application would require no expert knowledge, only the ability to follow well-established data collection and processing protocols (Wilkes *et al*., 2013; Appendix C).

It is possible to envisage **two alternative methods incorporating the hydrodynamic classification**, one requiring the prior delineation of habitat units and the other involving systematic data collection based on a reach-scale grid. The former application would require subjective choices regarding the boundaries between mesohabitats but the classification of habitat membership based on hydrodynamic measurements from the core of habitat units would represent an objective approach. The latter application would require no subjective judgements but would be time consuming and labour intensive. In either case, though a decision must be made regarding which classification model to use depending on target biota and river characteristics (*i.e.* near bed/benthic or point-six/pelagic), **the passing of hydrodynamic data through the appropriate classification tree represents a highly efficient and objective means of assigning habitat membership**. As the classification was developed using standardised data the methods could be applied at any discharge, though it would not be recommended at flows higher than Q_{50} due to the poor performance of the classifications for high flow time series (*e.g.* Figure 4.49). The suggested reason for this poor performance is the lessening effect of morphology on hydraulics as flow stage increases, a phenomenon reported by Clifford *et al*. (2002) and Emery *et al*. (2003).

6.3.2 Habitat modelling

Traditional ‘habitat-hydraulic’ or ‘HSI-based’ models (*e.g.* PHABSIM) have been criticised on numerous grounds, including their lack of transferability, their poor predictions and interpretability and their inadequate characterisation of habitat from an ecologically realistic perspective (S 1.5.2). Sound predictions of the response of biota to anthropogenic impacts and conservation and rehabilitation activities are required to guide management decisions. Mesoscale (*e.g.* Parasiewicz, 2001; Schneider *et al*., 2005) and bioenergetic (*e.g.* Hughes & Dill, 1990; Booker *et al*., 2004) models have separately been proposed as effective alternatives to traditional models. Together they have all of the required remedial properties (Table 1.9) yet, to the author's knowledge, there have been no attempts to combine the two approaches. An alternative, more simplistic incorporation of turbulent SC would involve replacing the mean velocity term in traditional habitat models such as PHABSIM (Figure 1.10) with the habitat suitability curve presented in Figure 5.10. If developed further, either of these techniques would **represent a more mechanistic approach to single species or species-by-species modelling**. Many commentators, however, have bemoaned the lack of habitat models at other ecological levels than species, such as the community-level (Murchie *et al*., 2008; Vaughan *et al*., 2009). Chapter 3 illustrated the utility of multivariate regression trees as a form of community-level modelling. This type of model is capable of considering any variable thought to affect, either directly or indirectly, the habitat selection of biota (De'ath, 2002). Though variables describing SC would be inappropriate due to their species-specific nature**, further understanding of general energetic relationships between biota and turbulence could lead to the inclusion of hydrodynamic variables in community-level models. Thus future approaches could be simultaneously mesoscale, bioenergetic, multivariate and community-level**.

6.3.3 River conservation and rehabilitation

River rehabilitation has become a key management activity, not least because it is crucial for achieving targets set by the WFD (Newson, 2002; Skinner & Bruce-Burgess, 2005). Despite the fact that it has become a lucrative industry (Bernhardt *et al*., 2005), very little PPA is carried out to appraise rehabilitation efforts and feedback into good practice (Clarke *et al*., 2003; Bernhardt *et al*., 2007). The major priorities for progress in these areas are similar to those for habitat assessment but, in addition, there is a requirement for flexible, generalisable design criteria for a range of habitats (Biron *et al*., 2004; Miller & Hobbs, 2007) and a need to establish standard approaches to PPA (Bernhardt *et al*., 2005; Vaughan *et al*., 2009). A major question in river restoration remains surrounding the failure of many projects to elicit a biological response (*e.g.*

Pretty *et al*., 2003; Jähnig *et al*., 2011), highlighting our incomplete understanding of ecological processes (Mika *t al*., 2010) such as the relationships between morphology, hydrodynamics and fish. There is a need to understand what makes the installation or removal of instream structures, such as woody debris (Crook & Robertson, 1999), fish passes (Larinier & Marmulla, 2004) or weirs (Garcia de Leaniz, 2008; Kemp & O'Hanley, 2010) work or not.

The morpho-hydrodynamic relationships identified in Wilkes *et al*., (2013) (Appendix C) and applied in Chapter 4 have the potential to guide and evaluate rehabilitation attempts, whatever the options for rehabilitation may be (*sensu* Figure 1.12). These relationships describe the interaction between flow and morphology (*e.g.* particle sizes, bed level) which results in a range of hydrodynamic features that are associated with different turbulence intensities, eddy sizes and orientation (Wilkes *et al*., 2013; Appendix C). Chapter 5 has shown, albeit for a single species, how these features can affect biota. Through erosional and depositional processes they also affect morphological change (Best, 1993), indirectly influencing community structure and potentially compromising the sustainability of rehabilitation solutions. An additional contribution from this thesis, therefore, is a **set of design criteria for common mesohabitats contained within Chapter 4**.

Several other opportunities to improve river restoration approaches identified in Chapter 1 (S 1.5.3) are worth revisiting in light of the findings contained in this thesis. Many commentators have highlighted the difficulties associated with defining a 'target' ecosystem when designing river restoration projects due to a lack of 'natural' or 'reference' conditions (*e.g.* Ward *et al*., 2001; Palmer *et al*., 2005). Identified by Maddock & Hill (2007) as 'pristine', **results presented in Chapter 4 for the Leigh Brook, and their subsequent incorporation into classification trees, represent a guide to reference conditions in this geographical context**. Target conditions are often based on the desire to increase spatial and temporal dynamicity in hydromorphic conditions (Biggs *et al*., 2005; Thoms *et al*., 2006; Palmer *et al*., 2007) and this thesis has both described that dynamicity at the mesoscale and related it to biological response. Recovery potential is another important consideration in optimising river restoration efforts (Brookes, 1992; Downs & Gregory, 2004; Newson & Large, 2006) and has been related to stream power and sediment supply (Figure 1.12). Because turbulence plays a key role in sediment transport processes (Bagnold, 1966; Best, 1993) it is the ideal basis for a river restoration design framework. Furthermore, it is also extremely relevant to the restoration of flow regimes encompassing flushing and channel maintenance flows (Petts, 1996; Poff *et al*., 1997; Bragg *et al*., 2005; Petts, 2009). **Ultimately, a simplified version of the classification procedure could be applied as a measure of rehabilitation performance that integrates complex hydromorphic factors with ecological relevance that are otherwise difficult to measure.**

The legislature (EC, 1979; 1992; UNESCO, 1994) sets strict targets for the conservation of individual species, including Atlantic salmon, and river habitats (S 1.3.4). Despite this conservation targets continue to be failed (*e.g.* Figure 1.14). Chapter 1 outlined the identification of key biophysical linkages determining juvenile salmonid production as a major priority. Chapter 5 makes a clear contribution to the knowledge in this area by showing that elevated turbulence results in increased energetic costs to Atlantic salmon parr in a way that affects their habitat selection. **Due to the morpho-hydrodynamic relationships identified above, this biophysical relationship means that parr response to management activities, such as the widespread addition of coarse substrata, may result in undesired outcomes** (*e.g.* Nislow *et al*., 1999; EA, 2003b).

Chapter 3 showed how community-level analysis can help to further our understanding of fish assemblage structure by integrating the effects of biological interaction, leading to new knowledge on the impacts of invasive salmonids on the native *G. platei* in the San Pedro River, which appeared to be mediated by flow depth (S 3.4). Existing knowledge of the impacts of salmonid introductions on galaxiids was previously limited to lentic habitats (Macchi *et al*., 2007; Arismendi *et al*., 2009; Habit *et al*., 2010; 2012; Correa *et al*., 2012). Chapter 3 also established other species of high conservation value as indicator species (*e.g. D. camposensis*, *P. gillissi*) and provided valuable new information on their mesoscale habitat affinities. Crucially, the results raise the **possibility of mesoscale predictive mapping of whole river basins**. This approach **represents a highly efficient means of biodiversity modelling** for ecosystem conservation and management purposes (Ferrier & Guisan, 2006).

6.3.4 Geomorphological and turbulence theory

The final set of implications arising from this research relate to geomorphological and turbulence theory. Firstly, the statistical framework for studying hydrodynamics suggests that turbulence is exported from the bed towards the surface (Nezu & Nakagawa, 1993). Thus turbulence intensity is expected to increase with proximity to the bed. The results presented in Figures B12 and B53, however, show that TKE could either increase or decrease with y, casting doubt on the applicability of turbulence theory developed in the laboratory to gravel and mixed bed rivers. The dimensionality of turbulence detected in mesohabitats also deviated from that expected based on theory, with $SDw:SDu$=0.88 and $SDv:SDu$=0.68 compared to 0.71<$SDw:SDu$<0.75 and 0.5<$SDv:SDu$<0.55 quoted in the theoretical literature (Nezu & Nakagawa, 1993). These deviations from theory have been ascribed to the high Re and depth-limited nature of flow in these hydraulically rough environments (Buffin-Bélanger & Roy, 1998; Lacey & Roy, 2007).

In terms of the coherent flow structure (CFS) framework (Appendix C), several findings presented in Chapter 4 further our understanding or question existing knowledge on the relationship between hydrodynamics and morphology at different scales (*i.e.* morpho-hydrodynamics). At a relatively small scale, CFSs associated with protuberant clasts and bedforms such as pebble clusters were shown to scale with measures of D. This supports the use of the Strouhal relationship (Eqn. 4.15) and corroborates previous findings showing that 0.18<S<0.2 (Clifford & French, 1993b; Lacey & Roy, 2008; Harvey & Clifford, 2009). At the macroturbulent scale, Roy *et al*. (2004) reported that the largest eddies rotating on a spanwise axis scaled with flow depth in a gravel bed river so that $3<ILS_u/h<5$, whereas observations from the laboratory suggest that the relationship may be closer to $ILS_u/h=1$ (Liu *et al*., 2001). Results from both study sites presented in Chapter 4, however, indicate that $ILS_u/h<1$ except in the case of runs and riffles at high flow (>Q_{35}) (Figure 4.53). The explanation for this scaling is unclear and further work is required in this area.

6.4 Future research priorities

This thesis highlights several areas that would benefit from further study. These areas pertain to the three approaches to modern river science identified at the outset (Figure 1.1), namely the mesohabitat concept, the hydrodynamics of river ecosystems and bioenergetic modelling.

Two research areas connected with the mesohabitat concept are ripe for further study. These relate to the ecological relevance and physical distinctiveness of mesohabitats. Though this thesis has made advances in these areas there is **still much work to be done to test the validity and transferability of the findings**. In terms of ecological relevance, Chapter 3 used community-level modelling to strengthen the ecological basis for mesohabitat classification and, in doing so, made a case for applying the same approach to other river types and biotic groups. In particular, the analysis of macroinvertebrate assemblage structure at the mesoscale, where only loose associations between mesohabitats and taxa generally identified to family level have been established (*e.g.* Principe *et al*., 2007; Hill *et al*., 2008; Reid & Thoms, 2008), would benefit from a community-level approach. There is a need to test the ability of models developed in Chapter 3 to predictively map fish communities in out-of-bag mesohabitats (*i.e.* those not sampled) along the study reach. If successful, this model could be extended to include the full range of mesohabitats found throughout the San Pedro system, which is characterised by high levels of endemism (Habit & Victoriano, 2012). This is particularly important given the threat of HEP construction and operation (Habit & Parra, 2012).

With respect to the physical distinctiveness of mesohabitats, Chapter 4 showed that a combination of variables describing turbulent flow could be used to good effect in classifying common mesohabitats. The hydrodynamic classification, however, was based on just two rivers without replication. There is a pressing need to validate this model on rivers spanning the gradient between relatively steep, pristine sites (*e.g.* Leigh Brook) and more sinuous, low gradient, impacted rivers (*e.g.* River Arrow). If successful, this validation **could lead to the application of the classification for habitat assessment and modelling purposes** in the ways suggested above.

The research area explored in Chapter 5 is in its infancy and there is much scope for further work in both the laboratory and the field. The next logical step following the results of the analyses would be to **test the ability of the GLM developed based on turbulent SC (Figure 5.10) to predict position choice in natural settings**. Though the results show that a hydrodynamic classification is relevant to the ecology of Atlantic salmon, there is a need to test its relevance to a range of other biota, including invertebrates and plants. **Further lab work is also required to calibrate SC models for a range of other fish species**, including species of high conservation value in developing countries where the threat of anthropogenic alteration is fiercest (*e.g.* Garcia *et al*., 2012). Finally, **further reductionist laboratory approaches are required to separate the effects of U and different measures of turbulence intensity and eddy characteristics on fish swimming performance and energetics**, with a view to establishing general relationships between turbulence and fish swimming performance. PIV is likely to be very important in this respect as it facilitates the direct measurement of eddy characteristics and avoids the need to make assumptions based on point measurements.

In summary, this thesis makes a major contribution to river research and management activities by strengthening the foundations of the mesohabitat concept in a way that is consistent with contemporary approaches incorporating hydrodynamics and bioenergetics. If the ideas and suggestions outlined above are developed and implemented they would result in real improvements in our understanding of ecohydraulic relationships for river habitat assessment, modelling, rehabilitation and conservation purposes.

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Appendix A

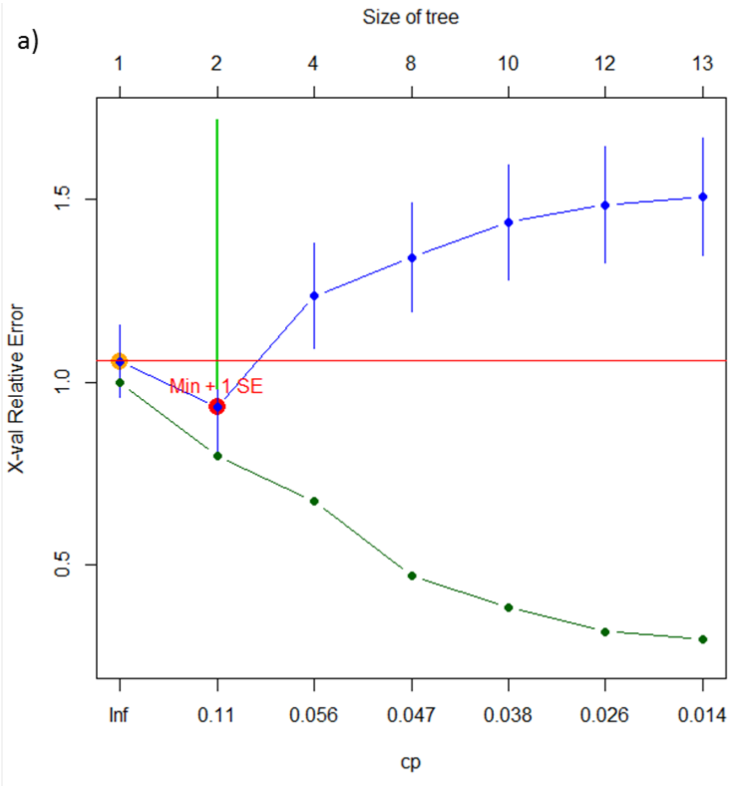
Table A1 – Raw species data from fish sampling within mesohabitats of the San Pedro River. See Table 3.4 for species codes.

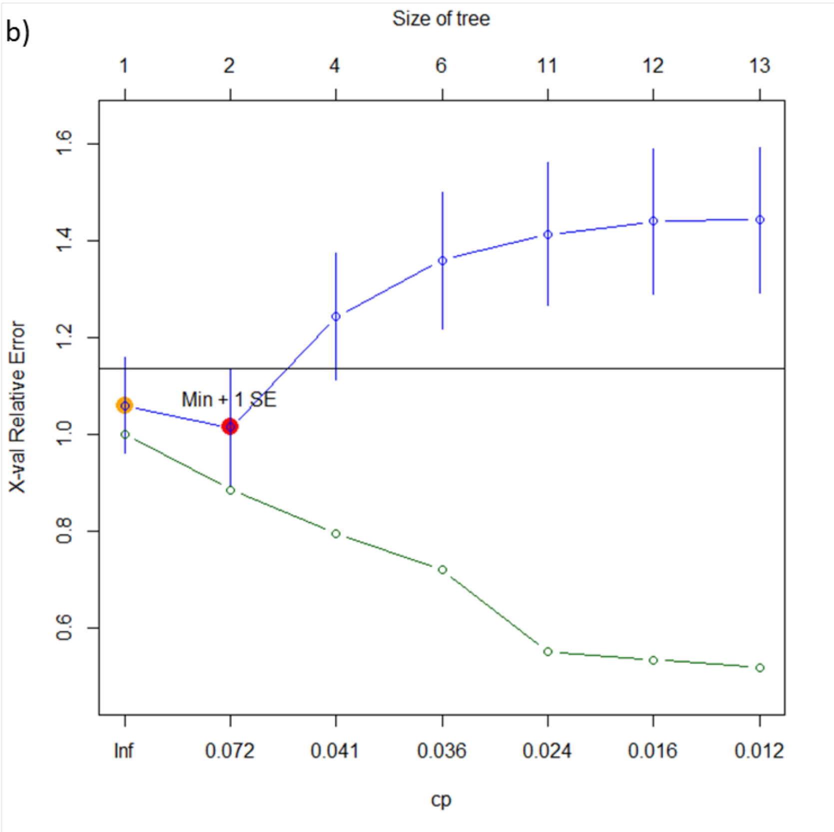
Habitat unit	Az	BaA	BaJ	Ca	Dc	Ga	Gm	Gp	GJ	OmA	OmJ	PgA	PgJ	Pt	St	Ta
LB1	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	0
LB10	0	0	0	2	0	0	61	12	3	0	0	6	0	0	0	0
LB14	1	0	0	0	0	0	32	0	239	2	0	104	0	13	1	0
LB16	0	0	0	1	0	0	65	0	7	2	0	10	0	6	1	0
LB17	0	0	0	0	2	0	0	0	16	4	0	14	0	5	0	0
LB19	0	0	0	0	4	0	1	0	25	0	3	23	0	5	0	0
LB2	0	0	0	0	1	0	0	1	7	0	0	0	0	0	0	0
LB24	0	0	0	0	3	0	0	0	0	3	0	1	0	13	1	0
LB28	0	0	0	0	1	0	25	4	73	2	0	10	0	7	0	0
LB29	0	0	0	0	0	0	2	2	39	2	0	9	0	10	0	0
LB33	1	0	0	0	2	0	3	1	10	3	0	11	0	6	1	0
LB34	1	0	0	0	3	0	11	0	0	1	0	35	0	1	0	0
LB35	0	0	0	0	0	0	10	1	30	1	0	13	0	1	0	1
LB36	0	0	0	0	0	0	0	0	40	0	2	30	0	0	0	0
LB37	0	0	0	0	0	0	50	1	19	5	0	408	0	3	0	0
LB4	0	0	0	0	1	0	67	1	0	0	0	1	0	0	0	0
LB49	0	0	0	0	0	0	0	6	9	0	0	7	0	0	0	0
LB5	0	0	0	0	0	0	0	0	3	0	0	10	0	0	0	0
LB51	0	0	0	2	0	0	302	262	230	0	0	25	0	0	0	7
LB52	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0
LB9	0	0	0	3	0	0	5	0	15	0	0	7	0	0	0	1
RB1	0	13	0	0	0	0	5	16	4	0	0	0	0	0	0	0
RB10	0	0	0	0	2	0	49	10	6	0	0	47	1	2	0	0
RB11	0	0	19	0	0	0	0	0	8	2	0	19	4	0	0	0
RB12	0	0	10	0	0	0	112	7	11	0	0	31	0	0	0	0
RB16	0	0	0	0	1	0	37	0	23	0	0	16	0	0	0	0
RB20	0	8	0	0	0	0	8	7	5	0	0	9	0	0	0	0
RB21	0	28	0	0	0	1	495	2	967	0	0	1	0	0	0	1
RB22	0	0	0	0	0	0	0	4	0	0	0	8	0	0	0	1
RB24	0	0	0	0	1	0	14	9	0	0	0	8	0	4	0	14
RB27	0	0	10	0	0	0	26	0	52	0	0	28	15	0	0	0
RB28	0	0	0	0	1	0	130	0	20	12	0	316	0	0	0	0
RB33	0	0	0	0	0	0	100	0	65	0	0	5	0	1	0	0
RB35	0	0	0	0	2	0	440	2	46	0	5	98	0	1	0	0
RB36	0	0	0	0	0	3	70	9	90	5	0	115	0	0	0	0

Table A1 continued

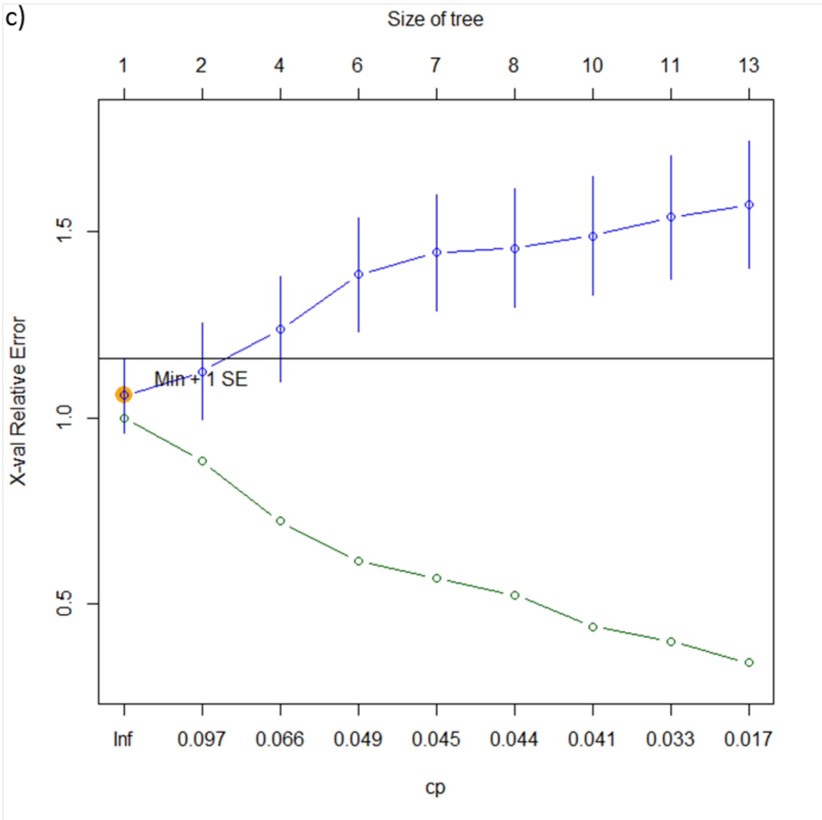
Habitat unit	Az	BaA	BaJ	Ca	Dc	Ga	Gm	Gp	GJ	OmA	OmJ	PgA	PgJ	Pt	St	Ta
RB40	0	7	0	0	0	0	54	32	0	0	0	6	0	0	0	0
RB6	0	2	0	0	0	1	12	0	7	0	0	9	0	0	0	1
RB9	0	0	0	0	0	0	5	5	0	0	0	1	0	0	0	0

Figure A2 - Cross-validation results showing RE (dark green) and CVRE (blue). Light green bars show the number of times that the solution was selected as best by the cross-validation procedure for the all variables both banks (a), above water (b), water's edge (c), below water (d) and all variables left (e) and right (f) banks scenarios.



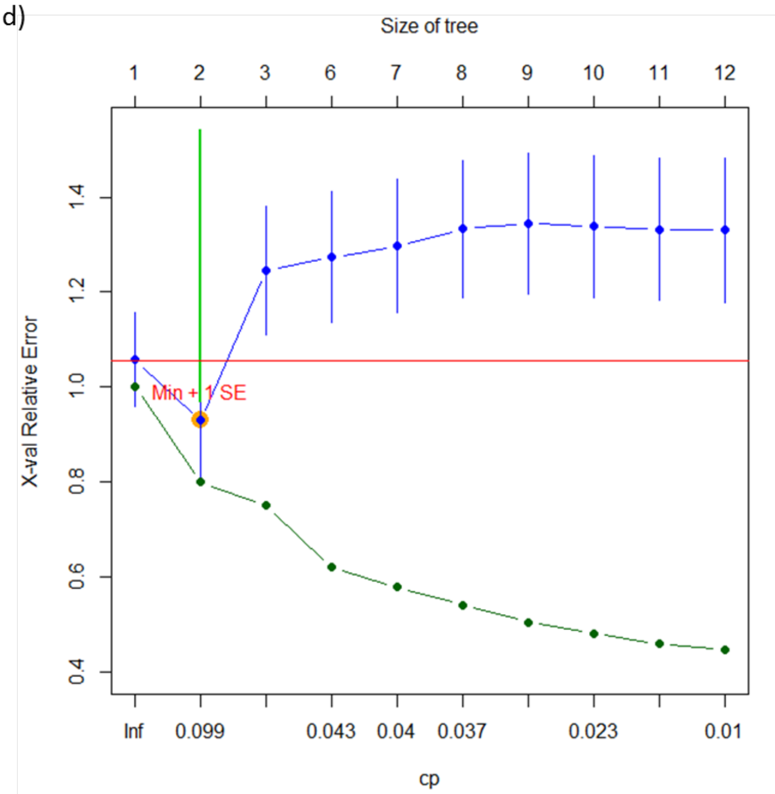


c)



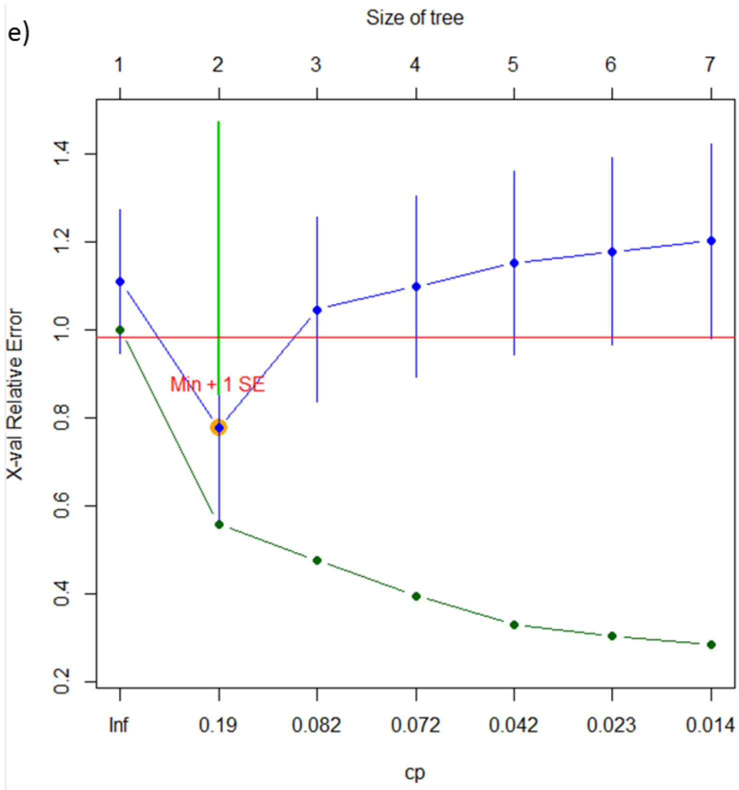
Size of tree
1
2
4
6
7
8
10
11
13
X-val Relative Error
1.5
1.0
0.5
Min + 1 SE
Inf
0.097
0.066
0.049
0.045
0.044
0.041
0.033
0.017
cp

d)



Size of tree
1
2
3
6
7
8
9
10
11
12
X-val Relative Error
1.4
1.2
1.0
0.8
0.6
0.4
Min + 1 SE
Inf
0.099
0.043
0.04
0.037
0.023
0.01
cp

e)


Size of tree
1
2
3
4
5
6
7
X-val Relative Error
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0.4
0.6
0.8
1.0
1.2
1.4
Min + 1 SE
Inf
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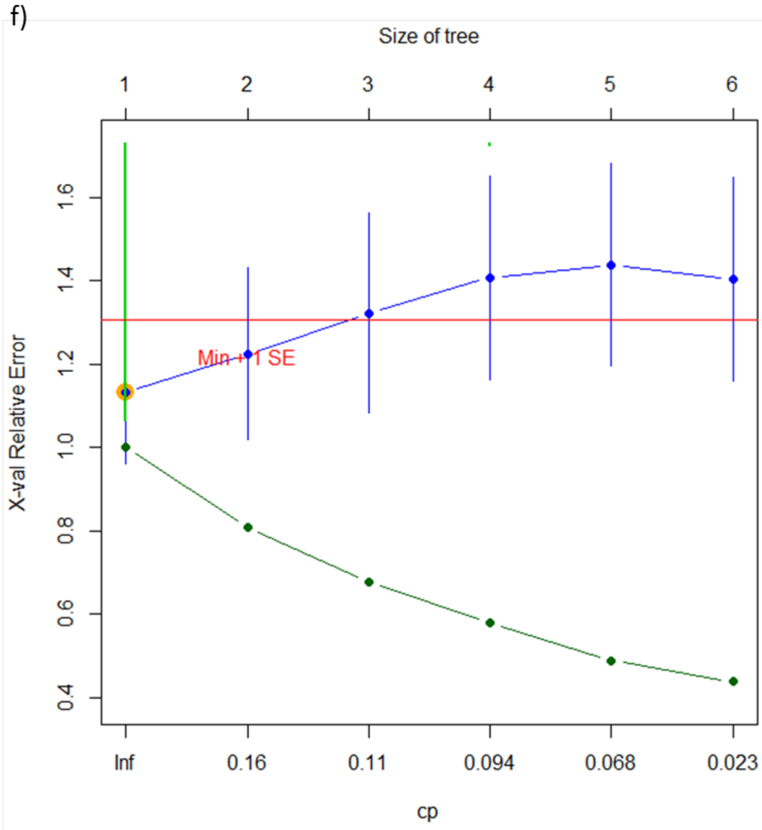
0.082
0.072
0.042
0.023
0.014
cp

f)


Size of tree
1
2
3
4
5
6
X-val Relative Error
0.4
0.6
0.8
1.0
1.2
1.4
1.6
Min + 1 SE
Inf
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0.11
0.094
0.068
0.023
cp

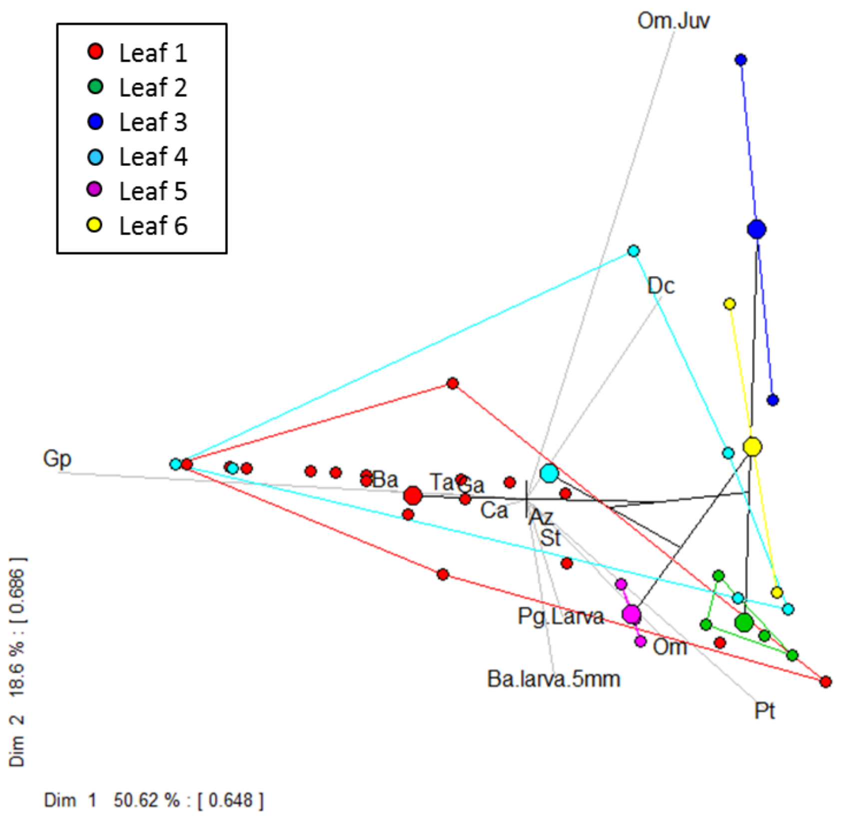


Figure A3 - PCA biplot of the first two axes from the six-leaf solution for the above water tree. Figures in square brackets denote the interset correlation for each dimension.

Table A2 – Species and tree variance for the six-leaf, above water tree. Figures in bold denote significant discriminator species at each split.

	AWDomSub	AWCover	AWNumSubSizes (left)	AWNumSubSizes (right)	AWDomSub (BedFrac)	Species total
Az	0.02	0	0.01	0.01	0	**0.22**
BaA	**0.95**	0	0	0	0	**8.75**
BaJ	0.09	0.28	0	0.94	1.15	**6.44**
Ca	0.03	0	0.01	0.01	0	**3.64**
Dc	0.57	0.35	0.15	0.16	2.48	**10.37**
Ga	0.14	0	0	0	0	**2.06**
Gp	**6.28**	0.83	0.02	1.43	0.07	**29.45**
OmA	**1.11**	0.01	0.63	0.14	0.09	**8.29**
OmJ	0.63	0.66	3.35	0.12	0	**7.91**
PgJ	0.1	0.12	0	0.41	0.5	**2.39**
Pt	1.29	1.61	0.9	0.03	0.03	**17.66**
St	**0.02**	**0.03**	0.03	0	0	**0.12**
Ta	**0.34**	0	0	0	0	**2.69**
Total	**11.56**	**3.89**	**5.09**	**3.26**	**4.32**	**100**

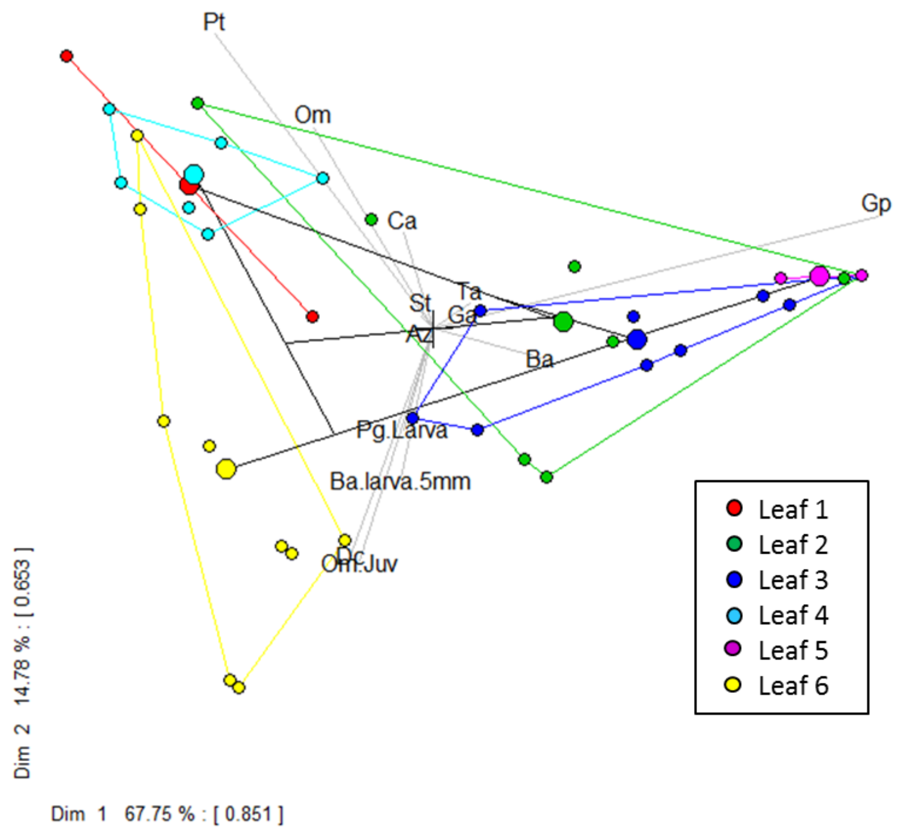


Figure A4 - PCA biplot of the first two axes from the six-leaf solution for the water's edge tree. Figures in square brackets denote the interset correlation for each dimension.

Table A3 – Species and tree variance for the six-leaf, water's edge tree. Figures in bold denote significant discriminator species at each split.

	WELowLay	BankLength (43)	WEWD2	WEMidLay	BankLength (13.5)	Species total
Az	0.02	0	0	0	0	**0.22**
BaA	0.95	2.53	0	**0**	0	**8.75**
BaJ	0.09	0.09	0.04	0.28	0.17	**6.44**
Ca	0.03	0.15	1.47	0.01	0.04	**3.64**
Dc	0.57	0.17	0.13	0.41	0.64	**10.37**
Ga	0.14	0.03	0.06	0	0	**2.06**
Gp	**6.28**	0.23	**3**	0.3	**8.65**	**29.45**
OmA	**1.11**	**0.12**	0.06	1.92	0.09	**8.29**
OmJ	0.63	0	0	0.63	0.4	**7.91**
PgJ	0.1	0	0	0.12	0.08	**2.39**
Pt	**1.29**	0.7	1.63	2.07	0.39	**17.66**
St	**0.02**	0	0	0.01	0	**0.12**
Ta	**0.34**	0.12	0.09	0	0	**2.69**
Total	**11.56**	**4.14**	**6.49**	**5.75**	**10.46**	**100**

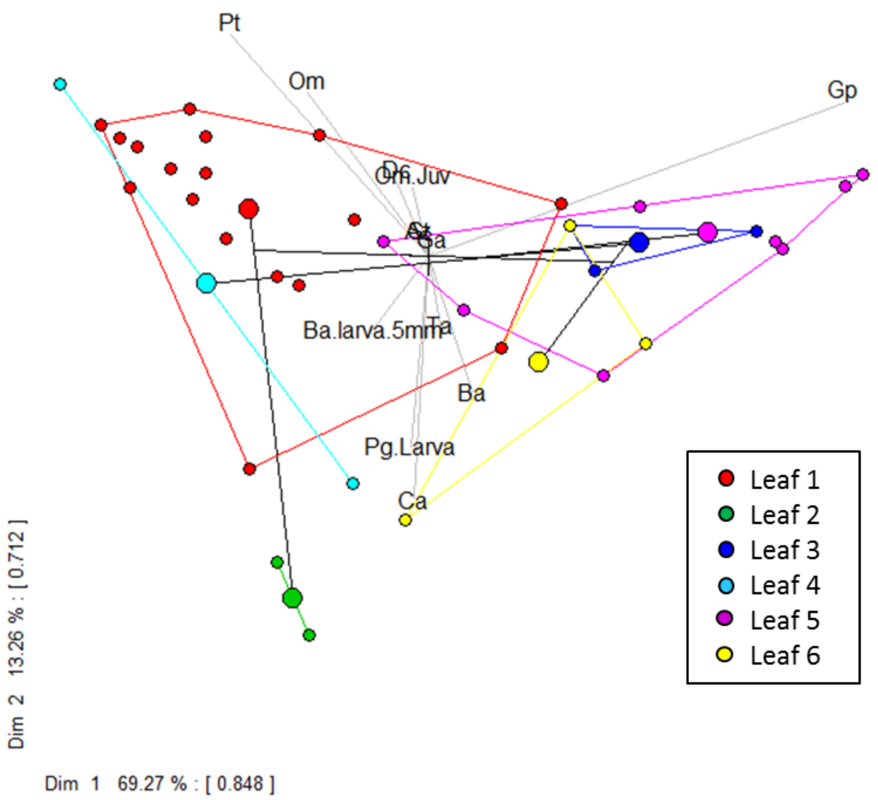


Figure A5 - PCA biplot of the first two axes from the six-leaf solution for the below water tree. Figures in square brackets denote the interset correlation for each dimension.

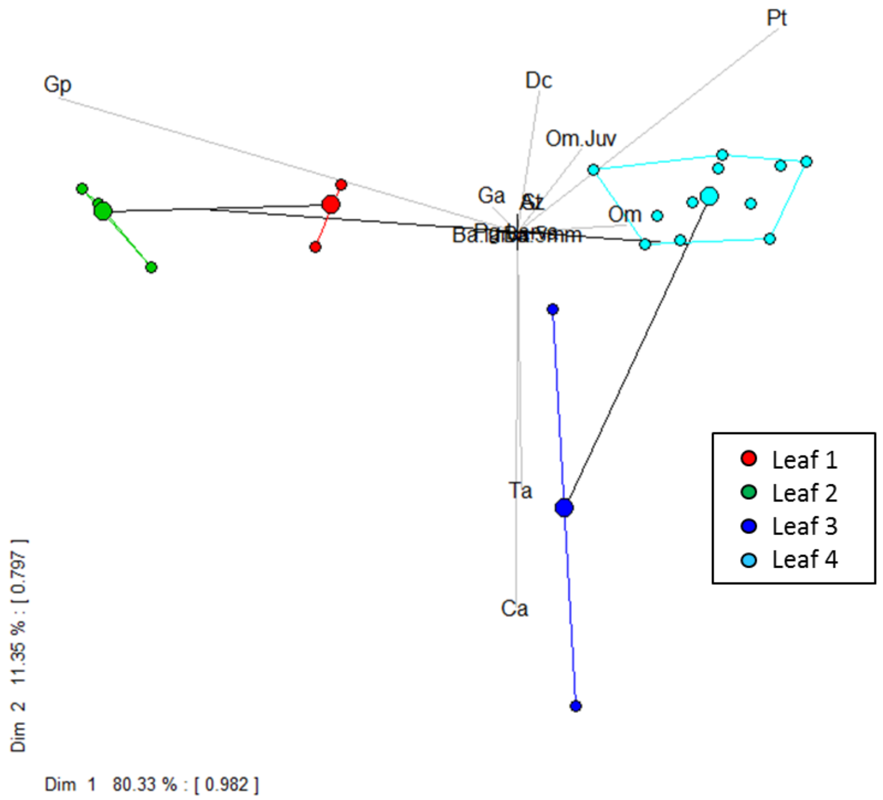


Figure A6 - PCA biplot of the first two axes from the four-leaf solution for the left bank tree. Figures in square brackets denote the interset correlation for each dimension.

