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Aquatic Habitat Characterization and Use in Groundwater versus Surface Runoff Influenced Streams: Brown Trout (Salmo trutta) and Bullhead (Cottus gobio)

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Aquatic Habitat Characterization and Use in Groundwater versus Surface Runoff Influenced Streams: Brown Trout (*Salmo trutta*) and Bullhead (*Cottus gobio*)

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A thesis submitted in partial fulfilment of the University's requirements for the degree of Doctor of Philosophy

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ABSTRACT

Riverine physical habitats and habitat utilization by fish have often been studied independently. Varying flows modify habitat composition and connectivity within a stream but its influence on habitat use is not well understood. This study examined brown trout (*Salmo trutta*) and bullhead (*Cottus gobio*) utilization of physical habitats that vary with flow in terms of size and type, persistence or duration, and frequency of change from one state to another, by comparing groundwater-dominated sites on the River Tern (Shropshire) with surface runoff-dominated lowland, riffle-pool sites on the Dowles Brook (Worcestershire).

Mesohabitat surveys carried out at two-month intervals on a groundwater-dominated stream and on a surface runoff-influenced stream showed differences in habitat composition and diversity between the two types of rivers. The temporal variability in mesohabitat composition was also shown to differ between the two flow regime types. In the groundwater-influenced stream, mesohabitat composition hardly varied between flows whereas in the flashy stream it varied to a great extent with discharge. Habitat suitability curves for brown trout and bullhead were constructed to predict the potential location of the fish according to flow. The resulting prediction maps were tested in the field during fish surveys using direct underwater observation (snorkelling).

Under the groundwater-influenced flow regime brown trout displayed a constant pattern of mesohabitat use over flows. Mesohabitats with non-varying characteristics over flows and with permanent features such as large woody debris, macrophytes or any feature providing shelter and food were favoured. Biological processes, such as hierarchy, life cycle and life stage appeared to play a key role in determining fish habitat use and to a greater extent than physical processes in these streams.

Bullhead observations in the flashy river showed that mesohabitat use varied with flow but that some mesohabitats were always favoured in the stream. Pools and glides were the most commonly used mesohabitat, due to their stability over flows and their role as shelter from harsh hydraulic conditions and as food retention zones. The presence of cobbles was also found to be determinant in bullhead choice of habitat. In this flashy environment, physical processes such as flow and depth and velocity conditions appeared to be a more decisive factor in bullhead strategy of habitat use than biological processes.

This research shows that:

1. Though differences in habitat use strategies between the two flow regimes can in part be attributed to differing ecology between the species, flow variability affects fish behaviour.
2. A stable flow regime allows biological processes to be the main driving force in determining fish behaviour and location. A highly variable environment requires fish to develop behaviour strategies in response to variations in hydraulic conditions, such as depth and velocity, which constitute the key factor in determining fish location.

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LIST OF ACRONYMS

BFI: Base Flow Index
CGU: Channel Geomorphic Unit
GIS: Geographic Information System
LWD: Large Woody Debris
MesoHABSIM: Mesohabitat Simulation model
NERC : Natural Environment Research Council
PHABSIM: Physical Habitat Simulation
RHS : River Habitat Survey
SFT : Surface Flow Type

CHAPTER 1

INTRODUCTION

1.1 CONTEXT OF THIS RESEARCH

Rivers have been a source of productivity and inspiration for mankind for thousands of years and yet only over the past century have we started to understand some of the processes governing running waters and affecting the organisms inhabiting them. The 20th Century witnessed an alarming decline in freshwater fish populations due in part to pollution, channelisation and river regulation (Davies *et al.*, 2000). This deterioration has generated a growing awareness of the unsustainable nature of traditional management practices and a move towards more environmentally-sensitive river management. In turn, river research has examined the nature of the decline in river health and the complex relationship between river morphology, hydrology and aquatic ecosystems (Norris and Thoms, 1999).

Despite the rapid growth of research on human impacts on freshwater ecology, there has been limited progress in developing models to link physical habitat dynamics using time scales appropriate to the population biology of large organisms (Petts *et al.*, 2006). The life cycle of species measured in years to decades (e.g. brown trout (Salmo trutta) and bull trout) is influenced by complex sequences of environmental variations (seasonal) and population dynamics reflect environmental conditions especially at key periods (spawning, migrations, juvenile stages) where biota is most vulnerable. It is a major scientific challenge to link physical and biological processes and there is a clear need to study environmental and habitat processes at a time scale relevant to biotic communities. It is especially important in the context of the EC Water Framework Directive, which requires monitoring of water bodies and that those reach good ecological status by 2015.

1.2 THE CONCEPTUAL BASIS

In this section, a chronological approach was taken to describe the development of the study of hydraulic ecosystems. Four main concepts were identified that first formed and influenced the basis for the dynamic description of hydraulic ecosystems: i) the river continuum concept, ii) the flood pulse concept, iii) hydraulic stream ecology, and iv) the riverine ecosystem synthesis.

1.2.1 The River Continuum Concept (Vannote et al., 1980)

This concept is based on the observation that a natural river constitutes a continuous flow of water from its source to the sea. As a result, ecological processes vary along the river according to their riparian environment (head water streams in mountains, lowland rivers in the middle of a floodplain, etc.) and along a continuous gradient of physical conditions. This concept constituted one of the first attempts to represent the ecological processes according to the physical environment surrounding the river and how these processes vary spatially from the headwaters to the river's estuary (Allan, 1995). In fact, the River Continuum Concept (RCC) first provided a link between the structure and function of rivers. Rivers and streams are categorized according to their size and each category (upland stream, large floodplain river, etc) is characterized by faunal assemblages and communities, and organic matter inputs. The RCC aimed at a global characterization of pristine running waters based on the main principle that the aim of the communities across a river are to present strategies that minimize energy loss so that the whole system from source to mouth is in energy equilibrium (Vannote *et al.*, 1980). As a result of the categorization, all the processes taking place in the river appear predictable.

Though a major step toward an integrated approach linking both physical conditions and instream biological processes, the RCC presents important limitations and assumptions that do not agree with the reality of instream environments. As it was first argued by Statzner and Higler (1985), physical conditions do not vary across a continuous gradient from source to mouth as some local conditions such as climate and land use for example can modify instream characteristics.

This concept was based on pristine rivers, which have become scarce over the past decades and most of the "natural" rivers, though relatively unimpacted in their geomorphology and hydrology, are nowadays subject to human impact to a certain extent. Finally this attempt of a global characterization of streams according to their size appears unrealistic given all the factors that influence instream environments: it is hardly expected that a small UK lowland stream will present the same characteristics as a stream of the same size in Africa given the differences in climate, biogeography and geology between the two regions.

1.2.2. The flood pulse concept (Junk et al., 1989)

While the River Continuum Concept aimed to described the longitudinal gradient of ecological variability along a river, the flood pulse concept focuses on the lateral connectivity between rivers and adjacent riparian zones and states that "the principle driving force for the existence, productivity and interactions of major biota in river-floodplains systems is the flood pulse" (Junk *et al.*, 1989, p.1). Unlike the RCC, the flood-pulse concept emphasizes that processes are not continuous in river-floodplain systems; they in fact vary in terms of timescale of occurrence and in predictability. It highlights the importance of riparian zones as a source of organic matter for instream ecosystems and the importance of floods as a link between terrestrial and aquatic ecosystems.

The concept was initially developed to explain the variation of water levels in Amazonian floodplains but its use was then extended to smaller river basins (Middleton, 2002) and more temperate systems (Tockner *et al.*, 2000). The interconnectivity between rivers and floodplains is a key driver to production, decomposition and consumption or organic matter. The floodplain provides a source of organic matter, hence nutrients, to the instream ecosystem while the latter favours seasonal vegetation succession. Hence this concept emphasizes the linkage between geomorphology, hydrology and biota.