Table A4 – Species and tree variance for the four-leaf, left bank tree. Figures in bold denote significant discriminator species at each split.

	Depth	WEMidLay	AWDomSub	Species total
Az	0.03	0	0.02	**0.44**
BaA	0	0	0	**0**
BaJ	0	0	0	**0**
Ca	0.12	0.03	3.15	**7.54**
Dc	0.09	2.64	0.37	**9.15**
Ga	0.32	0.66	0	**3.3**
Gp	**30.46**	**4.95**	0.11	**37.33**
OmA	**1.98**	0	0.09	**5.96**
OmJ	0.58	0	0.3	**13.67**
PgJ	0	0	0	**0**
Pt	**10.42**	0	2.59	**20.82**
St	0.03	0	0.02	**0.24**
Ta	0.08	0	**1.47**	**1.55**
Total	**44.11**	**8.29**	**8.12**	**100**

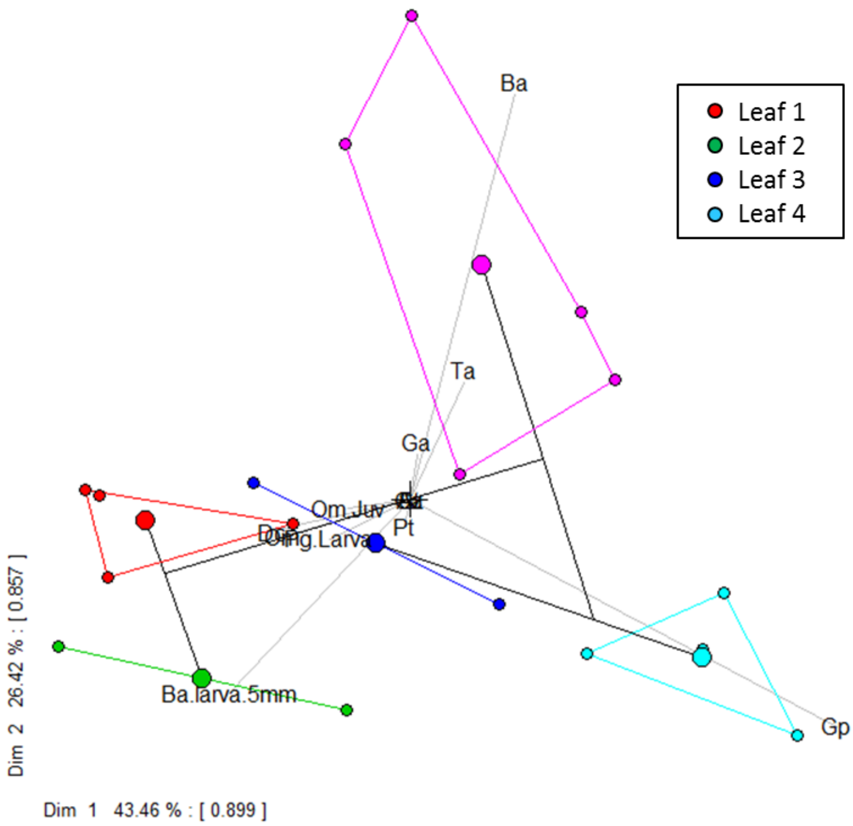


Figure A7 - PCA biplot of the first two axes from the four-leaf solution for the right bank tree. Figures in square brackets denote the interset correlation for each dimension.

Table A4 – Species and tree variance for the four-leaf, right bank tree. Figures in bold denote significant discriminator species at each split.

	WELowLay	**WEShape**	**BWWD1**	**AWCover**	**Species total**
Az	0	0	0	0	**0**
BaA	2.71	**0**	6.97	0.04	**15.15**
BaJ	**4.32**	5.76	0	0	**11.85**
Ca	0	0	0	0	**0**
Dc	1.99	1.78	0.01	0.02	**12.35**
Ga	0.09	0	0.03	0.14	**1.08**
Gp	**7.06**	0.42	4.52	5.43	**24.62**
OmA	1	0.64	0.09	0.38	**11.1**
OmJ	0.35	0.27	0	0	**3.09**
PgJ	0.74	0.09	0	0	**4.59**
Pt	0.5	0.01	0.92	3.81	**12.29**
St	0	0	0	0	**0**
Ta	0.41	0	0.54	0.04	**3.89**
Total	**19.17**	**8.98**	**13.08**	**9.85**	**100**

Appendix B

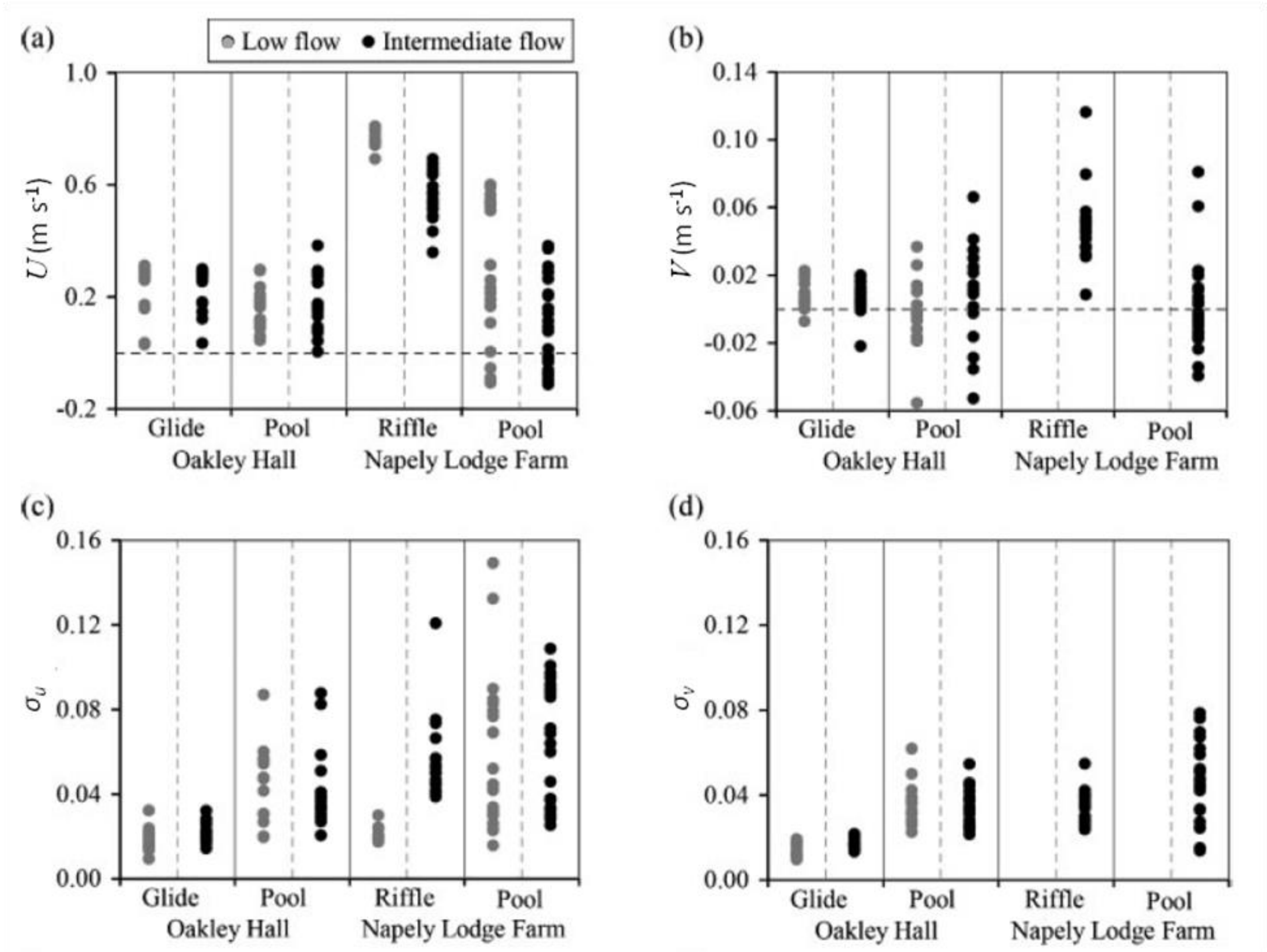


Figure B1 - Mean velocity (a, b) and standard deviation (c, d) for streamwise (*u*) and vertical (*v*) velocity components combined for all depths, locations and discharges within each Physical Biotope (PB). Low flow *v* data from Napely Lodge Farm missing. From Harvey & Clifford (2009).

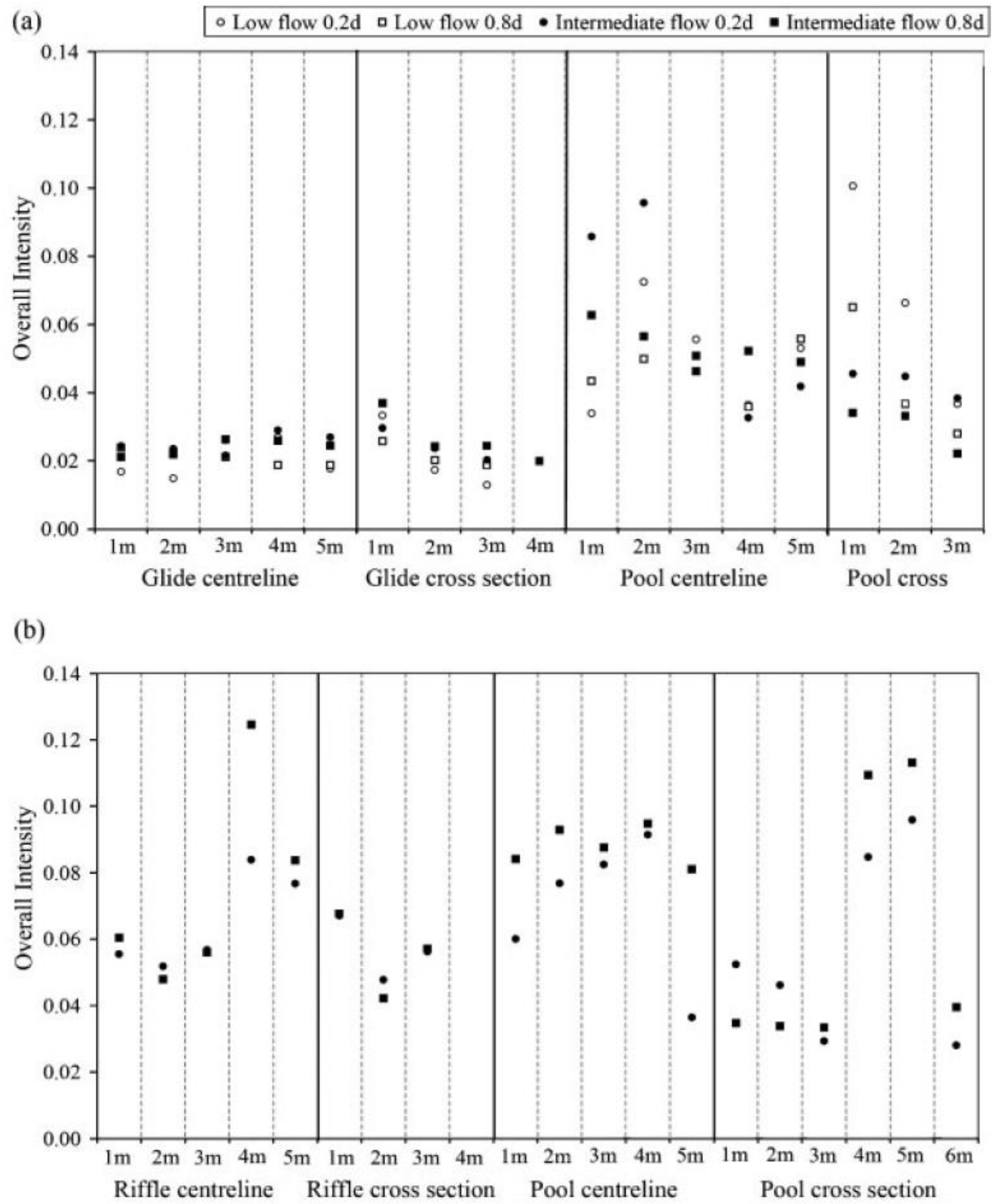


Figure B2 – Overall turbulence intensity (0.5[RMS_u+RMS_v]) for each velocity series. Results are plotted according to the location of the measurement (spaced 1 m apart along the centreline starting downstream, and cross-sectionally from the left bank) for different biotopes and flow stages. y/h=0.2 (0.2d) and 0.8 (0.8d) (a) Oakley Hall, (b) Napely Lodge Farm. Low flow data from Napely Lodge Farm missing. From Harvey & Clifford (2009).

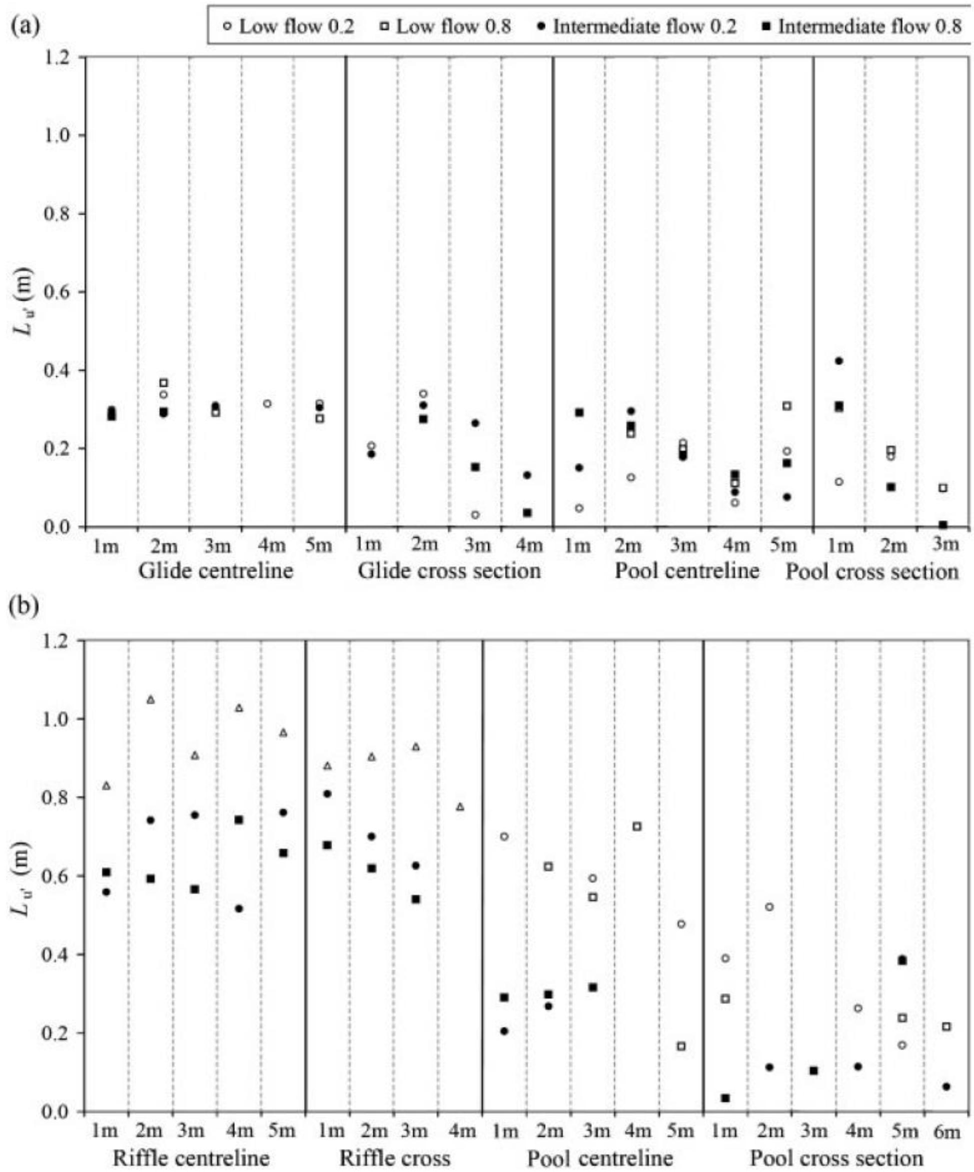


Figure B3 - Average eddy lengths (L_u) Results are plotted according to the location of the measurement (spaced 1 m apart along the centreline starting downstream, and cross-sectionally from the left bank) for different biotopes and flow stages. *y/h*=0.2 (0.2d) and 0.8 (0.8d) (a) Oakley Hall, (b) Napely Lodge Farm. From Harvey & Clifford (2009).

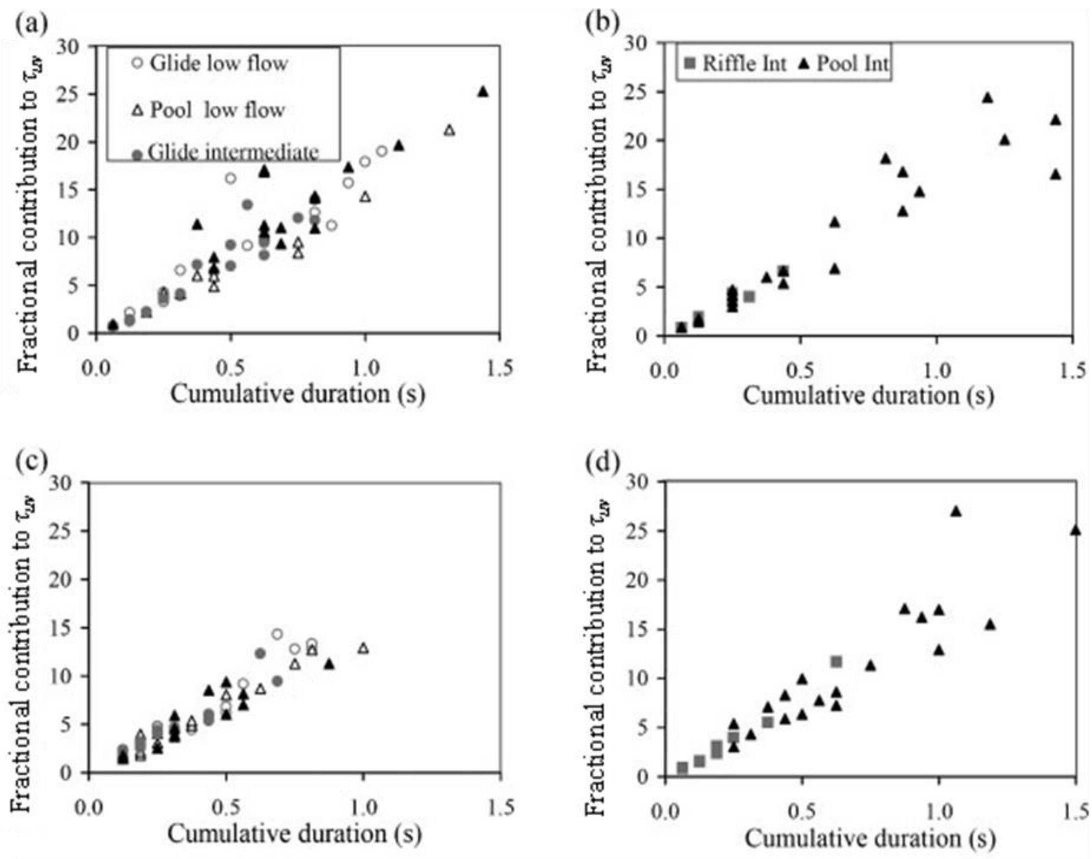


Figure B4 - Cumulative duration and fractional contribution to Reynolds shear stress (τ_{uv}) of each turbulent event type for each of the *uw* time series from the river Tern. Symbols represent series sampled from different Physical Biotopes (PBs) under 'low' and 'intermediate' discharges. (a) ejections (Oakley Hall), (b) ejections (Napely Lodge Farm), (c) sweeps (Oakley Hall), (d) sweeps (Napely Lodge Farm). Low flow data from Napely Lodge Farm missing. From Harvey & Clifford (2009).

Table B1 - Review of data quality for NDV and Flowtracker methods.

Site	Flow	PB	X (m)	Z (m)	y (m)	SNR	COR	mPST (% good)
NDV:								
Arrow	Int	Glide	0	4	0.06	23.11	94.51	98.47
Arrow	Int	Glide	0	4	0.216	23.62	94.9	98.05
Arrow	Int	Glide	0	5	0.06	23.8	93.97	98.05
Arrow	Int	Glide	0	5	0.176	24.05	95.49	96.16
Arrow	Int	Glide	0	6	0.06	23.74	93.34	99.03
Arrow	Int	Glide	0	6	0.184	24.07	95.48	95.75
Arrow	Int	Glide	0	7	0.06	24.54	91.61	95.47
Arrow	Int	Glide	0	7	0.232	24.09	94.5	99.31
Arrow	Int	Glide	2	4	0.06	24.47	98.18	97.98
Arrow	Int	Glide	2	4	0.324	23.95	94.42	98.45
Arrow	Int	Glide	2	5	0.06	23.74	94.63	98.53
Arrow	Int	Glide	2	5	0.236	24.29	95.38	98.31
Arrow	Int	Glide	2	6	0.06	24.36	97.65	96.95
Arrow	Int	Glide	2	6	0.196	24.88	98.17	96.7
Arrow	Int	Glide	2	7	0.06	24.86	96.61	98.42
Arrow	Int	Glide	2	7	0.208	27.54	97.17	98.12
Arrow	Int	Glide	4	4	0.06	22.89	95.34	97.57
Arrow	Int	Glide	4	4	0.32	23.14	95.39	97.91
Arrow	Int	Glide	4	5	0.06	23.15	95.79	96.59
Arrow	Int	Glide	4	5	0.232	23.36	95.24	95.53
Arrow	Int	Glide	4	6	0.06	23.2	95.7	97.51
Arrow	Int	Glide	4	6	0.156	23.09	97.01	98.37
Arrow	Int	Glide	4	7	0.06	22.29	97.31	99.41
Arrow	Int	Glide	4	7	0.1	22.28	98.28	96.85
Arrow	Int	Glide	6	3	0.06	23.49	96.39	99.97
Arrow	Int	Glide	6	3	0.324	23.57	94.32	97.68
Arrow	Int	Glide	6	4	0.06	23.87	95.24	97.24
Arrow	Int	Glide	6	4	0.304	23.7	96.19	99.07
Arrow	Int	Glide	6	5	0.06	23.49	95.96	99.64
Arrow	Int	Glide	6	5	0.248	23.91	96.64	97.16
Arrow	Int	Glide	6	6	0.06	23.11	97.75	96.89
Arrow	Int	Glide	6	6	0.1	23.23	98.24	99.33
Arrow	Int	Glide	8	3	0.06	23.12	95.23	98.45
Arrow	Int	Glide	8	3	0.312	22.91	94.89	97.42
Arrow	Int	Glide	8	4	0.06	22.42	94.22	96.74
Arrow	Int	Glide	8	4	0.276	22.62	96.25	96.49
Arrow	Int	Glide	8	5	0.06	22.83	94.65	96.65
Arrow	Int	Glide	8	5	0.208	23.14	97	95.23
Arrow	Int	Glide	8	6	0.06	22.47	96.9	97.59
Arrow	Int	Glide	8	6	0.1	23.09	97.71	99.04

Arrow	Int	Glide	10	3	0.06	22.95	93.78	96.55
Arrow	Int	Glide	10	3	0.3	22.98	95.38	99.53
Arrow	Int	Glide	10	4	0.06	22.81	95.11	97.38
Arrow	Int	Glide	10	4	0.248	23.24	96.62	96.92
Arrow	Int	Glide	10	5	0.06	22.89	94.88	98.18
Arrow	Int	Glide	10	5	0.178	23.03	97.31	99.74
Arrow	Int	Glide	10	6	0.06	22.8	95.11	96.64
Arrow	Int	Glide	10	6	0.092	22.74	97.62	97.33
Arrow	Int	Pool	1	4	0.06	22.64	96.37	82.22
Arrow	Int	Pool	1	4	0.13	21.17	90.42	89.94
Arrow	Int	Pool	1	5	0.06	25.02	89.17	98.25
Arrow	Int	Pool	1	5	0.248	24.53	94.59	98.69
Arrow	Int	Pool	1	6	0.06	24.15	85.87	99.44
Arrow	Int	Pool	1	6	0.296	23.73	94.44	98.71
Arrow	Int	Pool	1	7	0.06	28.32	98.86	99.58
Arrow	Int	Pool	1	7	0.216	23.41	98.6	97.74
Arrow	Int	Pool	1	8	0.06	35.12	99.7	98.27
Arrow	Int	Pool	1	8	0.14	26.54	98.66	99.98
Arrow	Int	Pool	4	5	0.06	21.27	91.96	99.88
Arrow	Int	Pool	4	5	0.108	21.32	92.32	98.71
Arrow	Int	Pool	4	6	0.06	23.88	95.59	97.54
Arrow	Int	Pool	4	6	0.312	23.03	96.52	96.96
Arrow	Int	Pool	4	7	0.06	21.76	94.84	99.34
Arrow	Int	Pool	4	7	0.26	21.29	94.73	89.04
Arrow	Int	Pool	4	8	0.06	24.73	99.17	95.36
Arrow	Int	Pool	4	8	0.20	25.96	97.49	78.94
Arrow	Int	Pool	7	5	0.492	31.31	94.28	99.72
Arrow	Int	Pool	7	6	0.48	28.59	91.45	95.01
Arrow	Int	Pool	7	7	0.43	31.5	96.76	75.78
Arrow	Int	Pool	7	8	0.368	33.21	98.54	96.57
Arrow	Int	Pool	7	9	0.06	33.59	98.29	95.26
Arrow	Int	Pool	7	9	0.32	32.42	98.38	95.98
Arrow	Int	Pool	10	5	0.54	30.03	96.64	81.93
Arrow	Int	Pool	10	6	0.492	27.27	94.7	98.37
Arrow	Int	Pool	10	7	0.38	30.03	96.57	95.42
Arrow	Int	Pool	10	8	0.06	29.52	97.94	96.79
Arrow	Int	Pool	10	8	0.292	28.68	97.93	95
Arrow	Int	Pool	10	9	0.06	33.88	98.3	97.53
Arrow	Int	Pool	10	9	0.192	29.43	98.51	96.08
Arrow	Int	Pool	13	3	0.06	32.73	99.05	97.21
Arrow	Int	Pool	13	3	0.188	27.94	98.72	98.33
Arrow	Int	Pool	13	4	0.06	24.39	97.5	95.52
Arrow	Int	Pool	13	4	0.348	23.06	97.59	95.63
Arrow	Int	Pool	13	5	0.36	21.64	94.72	96.72
Arrow	Int	Pool	13	6	0.06	21.66	94.36	98.16

Arrow	Int	Pool	13	6	0.3	21.63	96	98.45
Arrow	Int	Pool	13	7	0.06	21.4	98.61	98.57
Arrow	Int	Pool	13	7	0.212	21.29	97.41	97.18
Arrow	Int	Pool	13	8	0.06	21	98.49	95.98
Arrow	Int	Pool	13	8	0.144	20.91	93.28	95.7
Arrow	Int	Pool	16	3	0.06	22.52	96.88	97.99
Arrow	Int	Pool	16	3	0.14	22.32	96.63	99.4
Arrow	Int	Pool	16	4	0.06	22.21	98.51	96.93
Arrow	Int	Pool	16	4	0.168	22	95.51	95.11
Arrow	Int	Pool	16	5	0.06	21.91	92.24	99.41
Arrow	Int	Pool	16	5	0.184	21.77	95.32	98.79
Arrow	Int	Pool	16	6	0.06	22.22	95.93	96.35
Arrow	Int	Pool	16	6	0.12	21.89	96.27	97
Arrow	Int	Pool	16	7	0.06	21.81	98.62	97.1
Arrow	Int	Pool	16	7	0.096	21.7	97.4	97.57
Arrow	Int	Pool	16	8	0.06	21.57	97.6	95.34
Arrow	Int	Pool	19	3	0.06	31.47	87.24	83.15
Arrow	Int	Pool	19	3	0.14	23.1	91.17	99.54
Arrow	Int	Pool	19	4	0.06	22.75	86.93	99.34
Arrow	Int	Pool	19	4	0.108	22.62	92.8	96.53
Arrow	Int	Pool	19	5	0.06	22.43	85.44	99.92
Arrow	Int	Pool	19	5	0.108	22.49	92.89	97.15
Arrow	Int	Pool	19	6	0.06	22.27	92.45	96
Arrow	Int	Pool	19	7	0.06	21.91	88.43	99.68
Arrow	Int	Riffle	4	8	0.06	25.51	73.08	98.33
Arrow	Int	Riffle	6	4	0.06	29.58	87.41	97.75
Arrow	Int	Riffle	6	5	0.06	29.42	98.61	95.54
Arrow	Int	Riffle	6	6	0.06	29.01	83.32	97.22
Arrow	Int	Riffle	6	7	0.06	29.23	92.12	98.21
Arrow	Int	Riffle	8	5	0.06	28.78	98.04	97.39
Arrow	Int	Riffle	8	7	0.06	28.81	86.62	98.27
Arrow	Int	Riffle	8	8	0.06	29.42	84.83	96.27
Arrow	Int	Riffle	10	6	0.06	29.81	84.68	97.61
Arrow	Int	Riffle	10	7	0.06	30.41	70.03	98.54
Arrow	Int	Riffle	10	8	0.06	31.07	75.88	99.63
Arrow	Int	Riffle	10	9	0.06	30.4	87.89	96.05
Arrow	Int	Riffle	12	5	0.06	30.86	82.24	98.19
Arrow	Int	Riffle	12	6	0.06	30.24	93.06	98.55
Arrow	Int	Riffle	12	7	0.06	27.65	79.82	96.87
Arrow	Int	Riffle	12	8	0.06	28.1	73.68	96.1
Arrow	Int	Riffle	12	9	0.06	27.28	85.44	96.71
Arrow	Int	Run	0	9	0.06	22.63	97.19	95.59
Arrow	Int	Run	0	9	0.124	22.64	96.7	99.76
Arrow	Int	Run	0	10	0.06	22.53	94.62	95.2
Arrow	Int	Run	0	10	0.116	22.61	97.62	99.06

Arrow	Int	Run	2	5	0.06	20.22	97.76	96.82
Arrow	Int	Run	2	5	0.1	20.24	91.62	98.87
Arrow	Int	Run	2	6	0.06	20.31	93.38	99.78
Arrow	Int	Run	2	6	0.12	20.25	91.76	96.87
Arrow	Int	Run	2	7	0.06	22.77	95.69	98.22
Arrow	Int	Run	2	7	0.116	22.67	88.27	97.46
Arrow	Int	Run	2	8	0.06	22.6	96.68	99.71
Arrow	Int	Run	2	8	0.104	22.58	94.22	95.95
Arrow	Int	Run	2	9	0.06	22.56	94.92	97.67
Arrow	Int	Run	4	4	0.06	23.38	98.29	96.72
Arrow	Int	Run	4	4	0.116	23.25	97.65	97.5
Arrow	Int	Run	4	5	0.06	23.1	87.23	95.53
Arrow	Int	Run	4	6	0.06	23.1	95.13	98.09
Arrow	Int	Run	4	6	0.096	22.99	80.56	96.96
Arrow	Int	Run	4	7	0.06	23.1	95.23	98.83
Arrow	Int	Run	4	8	0.06	22.99	94.38	99.27
Arrow	Int	Run	4	9	0.06	31.75	93.65	95.19
Arrow	Int	Run	4	10	0.06	25.26	97.23	99.26
Arrow	Int	Run	6	3	0.06	23.31	98.62	95.71
Arrow	Int	Run	6	3	0.172	24.39	98.03	97.04
Arrow	Int	Run	6	4	0.06	21.54	94.48	98.05
Arrow	Int	Run	6	4	0.152	24.02	93.92	97.16
Arrow	Int	Run	6	5	0.06	23.79	95.34	98.89
Arrow	Int	Run	6	6	0.06	25.6	95.33	98.62
Arrow	Int	Run	6	7	0.06	25.27	96.77	98.49
Arrow	Int	Run	6	8	0.06	27.93	87.69	95.8
Arrow	Int	Run	6	8	0.088	30.51	85.33	97.39
Arrow	Int	Run	8	5	0.06	23.5	94.38	97.06
Arrow	Int	Run	8	5	0.228	25.86	93.85	96.38
Arrow	Int	Run	8	6	0.06	25.64	97.33	99.09
Arrow	Int	Run	8	6	0.128	25.16	89.57	97.55
Arrow	Int	Run	8	7	0.06	32.66	89.72	96.9
Arrow	Int	Run	8	7	0.096	30.38	86.68	96.5
Arrow	Low	Glide	0	4	0.06	21.73	97.28	99.23
Arrow	Low	Glide	0	4	0.2	21.96	97.71	96.95
Arrow	Low	Glide	0	5	0.06	22.97	96.73	96.59
Arrow	Low	Glide	0	5	0.164	22.71	97.79	95.07
Arrow	Low	Glide	0	6	0.06	21.95	94.3	95.82
Arrow	Low	Glide	0	6	0.17	22.3	97.44	89.3
Arrow	Low	Glide	0	7	0.06	21.8	96	99.8
Arrow	Low	Glide	0	7	0.22	18.39	50.39	80.39
Arrow	Low	Glide	2	4	0.06	21.66	96.81	97.4
Arrow	Low	Glide	2	4	0.296	21.77	95.33	96.2
Arrow	Low	Glide	2	5	0.06	21.98	94.18	95.92
Arrow	Low	Glide	2	5	0.212	22.28	94.94	96.88

Arrow	Low	Glide	2	6	0.06	22.13	96.55	99.44
Arrow	Low	Glide	2	6	0.18	22.16	97.39	99.06
Arrow	Low	Glide	2	7	0.06	21.81	98.36	97.4
Arrow	Low	Glide	2	7	0.18	23.04	98.5	95.87
Arrow	Low	Glide	4	4	0.06	20.88	98.15	96.38
Arrow	Low	Glide	4	4	0.288	24.99	98.65	95.75
Arrow	Low	Glide	4	5	0.06	22	98.34	95.56
Arrow	Low	Glide	4	5	0.22	21.55	98.13	98.85
Arrow	Low	Glide	4	6	0.06	21.63	98.71	97.49
Arrow	Low	Glide	4	6	0.114	21.61	98.66	98.54
Arrow	Low	Glide	4	7	0.06	32.39	99.63	96.56
Arrow	Low	Glide	4	7	0.086	21.64	99.04	95.13
Arrow	Low	Glide	6	3	0.06	21.06	98	95.07
Arrow	Low	Glide	6	3	0.296	21.02	98.42	96.17
Arrow	Low	Glide	6	4	0.06	20.84	98.3	97.49
Arrow	Low	Glide	6	4	0.272	20.6	98.32	96.24
Arrow	Low	Glide	6	5	0.06	20.7	98.31	97.26
Arrow	Low	Glide	6	5	0.196	20.58	98.3	97.98
Arrow	Low	Glide	6	6	0.06	20.36	98.72	98.44
Arrow	Low	Glide	6	6	0.092	20.33	98.56	95.57
Arrow	Low	Glide	8	3	0.06	21	97.75	97.03
Arrow	Low	Glide	8	3	0.296	21.18	98.04	96.8
Arrow	Low	Glide	8	4	0.06	21.37	97.79	96.82
Arrow	Low	Glide	8	4	0.238	21.09	98.21	96.15
Arrow	Low	Glide	8	5	0.06	21.34	98.34	98.96
Arrow	Low	Glide	8	5	0.16	21.13	98.26	95.9
Arrow	Low	Glide	8	6	0.06	20.59	98.69	96.48
Arrow	Low	Glide	10	3	0.06	21.57	97.02	99.94
Arrow	Low	Glide	10	3	0.284	21.68	97.77	97.31
Arrow	Low	Glide	10	4	0.06	21.44	97.48	98.29
Arrow	Low	Glide	10	4	0.236	21.66	97.8	98.53
Arrow	Low	Glide	10	5	0.06	21.31	97.81	96.67
Arrow	Low	Glide	10	5	0.168	21.17	98.05	97.81
Arrow	Low	Glide	10	6	0.06	20.71	98.46	96.22
Arrow	Low	Pool	1	4	0.06	27.97	85.77	98.31
Arrow	Low	Pool	1	4	0.11	22.64	85.07	98.75
Arrow	Low	Pool	1	5	0.06	19.76	86.63	98.86
Arrow	Low	Pool	1	5	0.22	22.97	90.98	97.61
Arrow	Low	Pool	1	6	0.06	25.70	90.16	97.32
Arrow	Low	Pool	1	6	0.29	27.62	88.66	98.27
Arrow	Low	Pool	1	7	0.06	19.77	91.61	98.96
Arrow	Low	Pool	1	7	0.20	27.69	85.94	99.12
Arrow	Low	Pool	1	8	0.06	27.46	86.38	96.78
Arrow	Low	Pool	1	8	0.12	27.52	85.70	97.61
Arrow	Low	Pool	4	5	0.06	26.04	94.49	96.79

Arrow	Low	Pool	4	5	0.09	26.41	92.22	95.91
Arrow	Low	Pool	4	6	0.06	27.24	93.46	95.53
Arrow	Low	Pool	4	6	0.28	20.77	85.97	95.51
Arrow	Low	Pool	4	7	0.06	26.82	87.64	98.52
Arrow	Low	Pool	4	7	0.25	20.07	90.12	98.24
Arrow	Low	Pool	4	8	0.06	23.12	91.16	97.47
Arrow	Low	Pool	4	8	0.20	26.80	92.08	99.74
Arrow	Low	Pool	7	5	0.48	26.47	85.40	95.55
Arrow	Low	Pool	7	6	0.48	27.32	87.26	96.32
Arrow	Low	Pool	7	7	0.41	20.44	88.56	96.35
Arrow	Low	Pool	7	8	0.33	20.63	92.40	96.91
Arrow	Low	Pool	7	9	0.06	21.09	93.92	99.57
Arrow	Low	Pool	7	9	0.32	28.17	88.94	97.80
Arrow	Low	Pool	10	5	0.52	20.23	86.56	95.56
Arrow	Low	Pool	10	6	0.46	28.49	94.23	98.26
Arrow	Low	Pool	10	7	0.38	19.18	94.27	96.87
Arrow	Low	Pool	10	8	0.06	28.54	89.35	99.31
Arrow	Low	Pool	10	8	0.31	20.89	93.20	97.84
Arrow	Low	Pool	10	9	0.06	21.89	87.76	98.52
Arrow	Low	Pool	10	9	0.18	20.18	90.60	97.76
Arrow	Low	Pool	13	3	0.06	25.22	89.30	99.08
Arrow	Low	Pool	13	3	0.17	19.95	90.69	98.59
Arrow	Low	Pool	13	4	0.06	26.97	91.41	97.79
Arrow	Low	Pool	13	4	0.32	26.30	89.54	98.81
Arrow	Low	Pool	13	5	0.36	22.35	92.46	96.15
Arrow	Low	Pool	13	6	0.06	24.89	85.43	97.09
Arrow	Low	Pool	13	6	0.28	21.88	86.06	97.03
Arrow	Low	Pool	13	7	0.06	21.03	93.12	95.80
Arrow	Low	Pool	13	7	0.19	27.74	92.13	99.70
Arrow	Low	Pool	13	8	0.06	25.43	85.32	99.30
Arrow	Low	Pool	13	8	0.13	23.75	86.31	98.60
Arrow	Low	Pool	16	3	0.06	22.38	91.82	95.62
Arrow	Low	Pool	16	3	0.12	27.50	91.30	98.85
Arrow	Low	Pool	16	4	0.06	28.58	90.94	97.02
Arrow	Low	Pool	16	4	0.14	26.91	88.50	97.49
Arrow	Low	Pool	16	5	0.06	26.00	86.36	96.78
Arrow	Low	Pool	16	5	0.17	19.34	86.95	97.75
Arrow	Low	Pool	16	6	0.06	20.29	93.37	97.99
Arrow	Low	Pool	16	6	0.10	26.92	92.23	96.41
Arrow	Low	Pool	16	7	0.06	21.28	91.41	99.38
Arrow	Low	Pool	16	7	0.09	24.57	92.49	99.64
Arrow	Low	Pool	16	8	0.06	19.04	86.18	98.21
Arrow	Low	Pool	19	3	0.06	22.81	89.57	96.20
Arrow	Low	Pool	19	3	0.12	28.04	89.44	98.05
Arrow	Low	Pool	19	4	0.06	19.75	88.51	97.33

Arrow	Low	Pool	19	4	0.10	21.06	85.49	95.64
Arrow	Low	Pool	19	5	0.06	28.63	86.89	97.85
Arrow	Low	Pool	19	5	0.10	23.13	86.19	96.53
Arrow	Low	Pool	19	6	0.06	19.22	87.55	97.87
Arrow	Low	Riffle	6	5	0.06	20.46	93.49	97.41
Arrow	Low	Riffle	6	6	0.06	34.45	80.87	95.72
Arrow	Low	Riffle	6	7	0.06	27.7	83.54	98.92
Arrow	Low	Riffle	8	7	0.06	23.04	73.54	95.39
Arrow	Low	Riffle	8	8	0.06	26.13	85.15	97
Arrow	Low	Riffle	10	6	0.06	27.53	86.63	98.17
Arrow	Low	Riffle	10	8	0.06	26.37	95.4	97.19
Arrow	Low	Riffle	12	8	0.06	27.67	69.43	98.51
Arrow	Low	Run	0	8	0.06	21.5	89.08	99.95
Arrow	Low	Run	0	8	0.096	21.53	93.94	98.94
Arrow	Low	Run	0	9	0.06	20.97	94.72	96.88
Arrow	Low	Run	2	5	0.06	20.83	90.67	97.32
Arrow	Low	Run	2	6	0.06	21.11	87.65	95.63
Arrow	Low	Run	2	7	0.06	21.52	76.08	95.65
Arrow	Low	Run	2	8	0.06	21.36	65.62	99.01
Arrow	Low	Run	2	10	0.06	43.46	100	99.09
Arrow	Low	Run	4	4	0.06	20.96	89.45	99.3
Arrow	Low	Run	4	4	0.088	19.56	87.01	95.82
Arrow	Low	Run	4	5	0.06	16.77	67.25	86.58
Arrow	Low	Run	4	6	0.06	22.11	84.65	95.89
Arrow	Low	Run	4	7	0.06	22.45	80.24	96.17
Arrow	Low	Run	4	8	0.06	22.04	92.86	96.25
Arrow	Low	Run	6	3	0.06	27.56	90.7	95.39
Arrow	Low	Run	6	3	0.152	23.57	89.27	95.62
Arrow	Low	Run	6	4	0.06	22.46	97.24	97.4
Arrow	Low	Run	6	4	0.168	21.93	93.94	98.7
Arrow	Low	Run	6	5	0.06	24.26	90	99.53
Arrow	Low	Run	6	5	0.092	22.54	89.1	95.03
Arrow	Low	Run	6	6	0.06	22.62	84.05	96.07
Arrow	Low	Run	6	7	0.06	22.3	92.52	97.43
Arrow	Low	Run	8	5	0.06	22.32	98.44	98.25
Arrow	Low	Run	8	5	0.26	21.77	97.71	96.18
Arrow	Low	Run	8	6	0.06	21.84	94.5	95.2
Arrow	Low	Run	8	6	0.144	21.78	94.32	99.9
Arrow	Low	Run	8	7	0.06	34.6	97.86	99.28
Leigh	Int	Glide	0	3	0.06	29.38	97.48	99.98
Leigh	Int	Glide	0	7	0.06	17.77	90.33	96.45
Leigh	Int	Glide	0	7	0.1	17.92	92.02	95.93
Leigh	Int	Glide	0	9	0.06	17.91	85.89	99.19
Leigh	Int	Glide	0	9	0.104	17.69	89.98	96.9
Leigh	Int	Glide	2	3	0.06	18.04	92.53	99.51

Leigh	Int	Glide	2	7	0.06	17.82	93	98.23
Leigh	Int	Glide	2	7	0.128	18.04	90.57	99.09
Leigh	Int	Glide	2	9	0.06	17.83	81.28	97.73
Leigh	Int	Glide	2	9	0.1	17.81	93.93	98.32
Leigh	Int	Glide	2	11	0.06	20.1	95.19	97.44
Leigh	Int	Glide	4	3	0.06	26.64	86.61	98.71
Leigh	Int	Glide	4	7	0.06	18.36	87.33	95.73
Leigh	Int	Glide	4	9	0.06	18.08	86.09	95.77
Leigh	Int	Glide	4	11	0.06	17.52	96.37	95.37
Leigh	Int	Glide	4	11	0.096	17.24	96.37	99.87
Leigh	Int	Glide	6	7	0.06	18.34	82.93	98.61
Leigh	Int	Glide	6	9	0.06	18.5	88.54	95.68
Leigh	Int	Glide	6	9	0.112	18.63	97.03	96.36
Leigh	Int	Glide	8	3	0.06	17.11	49.11	79.11
Leigh	Int	Glide	8	3	0.144	17.91	91.22	96.62
Leigh	Int	Glide	8	7	0.06	18.04	74.63	97.6
Leigh	Int	Glide	8	9	0.06	18.19	87.51	99.66
Leigh	Int	Glide	8	9	0.12	18.23	89.44	95.76
Leigh	Int	Glide	10	3	0.06	18.12	80.42	97.61
Leigh	Int	Glide	10	3	0.148	17.81	84.26	96.69
Leigh	Int	Glide	10	7	0.06	18.01	78.24	98.87
Leigh	Int	Pool	0	3.5	0.06	38.95	99.58	99.83
Leigh	Int	Pool	0	3.5	0.124	31.18	99.52	96.07
Leigh	Int	Pool	0	5	0.06	19.03	51.03	81.03
Leigh	Int	Pool	0	5	0.212	17	91.08	98.16
Leigh	Int	Pool	0	6.5	0.06	17.84	90.75	98.67
Leigh	Int	Pool	0	6.5	0.188	18.38	91.43	98.98
Leigh	Int	Pool	2	2	0.06	44.59	99.68	97.8
Leigh	Int	Pool	2	3.5	0.06	45.83	98.65	96.5
Leigh	Int	Pool	2	3.5	0.204	42.81	98.74	95.58
Leigh	Int	Pool	2	5	0.06	16.67	94.16	96.62
Leigh	Int	Pool	2	5	0.3	16.63	91.74	95.22
Leigh	Int	Pool	2	6.5	0.06	18.03	93.24	97.93
Leigh	Int	Pool	2	6.5	0.168	21.95	93.21	97.09
Leigh	Int	Pool	2	8	0.06	35.13	97.3	98.27
Leigh	Int	Pool	2	8	0.088	24.7	97.16	95.89
Leigh	Int	Pool	4	3.5	0.06	43.46	98.71	96.6
Leigh	Int	Pool	4	3.5	0.232	37.17	98.9	95.31
Leigh	Int	Pool	4	5	0.06	18.61	92.33	96.8
Leigh	Int	Pool	4	5	0.292	20.18	94.82	95.04
Leigh	Int	Pool	4	6.5	0.06	58.45	99.99	96.16
Leigh	Int	Pool	4	6.5	0.124	17.43	87.25	99.29
Leigh	Int	Pool	6	3.5	0.06	40.49	98.39	95.53
Leigh	Int	Pool	6	3.5	0.184	32.3	97.9	96.84
Leigh	Int	Pool	6	5	0.06	19.33	92.16	97.25

Leigh	Int	Pool	6	5	0.244	18.22	94.22	99.03
Leigh	Int	Pool	6	6.5	0.06	16.76	95.42	99.05
Leigh	Int	Pool	6	6.5	0.192	16.81	92.74	96.42
Leigh	Int	Pool	8	3.5	0.06	38.42	99.31	95.28
Leigh	Int	Pool	8	3.5	0.16	30.74	99.47	99.83
Leigh	Int	Pool	8	5	0.06	21.03	91.02	99.22
Leigh	Int	Pool	8	5	0.308	20.97	93.83	98.67
Leigh	Int	Pool	8	6.5	0.06	20.26	94.21	97.41
Leigh	Int	Pool	8	6.5	0.264	19.92	94.15	97.61
Leigh	Int	Pool	8	8	0.06	26.82	98.43	95.97
Leigh	Int	Pool	8	8	0.12	19.84	97.24	98.11
Leigh	Int	Pool	10	3.5	0.06	25.04	99.27	99.29
Leigh	Int	Pool	10	3.5	0.136	27.01	98.92	97.15
Leigh	Int	Pool	10	5	0.06	19.83	92.83	97.57
Leigh	Int	Pool	10	5	0.272	18.89	94.18	96.45
Leigh	Int	Pool	10	6.5	0.06	19.41	92.56	98.8
Leigh	Int	Pool	10	6.5	0.22	17.39	91.09	96.68
Leigh	Int	Pool	10	8	0.06	23.91	98.08	99.08
Leigh	Int	Pool	12	3.5	0.06	35.45	99.49	96.63
Leigh	Int	Pool	12	3.5	0.1	21.68	97.89	99.81
Leigh	Int	Pool	12	5	0.06	18.27	90.95	99.28
Leigh	Int	Pool	12	5	0.16	18.23	94.74	95.51
Leigh	Int	Pool	12	6.5	0.06	17.82	92.64	97.27
Leigh	Int	Pool	12	6.5	0.212	18	92.9	98.6
Leigh	Int	Riffle	0	5	0.06	20.86	95.01	99.01
Leigh	Int	Riffle	0	8	0.06	19.97	102.44	97.13
Leigh	Int	Riffle	2	6.5	0.06	23	109.48	98.77
Leigh	Int	Riffle	2	9.5	0.06	20.94	70.16	97.5
Leigh	Int	Riffle	4	9.5	0.06	16.89	48.89	78.89
Leigh	Int	Riffle	6	11	0.06	12.47	100.00	95.57
Leigh	Int	Riffle	8	9.5	0.06	26.07	86.41	95.92
Leigh	Int	Run	0	10	0.06	17.24	49.24	79.24
Leigh	Int	Run	0	11	0.06	22.84	89.15	96.39
Leigh	Int	Run	0	11.5	0.06	22.82	91.06	97.13
Leigh	Int	Run	2	10	0.06	32.01	93.86	95.36
Leigh	Int	Run	2	10.5	0.06	29.06	75.63	98.39
Leigh	Int	Run	2	11	0.06	30.6	83.01	96.44
Leigh	Int	Run	2	11.5	0.06	24.34	87.32	95.83
Leigh	Int	Run	4	10	0.06	22.8	84.42	95.44
Leigh	Int	Run	4	10	0.084	22.52	83.38	95.95
Leigh	Int	Run	4	10.5	0.06	22.1	71.09	99.28
Leigh	Int	Run	4	10.5	0.092	26.03	95.69	98.74
Leigh	Int	Run	4	11	0.06	27.82	94.82	96.57
Leigh	Int	Run	4	11	0.088	28.59	89.86	97.59
Leigh	Int	Run	4	11.5	0.06	24.9	87.58	96.47

Leigh	Int	Run	6	10	0.06	21.21	91.25	96.55
Leigh	Int	Run	6	10	0.1	21.58	87.47	97.23
Leigh	Int	Run	6	10.5	0.06	21.07	95.97	95.7
Leigh	Int	Run	6	11	0.06	21.05	71.71	95.73
Leigh	Int	Run	6	11	0.104	21.14	95.24	97.23
Leigh	Int	Run	8	10	0.06	22.06	85.09	99.18
Leigh	Int	Run	8	10.5	0.06	20.30	52.30	82.30
Leigh	Int	Run	8	10.5	0.096	18.7	84.94	97.13
Leigh	Int	Run	8	11	0.06	21.3	69	96.96
Leigh	Int	Run	8	11.5	0.06	21.08	79.54	97.14
Leigh	Int	Run	10	10	0.06	21.55	93.99	98.63
Leigh	Int	Run	10	10	0.12	18.45	89.92	97.41
Leigh	Int	Run	10	10.5	0.06	24.07	93.44	98.47
Leigh	Int	Run	10	10.5	0.12	18.92	74.07	95.95
Leigh	Int	Run	10	11	0.06	21.27	78.58	99.79
Leigh	Int	Run	10	11	0.096	20.95	81.61	97.85
Leigh	Int	Run	10	11.5	0.06	20.71	75.86	99.46
Leigh	Int	Run	12	10	0.06	19.55	80.76	95.94
Leigh	Int	Run	12	10	0.132	20.52	80.1	96.67
Leigh	Int	Run	12	10.5	0.06	20.43	69.92	95.63
Leigh	Int	Run	12	10.5	0.112	18.88	87.97	96.79
Leigh	Int	Run	12	11	0.06	19.24	68.75	96.41
Leigh	Int	Run	12	11	0.088	19.26	78.06	98.02
Leigh	Int	Run	12	11.5	0.06	19.42	79.44	99.64
Leigh	Int	Run	12	11.5	0.084	19.3	77.22	97.2
Leigh	Int	Run	12	12	0.06	21.14	86.17	95.48
Leigh	Low	Glide	0	7	0.06	27.54	99.57	98.97
Leigh	Low	Glide	0	7	0.096	17.4	98.05	96.37
Leigh	Low	Glide	0	9	0.06	18.89	97.74	99.07
Leigh	Low	Glide	0	9	0.112	21.89	98.56	99.93
Leigh	Low	Glide	2	9	0.06	26.91	98.69	98.78
Leigh	Low	Glide	2	9	0.1	18.85	97.97	98.05
Leigh	Low	Glide	2	11	0.06	39.67	99.95	95.84
Leigh	Low	Glide	2	11	0.128	20.54	98.91	95.55
Leigh	Low	Glide	4	3	0.06	33.43	99.33	96.66
Leigh	Low	Glide	4	7	0.06	30.53	98.77	98.3
Leigh	Low	Glide	4	9	0.06	36.03	96.46	95.55
Leigh	Low	Glide	4	11	0.06	39.84	99.34	98
Leigh	Low	Glide	4	11	0.088	26.89	98.77	95.66
Leigh	Low	Glide	6	9	0.06	22.52	92.22	98.79
Leigh	Low	Glide	6	9	0.092	36.78	92.9	95.32
Leigh	Low	Glide	8	3	0.06	24.62	99.25	97.24
Leigh	Low	Glide	8	3	0.124	21.49	98.93	97.46
Leigh	Low	Glide	8	9	0.06	27.17	98.13	98.51
Leigh	Low	Glide	8	9	0.13	27.89	98.35	97.02

Leigh	Low	Glide	10	3	0.06	33.08	99.81	98.37
Leigh	Low	Glide	10	3	0.136	20.47	98.79	98.04
Leigh	Low	Pool	0	3.5	0.06	25.01	99.25	96.64
Leigh	Low	Pool	0	3.5	0.104	20.81	98.8	98.17
Leigh	Low	Pool	0	5	0.06	17.95	97.57	98.56
Leigh	Low	Pool	0	5	0.188	17.8	97.73	97.63
Leigh	Low	Pool	0	6.5	0.06	39.8	99.96	96.21
Leigh	Low	Pool	0	6.5	0.164	39.74	99.99	96.81
Leigh	Low	Pool	2	3.5	0.06	44.4	99.72	97.88
Leigh	Low	Pool	2	3.5	0.172	29.16	99.75	99.11
Leigh	Low	Pool	2	5	0.06	41.32	99.84	99.91
Leigh	Low	Pool	2	5	0.268	23.3	98.56	96.26
Leigh	Low	Pool	2	6.5	0.06	40.56	99.76	99.1
Leigh	Low	Pool	2	6.5	0.148	35.43	99.76	95.64
Leigh	Low	Pool	2	8	0.06	38.65	99.95	95.97
Leigh	Low	Pool	4	3.5	0.06	42.71	99.61	99.05
Leigh	Low	Pool	4	3.5	0.216	34.36	99.74	97.05
Leigh	Low	Pool	4	5	0.06	24.16	98.25	97.9
Leigh	Low	Pool	4	5	0.268	23.9	98.46	96.98
Leigh	Low	Pool	6	3.5	0.06	39.35	99.77	99.91
Leigh	Low	Pool	6	3.5	0.116	34.94	99.26	99.47
Leigh	Low	Pool	6	5	0.06	26.47	99.43	95.73
Leigh	Low	Pool	6	5	0.26	22.69	98.8	96.03
Leigh	Low	Pool	6	6.5	0.06	40.76	99.99	99.92
Leigh	Low	Pool	6	6.5	0.116	28.53	99.88	97.25
Leigh	Low	Pool	6	8	0.06	41.47	99.98	99.5
Leigh	Low	Pool	6	8	0.108	29.17	99.91	96.38
Leigh	Low	Pool	8	3.5	0.06	30.81	99.95	96.86
Leigh	Low	Pool	8	3.5	0.084	39.21	99.72	95.43
Leigh	Low	Pool	8	5	0.06	23.39	99.08	96.69
Leigh	Low	Pool	8	5	0.244	19.89	98.71	98.44
Leigh	Low	Pool	8	6.5	0.06	43.49	99.2	96.29
Leigh	Low	Pool	8	6.5	0.24	34.95	99.84	95.33
Leigh	Low	Pool	8	8	0.06	37.39	99.92	96.37
Leigh	Low	Pool	8	8	0.152	33.75	99.98	99.16
Leigh	Low	Pool	10	3.5	0.06	28.69	99.37	96.9
Leigh	Low	Pool	10	3.5	0.096	23.47	99	96.28
Leigh	Low	Pool	10	5	0.06	37.36	99.89	99.11
Leigh	Low	Pool	10	5	0.248	28.44	99.16	99.91
Leigh	Low	Pool	10	6.5	0.06	34.25	99.61	96.11
Leigh	Low	Pool	10	6.5	0.228	24.62	99.48	97.38
Leigh	Low	Pool	10	8	0.08	29.88	99.71	96.14
Leigh	Low	Pool	12	3.5	0.06	21.81	98.87	96.25
Leigh	Low	Pool	12	5	0.06	43.4	99.21	95.24
Leigh	Low	Pool	12	5	0.18	19.97	98.45	98.59

Leigh	Low	Pool	12	6.5	0.06	24.15	98.98	96.15
Leigh	Low	Pool	12	6.5	0.228	17.2	97.58	95.47
Leigh	Low	Pool	12	8	0.06	35.72	99.79	96.99
Leigh	Low	Pool	12	8	0.132	27.28	99.7	96.57
Leigh	Low	Riffle	0	5	0.06	25.17	80.34	96.04
Leigh	Low	Riffle	2	5	0.06	25.64	96.86	96.25
Leigh	Low	Riffle	8	9.5	0.06	35.94	89.62	96.88
Leigh	Low	Run	0	11	0.06	23.25	87.73	95.87
Leigh	Low	Run	2	11	0.06	24.16	91.93	99.99
Leigh	Low	Run	4	10	0.06	25.5	89.31	95.29
Leigh	Low	Run	4	10.5	0.06	22.74	97.06	96.86
Leigh	Low	Run	4	11	0.06	23.3	95.79	97.73
Leigh	Low	Run	4	11.5	0.06	22.4	94.34	95.65
Leigh	Low	Run	6	10	0.06	44.86	98.48	99.91
Leigh	Low	Run	6	10.5	0.06	28.81	98.44	96.35
Leigh	Low	Run	6	11	0.06	33.08	93.61	99.77
Leigh	Low	Run	8	10	0.06	38.45	98.67	97.21
Leigh	Low	Run	8	10.5	0.06	33.45	94.71	96.44
Leigh	Low	Run	8	11	0.06	41.76	96.88	97.26
Leigh	Low	Run	10	10	0.06	36.79	99.68	97.79
Leigh	Low	Run	10	10.5	0.06	30.39	97.45	99.6
Leigh	Low	Run	10	11	0.06	34.85	97.76	96.36
Leigh	Low	Run	12	10	0.06	39.28	96.7	95.78
Leigh	Low	Run	12	10	0.116	35.04	97.89	96.45
Leigh	Low	Run	12	10.5	0.06	27.5	98.39	97
Leigh	Low	Run	12	10.5	0.088	31.47	98.77	99.06
Leigh	Low	Run	12	11	0.06	28.09	98.11	99.13
Leigh	Low	Run	12	11.5	0.06	27.33	97.45	99.45
Flowtracker:								
Arrow	High	Glide	0	7	0.06	19.3	>70	NA
Arrow	High	Glide	0	7	0.216	21.9	>70	NA
Arrow	High	Glide	4	3	0.06	21.5	>70	NA
Arrow	High	Glide	4	3	0.28	42.5	>70	NA
Arrow	High	Glide	4	7	0.06	24.5	>70	NA
Arrow	High	Glide	4	7	0.144	21	>70	NA
Arrow	High	Glide	4	11	0.06	22.7	>70	NA
Arrow	High	Glide	10	7	0.06	23.2	>70	NA
Arrow	High	Glide	10	7	0.24	24.5	>70	NA
Arrow	High	Pool	1	6	0.06	21.9	>70	NA
Arrow	High	Pool	1	6	0.3	22.3	>70	NA
Arrow	High	Pool	10	4	0.06	19.3	>70	NA
Arrow	High	Pool	10	4	0.408	20.6	>70	NA
Arrow	High	Pool	10	7	0.06	20.6	>70	NA
Arrow	High	Pool	10	7	0.48	19.3	>70	NA
Arrow	High	Pool	10	10	0.06	22.7	>70	NA

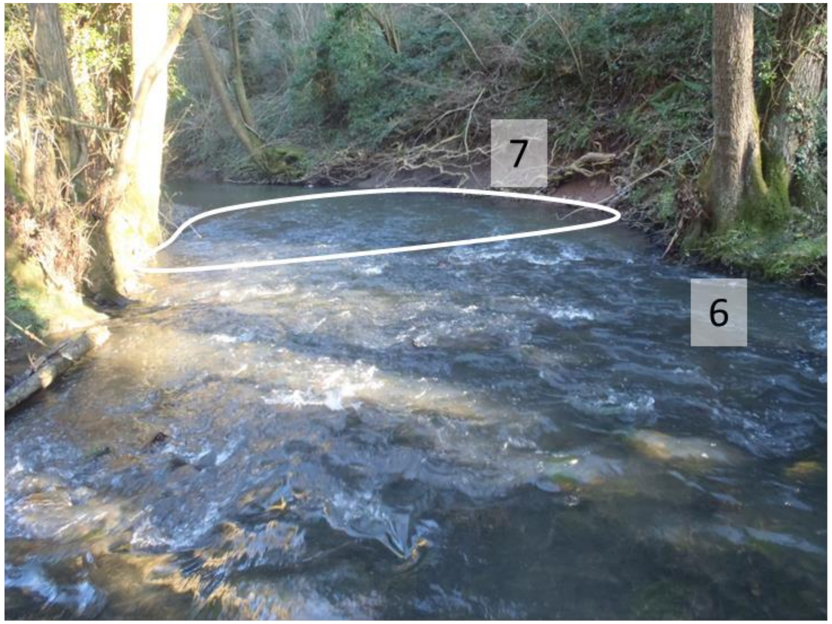
Arrow	High	Pool	10	10	0.328	19.7	>70	NA
Arrow	High	Pool	19	5	0.06	22.7	>70	NA
Arrow	High	Pool	19	5	0.176	21	>70	NA
Arrow	High	Riffle	0	10	0.06	18.4	>70	NA
Arrow	High	Riffle	6	3	0.06	18.4	>70	NA
Arrow	High	Riffle	6	7	0.06	18.9	>70	NA
Arrow	High	Riffle	6	7	0.148	18	>70	NA
Arrow	High	Riffle	6	10	0.06	18	>70	NA
Arrow	High	Riffle	12	7	0.06	21.5	>70	NA
Arrow	High	Run	0	9	0.06	21	>70	NA
Arrow	High	Run	0	9	0.1	20.6	>70	NA
Arrow	High	Run	4	4	0.06	19.9	>70	NA
Arrow	High	Run	4	7	0.06	18.9	>70	NA
Arrow	High	Run	4	10	0.06	18.4	>70	NA
Arrow	High	Run	8	6	0.06	18.9	>70	NA
Arrow	High	Run	8	6	0.16	19.3	>70	NA
Leigh	High	Glide	0	7	0.06	21.5	>70	NA
Leigh	High	Glide	0	7	0.152	21.5	>70	NA
Leigh	High	Glide	6	3	0.06	20.2	>70	NA
Leigh	High	Glide	6	3	0.124	20.2	>70	NA
Leigh	High	Glide	6	7	0.06	21.5	>70	NA
Leigh	High	Glide	6	7	0.144	21.5	>70	NA
Leigh	High	Glide	6	11	0.06	20.2	>70	NA
Leigh	High	Glide	6	11	0.124	20.2	>70	NA
Leigh	High	Glide	12	7	0.06	21	>70	NA
Leigh	High	Glide	12	7	0.12	21.5	>70	NA
Leigh	High	Pool	0	5	0.06	20.6	>70	NA
Leigh	High	Pool	0	5	0.28	20.6	>70	NA
Leigh	High	Pool	6	2	0.06	48.1	>70	NA
Leigh	High	Pool	6	5	0.06	22.3	>70	NA
Leigh	High	Pool	6	5	0.384	21	>70	NA
Leigh	High	Pool	6	8	0.06	20.6	>70	NA
Leigh	High	Pool	6	8	0.116	20.6	>70	NA
Leigh	High	Pool	12	6.5	0.06	20.6	>70	NA
Leigh	High	Pool	12	6.5	0.284	20.6	>70	NA
Leigh	High	Riffle	0	8	0.06	22.7	>70	NA
Leigh	High	Riffle	4	6.5	0.06	22.7	>70	NA
Leigh	High	Riffle	4	8	0.06	34.4	>70	NA
Leigh	High	Riffle	4	9.5	0.06	21	>70	NA
Leigh	High	Riffle	4	9.5	0.104	20.6	>70	NA
Leigh	High	Riffle	8	8	0.06	36.1	>70	NA
Leigh	High	Run	0	11	0.06	22.3	>70	NA
Leigh	High	Run	0	11	0.128	23.2	>70	NA
Leigh	High	Run	6	10	0.06	23.6	>70	NA
Leigh	High	Run	6	10	0.164	23.6	>70	NA

Leigh	High	Run	6	11	0.06	23.2	>70	NA
Leigh	High	Run	6	11	0.16	24	>70	NA
Leigh	High	Run	6	12	0.06	22.7	>70	NA
Leigh	High	Run	12	11	0.06	22.7	>70	NA
Leigh	High	Run	12	11	0.176	24	>70	NA

Table B2 – Characteristics of habitats mapped along a reach of the Leigh Brook. % refers to proportion of areal cover.

Habitat number	Width (m)	Length (m)	Full width? (Bank)	Macrophytes %	Trailing veg and roots %	Organic detritus %	Woody debris %	SFT Dominant	%	Subdominant	%	Present	%	Substrate Fine %	Gravel %	Cobble %	Boulder %
1	2.4	17.6	N (LB)	0	15	0	0	UW	95	BW	5			0	20	70	10
2	5.6	10.7	N (RB)	5	0	20	0	SM	75	UP	25			30	10	20	20
3	3.5	8.5	N (RB)	0	0	0	0	RP	75	SM	25			0	20	40	40
4	3.4	5	N (LB)	0	10	10	5	RP	70	UW	10	SM	20	20	10	20	20
5	7	22	Y	0	10	0	0	SM	90	UW	5	RP	5	20	10	30	40
6	6.3	9	Y	5-10	0	0	5	UW	60	BW	20	RP	20	0	10	30	60
7		4	Y	0	0	0	0	RP	100					10	10	30	40
8		32	Y	0	10	10	0	SM	95	UP	5			20	20	30	20
9	3.1	7	N (LB)	<5	20	0	0	UW	85	RP	10	BW	5	0	10	50	40
10	1.9	7	N (RB)	<5	0	0	0	UW	90	RP	10			0	10	50	40
11		37.6	Y/N	0	10	10	0	SM	80	RP	15	UP	5	40	0	20	30
12	2	21	N (LB)	0	5	0	0	UW	100					0	20	60	20
13	4P	21	N (cent	0	0	0	0	RP	100					0	80	20	0
14	7P	8	N (RB)	5-10	5	0	0	RP	40	BW	40	UW	20	10	10	30	50
15		49	Y	0	15	0	0	SM	90	RP	5	UP	5	15	0	30	55
16		9	Y	0	5	0	10	BW	50	UW	30	RP	20	0	10	50	40
17		10	Y	0	10	5	0	RP	90	SM	10			15	20	40	20
18		20	Y	0	0	15	5	SM	100					40	10	20	15
19		23	Y	0	20	5	0	SM	90	RP	10			20	20	25	35
20	1.2	15	N (RB)	0	20	0	0	UW	100					10	20	50	20
21	3	11	N (cent	0	0	0	0	RP	100					0	20	20	60
22	2.2	11	N (cent	0	10	0	0	UW	50	BW	10	RP	40	0	10	20	70
23	2.4	13	N (LB)	0	0	0	0	SM	60	RP	30	UW	10	10	20	50	20
24		12	Y	0	0	0	5	SM	90	RP	10			20	10	35	35
25		5	Y	0	5	0	0	UW	95	BW	5			5	15	30	50
26	3P	30	N (RB)	0	10	0	0	RP	70	UW	20	SM	10	0	20	20	60
27	4P	26	N (LB)	0	0	0	0	SM	100					20	40	40	0
28		14	Y/N	0	5	0	0	RP	60	UW	30	BW	10	0	30	50	20

Figure B5 – Photographs of habitat units mapped along a reach of the Leigh Brook.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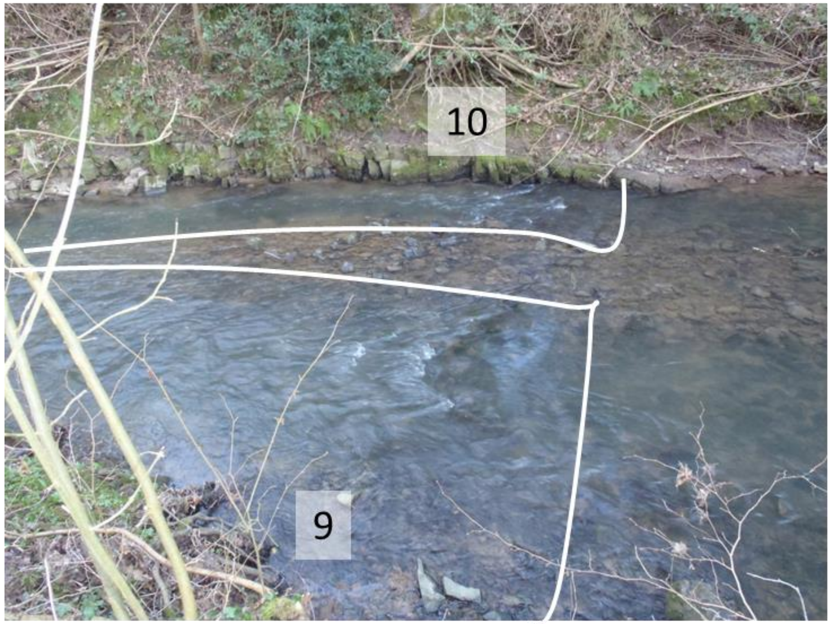
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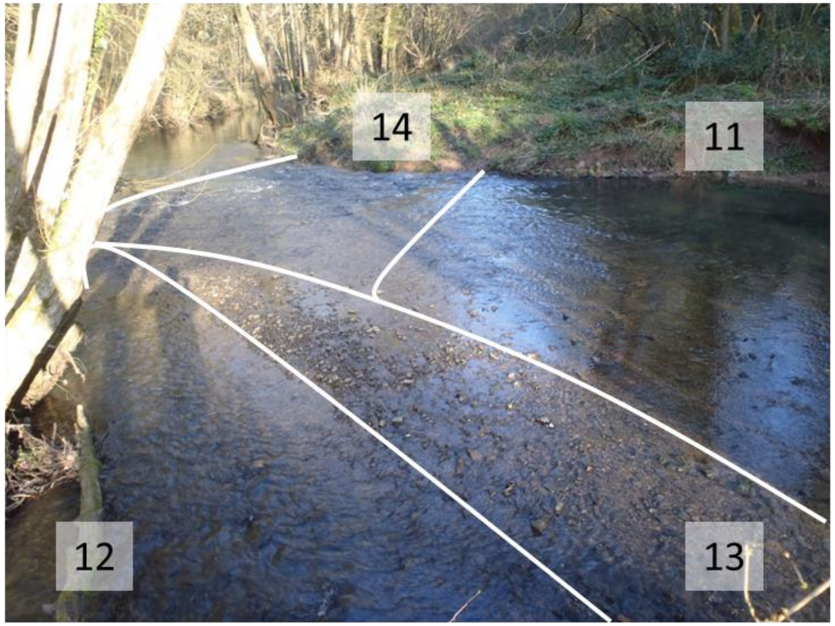
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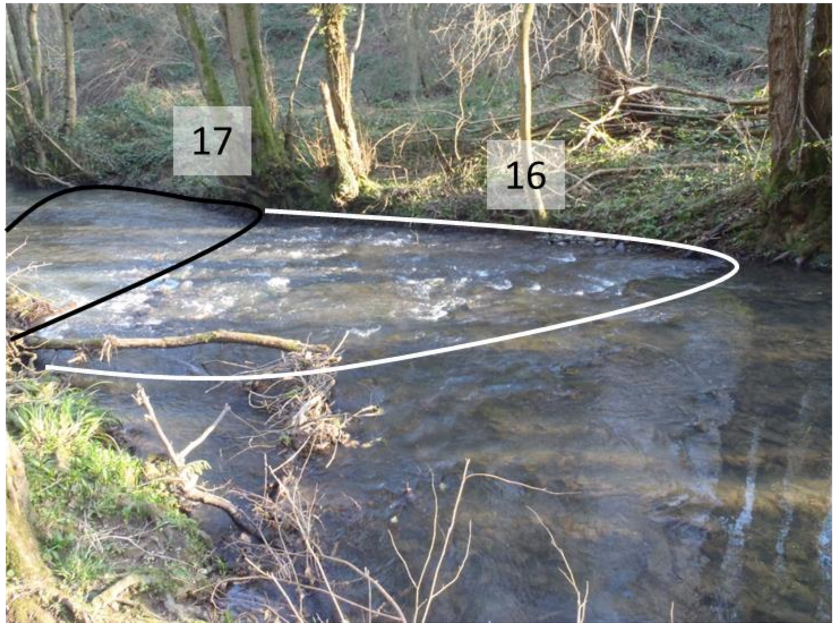
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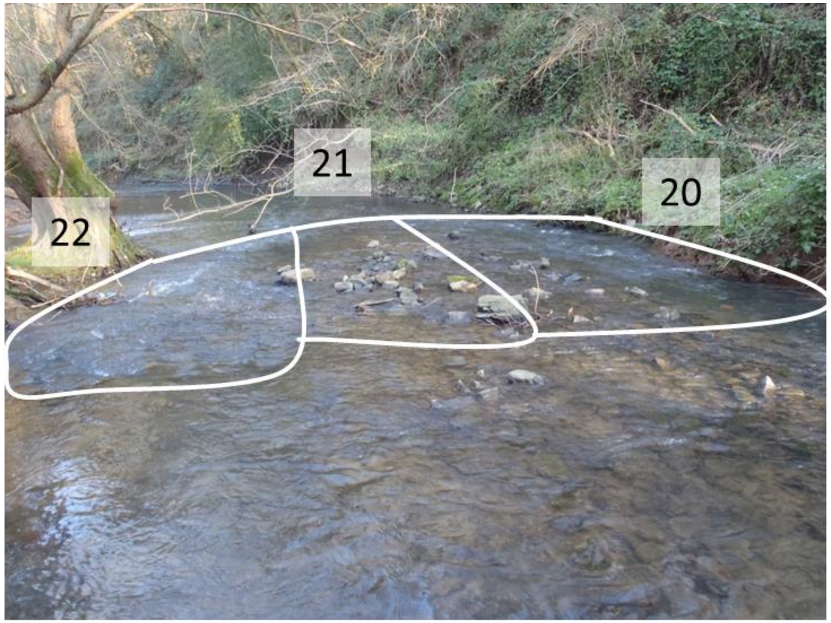
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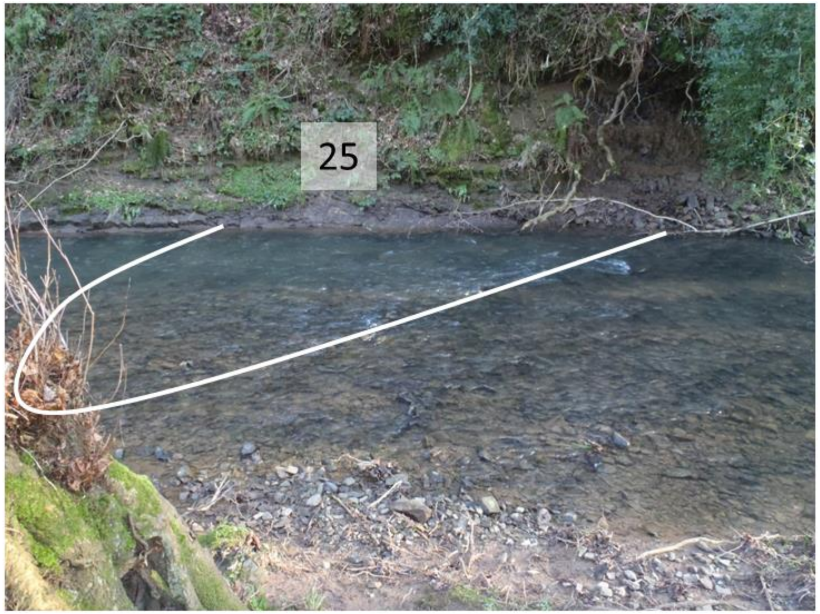
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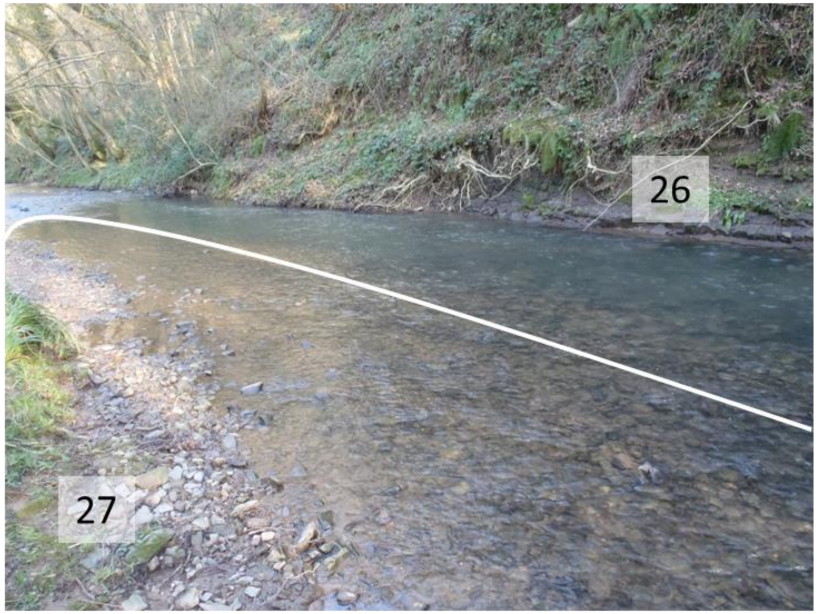
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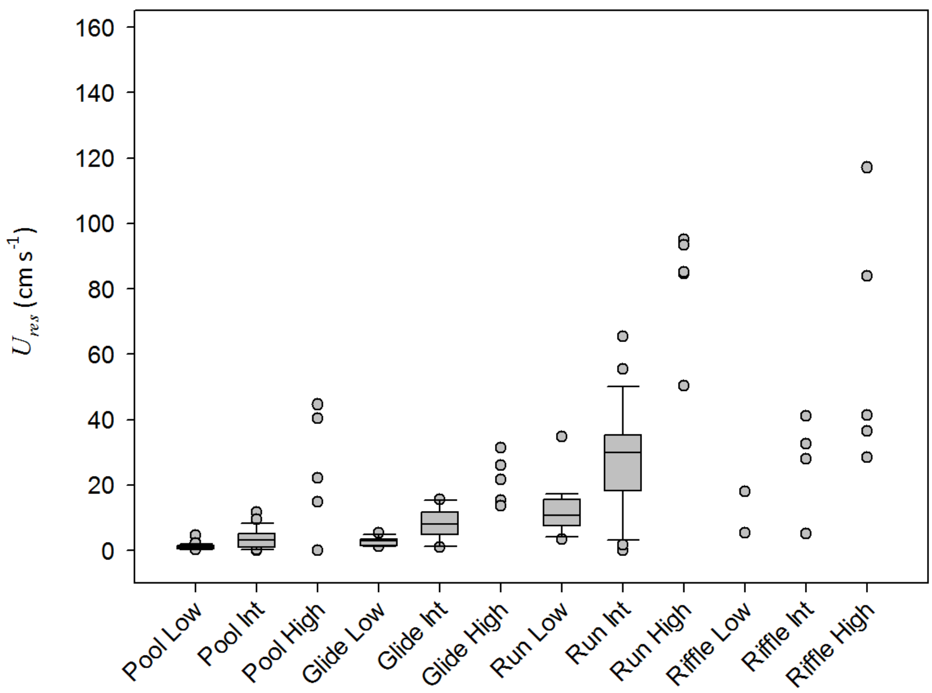


Figure B6 – Resultant velocity for Leigh Brook PBs including mean (horizontal lines), IQR (boxes), range up to 1.5IQR (whiskers) and outliers beyond 1.5 IQR (symbols). Only data points shown where sample size is limited (n<10).

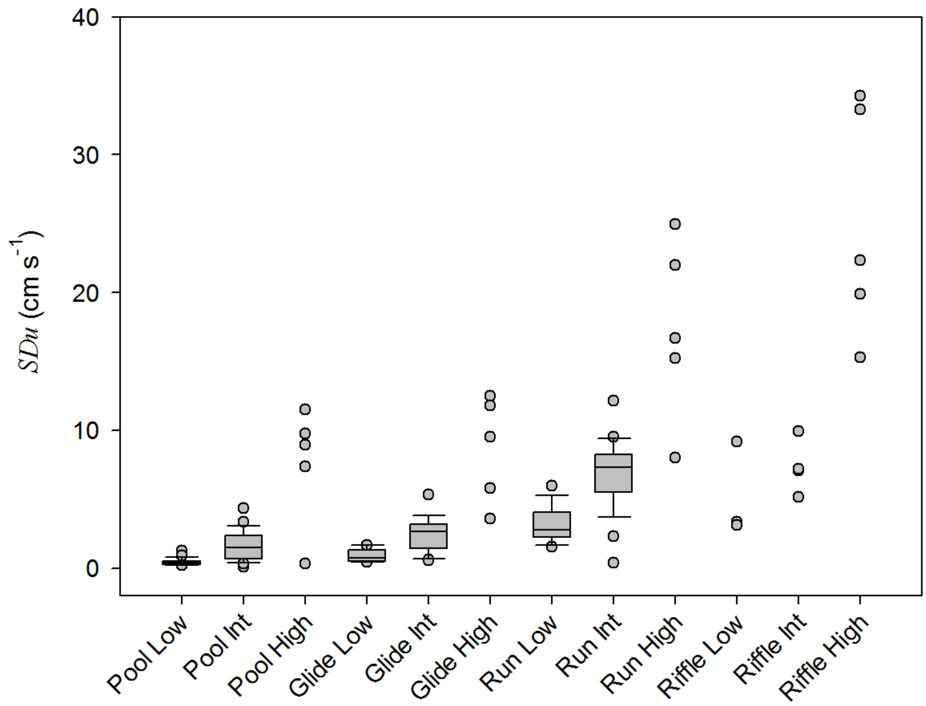


Figure B7 – Streamwise turbulence intensity for PBs of the Leigh Brook.