1.2.3. Hydraulic stream ecology (Statzner et al., 1988)

This concept was based on the knowledge that an organism's ecology and metabolism are influenced by flow characteristics. Using this approach, Statzner *et al.* (1988, p.2) sought to "link organismic responses to a more comprehensive treatment of the physical environment". Hydraulic stream ecology aimed at using simple measurements in the field such as mean velocity, depth and substrate, bottom roughness to calculate more complex hydraulic key variables that influence lotic organisms in running waters. This approach was first used on macroinvertebrates, showing that their distribution was linked to particular values of bottom roughness for example. This concept highlights the dynamic interactions that occur between river geomorphology (shape and form of the river), hydrology (movements of water throughout a river) and the ecology of organisms living in rivers (energy budget, life cycle, adaptation strategies). Statzner *et al.* (1988) further argue that this approach allows an increase in predictability of organism response to flow from the stream to the catchment scale, hence enhancing replicability of lotic ecology studies. Though hydraulic stream ecology highlights the importance of the interactions between flow and instream organisms behaviour, predictability might be only achievable for macroinvertebrates as these organisms are not very mobile compared to the flows they are subject to whereas fish are able to move to other habitats if the conditions are not optimal and that makes predicting their distribution far more challenging. Moreover, time scaling and temporal variability of organism responses to flow conditions were not studied to such an extent as spatial scaling. However, the philosophy behind this approach is still up to date these days as the interactions between instream biota and flow hydraulics constitute the major principle in 'Hydroecology' and 'Ecohydraulics'.

1.2.4. The Riverine Ecosystem Synthesis (Thorp et al., 2006)

This integrated model provides a framework for understanding riverine biocomplexity across a wide range of spatio-temporal scales and takes into account many aspects of the aquatic models proposed between 1980 and 2004 (Thorp *et al.*, 2006).

It first consider rivers as four-dimensional entities: the lateral and longitudinal dimensions are characterised by the riparian inputs, while the third dimension results from vertical interactions between the stream and the hyporheic zone and temporal variability constitutes the 4^{th} dimension. Secondly, and unlike the RCC, it considers that variations within the river ecosystem are not continuous but rather stochastic and that environmental conditions do not vary longitudinally. Indeed, it is based on the main property of rivers: the spatial zonation of hydrologic characteristics. Interactions between these hydrologic conditions and the local geomorphology create hydrogeomorphic patches which in turn create ecological "functional process zones" (FPZs). The distribution of these FPZs is not necessarily predictable and varies according to spatio-temporal scales. The REC is currently characterized by 14 tenets in order to predict patterns in species distribution and instream processes.

This approach encompasses the whole complexity of the riverine ecosystem as well as its interactions with terrestrial ecosystems and climatic factors. Hence, rivers are not just considered as a stream flowing in the middle of a terrestrial ecosystem anymore but as networks and open systems interacting with a range of factors across various spatial and temporal scales. The REC also emphasizes the unpredictable nature of riverine processes and the need to integrate spatio-temporal scales into river ecology studies. Its relevance to the current study lies in its taking into account of the hyporheic zone. Indeed one of the study sites, the River Tern, is groundwater influenced, so one may expect that some of the observations recorded during this project are a consequence of the interactions between the hyporheic zone and the stream.

1.2.5 Emergence and development of cross- disciplinary research

The four concepts described above present a common aim: in order to better understand the functioning of running water ecosystems, their study had to be undertaken beyond the boundaries of classic scientific disciplines. The new discipline of "hydroecology" or "ecohydrology" emerged at the beginning of the 1990s (1991 according to Hannah *et al.*, 2004). Since then, this interdisciplinary subject and way of looking at river ecosystems has grown and thus taken more importance as a scientific discipline. Hannah *et al.* (2004, 2007) illustrated that the number of scientific papers referring to this new discipline has steadily increased since the 1990s. They define ecohydrology as a "multidisciplinary concept which allows to encompass the whole ecosystem and the key interactions and processes at various spatial and temporal scales" (Hannah *et al.*, 2007, p.2). Newman *et al.* (2006) further stated that the aims of ecohydrology are to understand how hydrological processes influence the distribution, structure and dynamics of biotic communities and in turn how these communities can influence hydrology. The interactions between biological processes (organism ecology and biology) and physical processes (resulting from the physical environment) at various scales were also emphasized by Parsons and Thoms (2007) who used a hierarchical approach (catchment to patch) to better understand the processes and interactions between river processes and macroinvertebrate assemblages in the Murray-Darling Basin in Australia. Ecohydrology can be viewed as a bi-directional study of the interactions between physical processes and instream biota ecology, including any feedback mechanisms. Ecohydrology is often described by the term “Ecohydraulics”. If the two disciplines are similar in that they rely on multidisciplinary approaches to the study of aquatic ecosystems, Ecohydraulics is described as “the study of the linkages between physical processes and ecological responses in rivers, estuaries and wetlands” (Naiman *et al.*, 2007, p.3) and can be considered as a sub-discipline of Hydroecology together with the study of Environmental Flows (minimum flows necessary to maintain biota and ecological processes).

In the last year alone, numerous papers have been published that focus on the links between the physical environment and biological communities. Fisher *et al.* (2007) used “functional ecomorphology” to understand the linkages between river landscapes and biological processes at the river scale. Floodplain geomorphology was studied by Hamilton *et al.* (2007) as a way to predict biodiversity in a Peruvian river basin. Finally, several publications (Dollar *et al.*, 2007; Post *et al.*, 2007; Renschler *et al.*, 2007) focus on the key challenges and the best methods to bridge the gaps between the various disciplines involved in the study of riverine ecosystems, such as atmospheric research (impact of climate change of riverine systems), hydrogeology, ecology, geomorphology. The project presented in this thesis is embedded in the study of hydroecology and multidisciplinary research.

Indeed fish and environmental processes interact over a wide range of scales, and so management frameworks must incorporate a consideration of spatial and temporal scale (Imhof *et al.*, 1996). Rivers can be examined across a hierarchy of spatial scales, from the catchment (macro), reach, Channel Geomorphic Units or CGUs (meso) or at individual points (micro) (Frissell *et al.*, 1986). One criticism of past research is that patchiness has been measured by sampling at disparate points along a stream without mapping the heterogeneity of the system and understanding the influences between points. Another approach has considered the microhabitat scale i.e. studying local processes like turbulence and substrate type (Booker and Dunbar, 2004). However, Fausch *et al.* (2002) have suggested that when studying fish habitat, **macrohabitat** scale (maps or satellite pictures) and **microhabitat** scale (point characteristics) do not reveal features the most important to fish. These features are determined by channel morphology, habitat complexity and barriers to fish movement and are best viewed at an **intermediate** scale where the spatial arrangement of mesohabitats or CGUs such as pools and riffles are more influential.

A stream can be viewed as a mosaic of mesohabitats and it is at this scale that biotic interactions take place. However, studies of CGUs and habitat utilization by instream biota have often been carried out independently (Pedersen, 2003). There is a need to understand habitat connectivity and how this is linked spatially and temporally with fish ecology and behaviour, and to establish whether habitat dynamics represent a time scale that is appropriate to fish population dynamics, yet cross-scale studies that integrate both geomorphological processes and stream ecology are lacking. The next section presents further details on the aims of this study and the structure of this thesis.

1.3 OVERALL THESIS AIMS AND STRUCTURE

1.3.1. Aims, objectives and key research questions

This study aims to examine the relationship between river flow regime and the spatial and temporal habitat use dynamics for brown trout and bullhead at the mesoscale. It also aims to assess fish habitat use in relation to the spatial composition of CGUs.