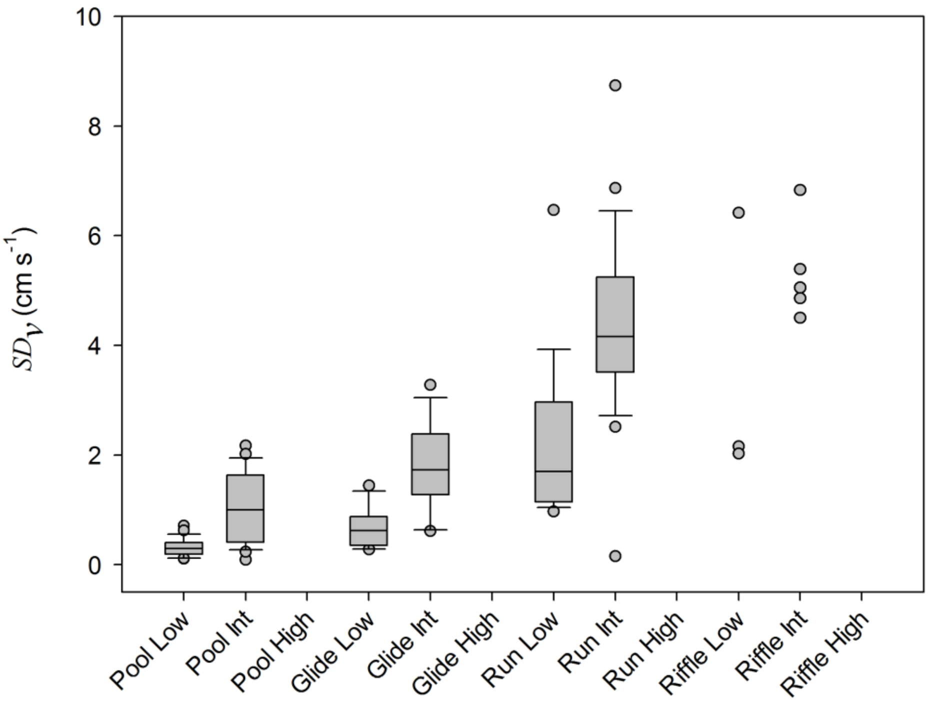


Figure B8 – Vertical turbulence intensity for PBs of the Leigh Brook.

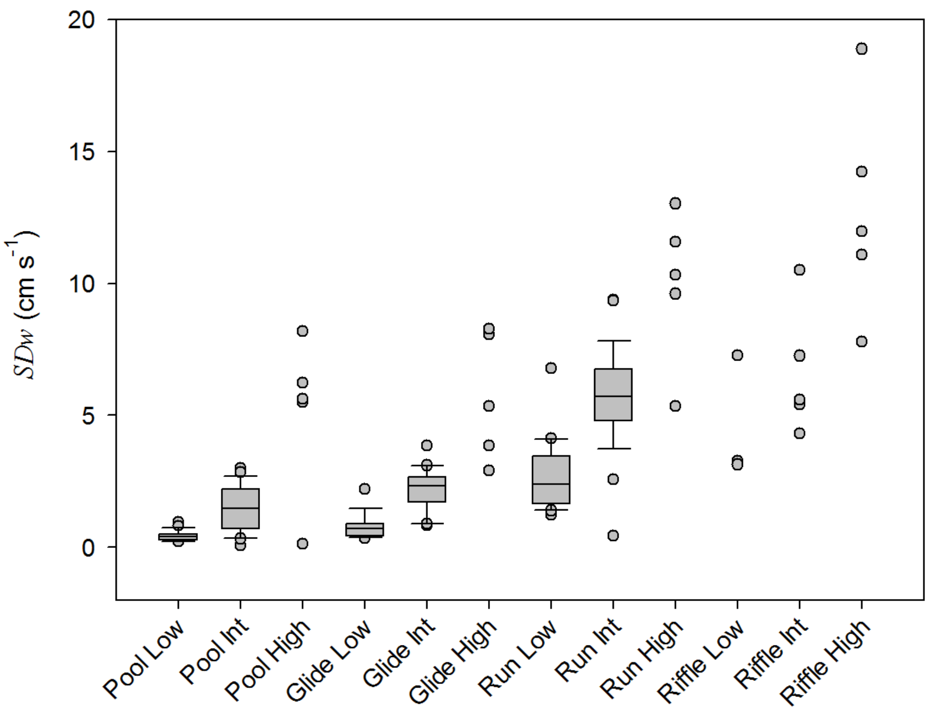


Figure B9 – Spanwise turbulence intensity for PBs of the Leigh Brook.

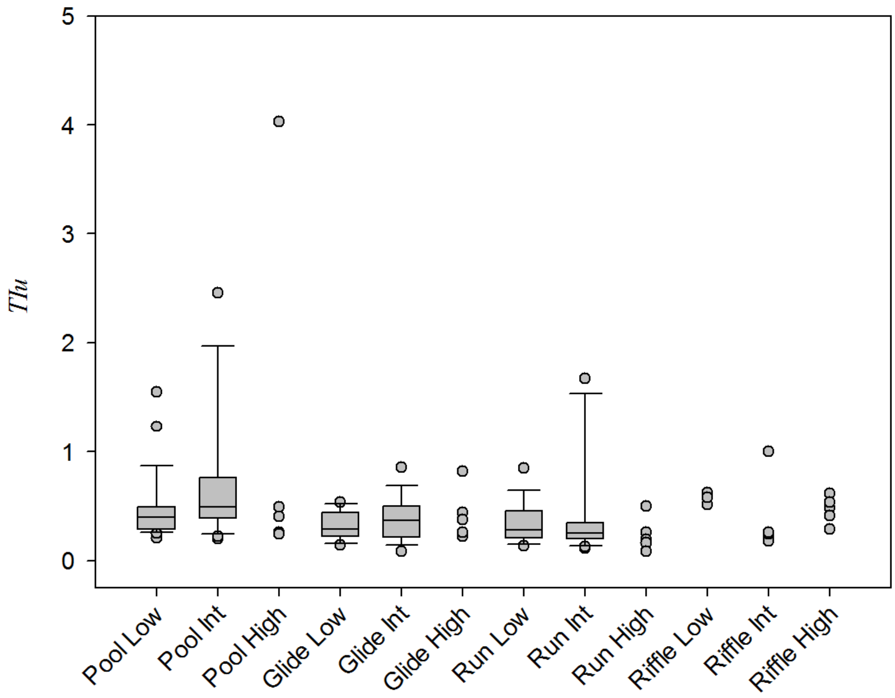


Figure B10 – Relative streamwise turbulence intensity for PBs of the Leigh Brook.

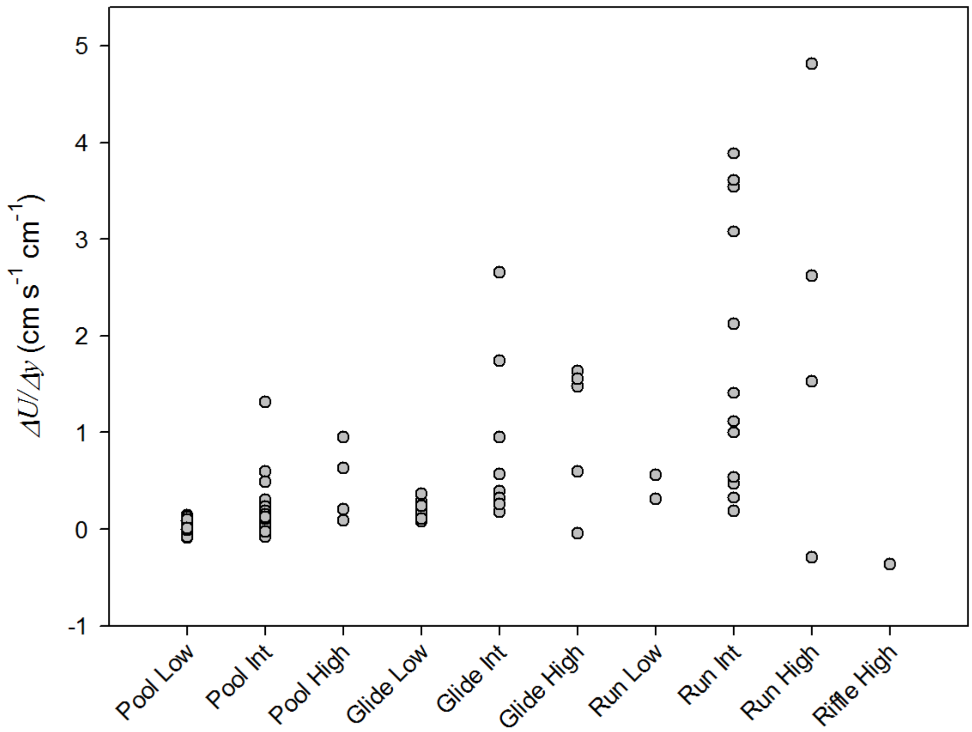


Figure B11 – Change in mean streamwise velocity with height above bed for PBs of the Leigh Brook.

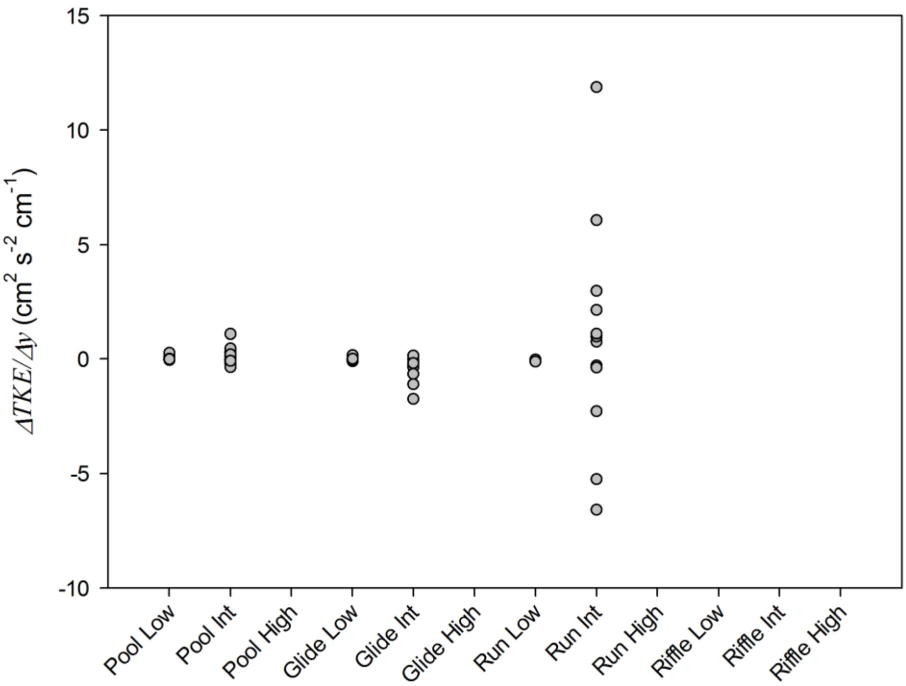


Figure B12 - Change in turbulent kinetic energy with height above bed for PBs of the Leigh Brook.

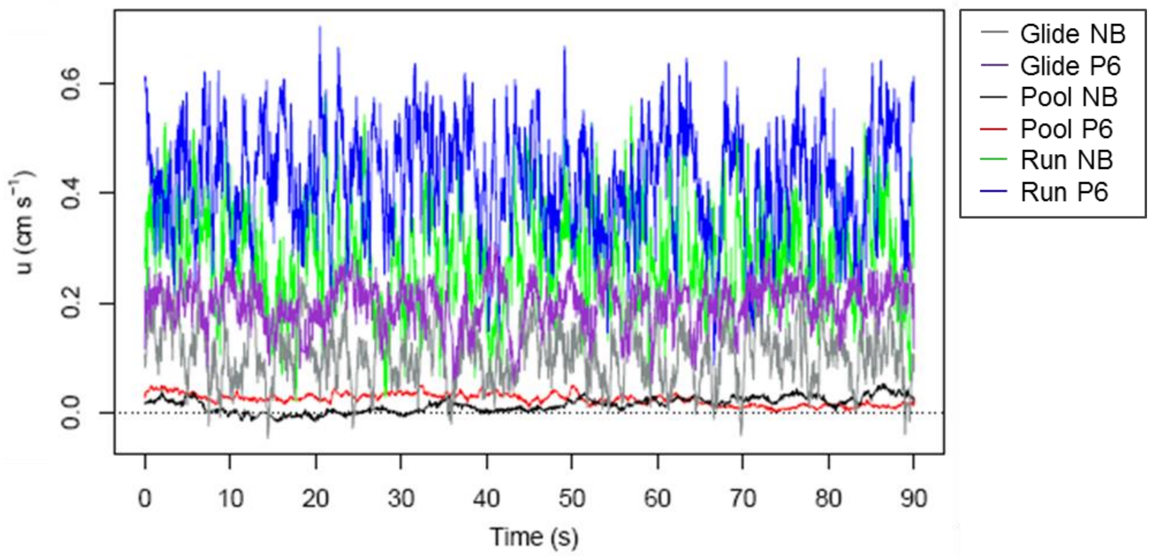


Figure B13 – Selected time series typifying the depth variability of the streamwise component for PBs of the Leigh Brook at intermediate flow. Near bed (NB) and point-six (P6) locations shown. No data available for the riffle.

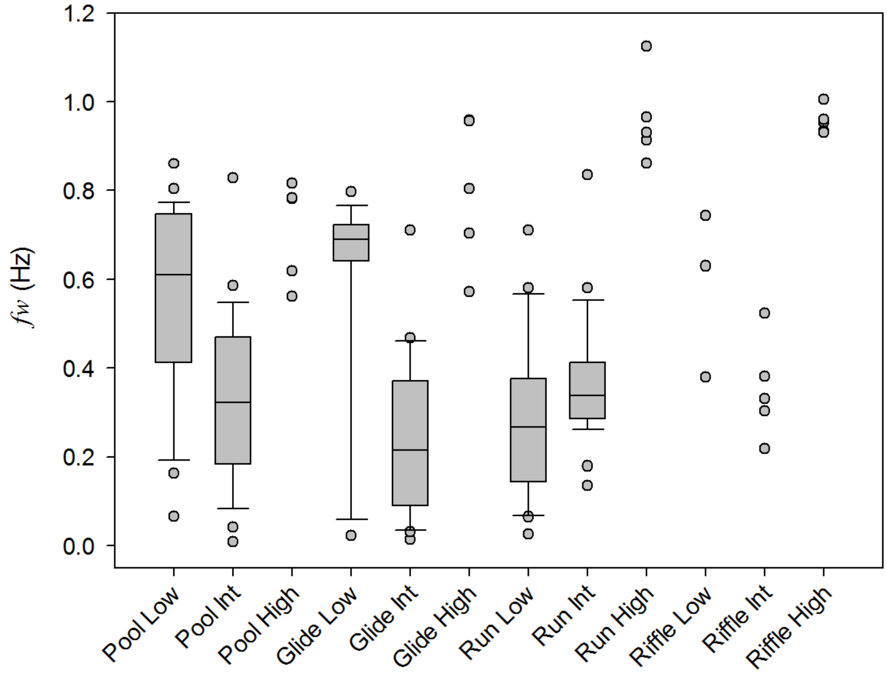


Figure B14 – Average eddy frequency of the spanwise component for PBs of the Leigh Brook.

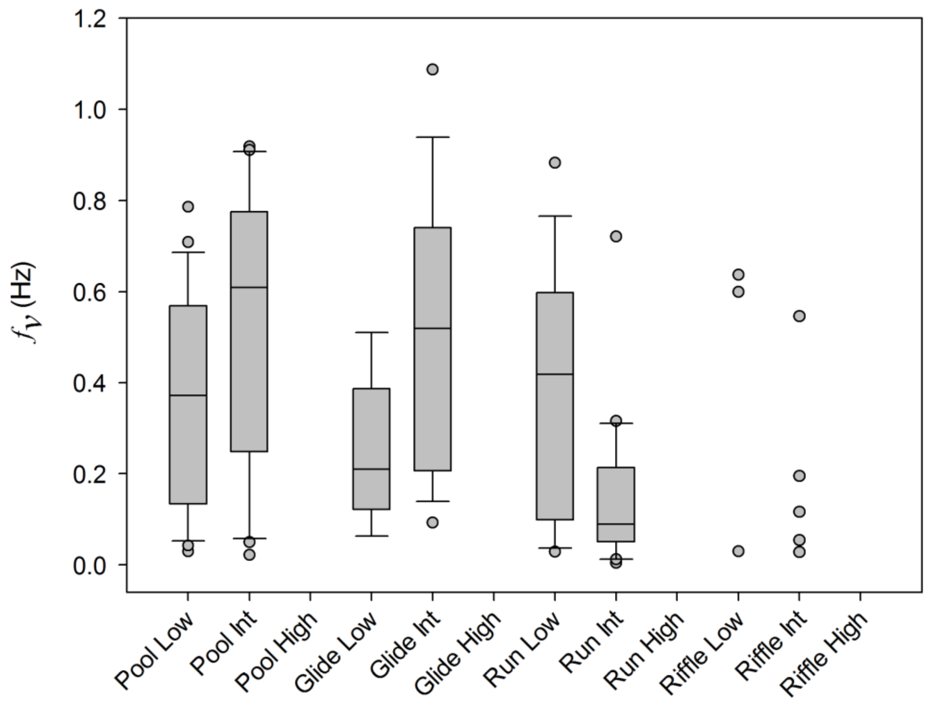


Figure B15 – Average eddy frequency of the vertical component for PBs of the Leigh Brook.

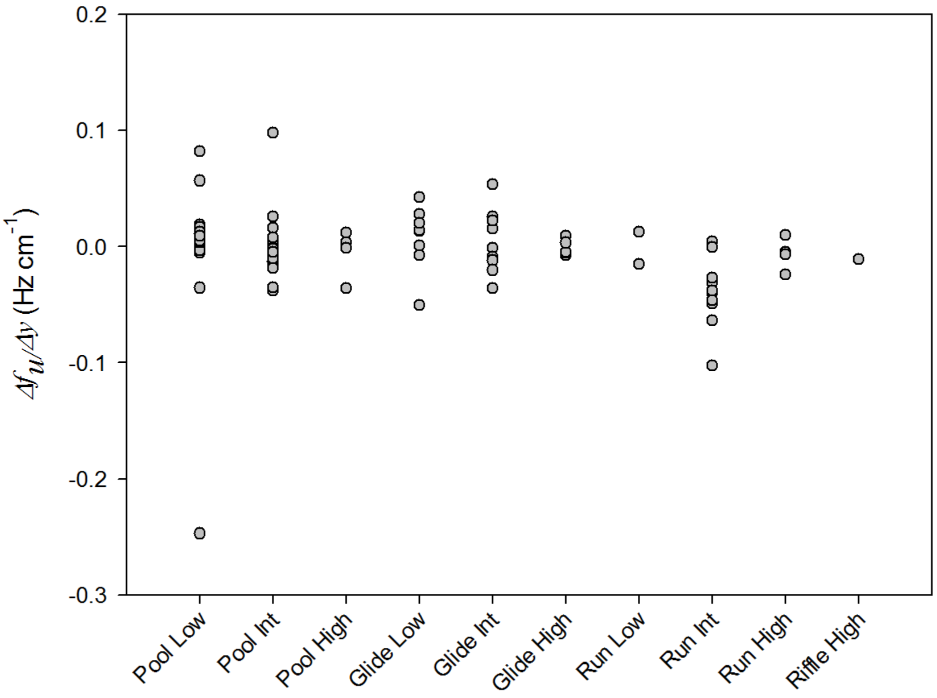


Figure B16 – Change in average streamwise eddy frequency with height above bed for PBs of the Leigh Brook.

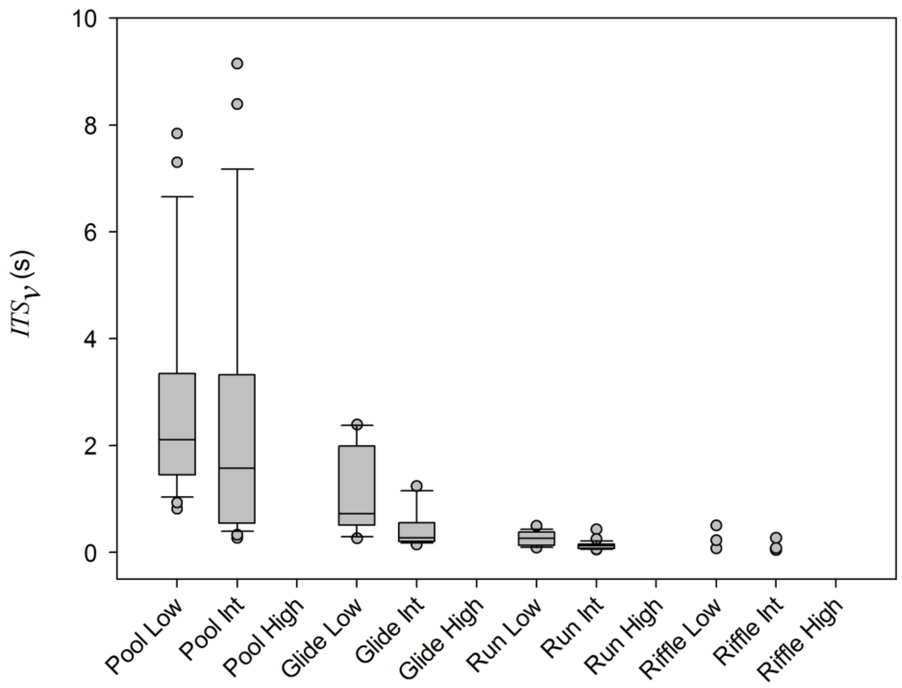


Figure B17 – Integral time scale of the vertical component for PBs of the Leigh Brook.

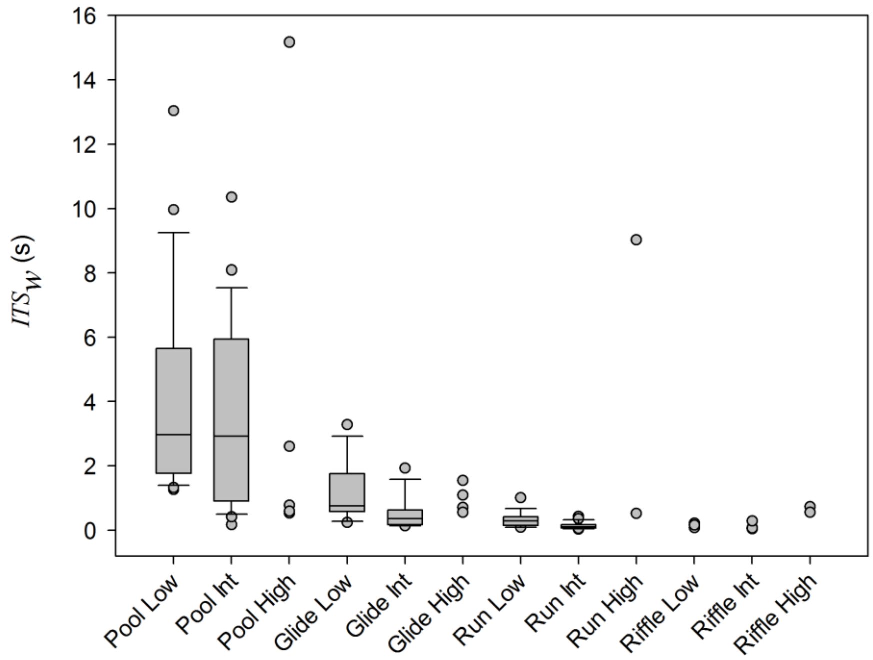


Figure B18 – Integral time scale of the spanwise component for PBs of the Leigh Brook.

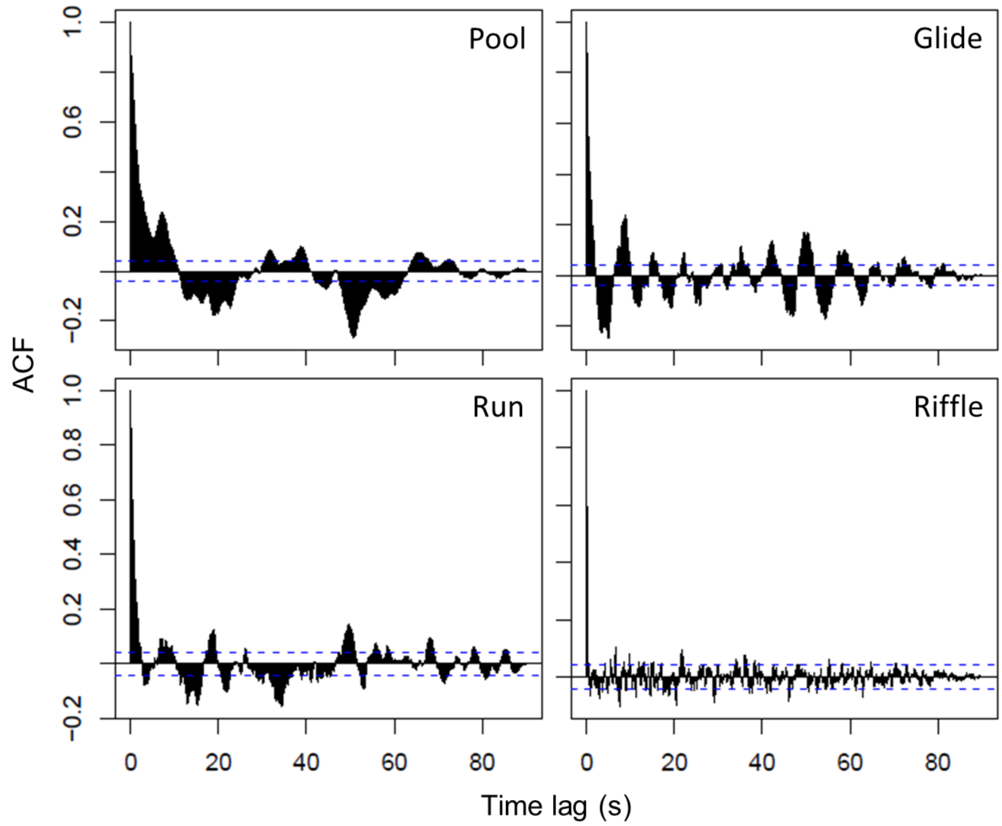


Figure B19 – Selected ACFs typifying the streamwise component for PBs of the Leigh Brook at low flow. Dashed lines indicate bounds of non-significant ($p>0.05$) correlation.

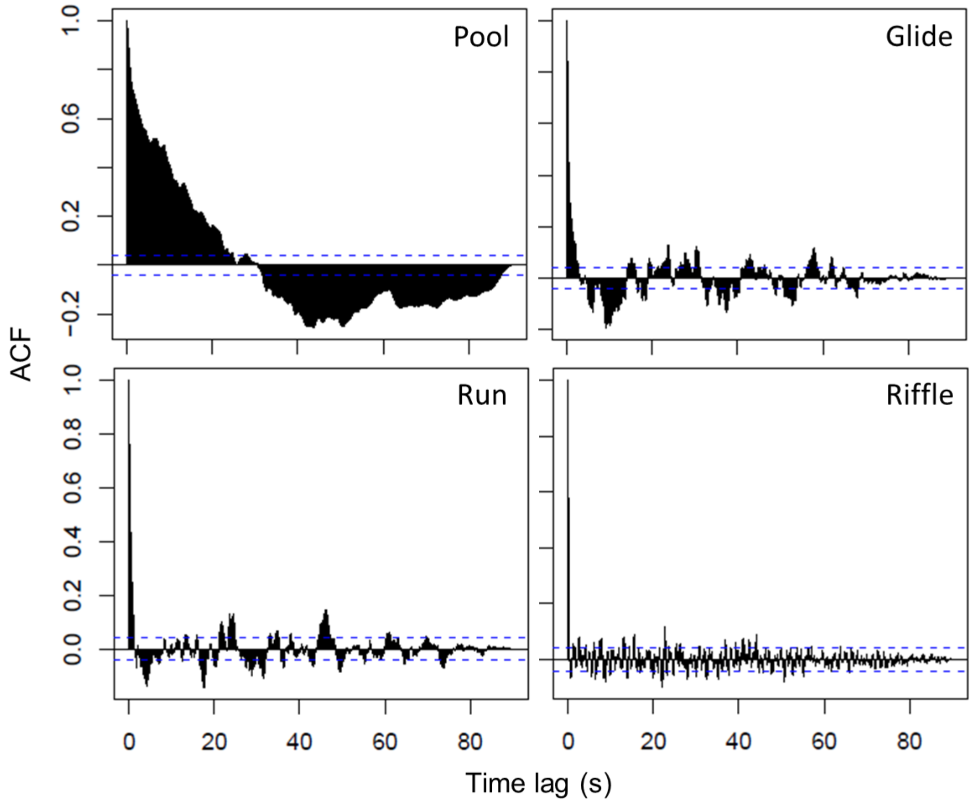


Figure B20 – Selected ACFs typifying the streamwise component for PBs of the Leigh Brook at intermediate flow. Dashed lines indicate bounds of non-significant (p>0.05) correlation.

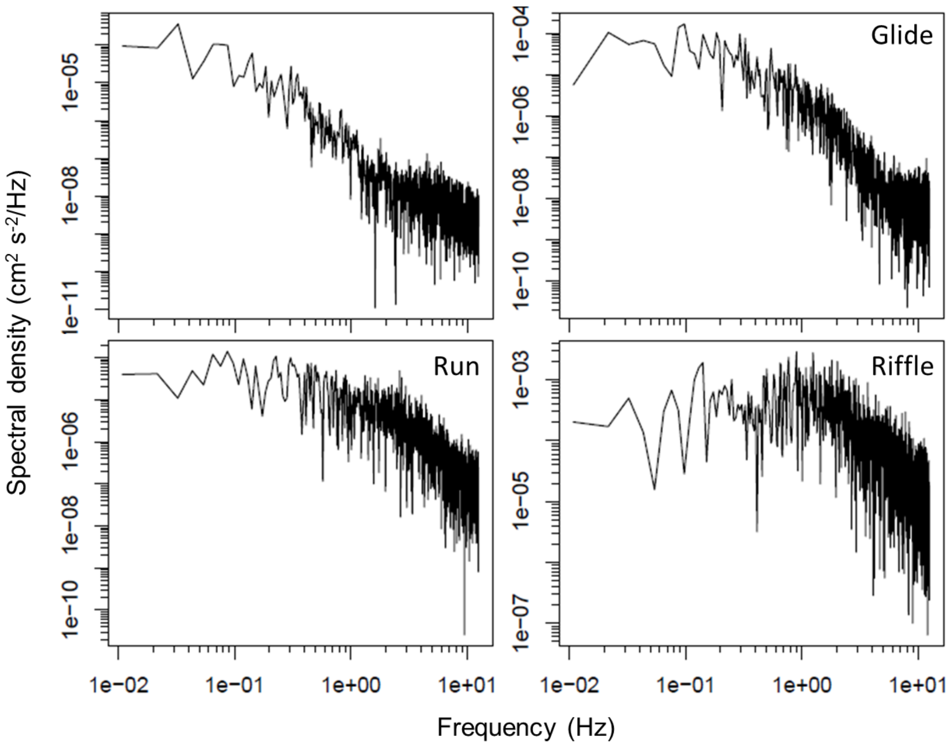


Figure B21 – Selected velocity power spectra typifying the vertical component for PBs of the Leigh Brook at low flow.

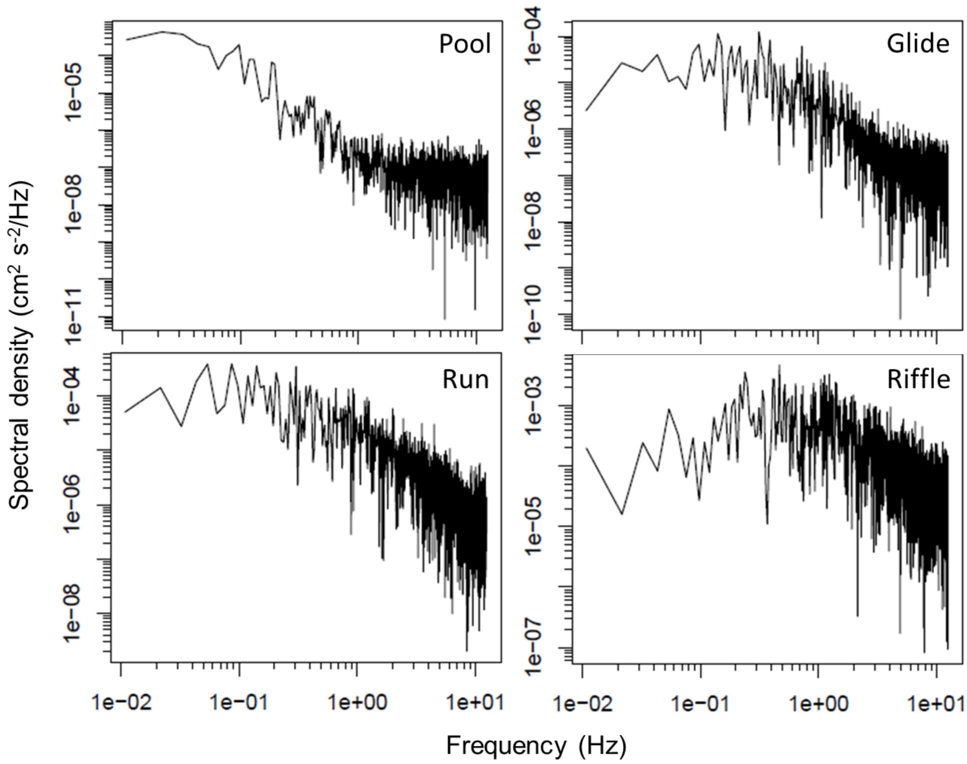


Figure B22 – Selected velocity power spectra typifying the spanwise component for PBs of the Leigh Brook at low flow.

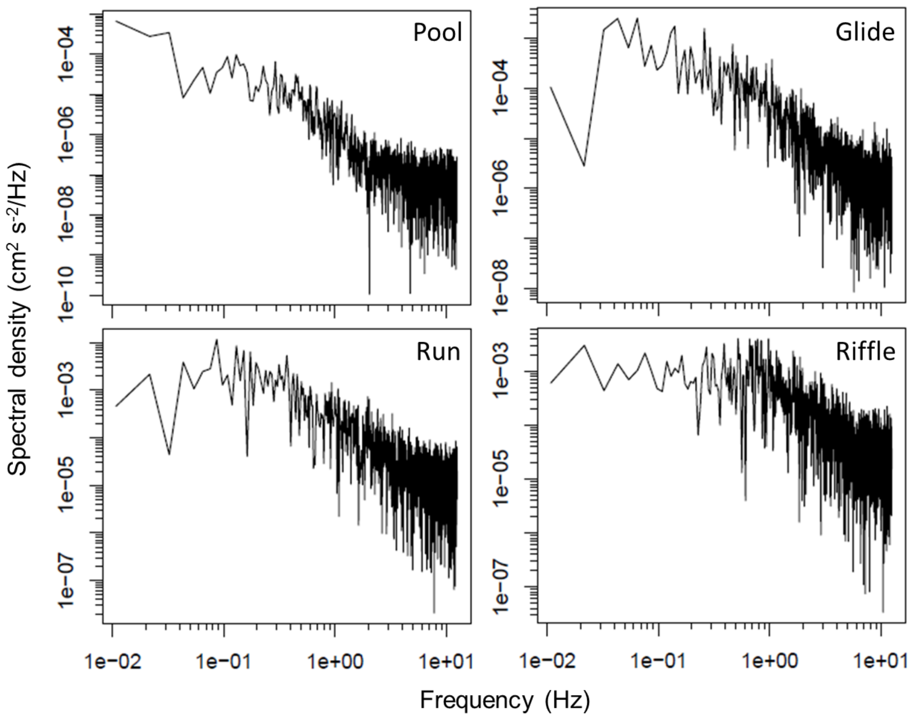


Figure B23 – Selected velocity power spectra typifying the streamwise component for PBs of the Leigh Brook at intermediate flow.

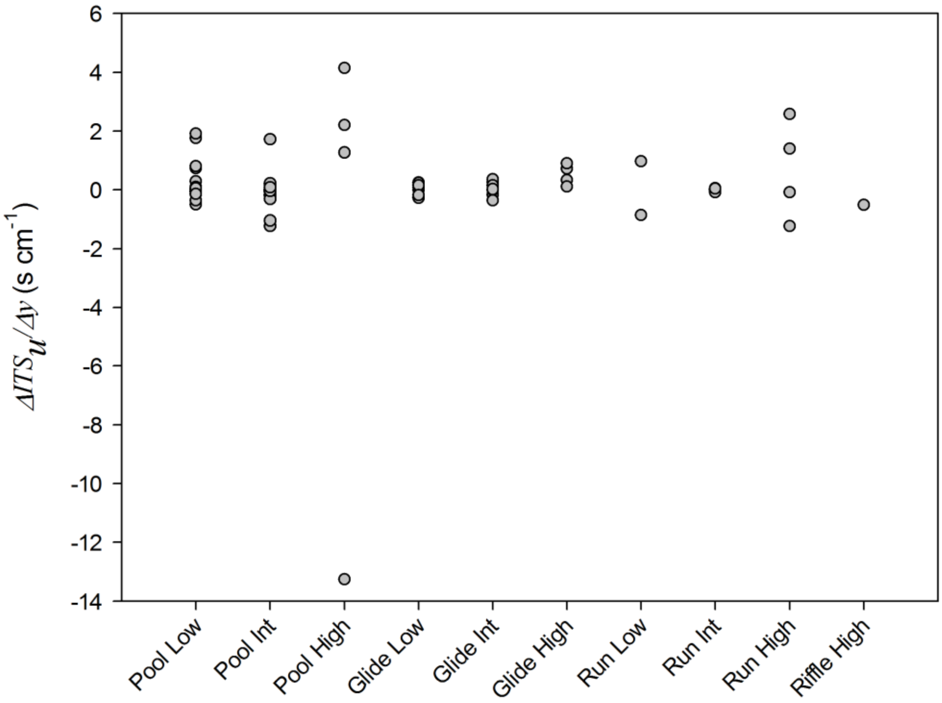


Figure B24 – Change in integral time scale of the streamwise component with height above bed for PBs of the Leigh Brook.

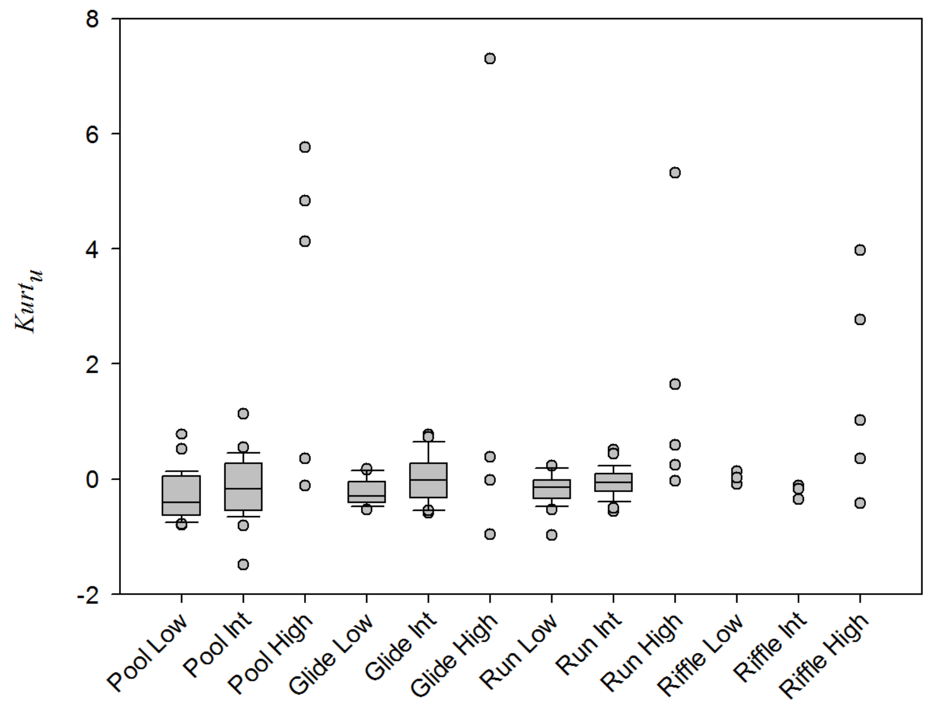


Figure B25 – Kurtosis of the streamwise component for PBs of the Leigh Brook.

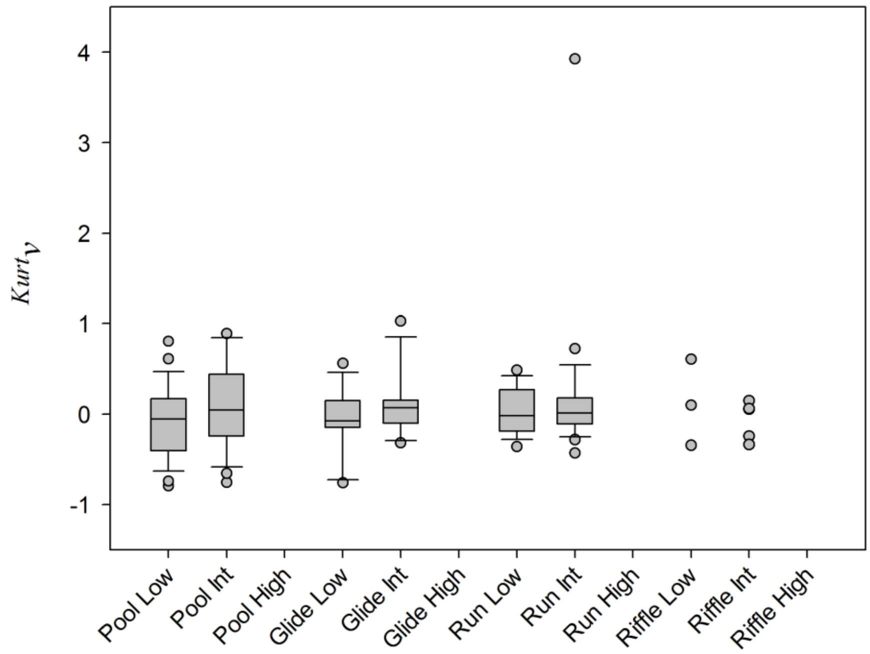


Figure B26 – Kurtosis of the vertical component for PBs of the Leigh Brook.

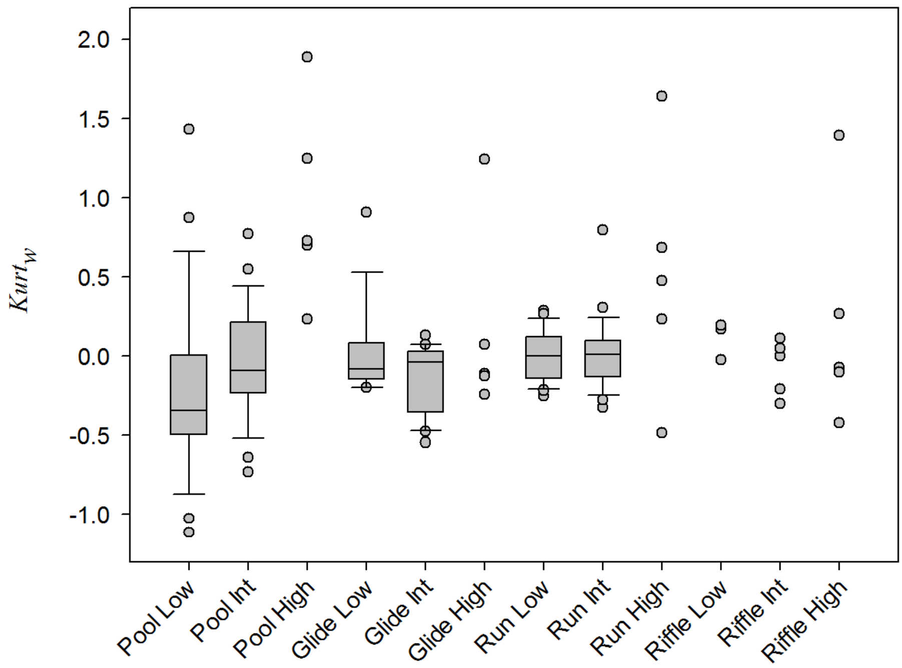


Figure B27 – Kurtosis of the spanwise component for PBs of the Leigh Brook.

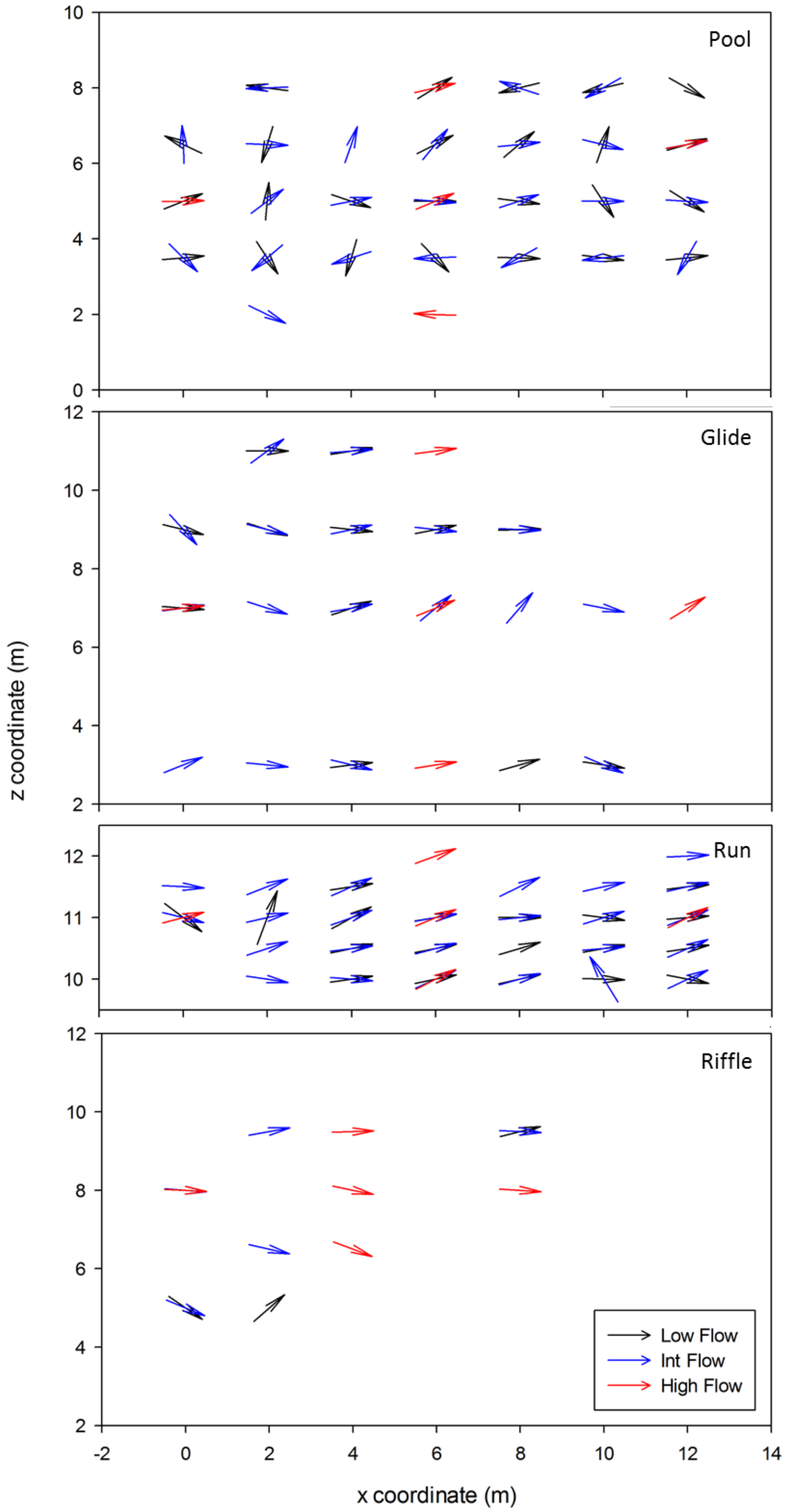


Figure B28 – Primary horizontal velocity vector for PBs of the Leigh Brook.

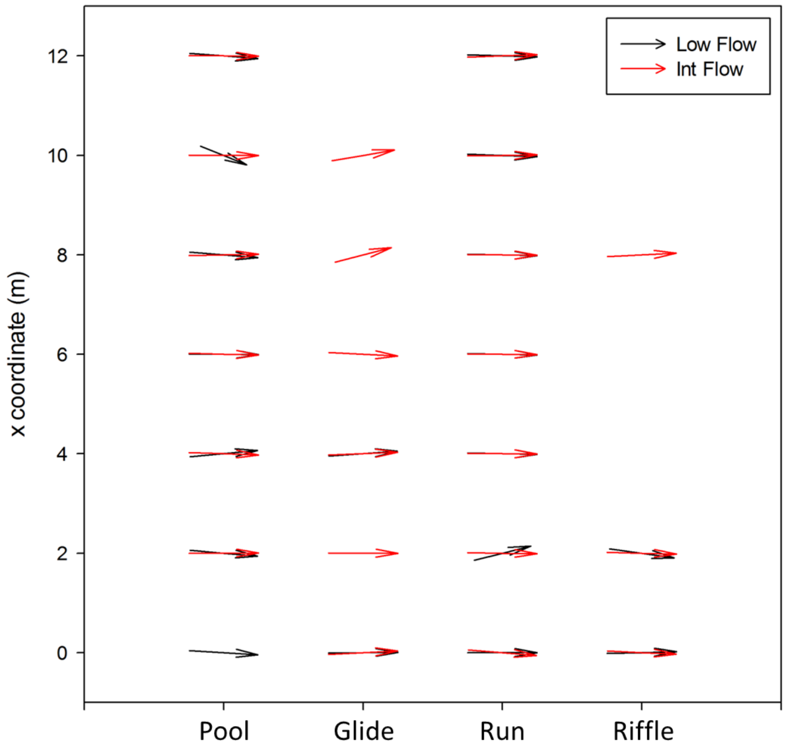


Figure B29 – Primary vertical velocity vector for the centreline of PBs of the Leigh Brook.

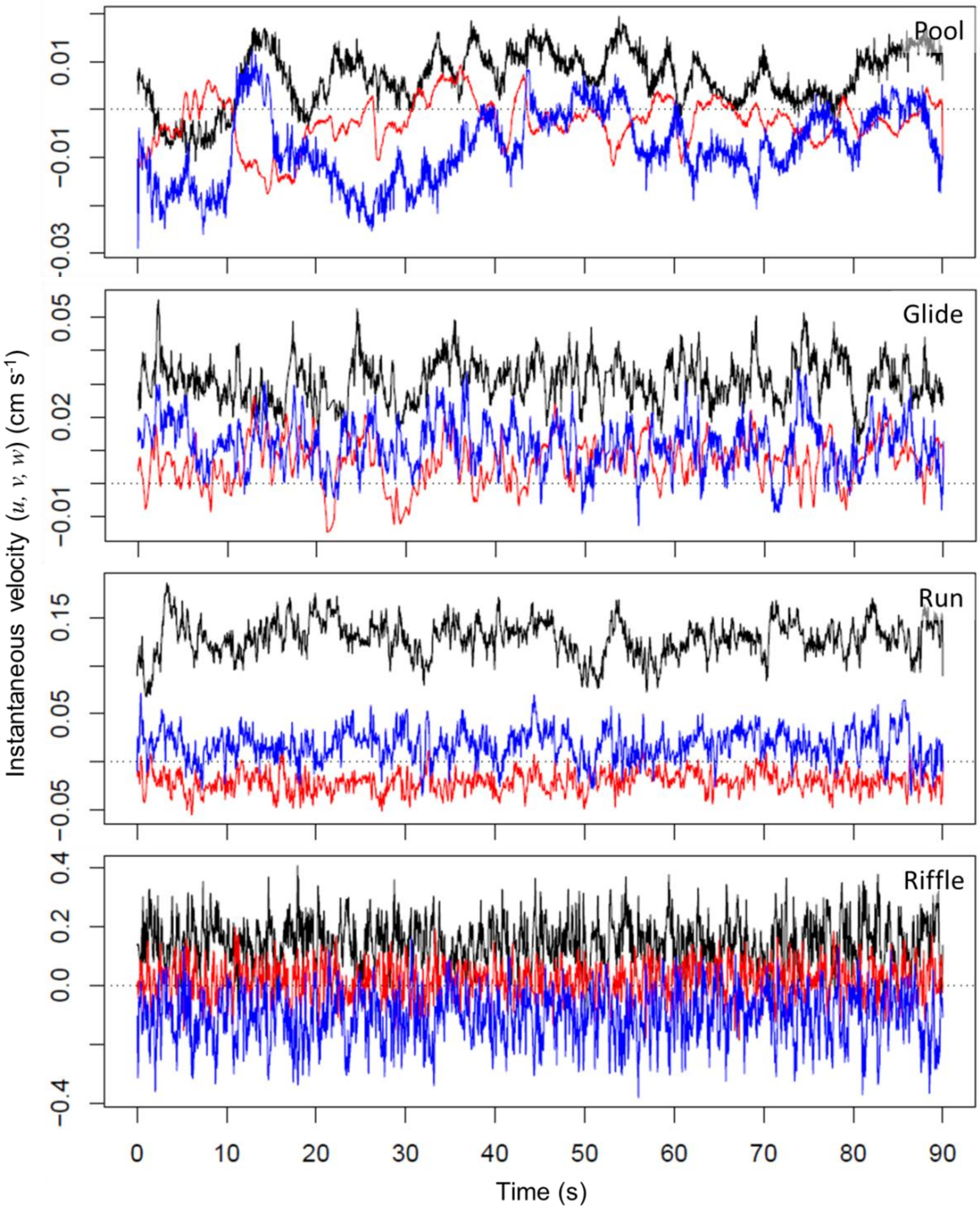


Figure B30 – Selected time series typifying three-dimensional velocities in PBs of the Leigh Brook at low flow. Based on un-rotated data (black=u, red=v, blue=w).

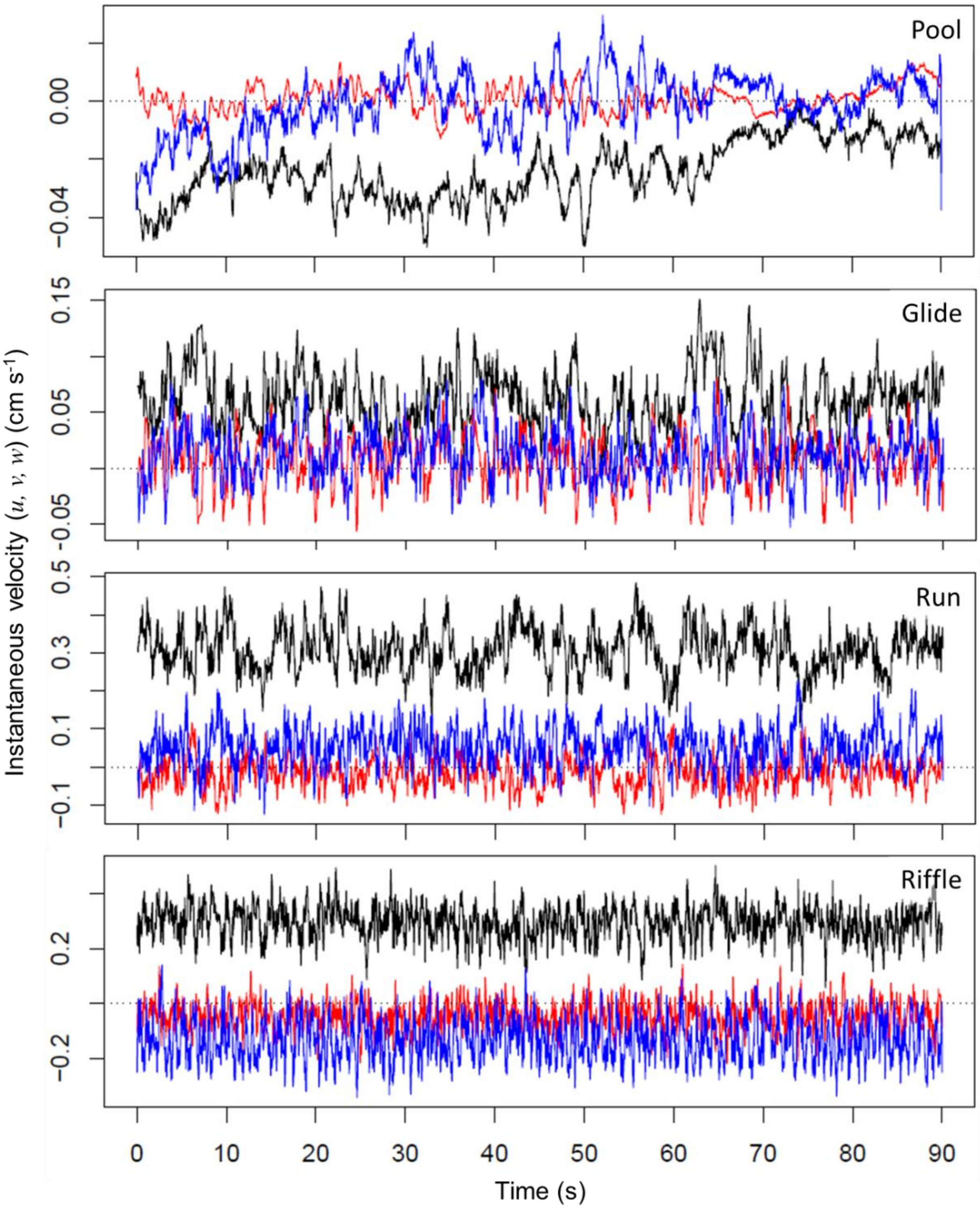


Figure B31 – Selected time series typifying three-dimensional velocities in PBs of the Leigh Brook at intermediate flow. Based on un-rotated data (black=u, red=v, blue=w).

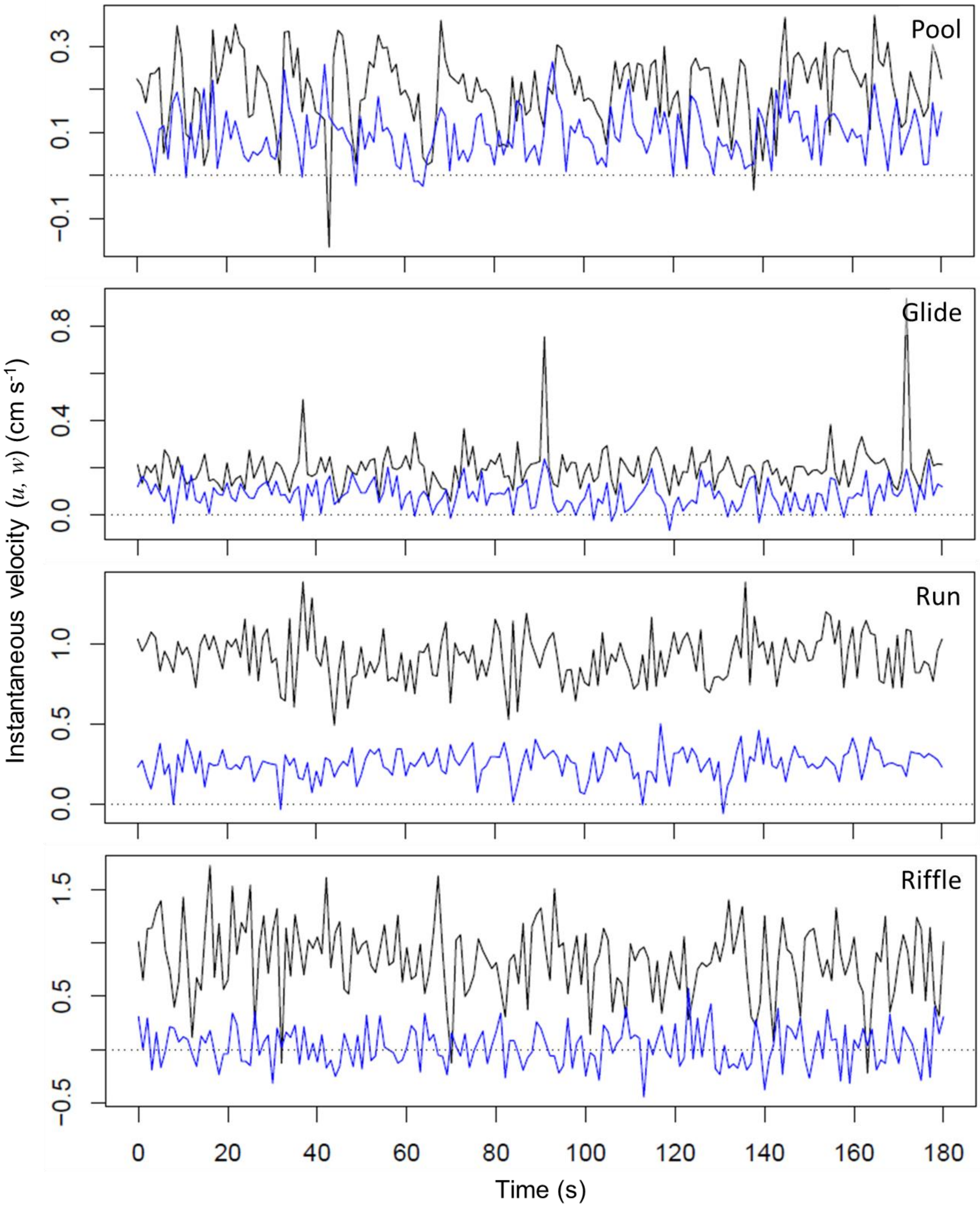


Figure B32 – Selected time series typifying two-dimensional velocities in PBs of the Leigh Brook at high flow. Based on un-rotated data (black=u, blue=w).

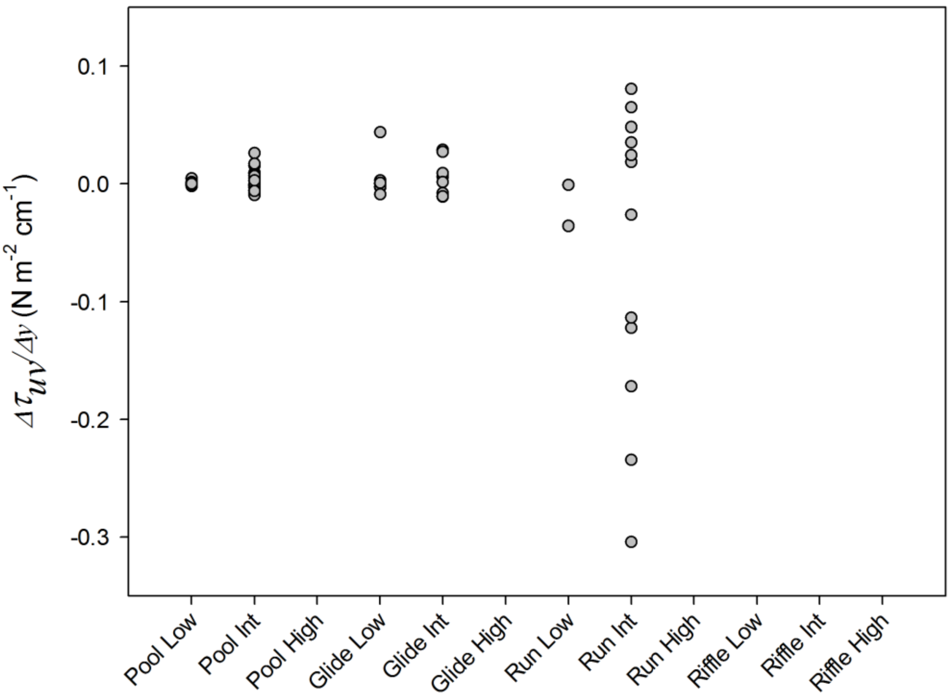


Figure B33 – Change in Reynolds shear stress on the streamwise-vertical plane with height above bed for PBs of the Leigh Brook.

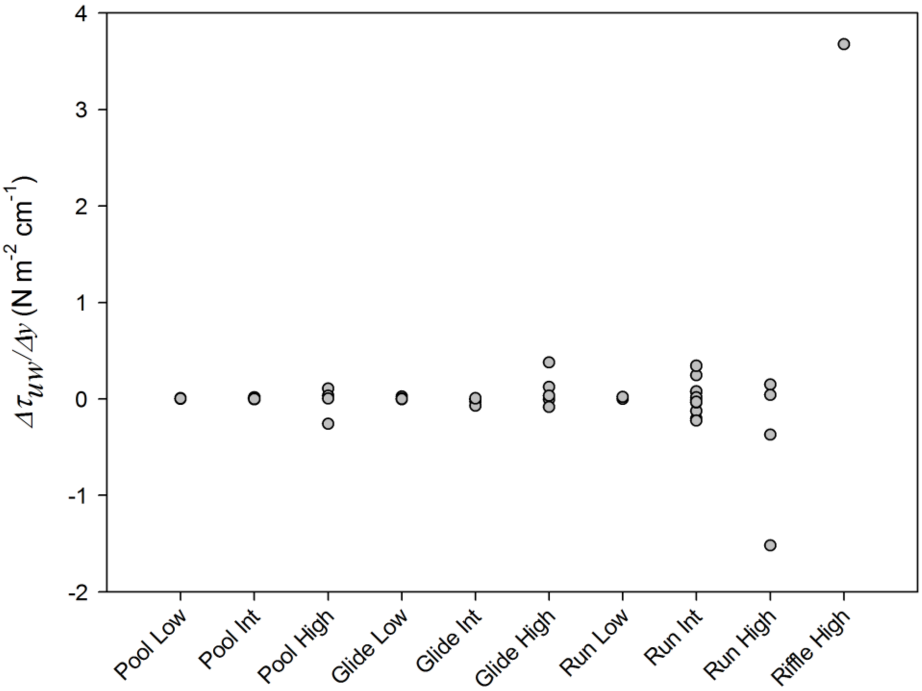


Figure B34 – Change in Reynolds stress on the streamwise-spanwise plane with height above bed for PBs of the Leigh Brook.

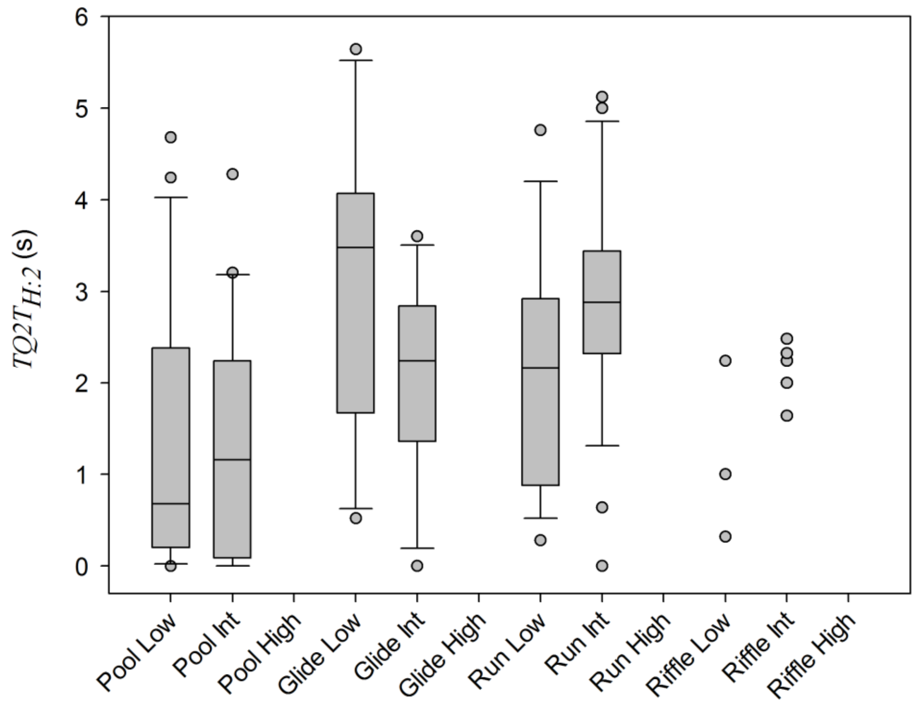


Figure B35 – Cumulative duration of ejections (Q2) for PBs of the Leigh Brook.

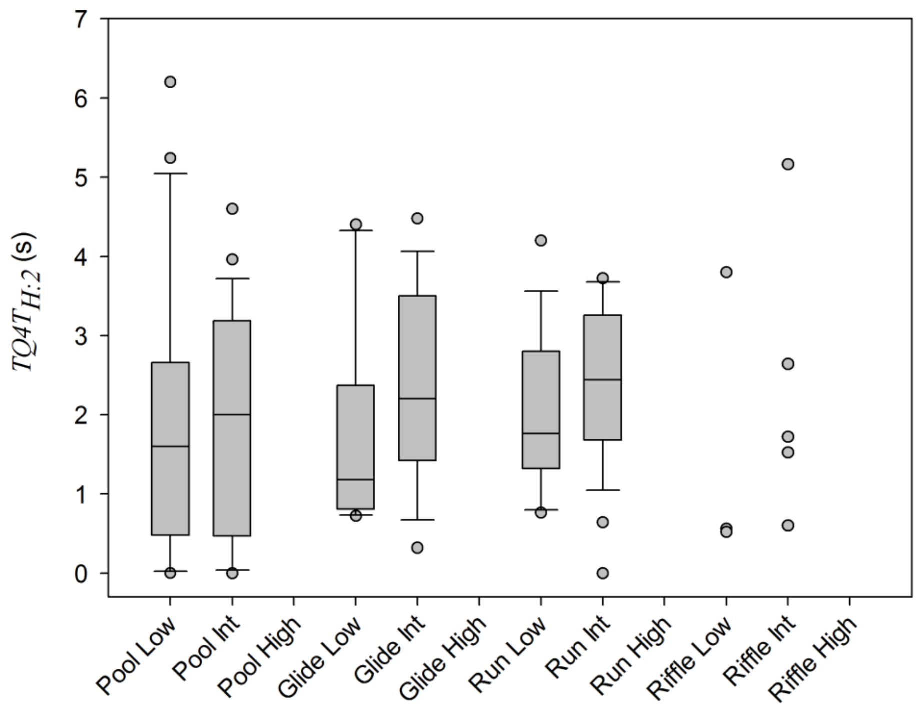


Figure B36 – Cumulative duration of sweeps (Q4) for PBs of the Leigh Brook.

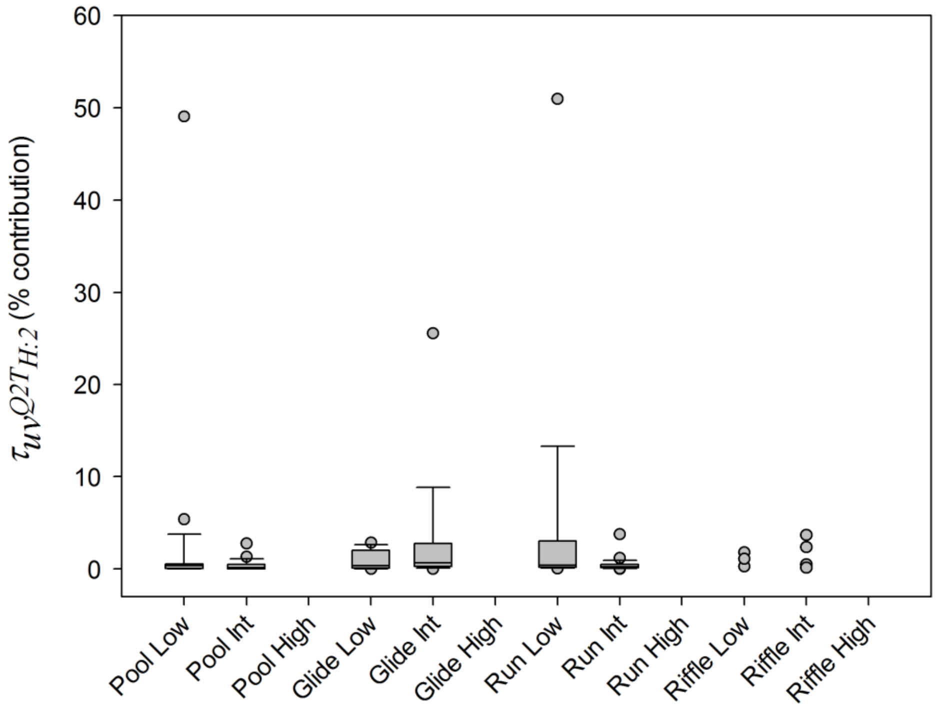


Figure B37 – Fractional contribution to Reynolds shear stress from ejections (Q2) for PBs of the Leigh Brook.

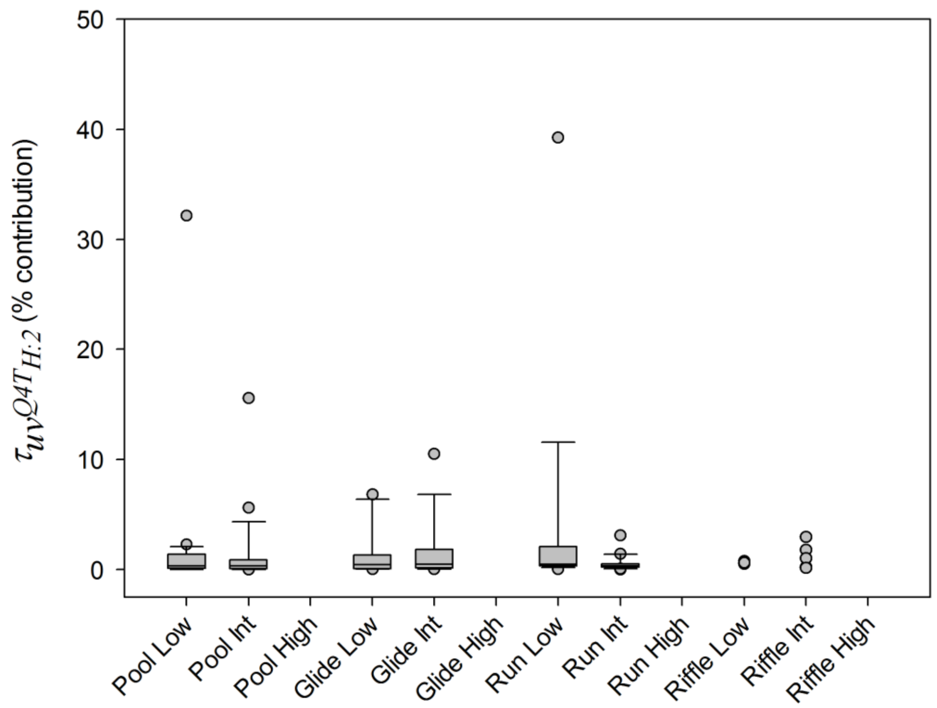


Figure B38 – Fractional contribution to Reynolds shear stress from sweeps (Q4) for PBs of the Leigh Brook.

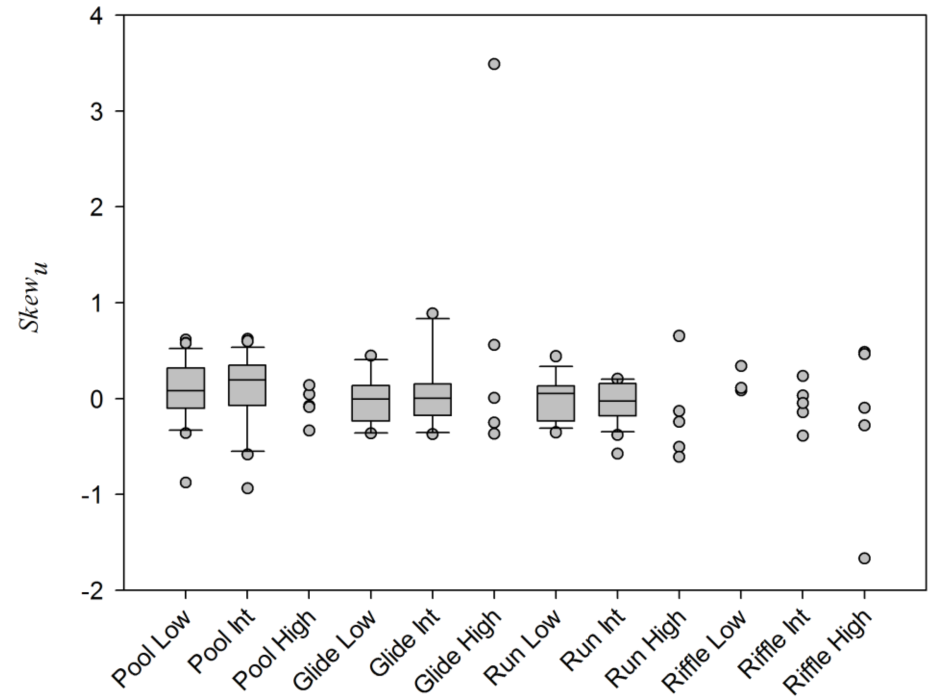


Figure B39 – Skewness coefficient of the streamwise component for PBs of the Leigh Brook.

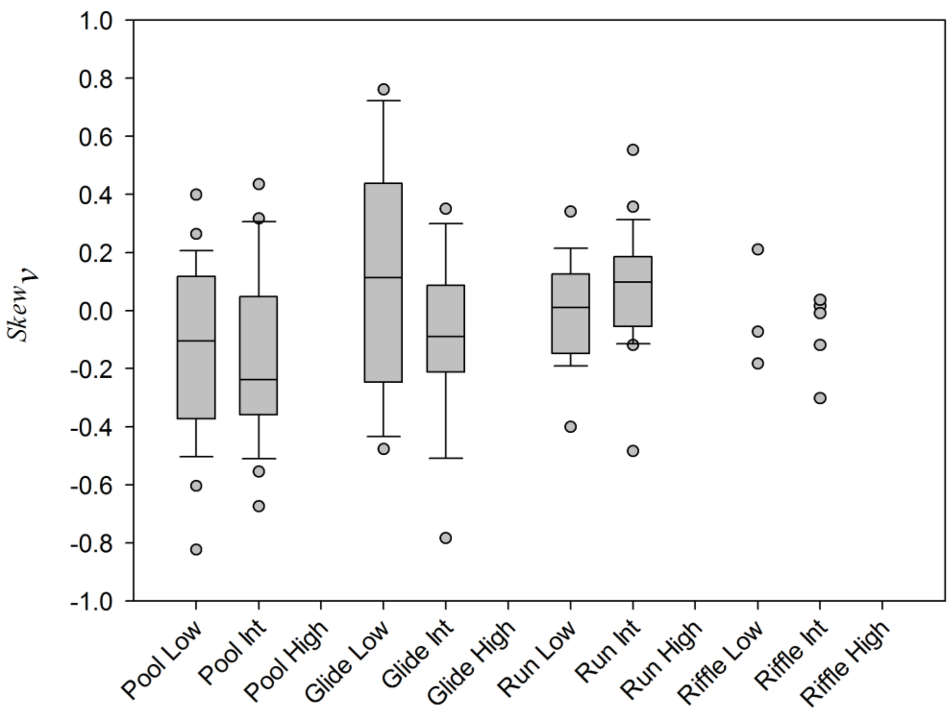


Figure B40 – Skewness coefficient of the vertical component for PBs of the Leigh Brook.

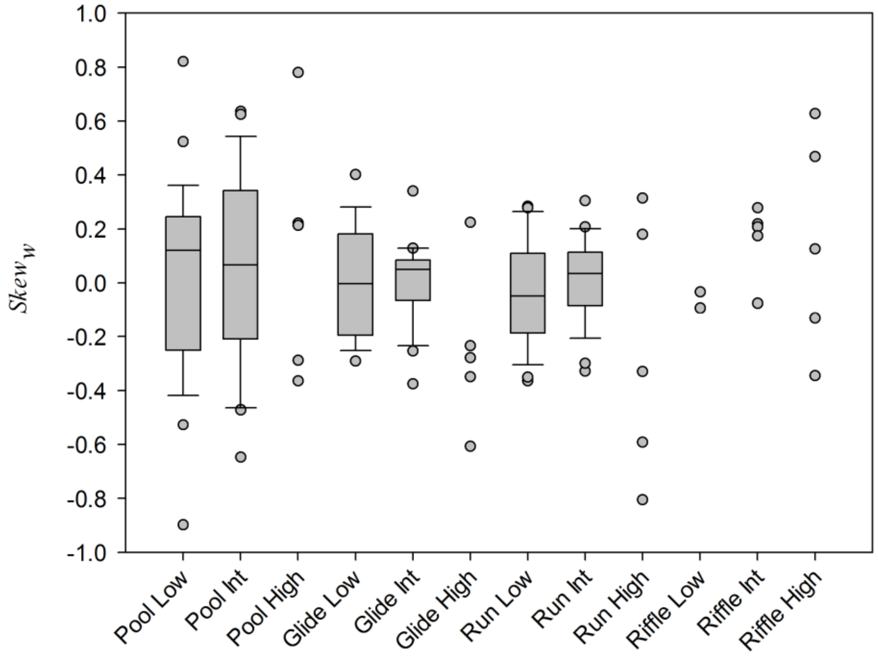


Figure B41 – Skewness coefficient of the spanwise component for PBs of the Leigh Brook.

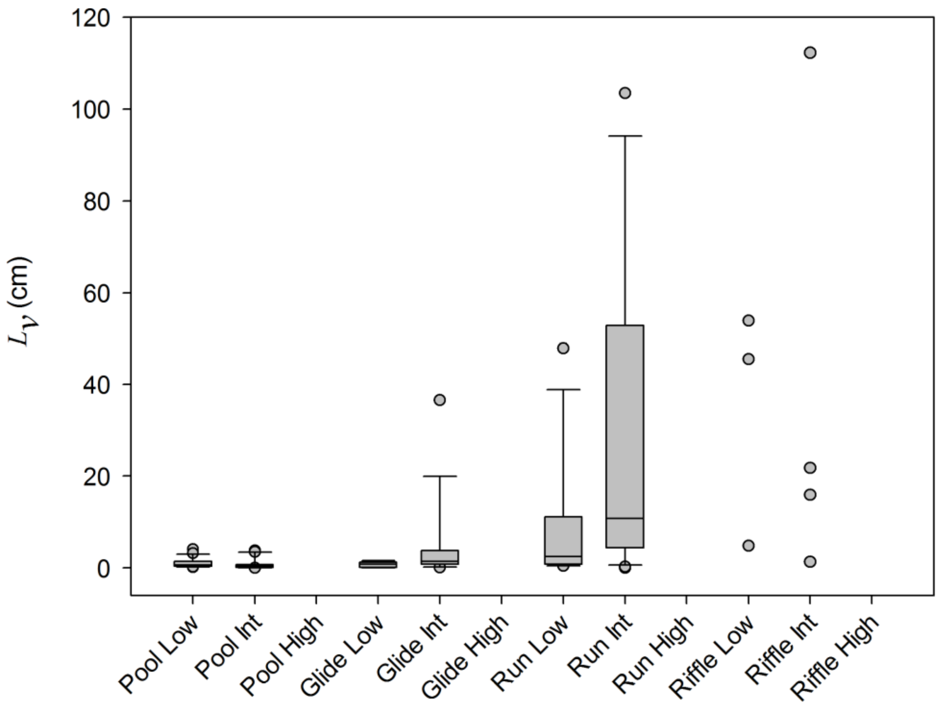


Figure B42 – Average eddy depth for PBs of the Leigh Brook. Based on un-rotated data.