The objectives are:

1. Characterise the above species' habitat in groundwater and surface run-off influenced streams.
2. Use an intermediate scale (mesohabitat) approach to understand the implications of spatial pattern and habitat connectivity in streams.
3. Evaluate the temporal dynamics of habitat use and species' response to habitat variability in relation to flow regime.
4. Use field evidence to evaluate the accuracy and reliability of HSI curves constructed with previously published data.

A number of key research questions have also been defined relating to these objectives and they are stated below.

RQ_1. Do different types of natural flow regimes result in different types of stream geomorphology and hence in different patterns of mesohabitat composition?

RQ_2. How does instream mesohabitat composition vary over the range of flows experienced by a river according to its flow regime?

RQ_3. Is there a pattern of mesohabitat use displayed by the fish populations studied and if so what is it?

RQ_4. Does mesohabitat use by fish follow the same pattern as mesohabitat variability, i.e. is it influenced only by flow?

RQ_5. Are other factors involved in fish habitat use?

RQ_6. What role is played by factors such as seasonality, habitat availability, life-stage and social interactions in the pattern of habitat use displayed by the surveyed population?

RQ_7. What are the key habitat characteristics that determine fish location?

1.3.2. Relevance of the chosen fish species

Brown trout (Salmo trutta) and Bullhead (Cottus gobio) are abundant in rivers and streams of England and often found living in sympatry (Natural England online, date unknown). Both species had been previously recorded in the streams used for this study. In the River Tern at Norton in Hales, both species were recorded and accounted for nearly all the individual fish surveyed by electrofishing (Pinder *et al.*, 2003). The presence of bullhead and brown trout was also recorded in the Dowles Brook (Natural England online, date unknown) although no background data on their population were available. The two species have differing ecology: bullhead is a benthic fish and a poor swimmer while brown trout lives mainly in the water column and with good swimming capacity. Therefore this study selected these two species to investigate how fish with differing ecology respond to similar patterns of flow and mesohabitat variability. Both species are considered as indicators of stream naturalness and good water quality: Bullhead is very sensitive to physical habitat degradation via instream channel regulation and removal of instream coarse substrate. Such degradation has occurred to a great extent in continental Europe and as a result a sharp decline in bullhead populations has been observed, prompting the classification of this species as endangered under the E.U Habitat Directive. Brown trout require well oxygenated waters in general good water quality and is thus seen as a good indicator of river naturalness and absence of pollution. While a lot is understood about brown trout ecology and life-cycles (Elliot, 1994), less is known about its habitat use in relation to flow regime and mesohabitat connectivity. Little is known about its ecology (Tomlinson and Perrow, 2004). Therefore these two species will complement each other and provide the ecological importance for the study. A summary of the literature on brown trout and bullhead is provided in Chapter 2, section 2.6.

1.3.3 Thesis structure

Following this introductory chapter (Chapter 1), this thesis includes five further chapters. These present a critical review of relevant literature (Chapter 2), the materials and methods used to carry out the investigation presented in this thesis (Chapter 3), two research chapters devoted to addressing specific research questions on brown trout and bullhead habitat use constructed from the knowledge gaps identified in the literature review

(Chapter 4 and 5) and a final chapter that provides a research summary, discussion of the results of the investigation and conclusions (Chapter 6).

Chapter 2 reviews the published literature concerning a number of specific areas of interest and relevant to the study, including hydrological and physical processes with specific links to temporal and spatial scale consideration; flow regime and its influence on instream processes and ecology; mesohabitat description, characterization and hydraulics at the reach scale; fish behaviour and how biotic and abiotic factors impact on it. From this review a number of distinct research gaps and questions were identified that form the focus of the research presented thereafter. Chapter 3 introduces the study sites within the Dowles Brook Catchment in Worcestershire and the Tern Catchment in Shropshire, detailing their physical and ecological characteristics. It also describes the overall experimental design, including detail on the method used for mesohabitat mapping and fish habitat characterization and the fish sampling protocol and strategy. Details of the tools and techniques used for data analysis are also presented. Chapter 4 focuses on the study of habitat use by brown trout in a groundwater-fed stream, i.e. the River Tern. It presents the results of mesohabitat composition monitoring over a range of flows as well as trout response to flow and mesohabitat pattern of variability. This section also discusses proposed hypotheses and explanations of the results. Chapter 5 discusses the results of the study of bullhead habitat use under two types of flow regimes and its response to mesohabitat and flow variability. A comparison of the types of flow regimes in terms of mesohabitat variability and fish response is presented as well as a discussion of the results. Finally, Chapter 6 brings together the results from the two previous chapters in relation to the thesis aims and compares them to previously published studies. Conclusions are drawn and suggestions for further research are proposed. Figure 1.1 presents a flow chart with the structure of the thesis.

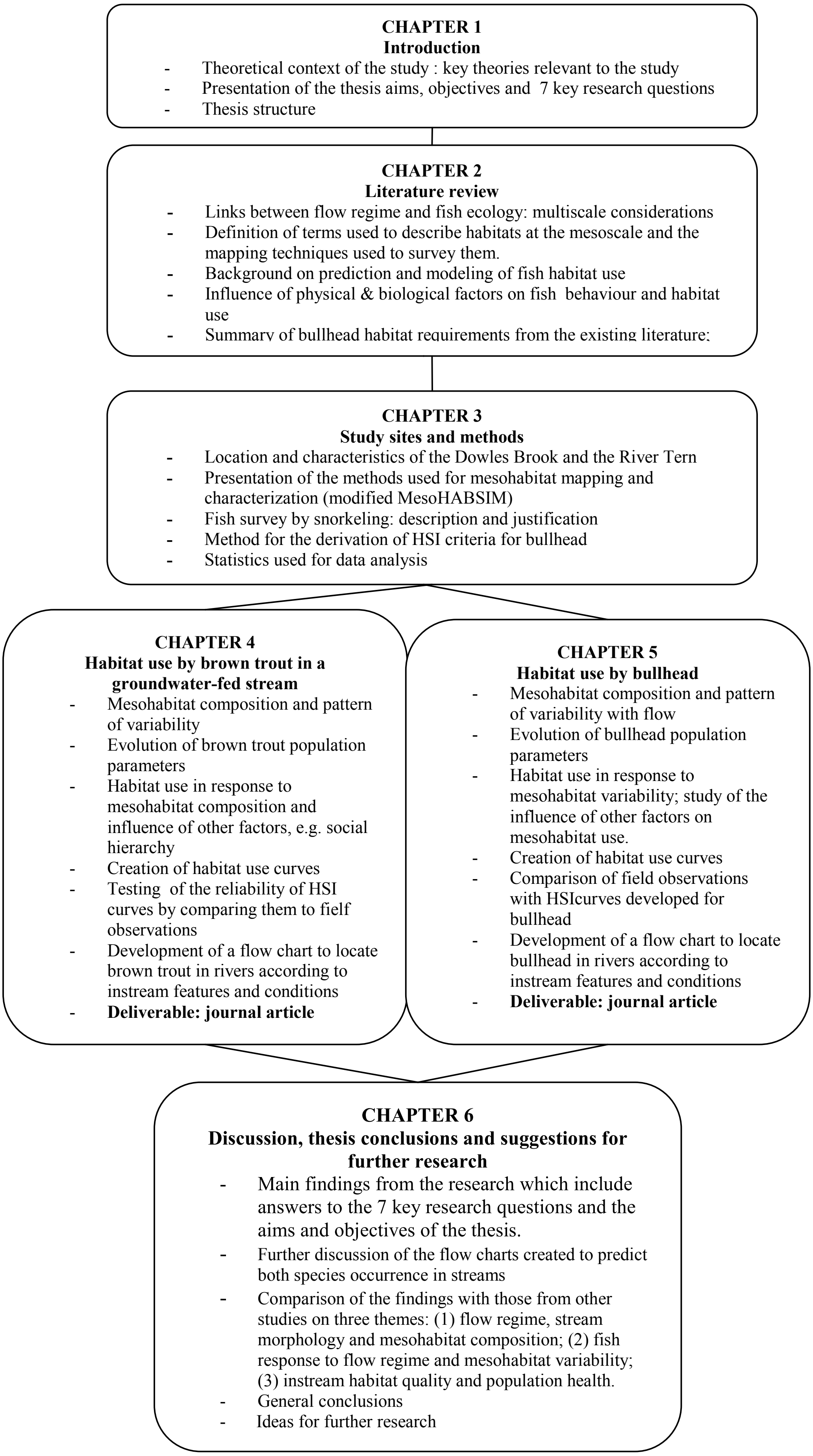


Figure 1.1. Structure of the thesis

CHAPTER 2

LITERATURE REVIEW

2.1 INTRODUCTION

River catchments are complex ecosystems where physical (abiotic) processes interact with biota over a wide range of spatial and temporal scales. Rivers can be compared to arteries and catchments to the heart so that the riverine ecosystem reflects the degree of human disturbance on the catchment. To understand, manage and protect efficiently these ecosystems, it is necessary to assess the health status of rivers and of the habitats they provide for aquatic biota in general, and in the particular case of this study, for fish. Each river catchment is characterised by its own unique combination of flow regime and bed morphology which in turn governs stream health, the array of instream habitats found as well as the distribution of aquatic organisms (Bunn and Arthington, 2002). This thesis is concerned with hydroecology, and the links that exist between hydrology, fluvial geomorphology and ecology along river corridors. It also considers how habitat composition affects fish distribution in relation to flow regime over seasonal and annual timescales.

The following critical review aims to set the multidisciplinary context in which this research has been developed and carried out as well as define the knowledge gaps it has tried to address. Figures 2.1 and 2.2 introduce the multidisciplinary context and identify the various processes and interactions over a variety of scales that were considered during the research. Section 2.2 focuses on one of the major considerations in this research project, i.e. the scale of investigation. Figure 2.1 describes current knowledge with respect to flow regime and how it determines (i) the various physical processes that take place at the stream scale as well as (ii) habitat composition. It also shows the several variables that interact with flow regime both at the catchment (floods/droughts) and the reach scale (temperature regime, vegetation, sediment load in the stream) and how these interactions fit in with the focus of this research: the influence on mesohabitat composition and ultimately the possible effects on fish under good water quality conditions. This is discussed further in section 2.3. Habitat composition and variability as well as the different techniques that can be used to map them in a river are discussed in section 2.4 (see Figure 2.2).

A summary of the various parameters relevant to the understanding and description of instream habitats according to scale are presented in section 2.5. In section 2.6, the research gaps identified in the literature are discussed, and how the current project aimed to address some of the gaps is detailed. Figure 2.2 presents habitat characteristics on the one hand and the variables related to fish ecology on the other. The present research has sought to identify the links between the two components. Fish ecology and the factors, both biological and physical, affecting fish habitat use are discussed in section 2.7.

Cowx and Welcomme (1998) stated that the productivity of any riverine habitat was determined by four factors:

- Flow regime
- Water quality
- The physical nature of the floodplain
- The energy budget of the total diversity of biota present in the system.

This statement i.) emphasizes the key role that flow regime plays in riverine ecosystems as it is the principal determinant of the physical parameters fish are subjected to and ii.) indicates the complexity of the interactions that occur within rivers. Instream disturbance, due to high flow variability can be considered as a driving force for instream communities and influencing the spatial heterogeneity of habitats. In turn this can be viewed as the availability for refuge for instream biota (Scarsbrook and Townsend, 1993) particularly against high variability in water velocity (Jowett and Duncan, 1990; Newson and Newson, 2000). This determines the location of fish and other organisms in a stream. The influence of flow regime on instream and riparian vegetation is discussed in section 2.3.4. Benthic macroinvertebrates are also subject to instream discharge variability and the impact this has on their habitat patches. Jowett (2003) showed that macroinvertebrate abundance was highest where substrate was the most stable and disturbance was less frequent; accumulation of fine sediments from high flow events reduced macroinvertebrates abundance considerably. Fish habitat use with respect to discharge is more difficult to assess as they are mobile organisms, thus less dependent on the local constraints resulting from flow variability. Under natural flow conditions, organisms are perfectly adapted to the habitat conditions inherent to a stream (Poff, 2004). This concept has led to the use of fish assemblages and their variations as means to determine the status (natural, human influenced, etc.) and level of disturbance of a particular river (Pusey *et al.*, 1993; Poff *et al.*, 1997; Schmutz *et al.*, 2005; Vehanen *et al.*, 2004). However, data and information on how particular fish species/populations respond in terms of behaviour and habitat use to modifications of habitat characteristics from flow variability are lacking.

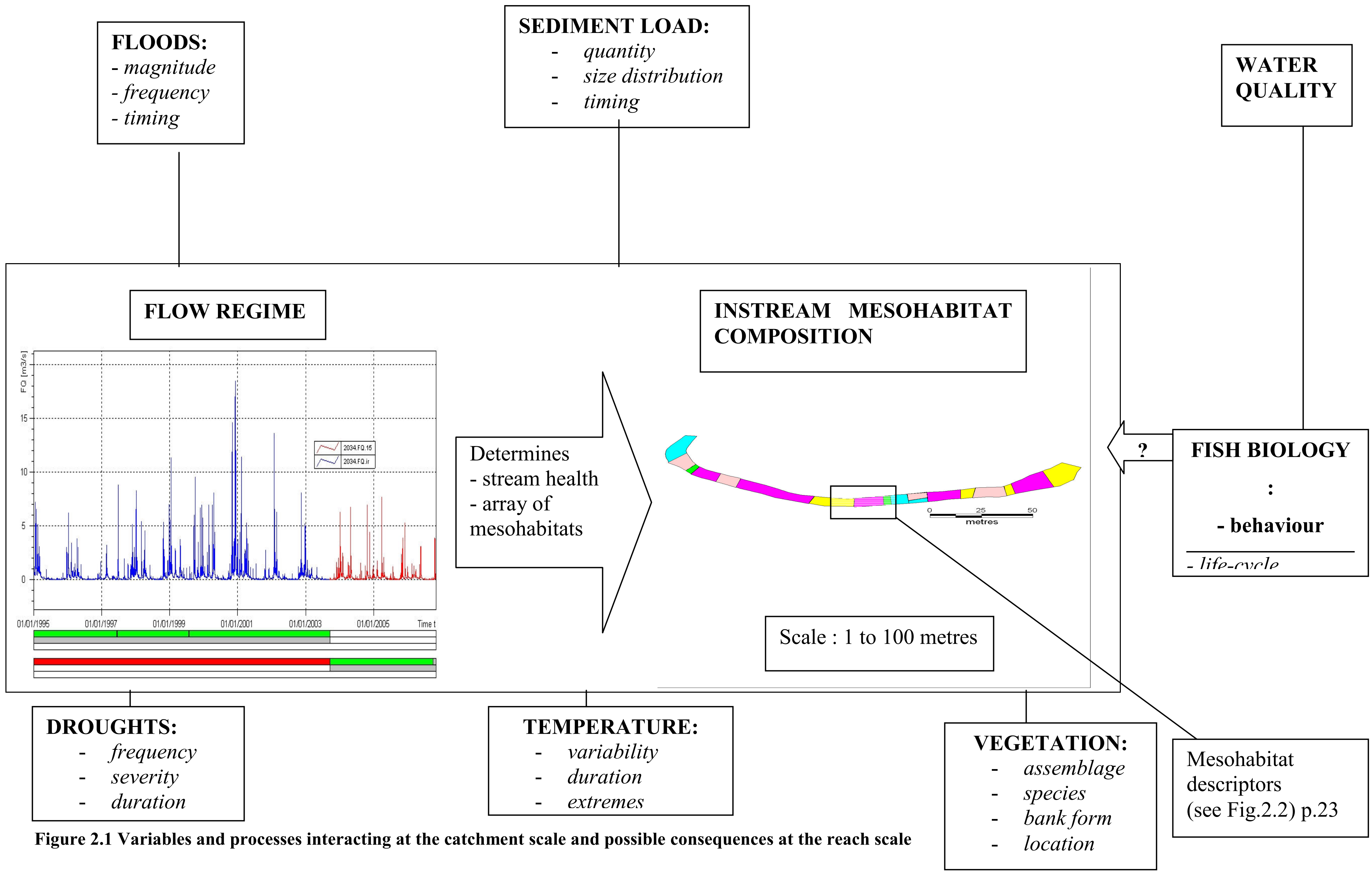


Figure 2.1 Variables and processes interacting at the catchment scale and possible consequences at the reach scale