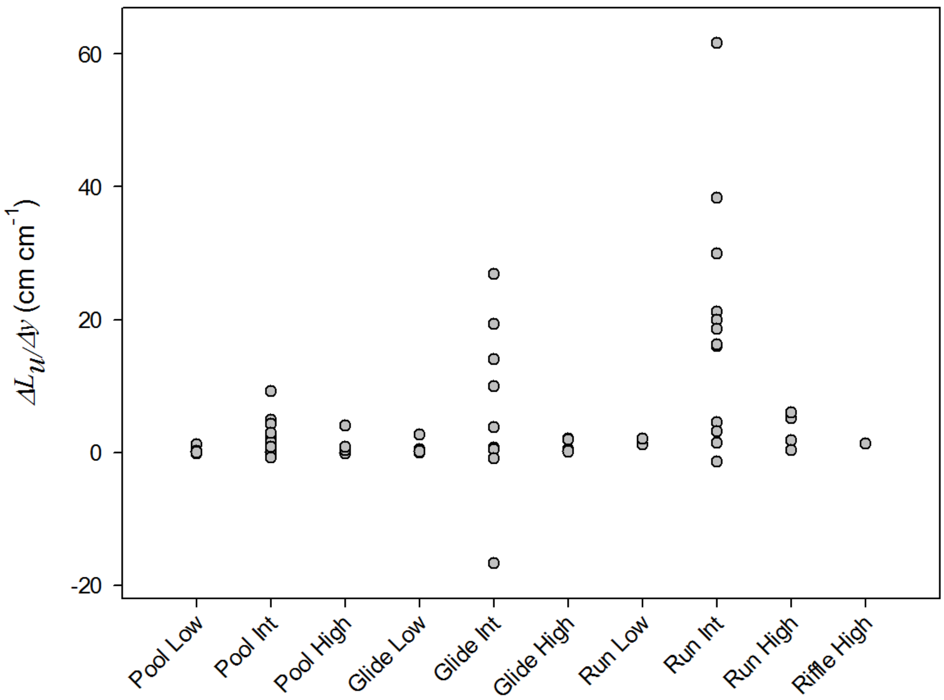


Figure B43 – Change in average eddy length with height above bed for PBs of the Leigh Brook.

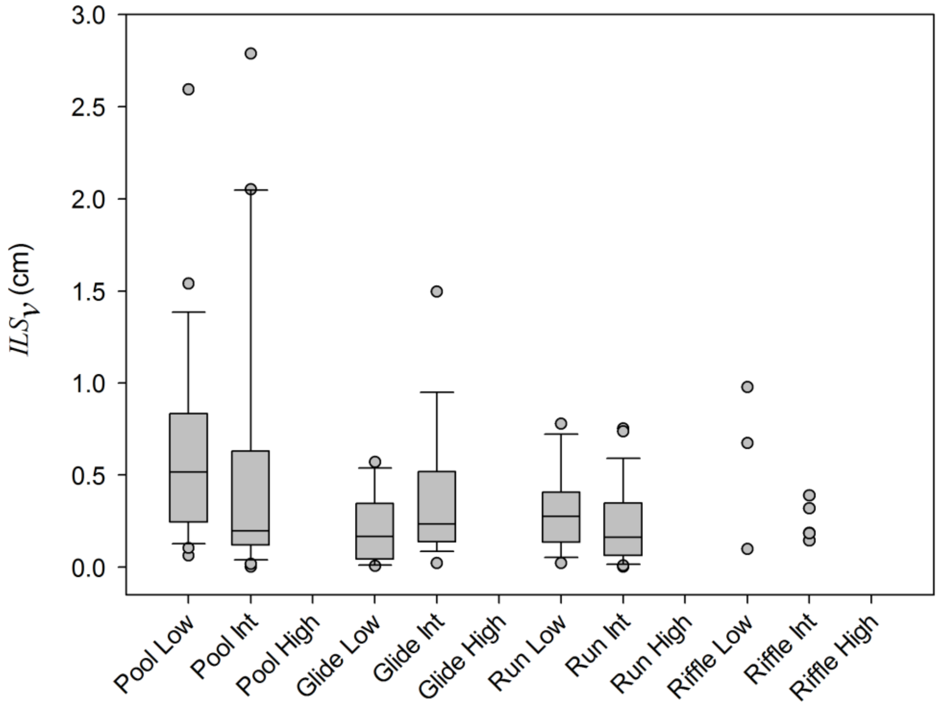


Figure B44 – Integral length scale of the vertical component for PBs of the Leigh Brook. Based on un-rotated data.

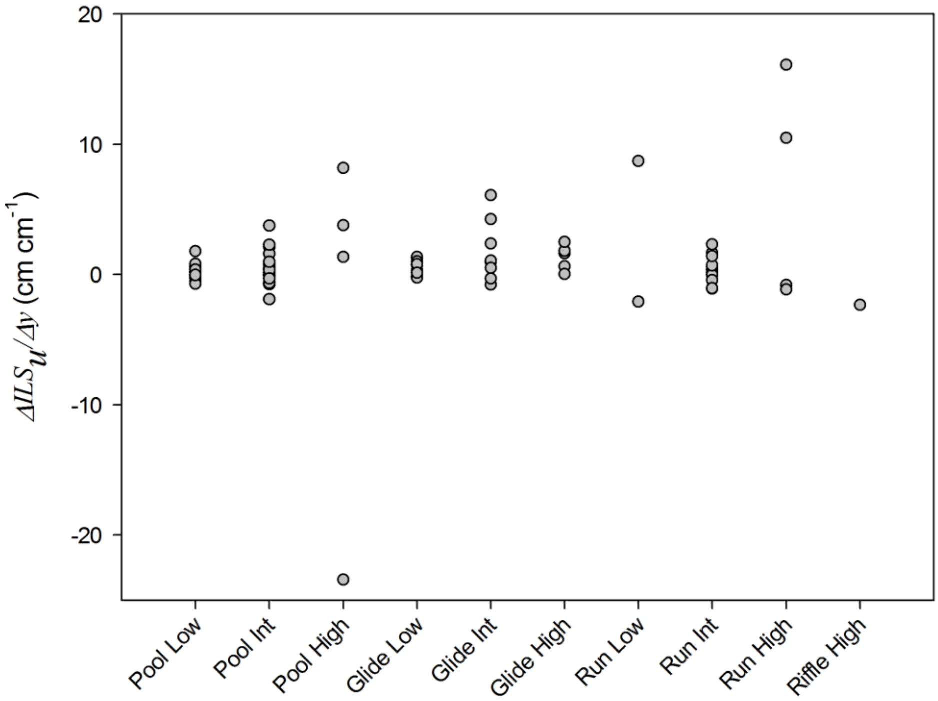
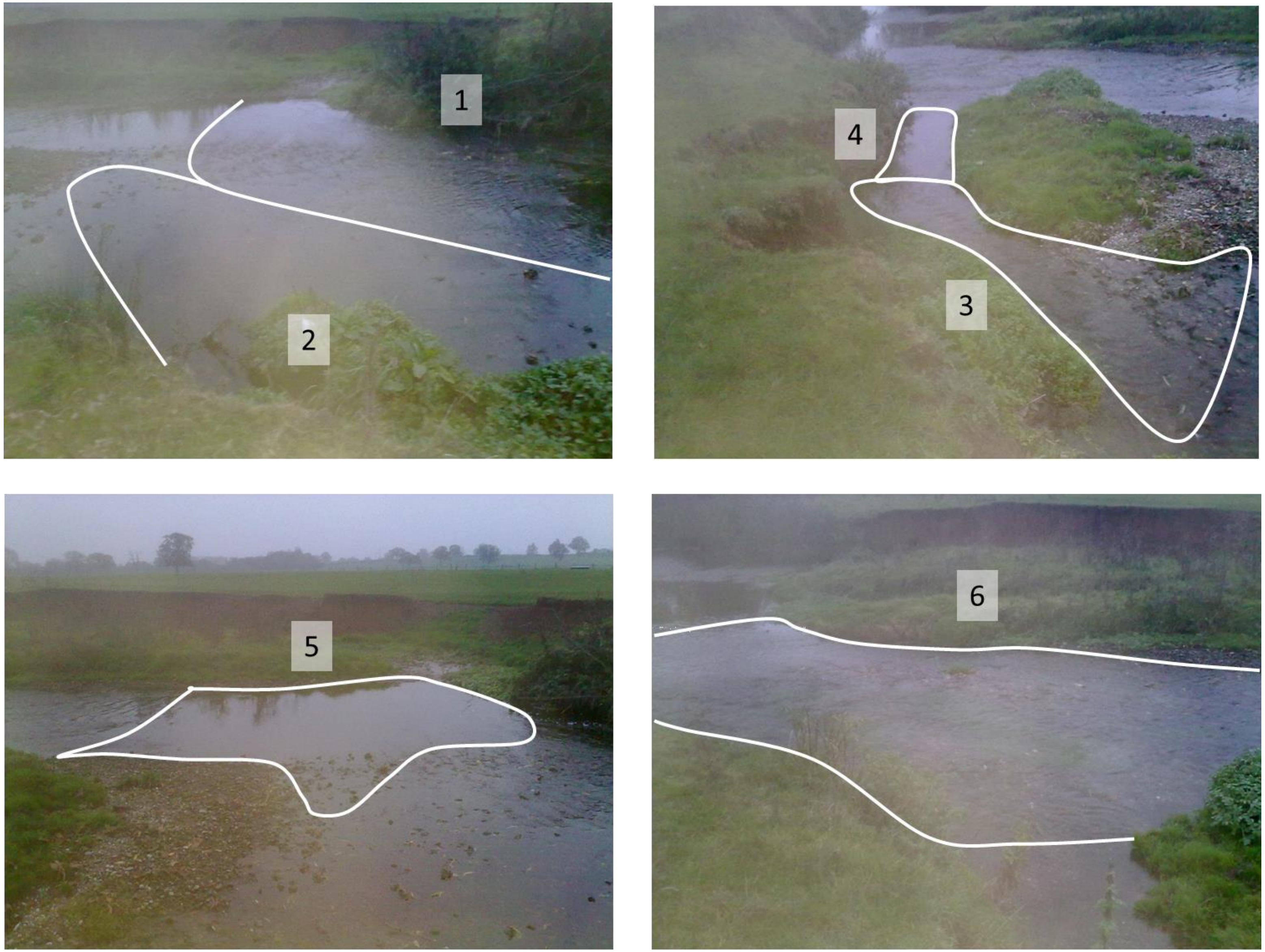


Figure B45 – Change in integral length scale of the streamwise component with height above bed for PBs of the Leigh Brook.

Table B3 – Characteristics of habitats mapped along a reach of the River Arrow. % refers to proportion of areal cover.

								SFT						Substrate				
Habitat number	Width (m)	Length (m)	Full width?	Macrophyte %	TV & roots %	LWD %	Detritus %	SFT	%	SFT	%	SFT	%	Fine %	Gravel %	Cobble %	Boulder %	Notes
1	4	6	N	5	5	0	0	UW	90	RP	10			0	60	40	0	Rancunculus
2	4	7	N	0	0	0	0	RP	70	SM	30			5	70	25	0	
3	1	5	N	0	<5	0	0	UW	90	RP	10			0	100	0	0	LB of mid-channel bar
4	1	3	N	0	<5	0	0	SM	80	RP	20			0	100	0	0	LB of mid-channel bar
5	5	5	N	0	<5	<5	0	RP	20	SM	60	NP	20	15	65	20	0	RB of mid-channel bar.
6	5	10	Y	40	<5	0	0	UW	85	RP	15			0	90	10	0	Rancunculus
7	2	9	Y	10	5	5	0	NP	100					20	40	40	0	Seasonal marginal veg
8	5	6	Y	10	<5	0	0	RP	75	UW	25			5	80	15	0	Rancunculus
8a	2	7	N	10	<2	0	0	SM	50	RP	50			0	90	10	0	Rancunculus
9	6	16	Y	5	10	5	10	SM	20	NP	80			20	30	40	0	Seasonal marginal veg
10	6	10	N	0	<5	0	0	SM	75	RP	25			0	100	0	0	
11	5.5	20	Y	0	<5	0	0	NP	100					10	20	70	0	
12	6	8	Y	0	0	0	0	SM	80	RP	20			0	80	20	0	
13	7	8	Y	<5	<2	0	0	UW	90	BW	10			0	70	30	0	
14	6	8	N	0	<5	0	0	RP	40	SM	30	NP	30	30	40	30	0	Recirculation/eddy pool
15	8.5	16	Y	0	5	5	0	SM	100					60	20	20	0	Very deep
16	7	7	Y	0	<2	10	0	SM	90	RP	10			10	80	10	0	
17	6.5	8	Y	<2	<5	0	0	RP	100					5	40	55	0	
18	8.5	48	Y	5	5	0	15	NP	70	RP	10	SM	10	10	25	25	25	Seasonal marginal veg
19	6	6	Y	0	<5	0	0	SM	65	RP	35			0	50	25	25	
20	6.5	6.5	Y	5-10	<2	0	0	UW	70	RP	20	BW	10	0	50	20	30	Rancunculus
21	6	19	Y	5	5	0	0	SM	65	NP	20	SM	15	10	40	20	30	Seasonal marginal veg
8a	2	7	N	10	<2	0	0	SM	50	RP	50			0	90	10	0	Rancunculus

Figure B46 - Photographs of habitat units mapped along a reach of the River Arrow.

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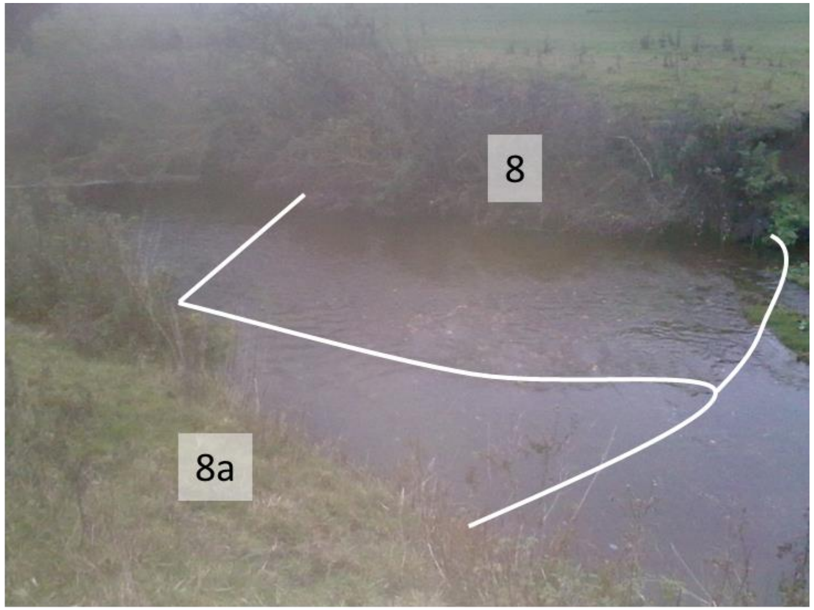
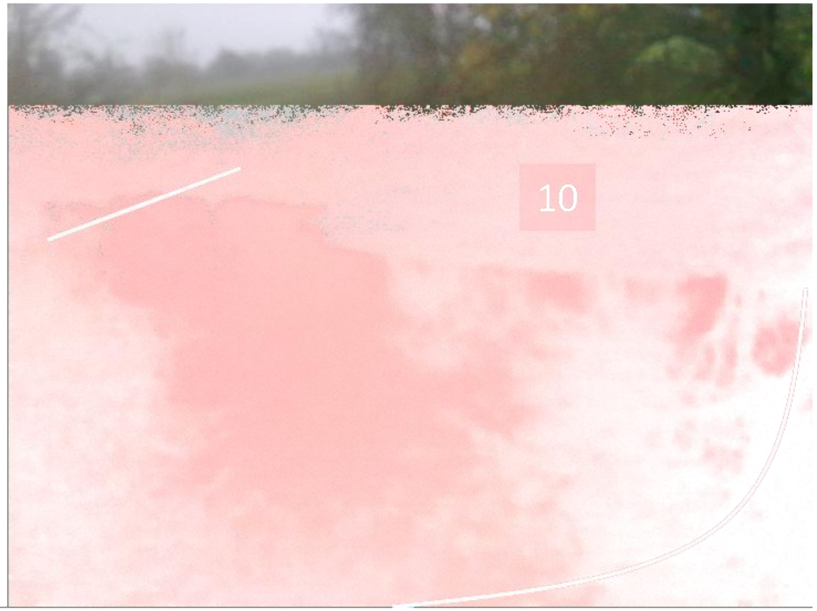

8
8a

9

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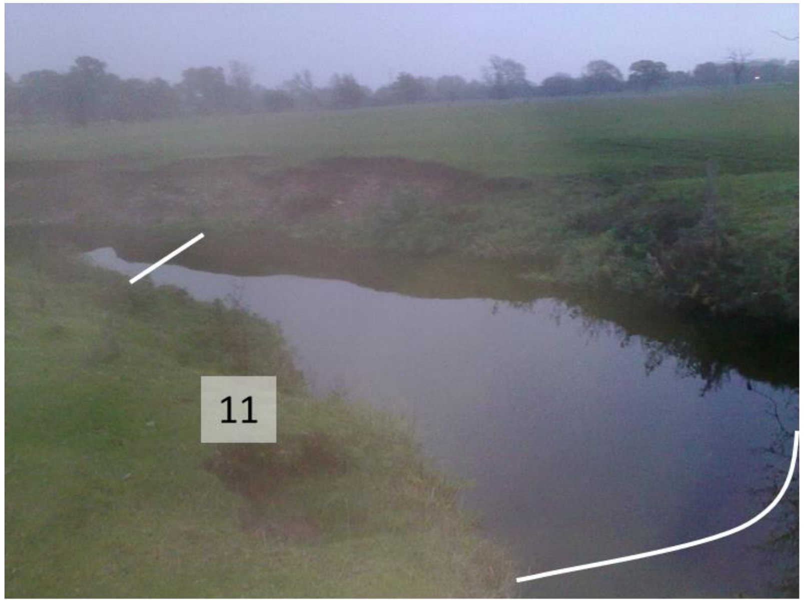
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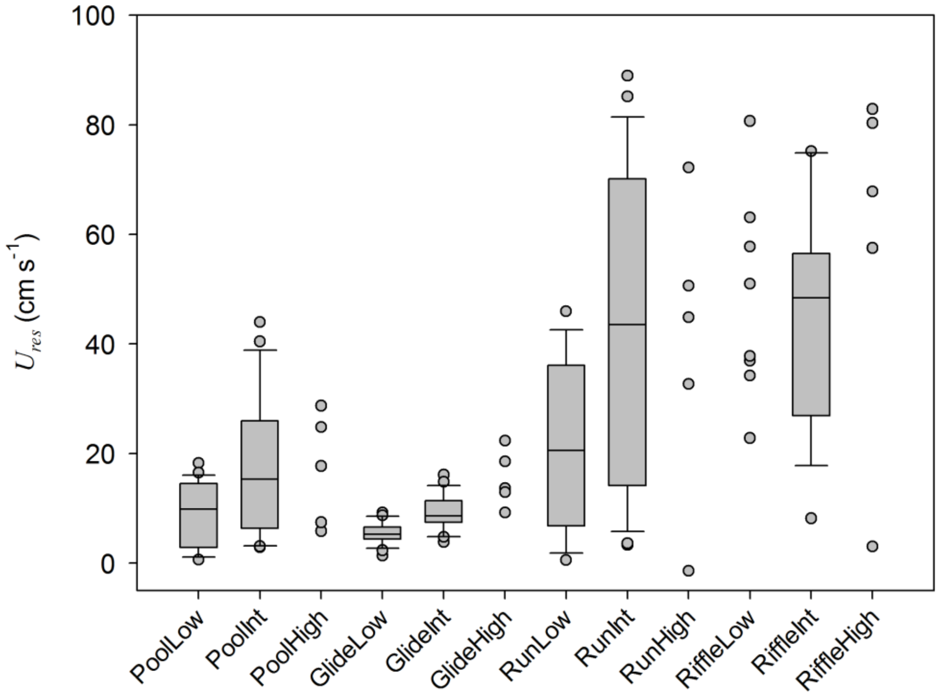

Figure B47 – Resultant velocity for River Arrow PBs including mean (horizontal lines), IQR (boxes), range up to 1.5IQR (whiskers) and outliers beyond 1.5 IQR (symbols). Only data points shown where sample size is limited (n<10).

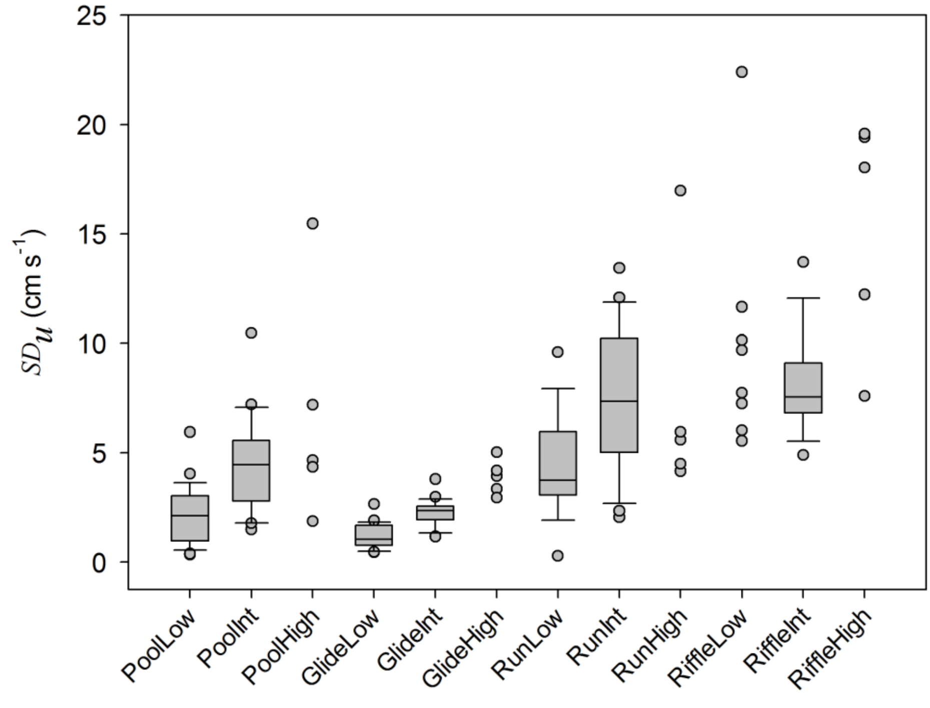

Figure B48 – Streamwise turbulence intensity for PBs of the River Arrow.

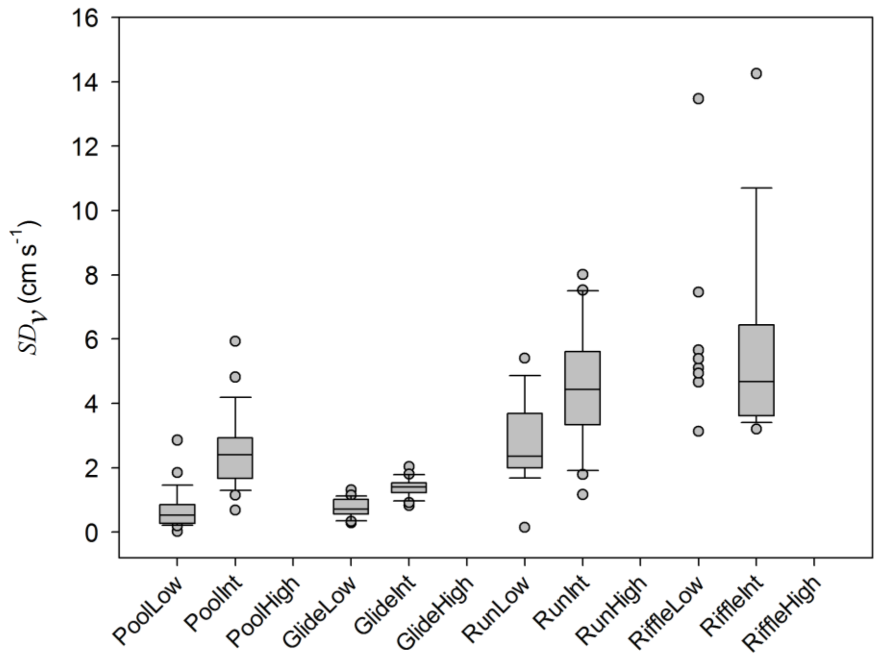

Figure B49 – Vertical turbulence intensity for PBs of the River Arrow.

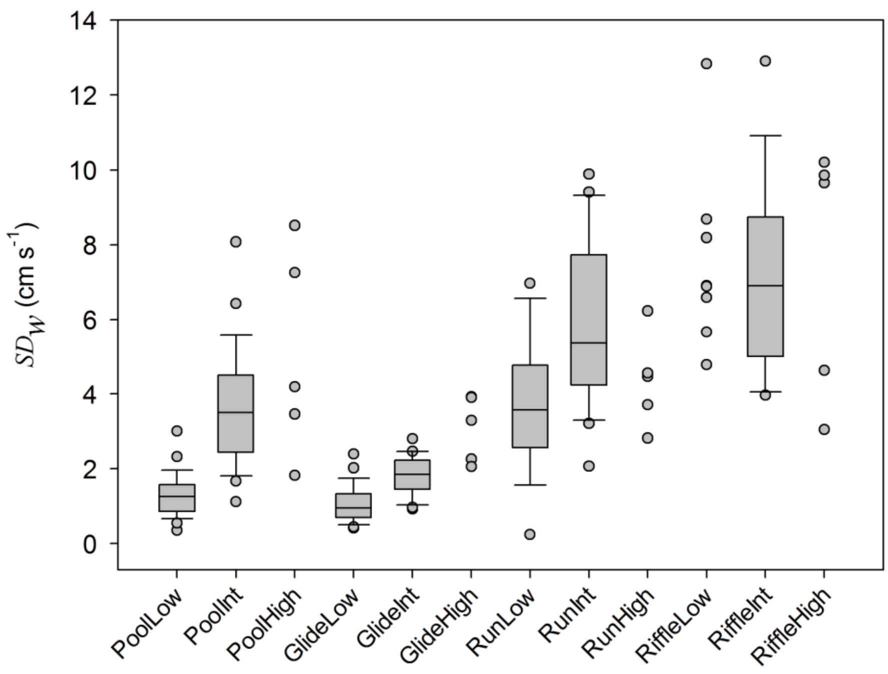

Figure B50 – Spanwise turbulence intensity for PBs of the River Arrow.

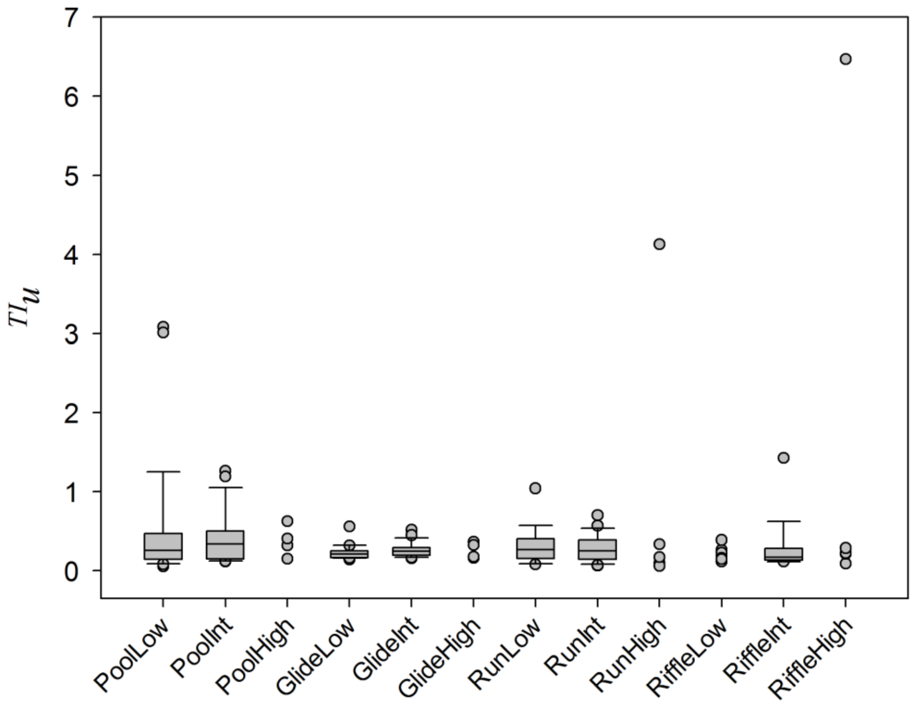

Figure B51 – Relative streamwise turbulence intensity for PBs of the River Arrow.

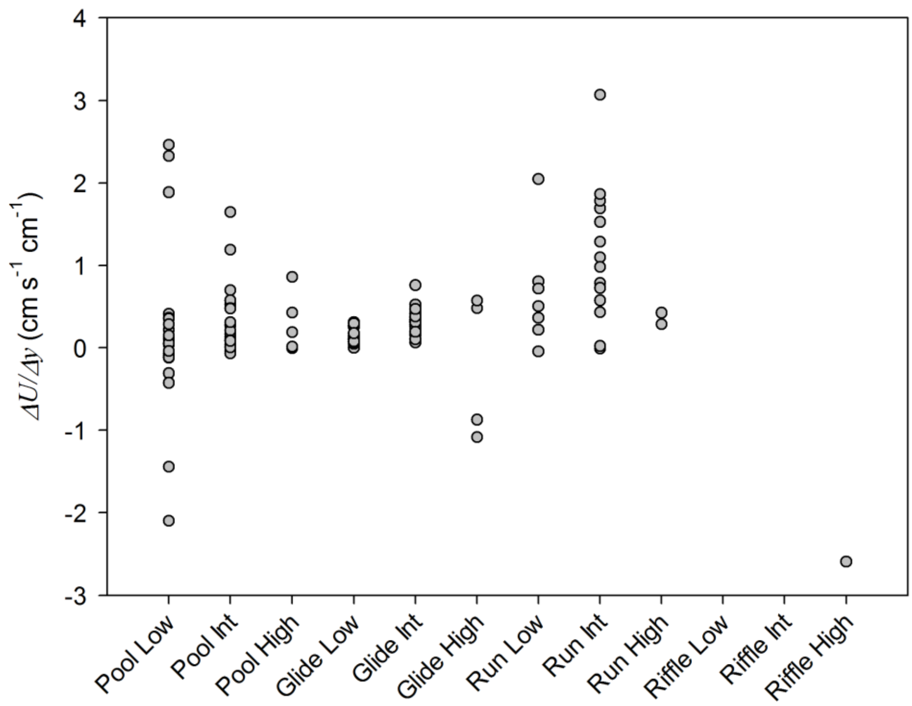

Figure B52 – Change in mean streamwise velocity with height above bed for PBs of the River Arrow.

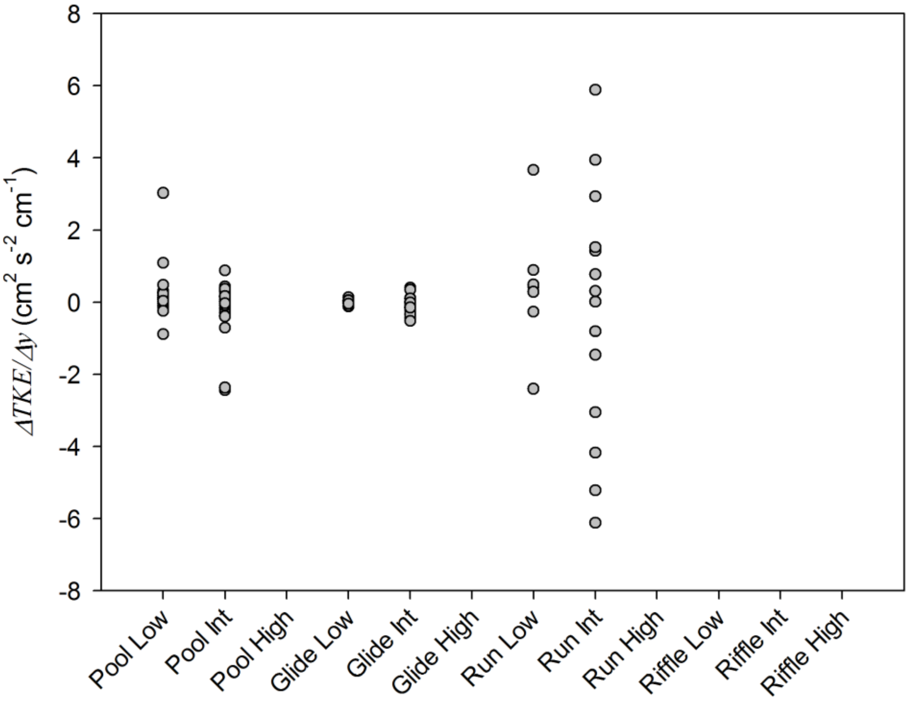

Figure B53 - Change in turbulent kinetic energy with height above bed for PBs of the River Arrow.

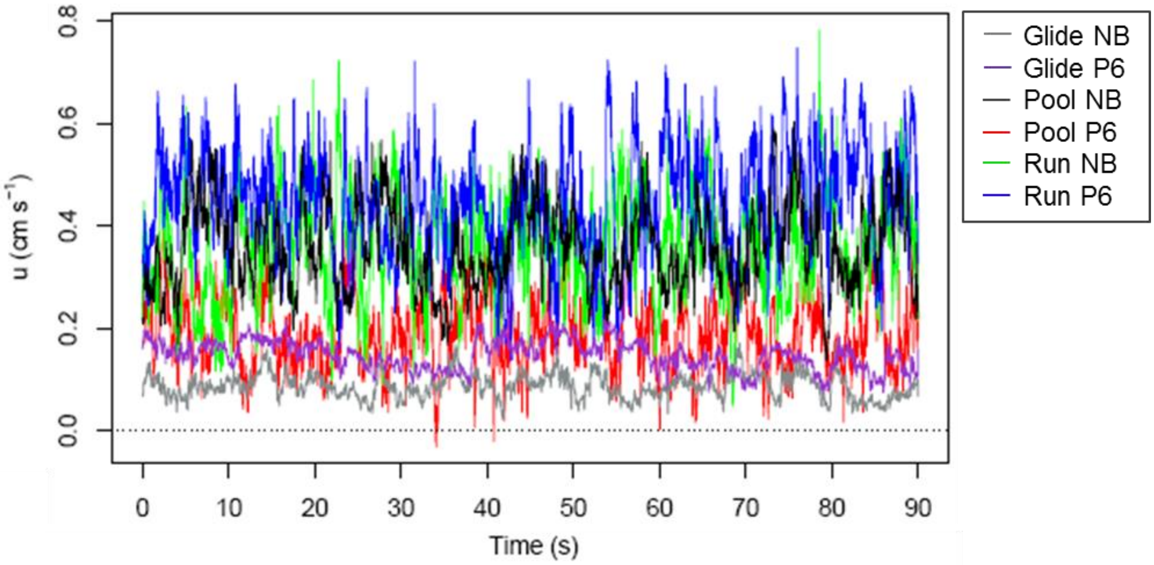

Figure B54 – Selected time series typifying the depth variability of the streamwise component for PBs of the River Arrow at intermediate flow. Near bed (NB) and point-six (P6) locations shown. No data for the riffle.

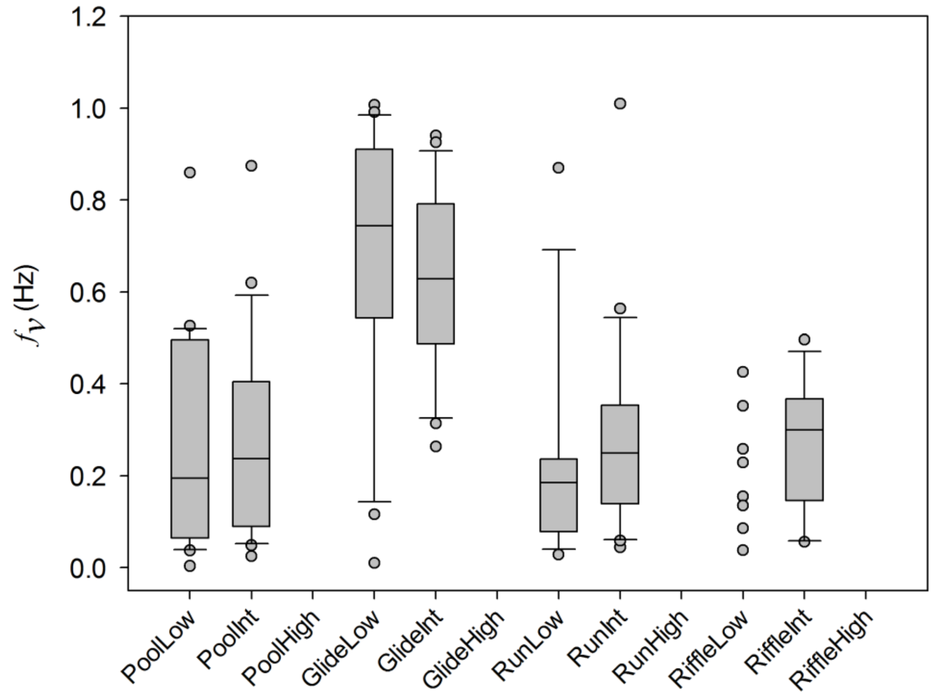

Figure B55 – Average eddy frequency of the vertical component for PBs of the River Arrow.

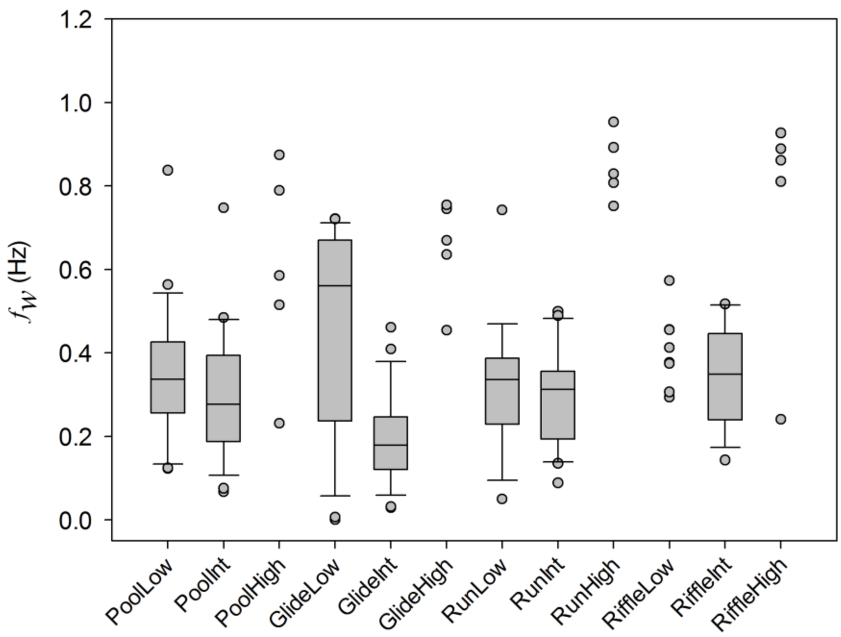

Figure B56 – Average eddy frequency of the spanwise component for PBs of the River Arrow.

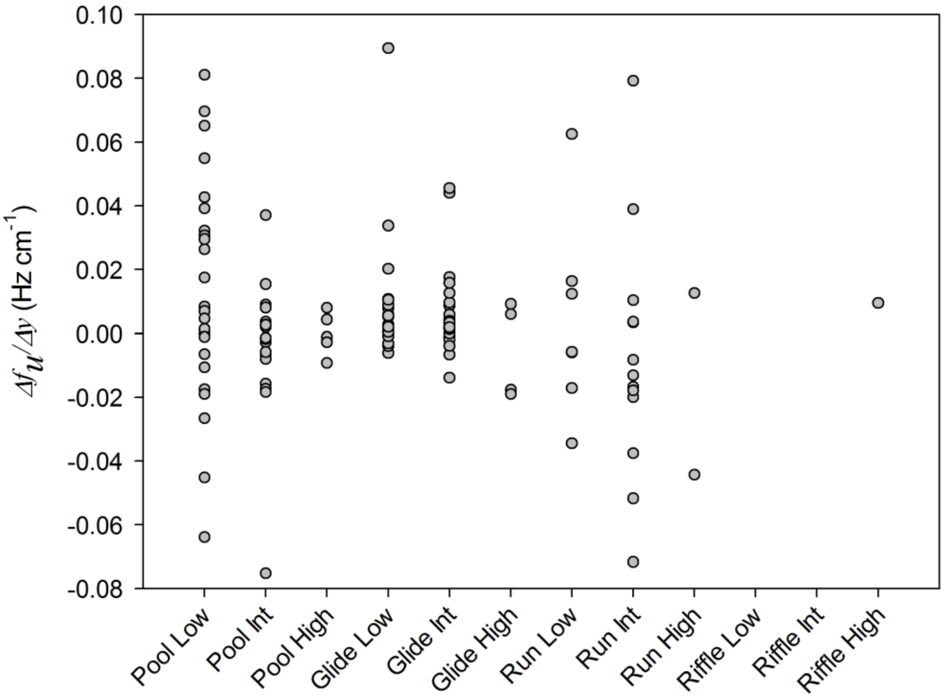

Figure B57 – Change in average streamwise eddy frequency with height above bed for PBs of the River Arrow.

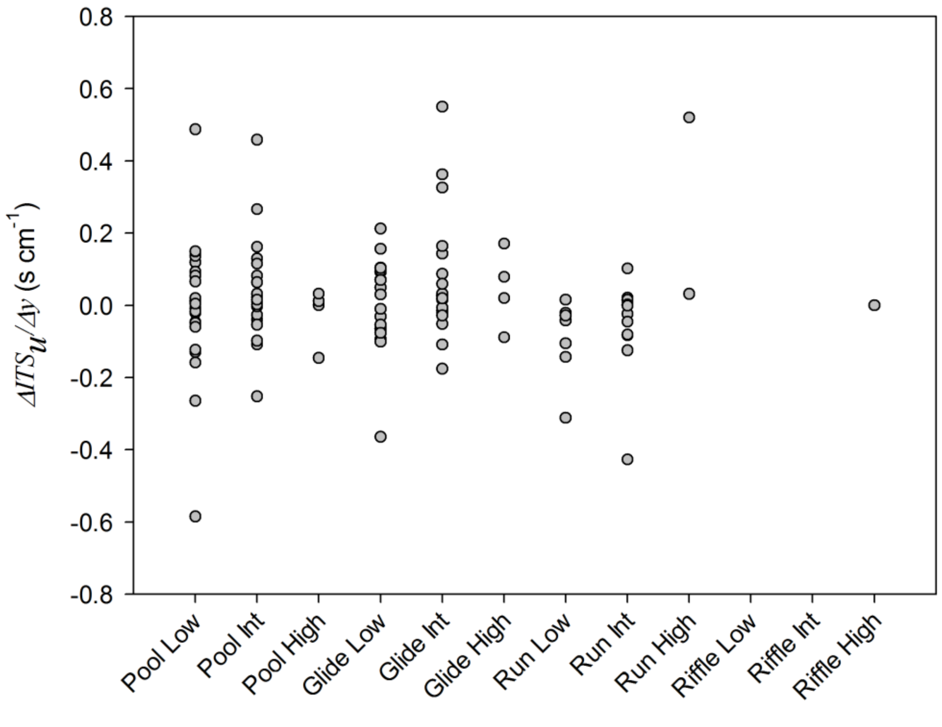

Figure B58 – Change in integral time scale of the streamwise component with height above bed for PBs of the River Arrow.