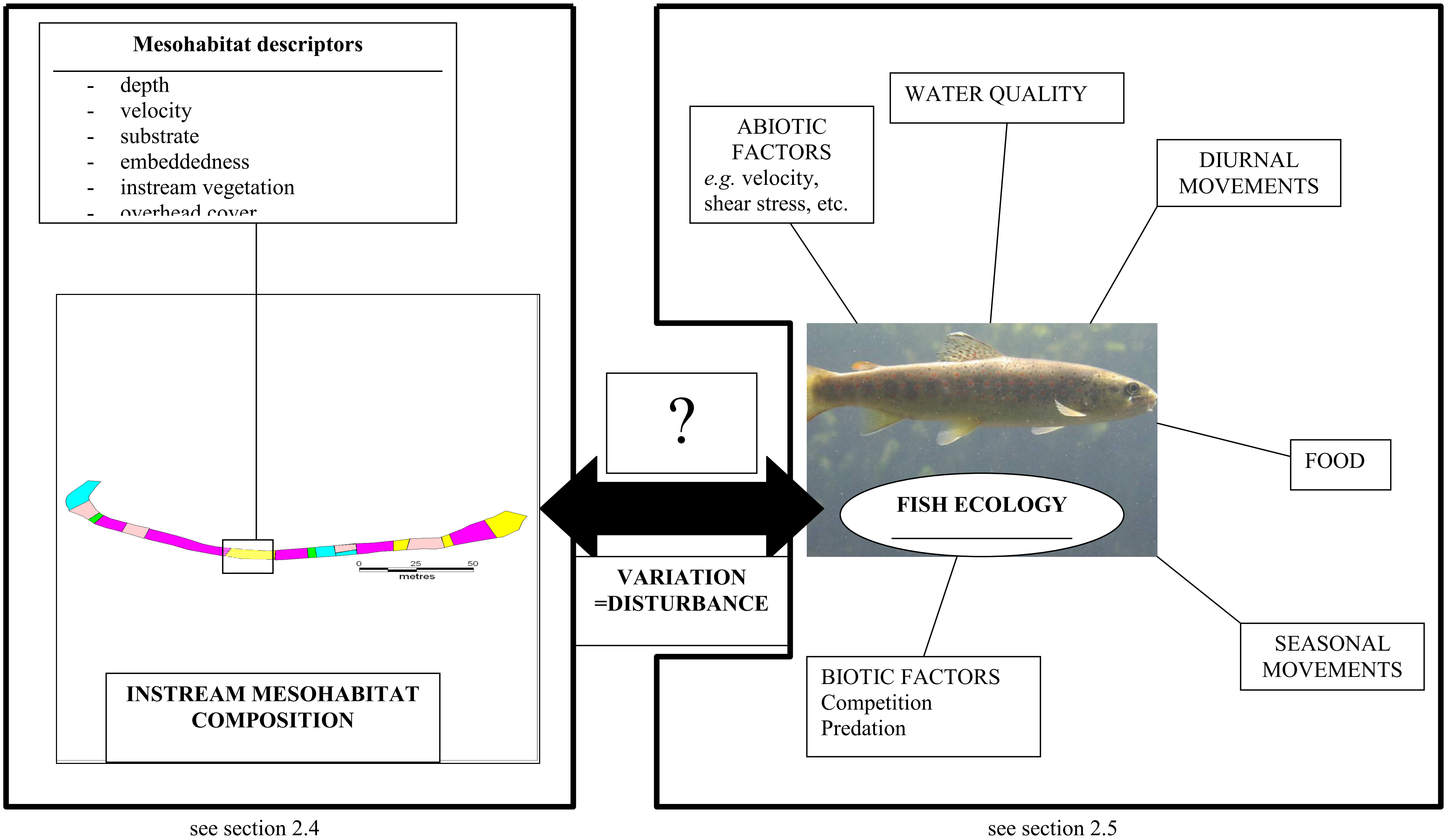


Figure 2. 2 Linking physical habitat characteristics and fish ecology: the big picture

2.2 BACKGROUND TO SCALE CONSIDERATION

As very mobile organisms, fish are not restrained to just one part of a drainage network. However their range may be limited by both water quality (especially temperature) and channel morphology changes along the river continuum. Their movements can range from over a few metres to hundreds of kilometres in the case of migrating species (Lucas, 2000). As a result, fish and environmental processes interact over various scales from the catchment down to the microhabitat scale. Lewis *et al.* (1996) stressed how ecological processes and structures are multi-scaled. This is illustrated by Figure 2.3 below, which was drawn after Stanley & Boulton (2000) and Fausch *et al.* (2002) and summarizes the spatial and temporal scales over which physical processes and species interact in aquatic ecosystems, as well as the current level of understanding of these interactions.

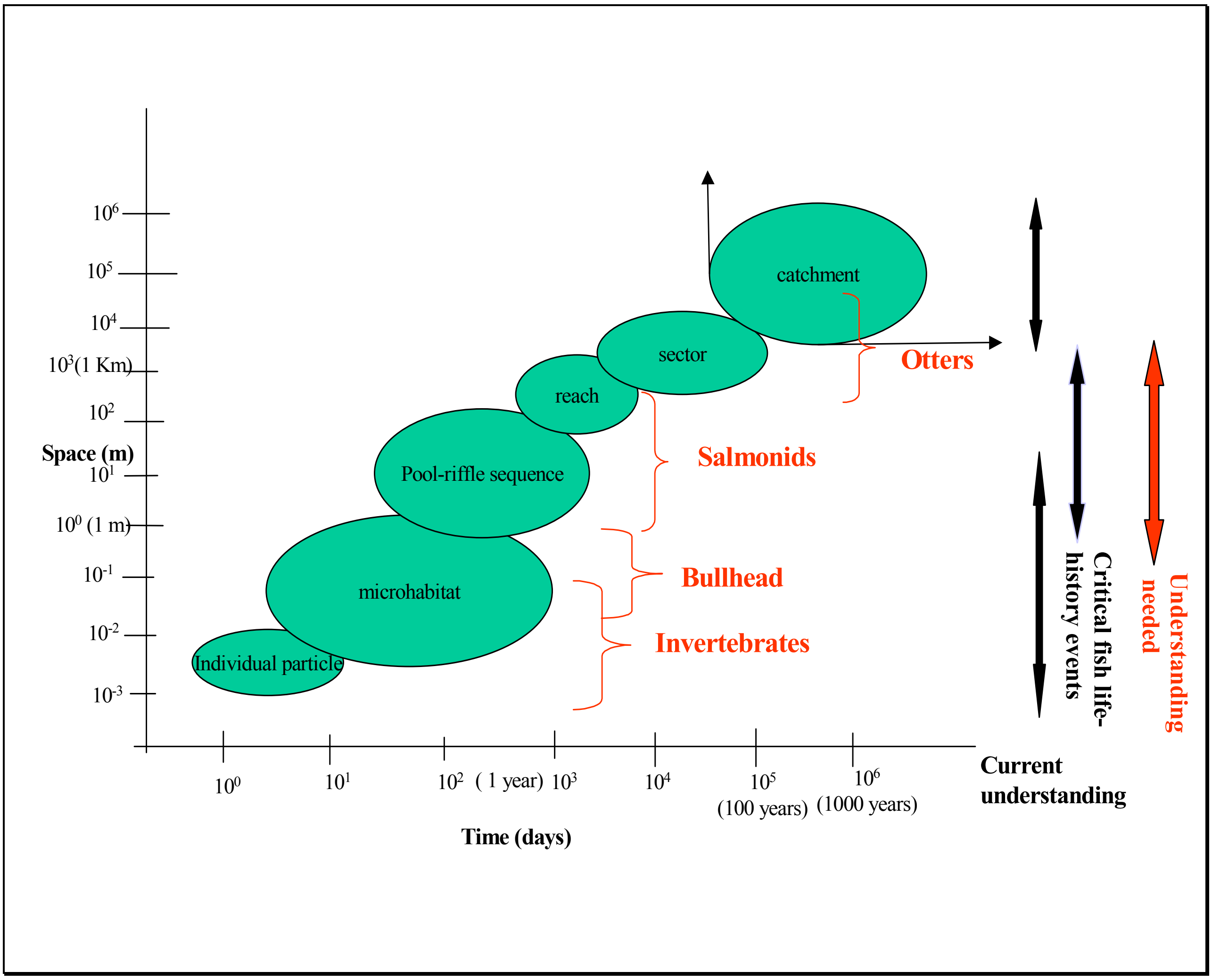


Figure 2.3 Temporal and spatial scales of riverine processes and ecology (drawn from Stanley and Boulton, 2000, and Fausch *et al.*, 2002).

Figure 2.3 shows that one of the main difficulties when studying riverine ecosystems is the large number of scales at which processes take place both in space and time. As a result, study of the processes occurring at a particular scale has to be put into the context of this interconnectivity. Understanding the processes occurring at the intermediate scale (located from the pool-riffle sequence to the sector scale in Figure 2.3) is an area that has received increasing attention over the past decade. However linkages between fish species and these processes have seldom been investigated.

At the catchment scale (scale of 100 km and more), physical processes such as the shaping of river valleys and the evolution of landscape geomorphology take place over several decades, hundreds or even thousands of years. At the sector scale (river scale around 10km) changes in sediment loads such as the formation and erosion of bed and banks takes place over several decades. At the reach scale, physical processes are more easily observed from a human perspective. At the other end of this scale, if one considers a single particle, whether it be plankton or a sand particle, its pattern of evolution takes place at a very small spatial scale around a millimetre and over one up to a few days. Moreover, at the catchment scale, geologic and climatic factors among others determine the catchment hydrology (variability in discharge and flow regime over inter-annual time scales), which in turn influences the hydraulics at a sector/reach scale, i.e. depth and velocity parameters and their variations. On top of this space/ time matrix, one has to consider riverine organisms interacting with these different ecosystems. Invertebrates, given their limited mobility, will be better studied at the microhabitat scale (around an area of 1 m^2) and a year is appropriate to study their life cycle. Higher in the food web, organisms such as fish are more mobile and have a longer life cycle. As a result, their study requires a larger area, such as a riffle-pool sequence up to a sector over several years to study the whole life cycle of fish species, from hatching to spawning and the various growth stages as well as their migratory behaviour when relevant.

Therefore, management frameworks must incorporate a consideration of spatial and temporal scale (Imhof *et al.*, 1996). River ecosystems can be examined across a hierarchy of spatial scales, from the catchment (macro), reach, Channel Geomorphic Units or CGUs (meso) or at individual points (micro) (Frissell *et al.*, 1986). The macroscale takes into consideration the processes taking place within the catchment such as for example, the amount of precipitation received, the amount of runoff or in which rivers salmonid populations are found. It thus gives a broad view of a situation, but this scale cannot explain processes taking place in a particular location within a river. On the contrary, the microscale focuses on very local processes such as invertebrate assemblages at a local patch and the local depth and velocity parameters. It thus gives a very detailed description of conditions and processes at a particular point but extrapolation of these observations at a larger scale can be problematic.

Fausch *et al.* (2002) have suggested that when studying fish habitat, macrohabitat scale (maps or satellite pictures) and microhabitat scale (point characteristics) do not reveal the features most important to fish. These features, such as barriers to fish movement or spawning habitat are determined by channel morphology and habitat complexity. They are best viewed at an intermediate or meso-scale, which takes into account the spatial arrangement of mesohabitats or CGUs such as pools and riffles over spatial scale of 1-100 m^2. Using this intermediate scale, a stream can be viewed as a mosaic of mesohabitats where interactions between fish and their physical habitat take place. However, Pedersen (2003) made the criticism that most studies of CGUs and habitat utilization by instream biota had so far often been carried out independently or separately. Habitat connectivity needs to be understood as well as how it is linked spatially and temporally to fish ecology and behaviour, yet cross-scale studies that integrate both geomorphological processes and fish ecology have so far been scarce. For the past two decades, focus on the mesoscale to investigate river hydroecology has increased and studies have sought to establish the factors governing mesohabitat composition and distribution in rivers. However, at the basin scale, prediction of such composition is difficult as it is influenced by climatic and regional factors as well as river types (Cohen *et al.*, 1998).

2.3 FLOW REGIME: A KEY DRIVER TO CATCHMENT HYDROLOGY AND HYDROECOLOGY

Flow regime was defined by Musy and Higgy (2003) as the summation of all the hydrologic characteristics of a river as well as its temporal evolution, measured in terms of discharge variability. As shown by Figure 2.1, natural flow regime determines as well as depends on a wide range of physical parameters both at the catchment and reach scale. The natural flow regime results from the interactions of climate (precipitation and temperature) with the catchment geology and vegetation. Human impact can alter significantly the pattern of discharges through direct manipulation (e.g. reservoir releases, abstraction, increase) and indirect effects (e.g. urbanisation, deforestation, land drainage) (Cowx and Welcomme, 1998; Bunn and Arthington, 2002). As a result each catchment presents its own, particular flow regime, with local variations. Flow regime has a key role in preserving the ecological integrity of rivers and streams, as shown by Figure 2.4, drawn after Lytle and Poff (2004).

Figure 2. 4 Flow regime characteristics and their influence on ecological integrity (from Lytle and Poff, 2004)

Figure 2.4 shows that flow regime influences all the components of riverine ecosystems and that any modification to a river's flow regime will impact on every component of the ecosystem. It is thus necessary to understand the mechanisms linking flow regime and ecosystem processes and interactions in order to protect and manage rivers in a sustainable manner.

Numerous hydrological indices can be used to characterize a natural river's flow regime. In their review of the ecological methods used to determine environmental flows, Bragg *et al.* (2005) defined three main classes of methods to describe flow regime:

- River flow statistics: for example Q_{50} (median flow), Q_{95} (index of low flow rate); Jowett and Duncan also mentioned mean annual flow, mean annual low flow and maximum flow (Jowett and Duncan, 1990) that are easily calculated for gauged rivers.
- Methods that estimate hydrological variables from ungauged sites e.g. flow duration curve.
- Indicators of change in hydrological regimes as a result of climate change.

River flow statistics are the most commonly used attribute to describe a river's flow response. However these statistics are so numerous that comparison of different stream responses to discharge can be difficult. The present study focused on two types of natural flow regimes: surface runoff influenced and groundwater influenced.