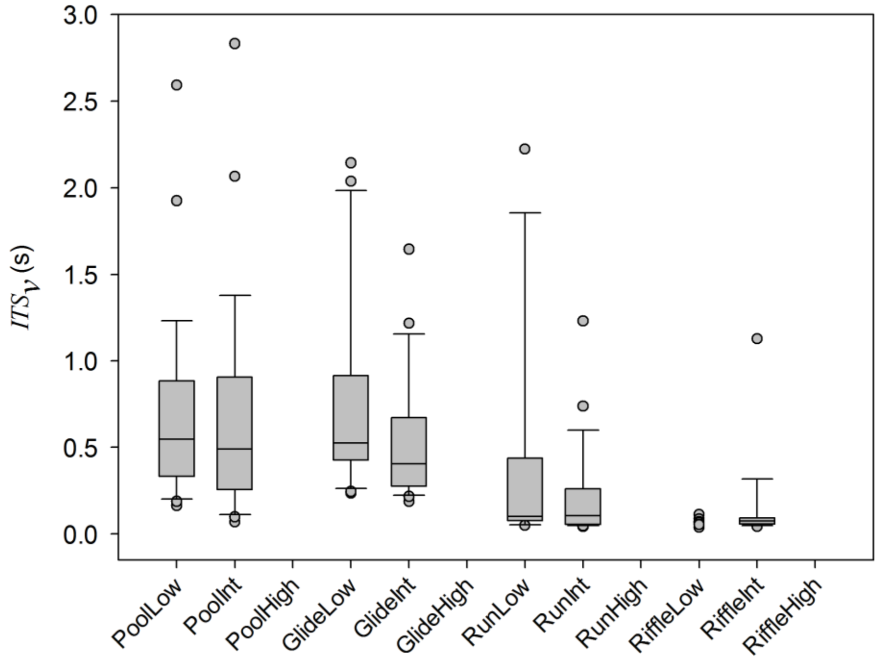

Figure B59 – Integral time scale of the vertical component for PBs of the River Arrow.

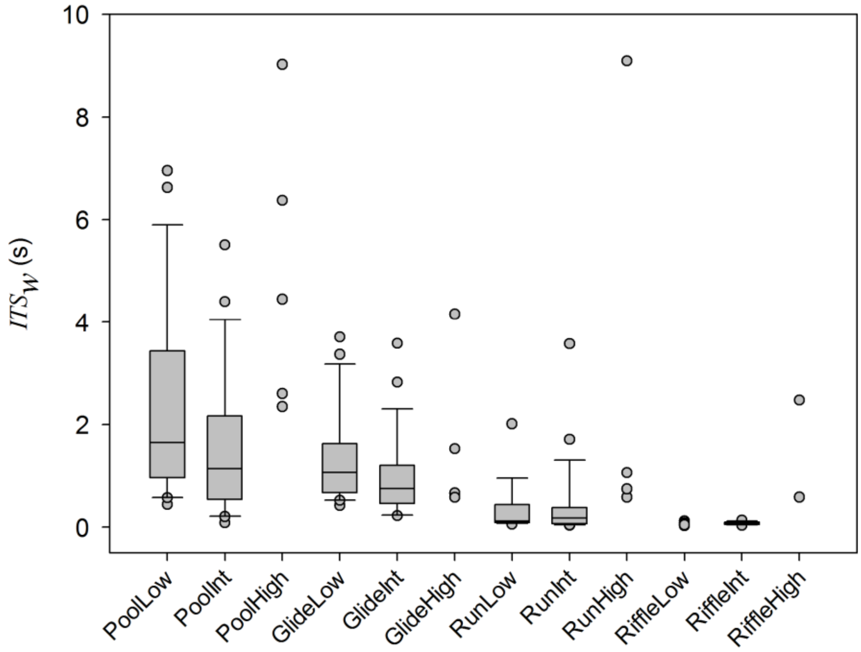

Figure B60 – Integral time scale of the spanwise component for PBs of the River Arrow.

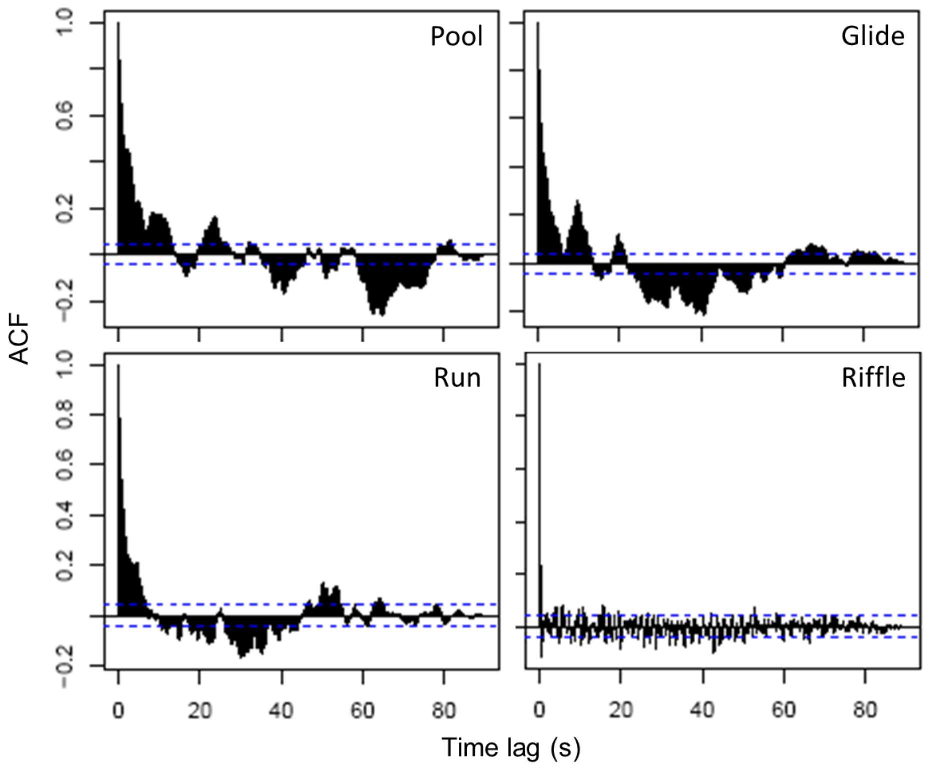

Figure B61 – Selected ACFs typifying the streamwise component for PBs of the River Arrow at low flow. Dashed lines indicate bounds of non-significant ($p>0.05$) correlation.

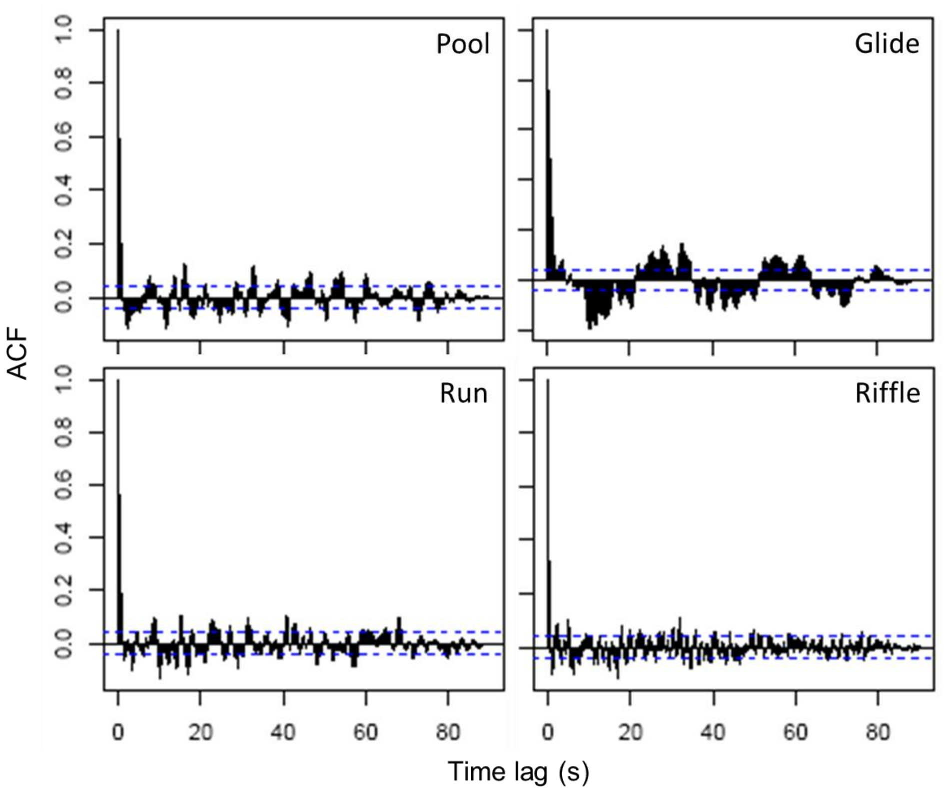

Figure B62 – Selected ACFs typifying the streamwise component for PBs of the River Arrow at intermediate flow.

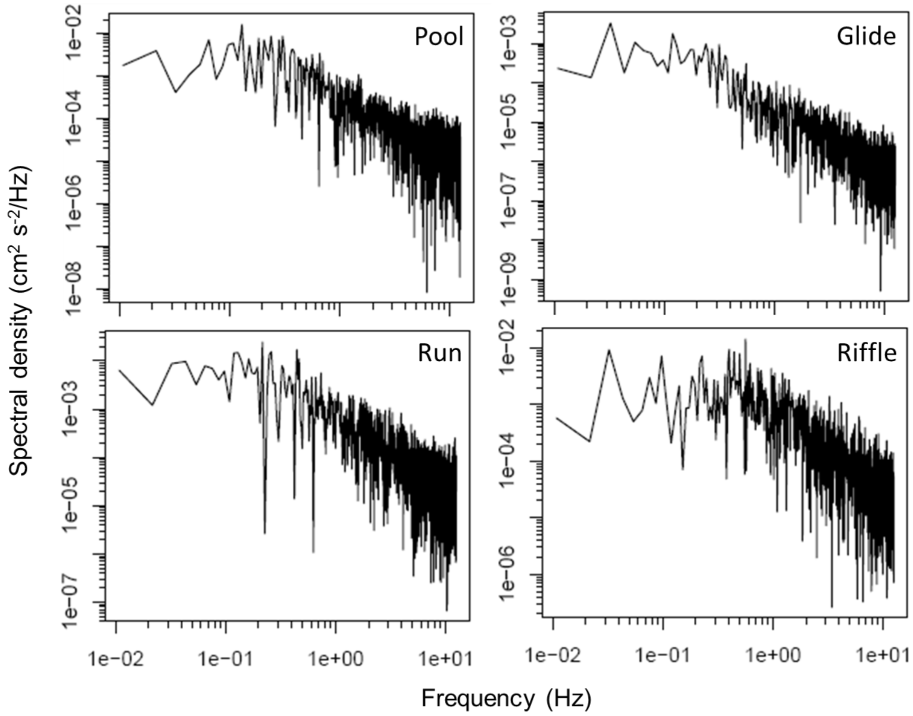

Figure B63 – Selected velocity power spectra typifying the streamwise component for PBs of the River Arrow at intermediate flow.

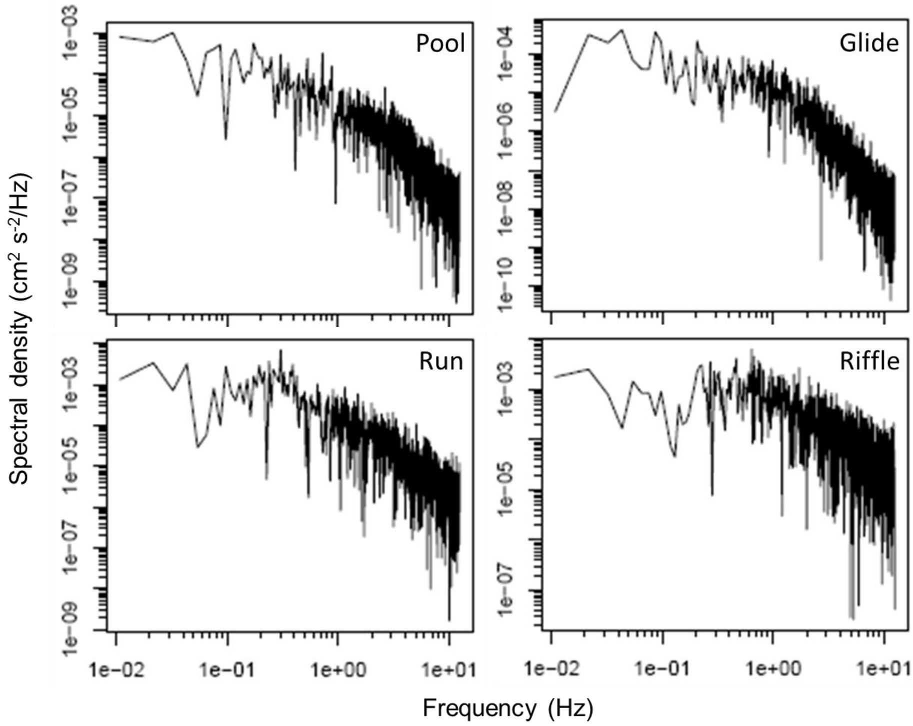

Figure B64 – Selected velocity power spectra typifying the vertical component for PBs of the River Arrow at low flow.

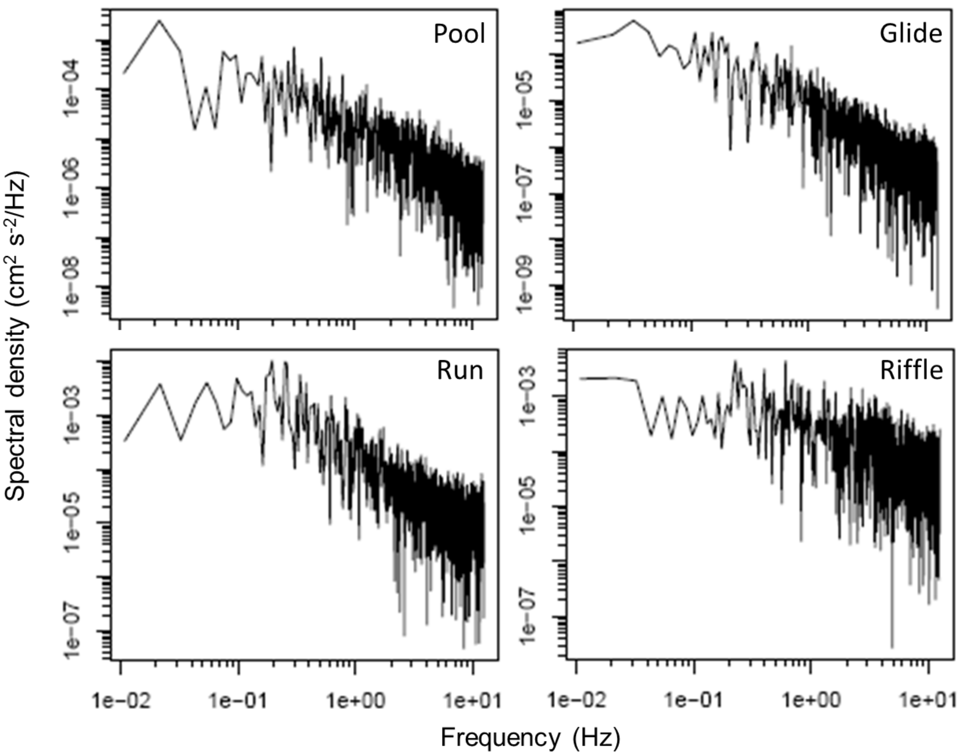

Figure B65 – Selected velocity power spectra typifying the spanwise component for PBs of the River Arrow at low flow.

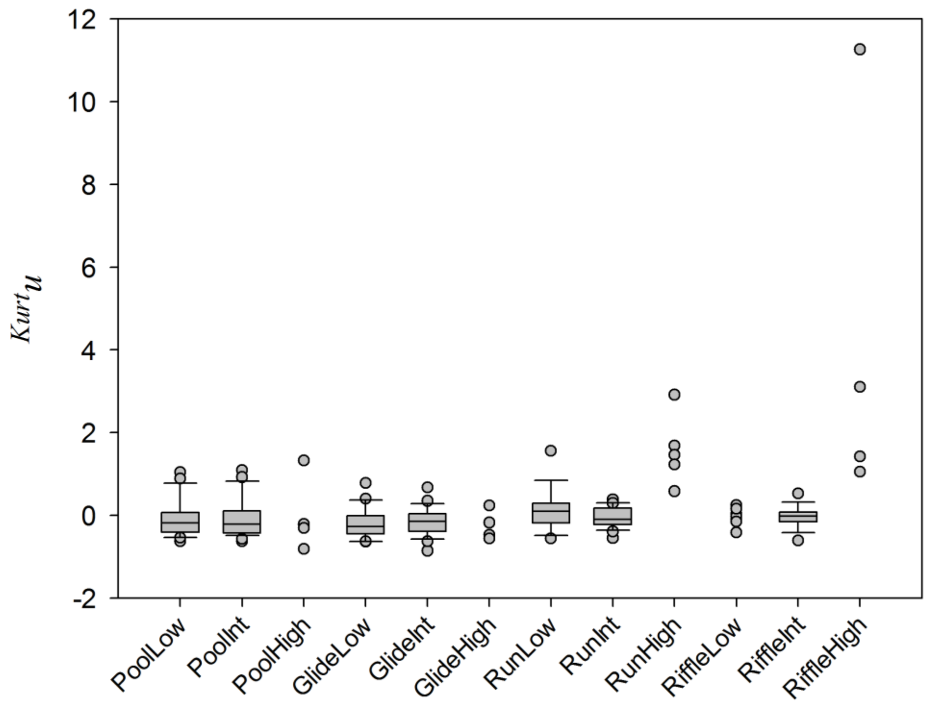

Figure B66 – Kurtosis of the streamwise component for PBs of the River Arrow.

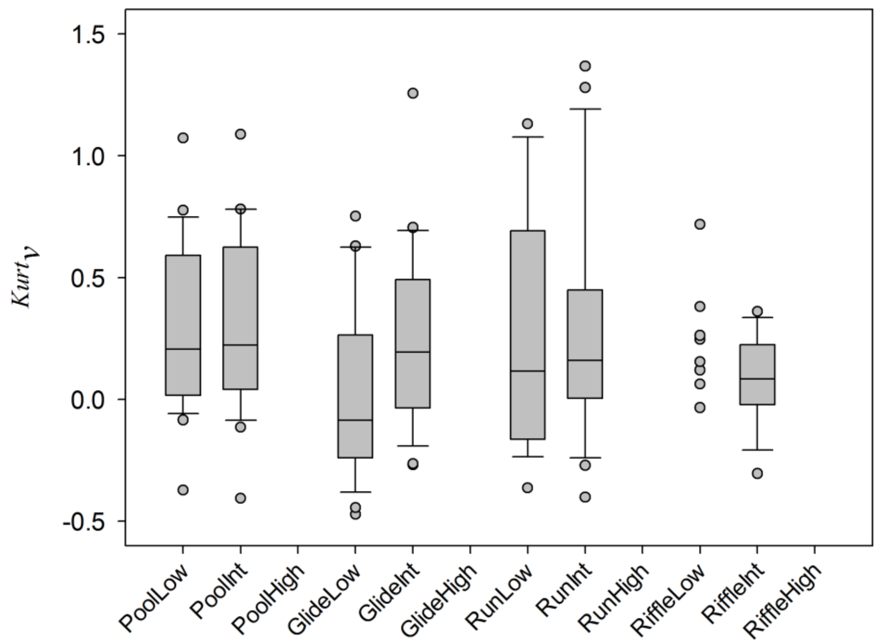

Figure B67 – Kurtosis of the vertical component for PBs of the River Arrow.

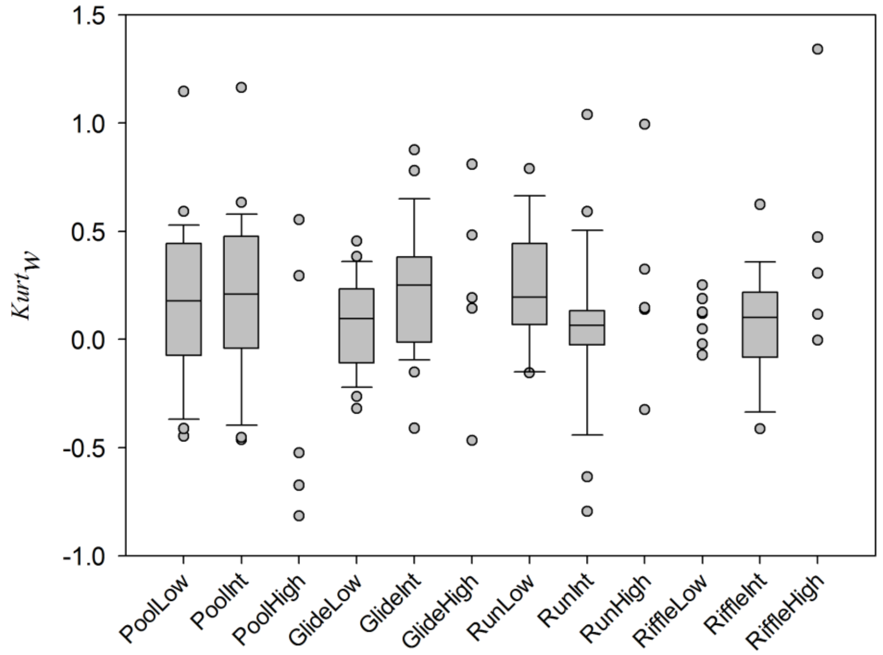

Figure B68 – Kurtosis of the spanwise component for PBs of the River Arrow.

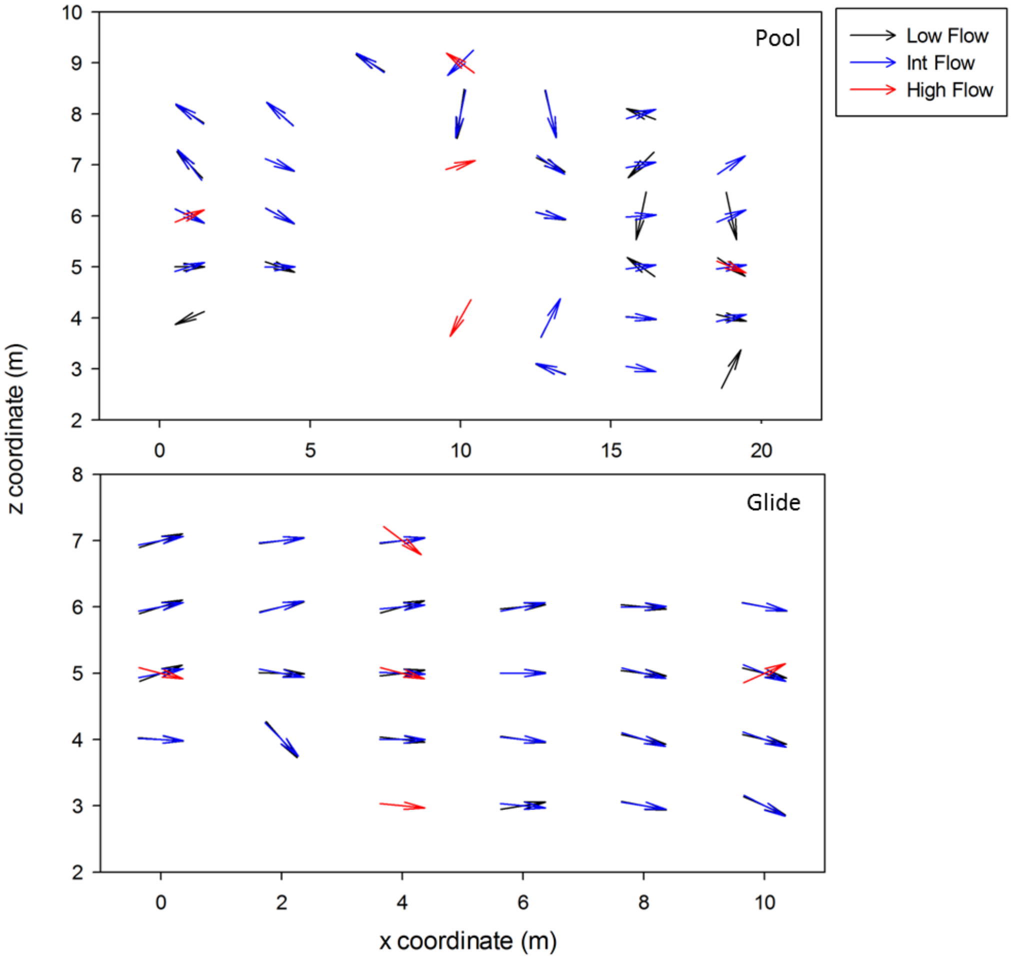

Figure B69 – Primary horizontal velocity vector for the pool and glide at the River Arrow.

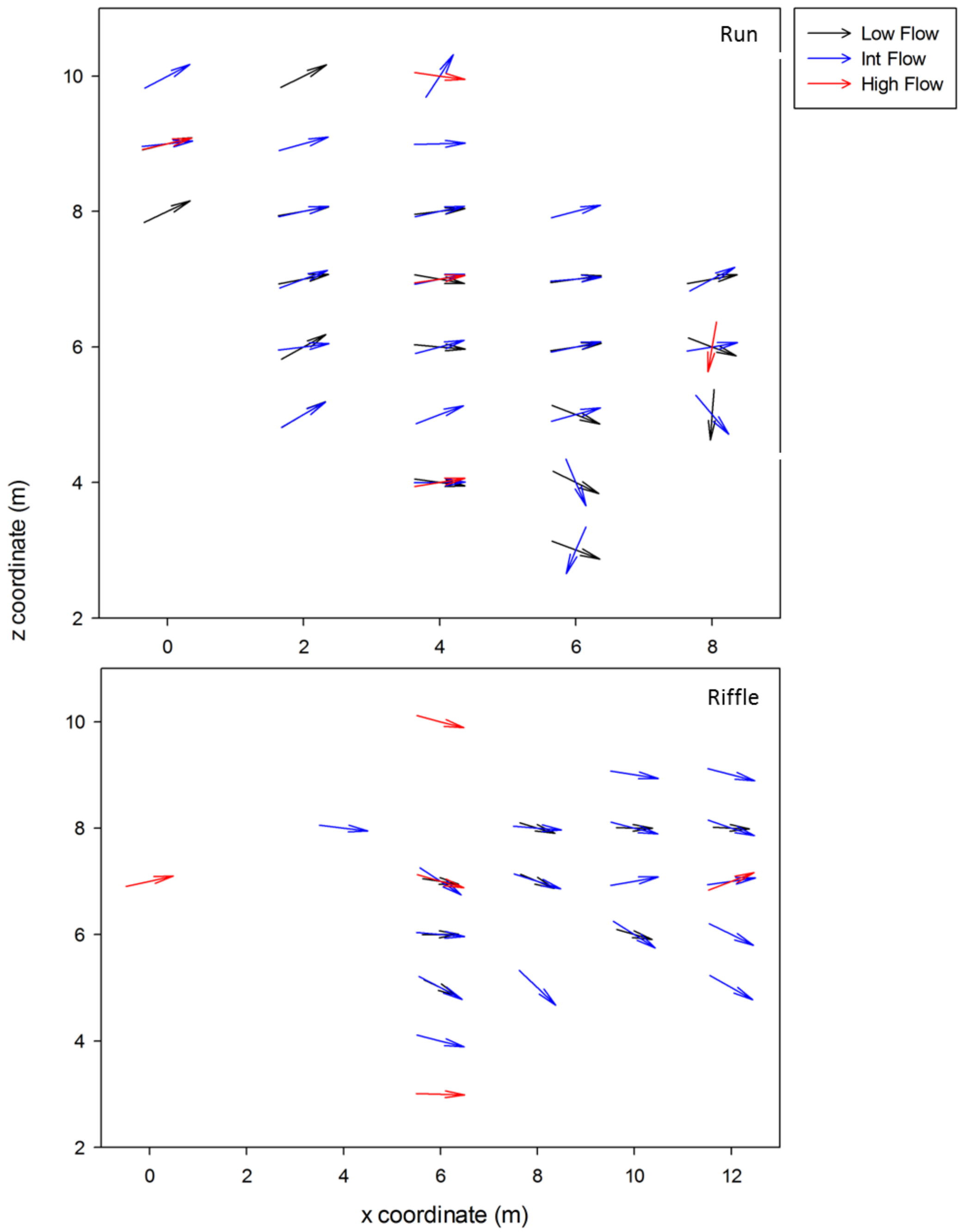

Figure B70 – Primary horizontal velocity vector for the run and riffle at the River Arrow.

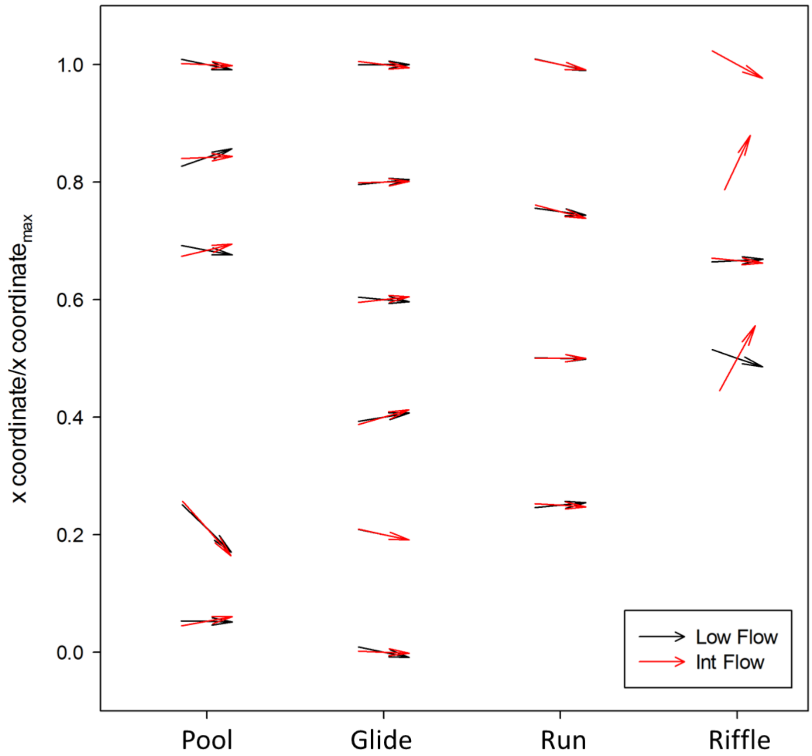

Figure B71 – Primary vertical velocity vector for the centreline of PBs of the River Arrow.

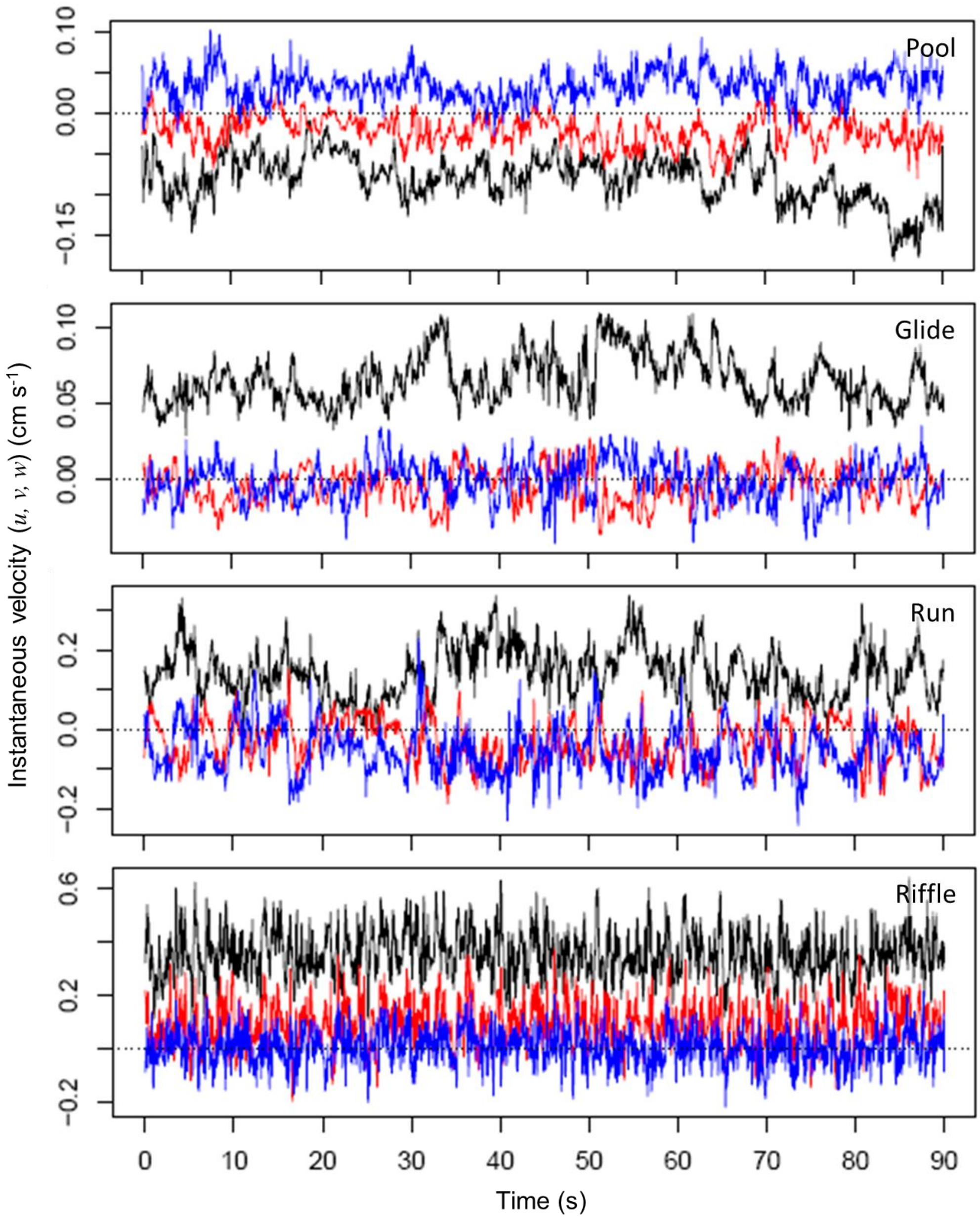

Figure B72 – Selected time series typifying three-dimensional velocities in PBs of the River Arrow at low flow. Based on un-rotated data (black=u, red=v, blue=w).

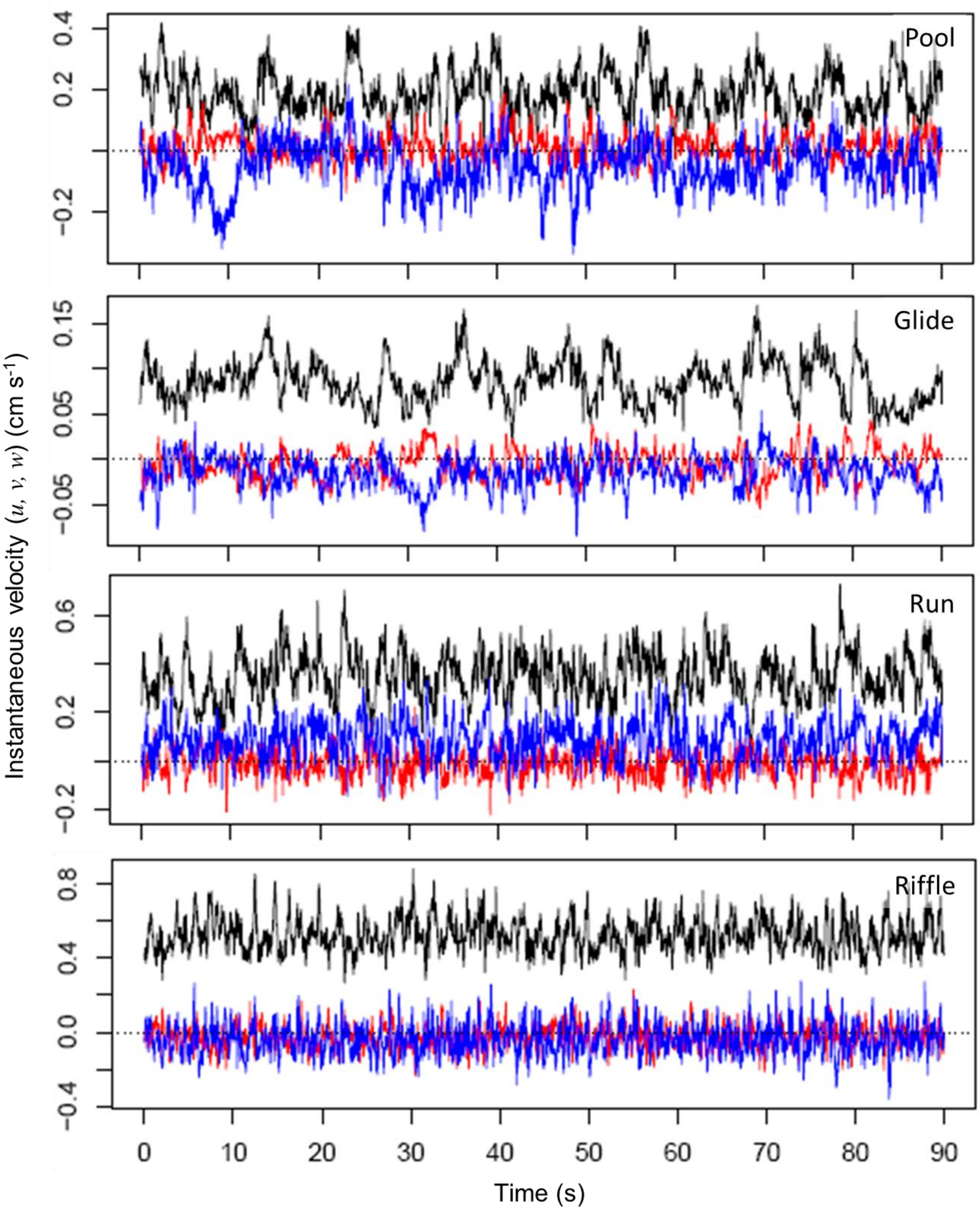

Figure B73 – Selected time series typifying three-dimensional velocities in PBs of the River Arrow at intermediate flow. Based on un-rotated data (black=u, red=v, blue=w).

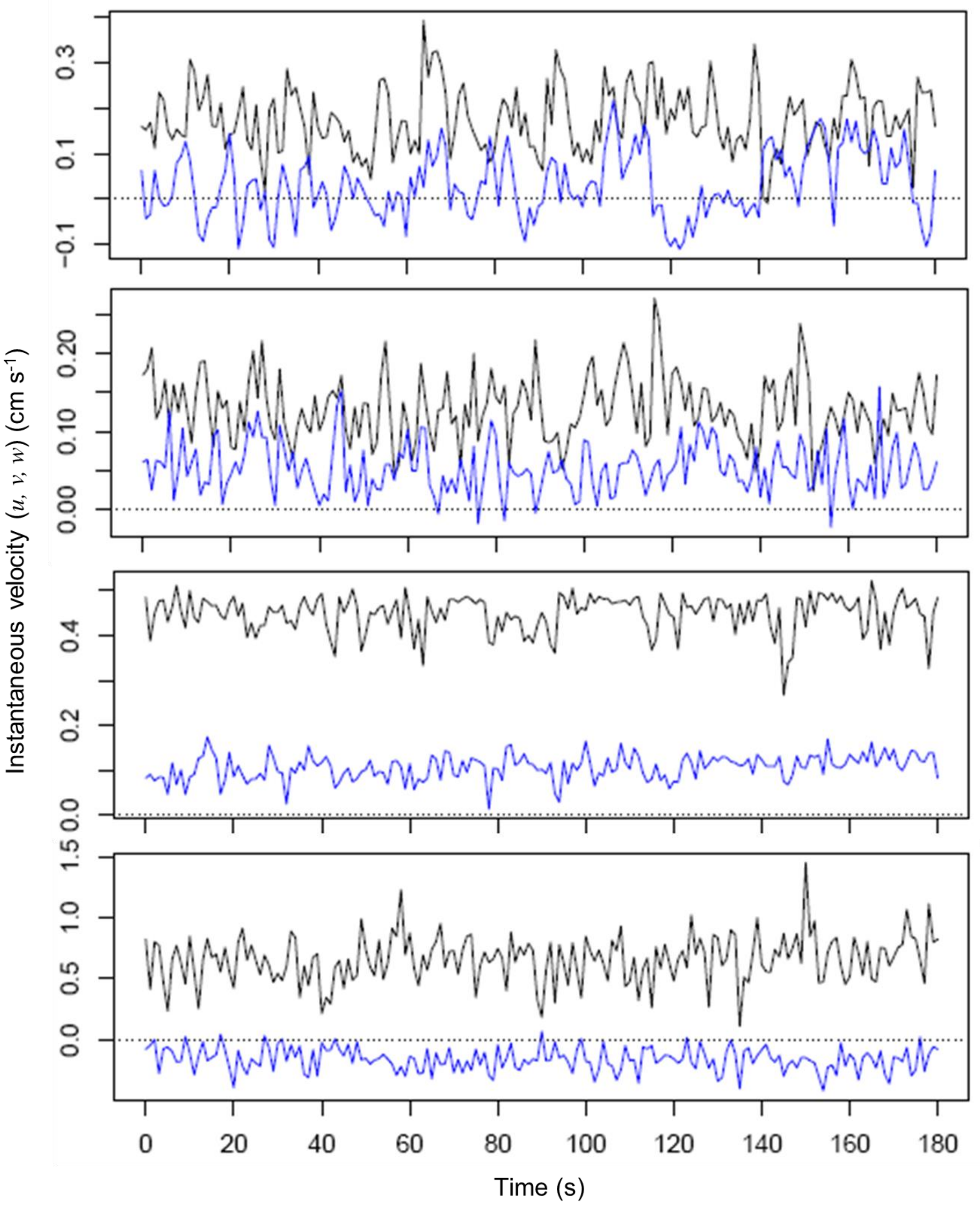

Figure B74 – Selected time series typifying two-dimensional velocities in PBs of the River Arrow at high flow. Based on un-rotated data (black=u, blue=w).