Surface runoff influenced streams, e.g. the upland rivers in the U.K., receive most of their water directly from rainfall or snowmelt and hence result in very quick and dramatic responses to precipitation or lack of precipitation, translated by rapid increases/decreases in discharge. Prolonged periods of precipitations often result in rapid flooding, as was the case in July 2007 for the River Severn catchment. On the contrary, dry periods result in a rapid and pronounced drop of the amount of discharge in the stream. Rivers characterized by this type of flow regime are described as 'flashy'. The degree of flashiness describes the influence of groundwater on the stream and/or as the response of the stream to runoff and precipitation. The Base Flow Index (BFI, Mash and Lees, 2003) is a good indicator of the inverse of flashiness of a stream as it represents the percentage of groundwater input in the stream: the higher the BFI the greater the influence of groundwater on the stream. Jowett and Duncan added another index, which is the overall flow variability and is described as Q_{10}/Q_{95} (Jowett and Duncan, 1990).

Groundwater influenced streams, e.g. the Tern Catchment which has also been studied during this project (see chapter 4), displays a regulated discharge pattern as most of the water it receives comes from springs and interactions with the underlying aquifer (NERC LOCAR research programme, 2003). The result is a slower response to precipitation depending on the retention capacity of the aquifer as well as the level of the water table. Consequently, periods of floods and droughts last much longer than in surface runoff influenced catchments (Ward and Robinson, 2000).

The following section outlines the factors that flow regime influences or interacts with over a variety of scales and which are of fundamental importance when considering riverine habitat and its characteristics. Sections 2.3.1 to 2.3.3 focus on influences at the catchment scale while sections 2.3.4 to 2.3.6 focus on the sector scale.

2.3.1 Influence of flow regime on droughts and floods events

The flow regime results from the interaction between climatic, geologic and hydrologic factors, hence it varies geographically. As Poff (1996) showed in his work on the hydrology of unregulated streams in the United States, streams with similar hydrological characteristics (e.g. rainfall and snowmelt influenced, stable groundwater, perennial run-off) tend to be found in a same geographic region or in regions of similar topography, geology and climate. Stromberg *et al.* (2007) added that flow regime and, as a result, flood hydrographs are the mirror of climatic conditions. Their work in rivers of the arid south-western United States showed that flood patterns were highly variable and that they reflected the climatic conditions of these areas (Stromberg *et al.*, 2007).

In their study on the geomorphology of spring-fed rivers, Whiting and Stamm (1995) determined that the principal characteristics of this type of river as opposed to those influenced by direct runoff from rainfall and/or snowmelt is the narrow range of discharges they experience. They concluded that one of the main factors influenced by groundwater-fed flow regime is the flood regime: high flows are less frequent than in surface runoff dominated rivers and the flow hydrographs are much more stable. Indeed the time of response from precipitation tends to be greater in groundwater-fed streams, as already established in section 2.3. This can lead to extended low flow/ high flow periods as opposed to runoff influenced rivers that may respond with a peak of discharge within hours after a flow event. Samaniego and Bardossy (2007) examined the relationship between macroclimatic circulation patterns and flood and drought characteristics. They found that flood and drought patterns were not obviously related to climatic circulation conditions but also were driven by the local morphology of the water basin, its land cover as well as the amount of runoff experienced, the latter being the main characteristic of a river flow regime (Samaniego and Bardossy, 2007).

2.3.2 Flow regime and sediment load

Impacts of flow regime on sediment transport have been highlighted by studies focusing on regulated rivers and the consequences of impoundment and dam construction (Osmundson *et al.*, 2002; Ortlepp and Mürle, 2003; Petts and Gurnell, 2005; Le *et al.*, 2007). Through the transport and accumulation of sediments, the natural flow regime influences river channel morphology. Hence river habitat diversity is a function of the frequency of high flows that erode potential accumulations of fine sediments from some areas while depositing new substrata in other parts of the river. Yarnell *et al.* (2006) emphasize the role of the interactions between discharge fluctuations and sediment supply and transport in creating instream habitat heterogeneity: they conclude that instream physical habitat complexity is enhanced by moderate sediment supply and a varied flow regime at the catchment scale together with interactions between local hydraulic processes and instream features such as woody debris which favour differential erosion and deposition processes. Surface runoff also facilitates the input of sediment along river systems through sediment pulses as a result of interactions with riparian zones. Reservoirs, through their impact on frequency and magnitude of discharge, reduce the flood regime and hence sediment supply and sediment transport to downstream parts of rivers. However, Poff *et al.* (2006) concluded in their work on flow regime and the geomorphic context, that the type of flow regime alone does not reflect the importance of bed load transport in a river system. Bed load transport also depends on the channel geomorphology and similar types of flow regimes present different types of sediment transport regimes.

2.3.3 Impacts on water temperature regime (catchment scale)

Temperature patterns within a stream are influenced by a variety of factors, including location, climate and elevation, orientation/aspect (Allan, 1995). These external factors determine the net heat energy to enter a river system in the same way as they influence the volume of water entering a river. Unlike lakes, river waters display far more mixing and vertical thermal stratification hardly occur in streams. River temperatures, as well as being influenced by seasonal and daily time scales, display a different evolution according to flow regime. How temperature values are then distributed within a stream is function of the stream morphology, the presence and importance of the hyporheic zone and the importance of riparian vegetation (Poole and Berman, 2001). In groundwater-influenced rivers, interactions with the groundwater table mean that temperatures fluctuate less. However differences in temperatures can be observed in different parts of the stream according to the location of the groundwater input (e.g. downstream end of riffles) (Bilby, 1984; Maddock *et al.*, 1995). This results in the stream temperatures being slightly cooler in summer and higher in winter, therefore avoiding drastic seasonal changes in temperatures for stream biota. As a result stream temperature regime is both dependent on the interactions between external drivers and internal, instream components.

2.3.4 Consequences for water quality (sector/reach scale)

River water naturally contains a wide variety of chemical compounds as well as organic matter and nutrients. Rainfall constitutes a major source of input in this respect and since rainfall and runoff vary geographically, water quality is influenced likewise, depending on the climatic conditions and the proximity to the sea among other factors (Allan, 1995). Under natural conditions, depending on the geology of the catchment and the amount of runoff this area experiences, the chemical composition of river water will vary spatially and temporally, which can be quantified by the use of isotopes for example so as to determine the source of water input (Musy and Higgy, 2003). Variations in water quality have implications for instream biota. Particularly, human activities can seriously affect water quality, for example as a result of wastewater discharge, mine washing, runoff of pesticides, etc. Two studies by Beaumont *et al.* (1995; 2003) described the effects of low pH and high concentrations of copper and other heavy metals such as aluminium and zinc on brown trout physiology and swimming performance. They concluded that (i) swimming performance was impaired by four days of exposure to high concentrations of copper at low pH and (ii) the latter two factors influence plasma ammonia concentration, which at high values affect several key enzymes of energy metabolism, hence altering muscle activity and alternatively the nervous system. Hence variability in water quality can have severe effects on instream biota, maybe they be fish or organisms in lower part of the riverine food web.

2.3.5. Influence of vegetation on flow and local hydraulics

Both instream and riparian vegetation are part of the primary-producer community, and are subject to discharge fluctuations induced by natural flow regime, whether surface runoff influenced or groundwater fed (Stromberg *et al.*, 2007). While instream vegetation is directly influenced by discharge in the river channel, the vegetation present in floodplains depends on levels of groundwater tables as well as disturbances such as floods. Natural flow variability determines plant species richness and diversity, with floods acting as disturbances that reset plant community structure. In turn, riparian vegetation influences soil water retention hence the amount of runoff that goes into a river. Indeed, timber harvesting and intensive grazing in upper reaches of river systems have been found to considerably decrease the level of infiltration and increase the amount of runoff and sediment entering rivers (Miller *et al.*, 2002). The review on riparian bank seeds structures and processes by Goodson *et al.* (2001) emphasized the role of flow regime on riparian vegetation. Short-term fluctuations such as floods can be damaging to vegetation, particularly in their early stage of development either by direct physical damage to the plant or by burying seeds under sediments and thus preventing germination. Longer-term variations (over several weeks) result in gradual changes in riparian vegetation cover, with the final result often being a very diverse vegetation community along the river banks (Goodson *et al.*, 2001).