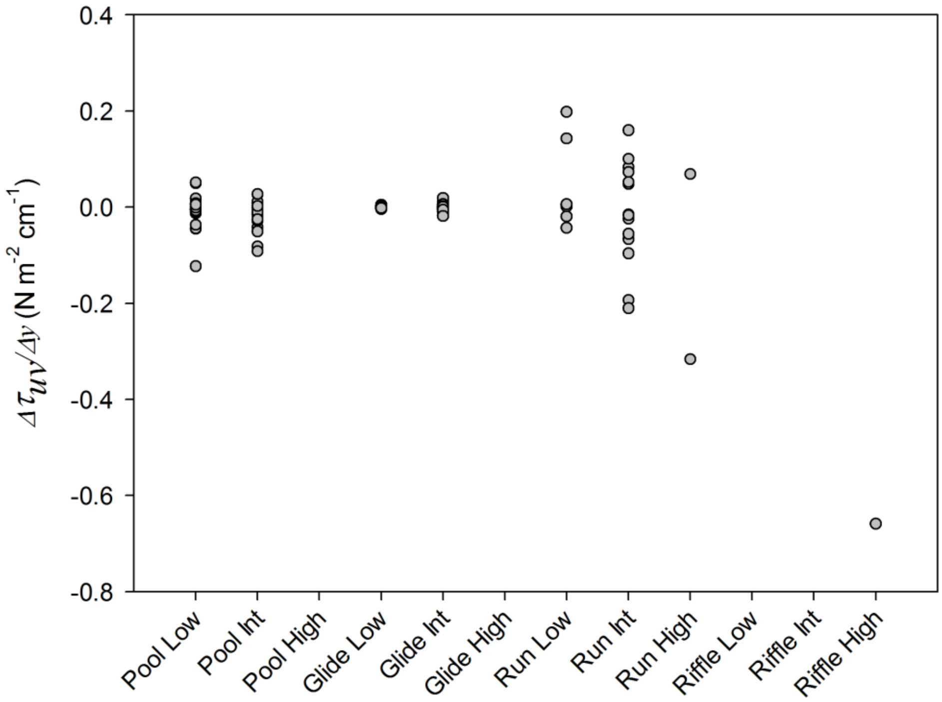

Figure B75 – Change in Reynolds shear stress on the streamwise-vertical plane with height above bed for PBs of the River Arrow.

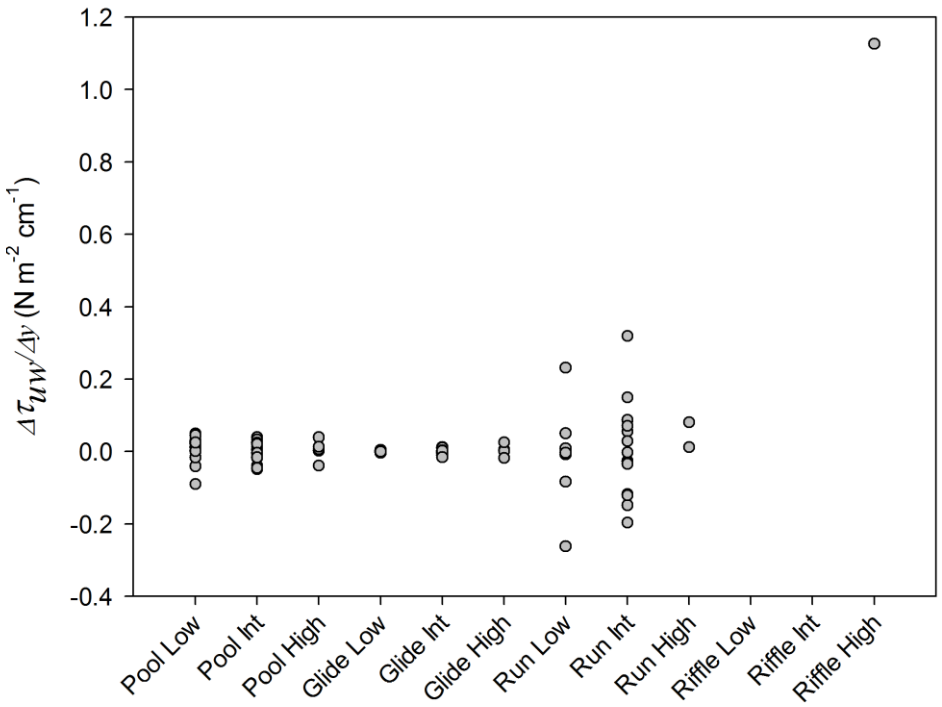

Figure B76 – Change in Reynolds stress on the streamwise-spanwise plane with height above bed for PBs of the River Arrow.

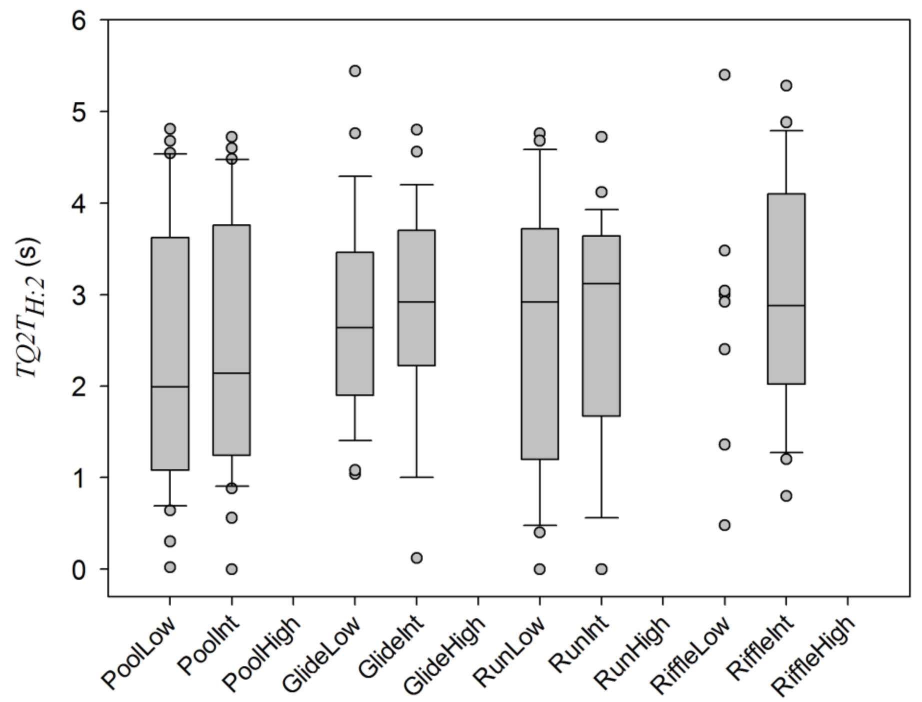

Figure B77 – Cumulative duration of ejections (Q2) for PBs of the River Arrow.

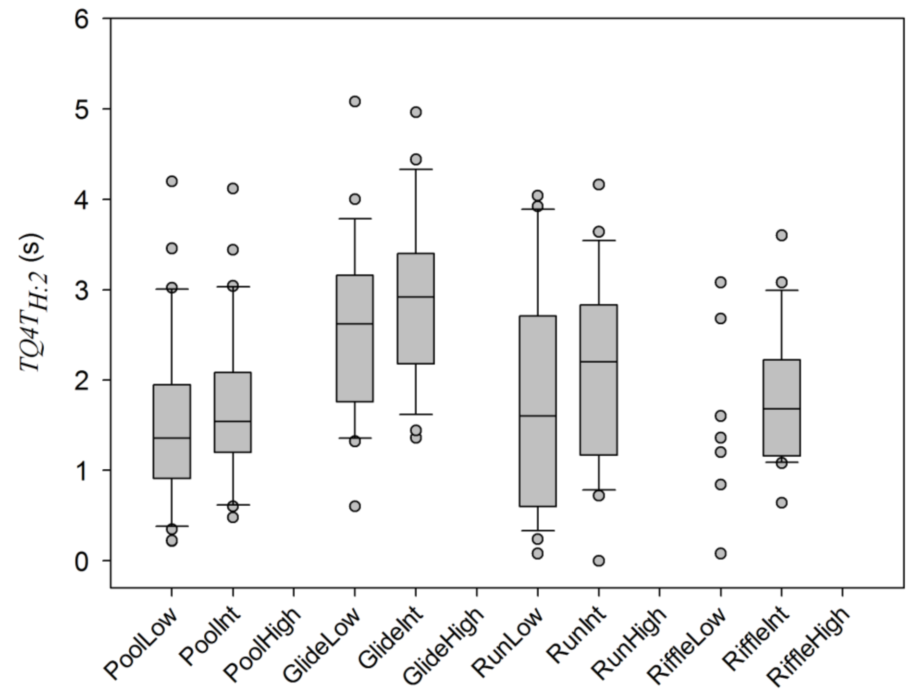

Figure B78 – Cumulative duration of sweeps (Q4) for PBs of the River Arrow.

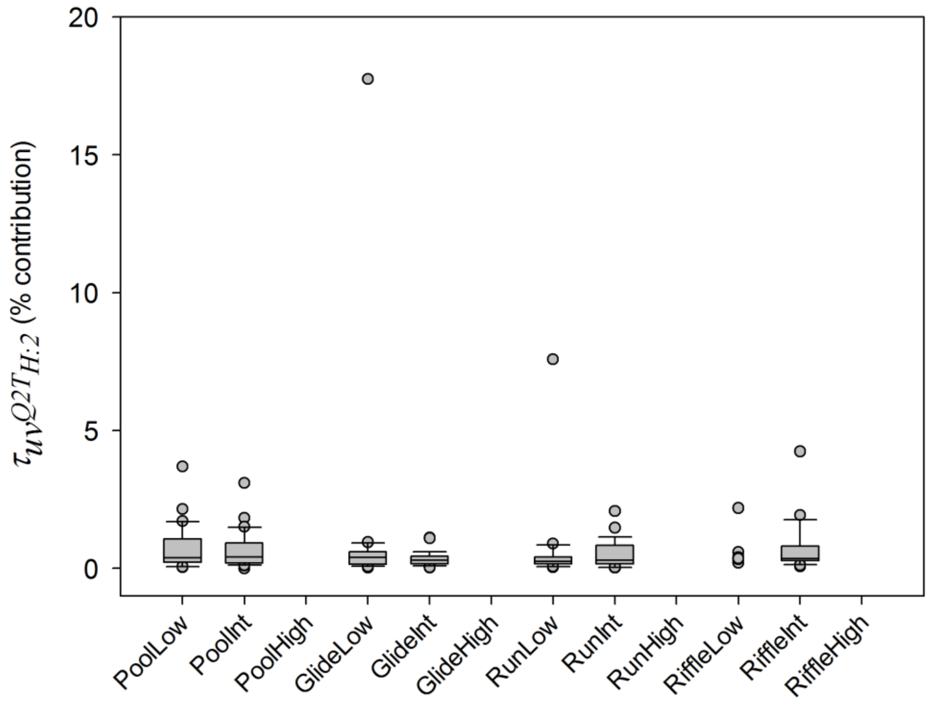

Figure B79 – Fractional contribution to Reynolds shear stress from ejections (Q2) for PBs of the River Arrow.

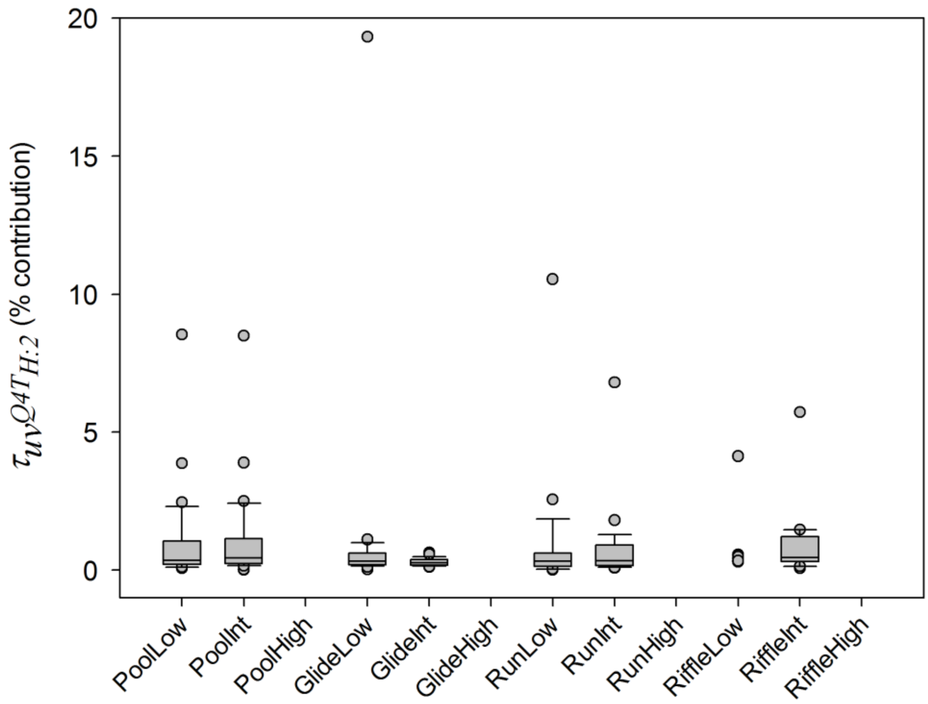

Figure B80 – Fractional contribution to Reynolds shear stress from sweeps (Q4) for PBs of the River Arrow.

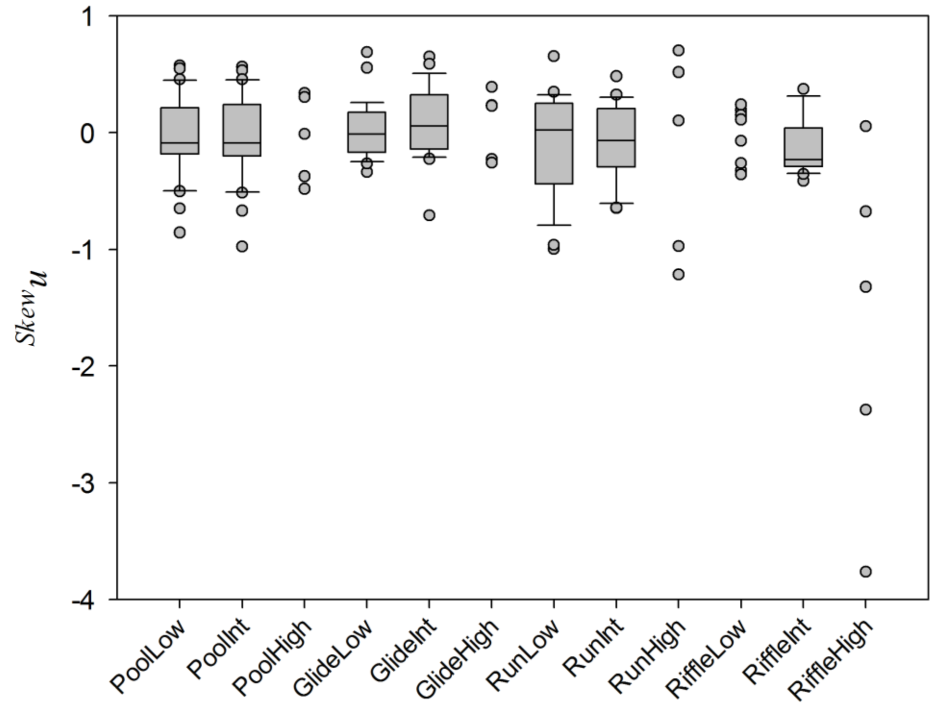

Figure B81 – Skewness coefficient of the streamwise component for PBs of the River Arrow.

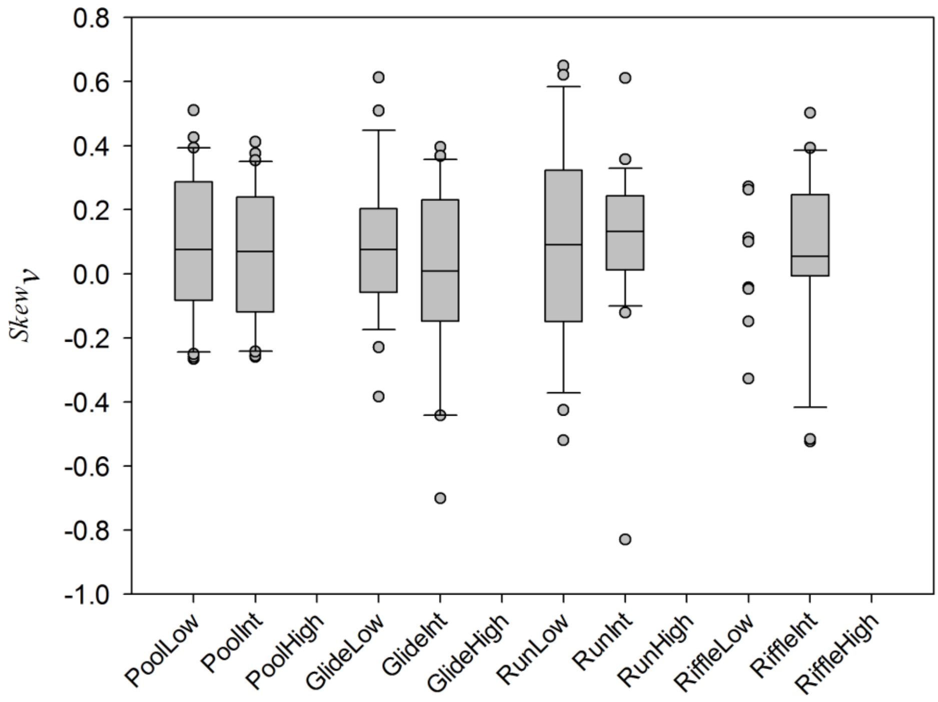

Figure B82 – Skewness coefficient of the vertical component for PBs of the River Arrow.

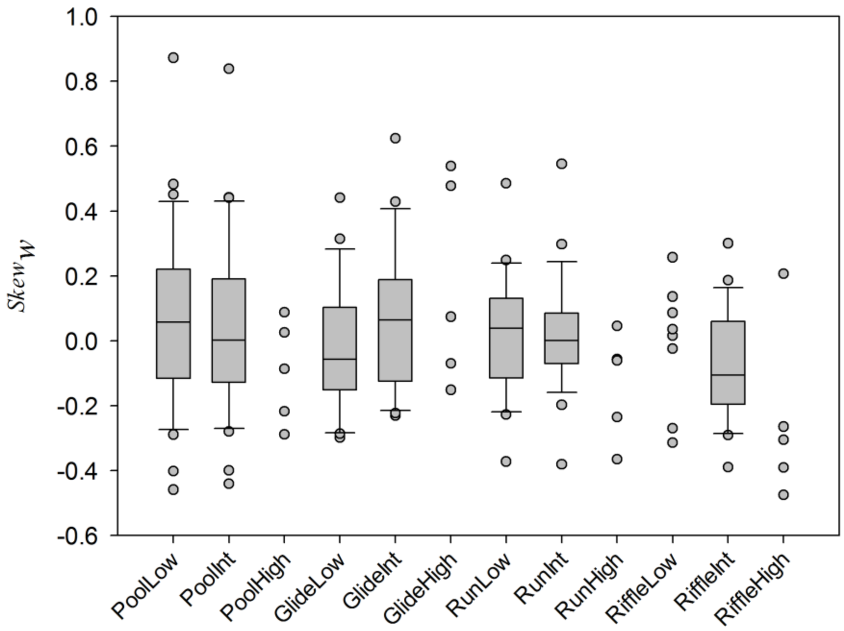

Figure B83 – Skewness coefficient of the spanwise component for PBs of the River Arrow.

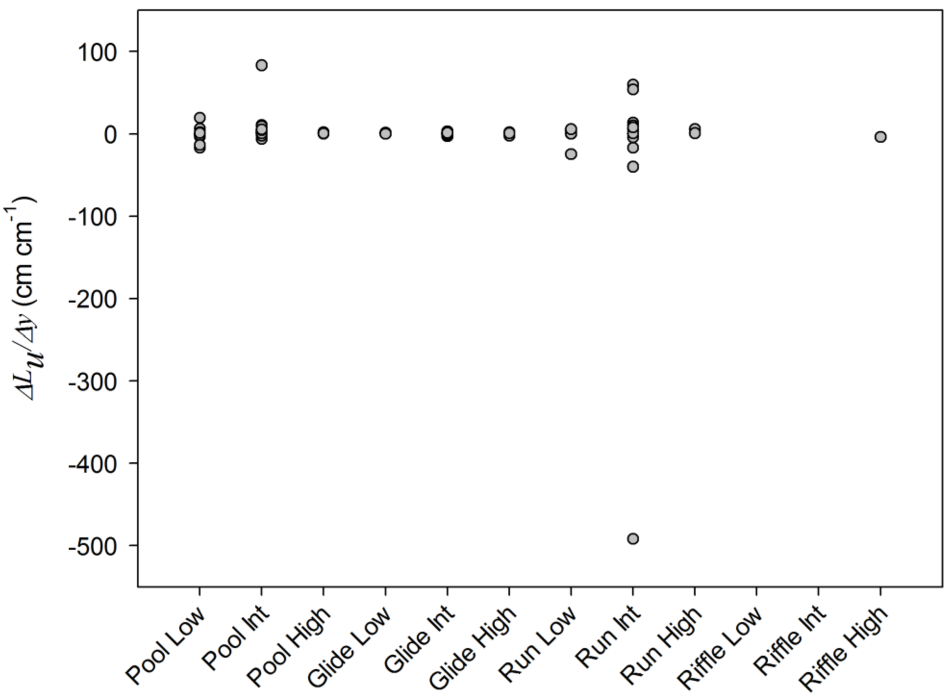

Figure B84 – Change in average eddy length with height above bed for PBs of the River Arrow.

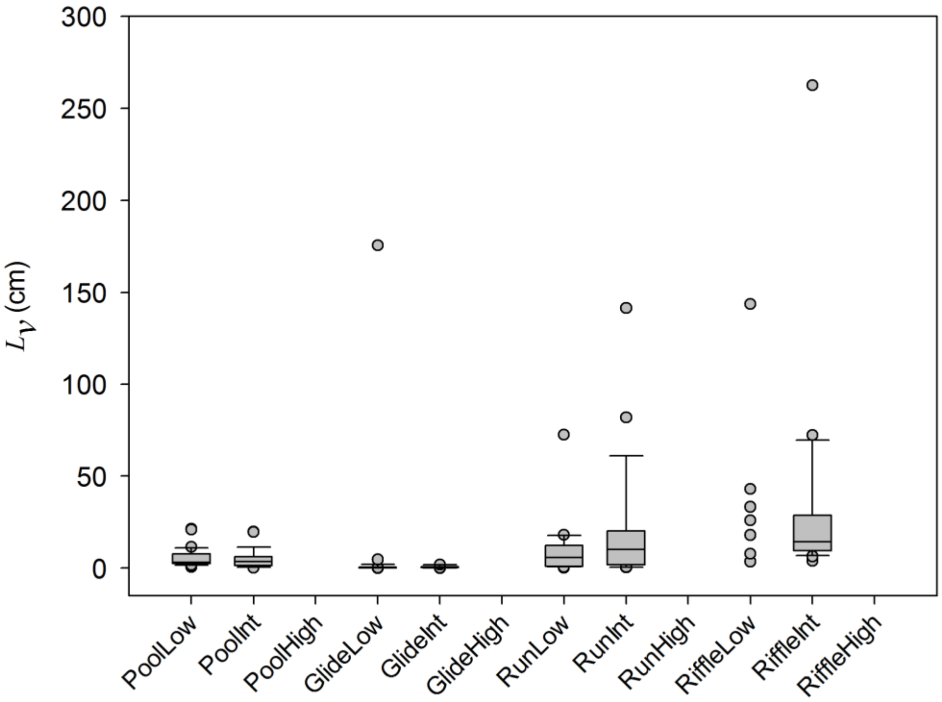

Figure B85 – Average eddy depth for PBs of the River Arrow. Based on un-rotated data.

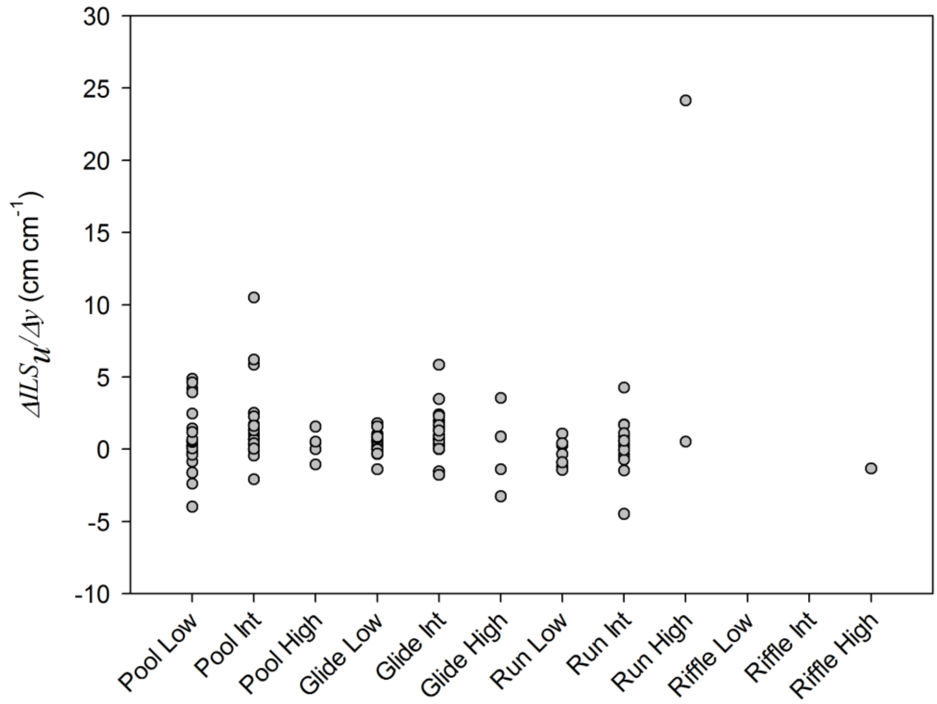

Figure B86 – Change in integral length scale of the streamwise component with height above bed for PBs of the River Arrow.

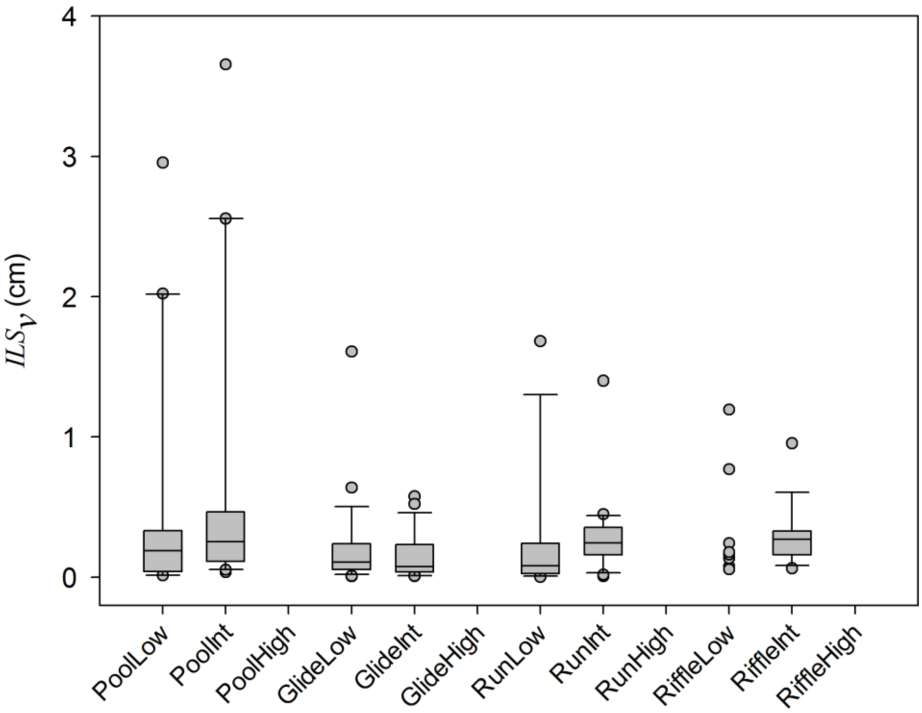

Figure B87 – Integral length scale of the vertical component for PBs of the River Arrow. Based on un-rotated data.

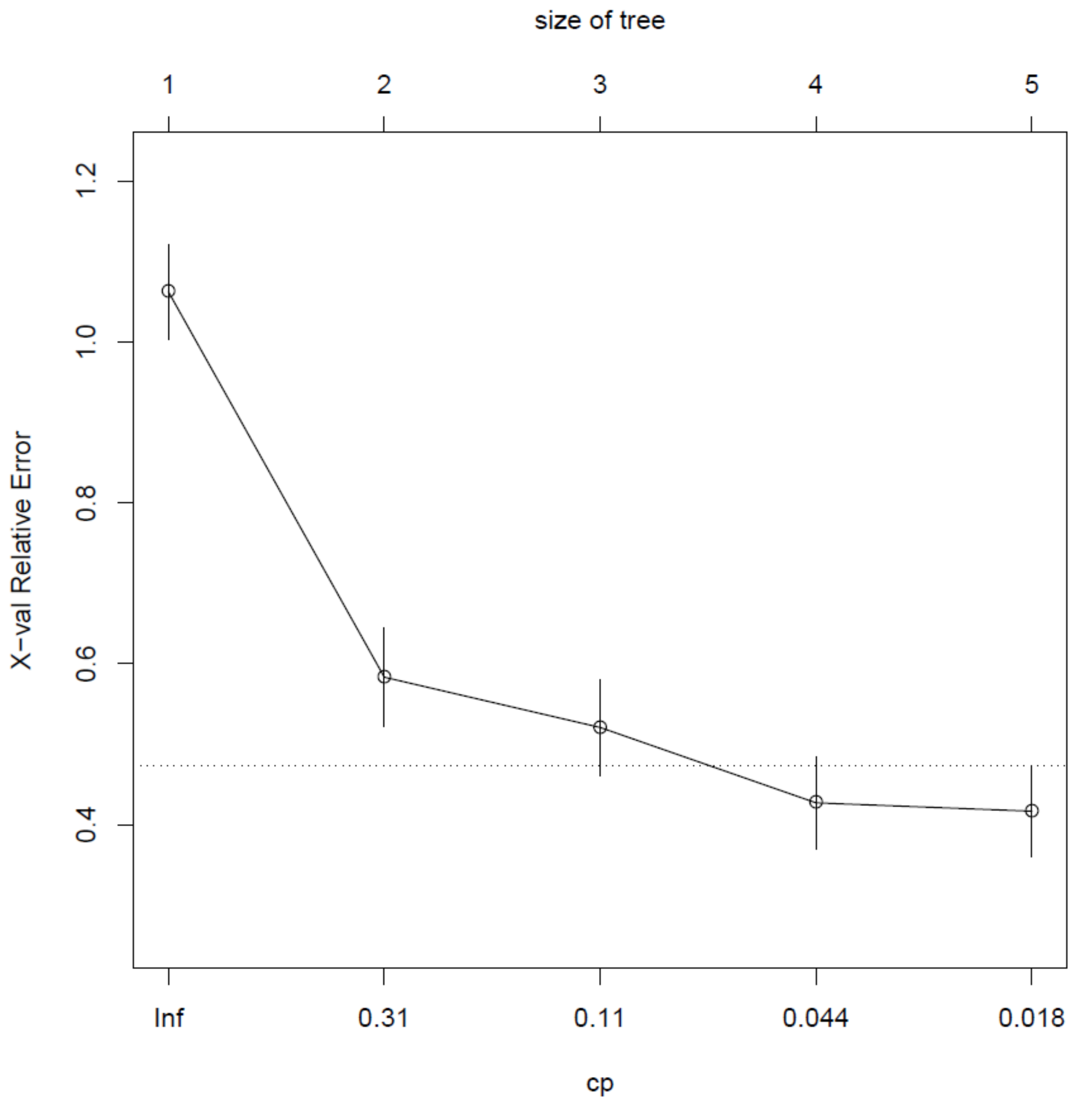

Figure B88– Cross validated relative error (CVRE) for classification trees with different numbers of terminal nodes (size of tree) for the Leigh Brook, near bed, all flows (LB NB All) scenario. Vertical bars represent the standard error (SE) of CVRE and the dashed line indicates the CVRE+1SE of the tree with the lowest CVRE. The tree chosen was the smallest tree within 1SE of the tree with the lowest CVRE (=4).

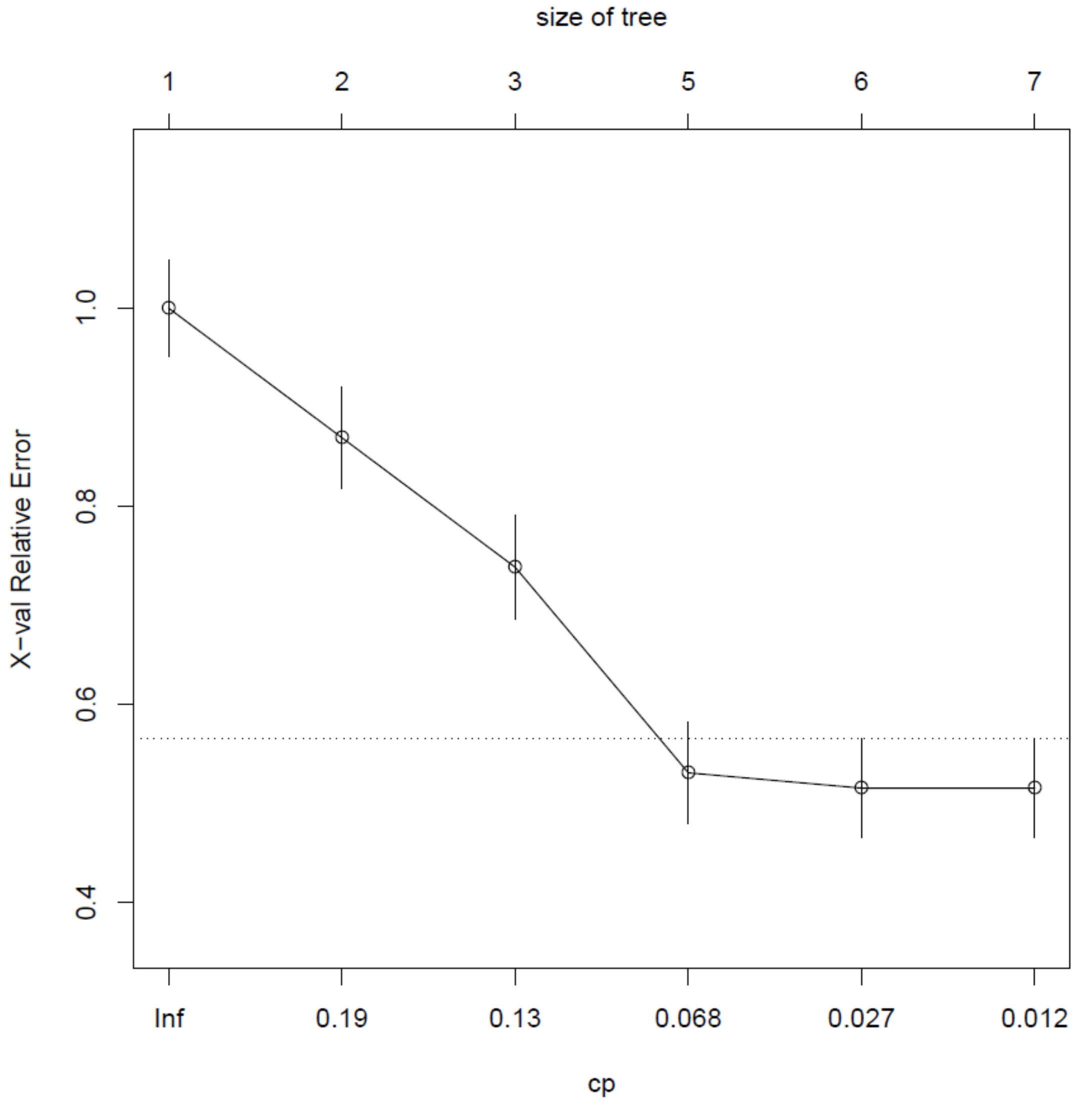

Figure B89 – Cross validated relative error (CVRE) for classification trees with different numbers of terminal nodes (size of tree) for the River Arrow, near bed, all flows (RA NB All) scenario. Vertical bars represent the standard error (SE) of CVRE and the dashed line indicates the CVRE+1SE of the tree with the lowest CVRE. The tree chosen was the smallest tree within 1SE of the tree with the lowest CVRE (=5).

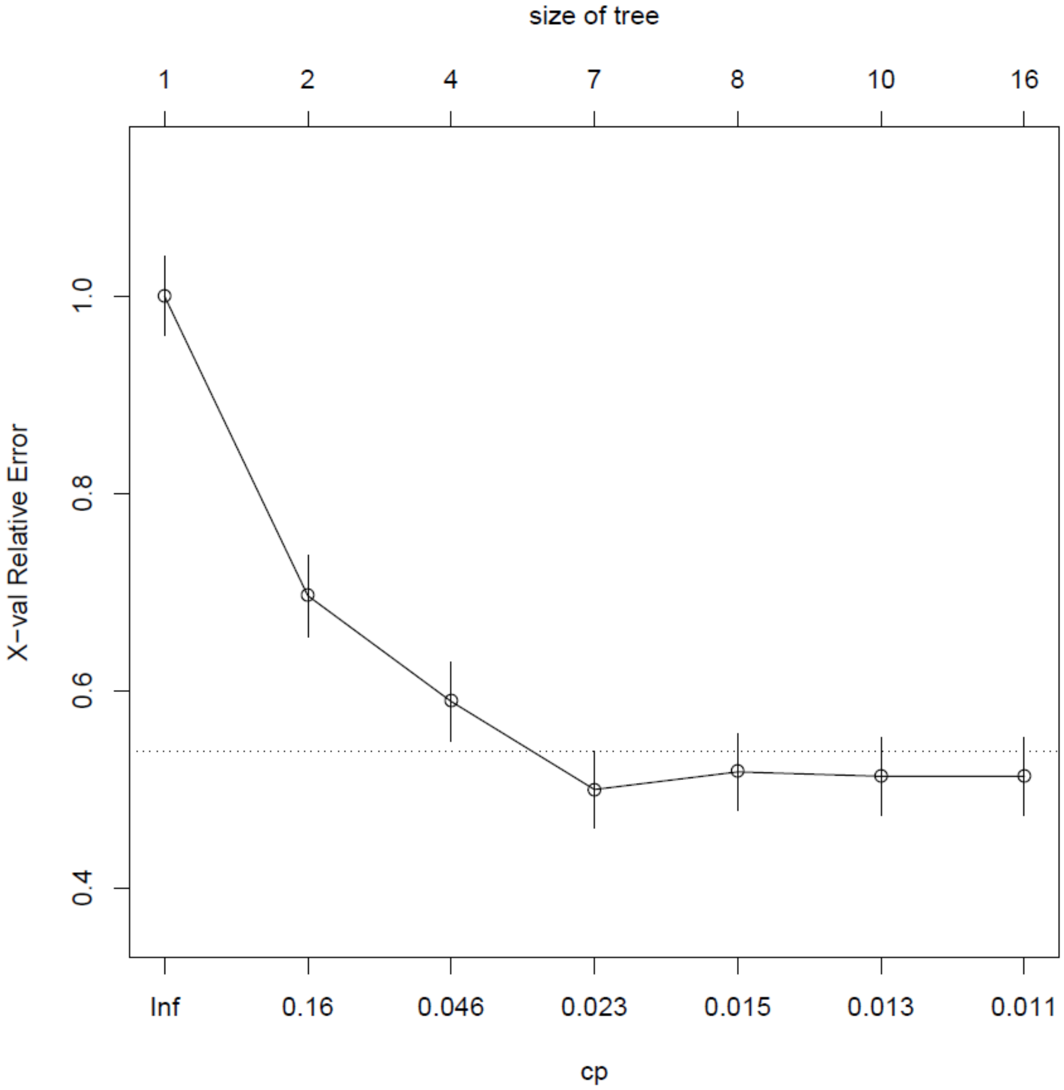

Figure B90 – Cross validated relative error (CVRE) for classification trees with different numbers of terminal nodes (size of tree) for the both sites, point-six, all flows (Both P6 All) scenario. Vertical bars represent the standard error (SE) of CVRE and the dashed line indicates the CVRE+1SE of the tree with the lowest CVRE. The tree chosen was the smallest tree within 1SE of the tree with the lowest CVRE (=7).

Appendix C

Incorporating Hydrodynamics into Ecohydraulics: The Role of Turbulence in the Swimming Performance and Habitat Selection of Stream-Dwelling Fish

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