2.3.6. Flow regime and mesohabitat composition

The physical habitat composition of a stream and the corresponding hydraulic parameters are considered as the basic elements to river health assessment (Maddock, 1999). Flow regime influences the mesohabitat composition of rivers (Bunn and Arthington, 2002) by its interactions with river geomorphology. The latter is itself driven by the interactions between the sediment supply to the stream and its sediment transport capacity. Yarnell *et al.* (2006) hypothesise that greater physical habitat heterogeneity, known to enhance biotic species richness, is best achieved in streams characterized by a moderate relative sediment supply (defined as the sediment supply over the transport capacity ratio) either by local erosion or deposition depending on abundance of less mobile instream structures such as large woody debris and boulders. Their study emphasized the dynamic nature of the interactions between the variability of instream hydraulic variables, sediment supply, sediment size and texture, and transport capacity in defining instream landscapes and their diversity.

Flow variability from a natural flow regime greatly affects mesohabitat composition and diversity. Indeed, Maddock *et al.* (2005) comparison of regulated and unregulated reaches of the Soca River in Slovenia showed that the unregulated reaches showed greater diversity of mesohabitats (or CGUs) and that individual CGUs were longer than in regulated reaches. As a result, regulation presented rivers with a lack of connectivity between physical habitats. Similarly, Jowett and Duncan (1990) show that stream morphology is also influenced by discharge variability in New Zealand, where rivers presenting less flow variability are more longitudinally uniform than rivers with high flow variability. As a result physical habitat variability is thus expected to be greater under surface runoff influenced flow conditions. Groundwater-fed rivers, which are naturally regulated by their interactions with aquifers, appear to present less variability of mesohabitat composition with discharge.

Kemp *et al.* (1999) further investigated the factors driving mesohabitat composition and diversity in natural and semi-natural streams in the East midlands of the UK and concluded that different drivers exist at different scales: flow regime through its interactions with geomorphology influences mesohabitat diversity at the reach scale; variability in other drivers such as instream hydraulics and particularly depth, determine habitat diversity with low variability in depth along the reach resulting in low habitat diversity. This latter conclusion emphasizes the cross-scales interactions that result in particular mesohabitat assemblages in rivers.

2.4 THE MESOSCALE APPROACH: DESCRIPTION AND RELEVANCE TO THE PRESENT STUDY

Most studies investigating fish habitat use have done so at the microscale, i.e. with reference to the habitat characteristics at the individual fish location such as velocity at a fish focal point for example. The advantage of the mesoscale (or intermediate) approach is that it allows to study how habitat connectivity (or lack of it) influences fish habitat use and how a particular fish population responds in terms of habitat use to habitat composition. Fausch *et al.* (2002) emphasized in particular that features important to fish ecology such as barriers to fish movements can only be seen and taken into consideration at an intermediate scale.

At this particular scale a habitat is a portion of river generally between 1 and 100 metres long, defined by particular values of depth and velocity as well as surface flow type, which constitutes a habitat for riverine organisms such as macroinvertebrates and fish.
Many terms exist to describe habitats at the mesoscale, depending on the research context of the study (hydrology, geomorphology, ecology). Table 2.1 presents a summary of the terms used to describe habitats at the mesoscale.

All terms except "functional habitats" are based on the physical characteristics of the habitat and the interactions between these characteristics and flow. Thomson *et al.* (2001) criticized this approach because the definition according to surface flow types prevents other important habitat parameters such as variations in substrate, macrophytes and organic matter from being readily taken into account. The variety of definitions presented in Table 2.1 shows the two different approaches taken in aquatic sciences when describing physical habitat: the "top down "approach which means the use of habitat units is implicit in their physical characteristics; and the "bottom up" approach in which the habitat characteristics and conditions are derived from the biological communities inhabiting the stream (Newson *et al.*, 1998). Hence the concept of "functional habitat" is characteristic of the "bottom up" approach whereas all the other terms described in Table 2.1 fit the "top down" approach. For the purposes of this study, the concept of functional habitat could not be considered as it is based on macroinvertebrate assemblages. All the other terms used to describe habitats at the mesoscale are relevant to the present work.

Table 2.1. Summary of the terms used to describe habitats at the mesoscale.

Term	Definition	Author
Physical Biotope	Habitat described based upon the physical characteristics, particularly the associated flow type	Padmore, 1997a
Functional Habitat	Habitat which holds a distinct macroinvertebrate assemblage among all the habitats recognizable from the river bank. The definition is based on substrate type and vegetation components	Harper *et al.*, 1995; Newson *et al*, 1998 ; Kemp *et al.*, 1999.
Physical habitat	Habitat determined by the interaction between channel geomorphological features and flow regime (variation in discharge levels). Physical habitats are therefore dynamic in space and time	Maddock, 1999.
Mesohabitat	1. Habitat described on the basis of its substratum type;	Armitage and Pardo, 1995
	2.“A single habitat type (pool, riffle, run) one to ten channel widths in length”	Stewart *et al.*, 2005
	3. medium-scale habitat arising through the interactions of hydrological and geomorphological forces	Tickner *et al.*, 2000
Channel Geomorphic Unit (CGU)	Instream landform that reflects a distinct form-processes association	Thomson *et al.*, 2001
Hydraulic habitat	“The state of flow and local flow configuration in which stream biota live”	Newbury and Gaboury, 1993.

Surface flow type is a major descriptor of physical habitats and it is the interaction between flow and particular instream physical characteristics that will create particular habitat types. Hence discharge and its variability will influence habitat composition and occurrence in streams. How particular habitats will occur in streams at a given discharge depends on their geomorphological nature and the sediment processes governing these habitats, i.e. erosion versus deposition (Newson *et al.*, 1998, Fig. 6 p.441). Padmore (1998) and Newson *et al.* (1998) also stated that mesohabitats or morphological units result from the transport of water and sediments from mountains to coast, and as such are either depositional or erosional features that act as local controls for velocity and sediment transport. Particular values of depth and velocity within a stream and hence within morphological units are strongly stage dependent (Clifford *et al.*, 2006). Flow regulation impacts on the CGU composition in rivers with more fragmentation of mesohabitat and shorter CGUs (Maddock *et al.*, 2005) thus resulting in a lack of connectivity that could affect fish behaviour. Moreover the type of mesohabitats present in regulated rivers varies from that in natural rivers. For example, Newson *et al.* (1998) found that a high proportion of glides in a channel is characteristic of channels subject to regulation (natural or not). Discharge regulation also results in a decrease in CGU diversity as a result of the reduced hydrological variability and sediment transport frequency.

As more studies use the mesoscale approach, focus has increased on the methodologies used to identify mesohabitats and on the mapping techniques that aim to describe the diversity of instream mesohabitats. Indeed, when identifying mesohabitats, three major difficulties arise:

- Experience is required in order to be consistent and confident in the identification of mesohabitats during a river mapping survey.
- Operator variability: each surveyor may have identify a mesohabitat differently (shallow run versus riffle for example)
- The same mesohabitat type can be identified differently according to the survey method used and the country/ continent of origin. Similar terms are used by different methods to describe different features.
-

Mesohabitats are most often associated with particular depth-velocity conditions (Kemp *et al.*, 1999). With respect to the latter, Jowett (1993) developed an objective method to identify pools, riffles, etc using physical parameters such as depth and velocity to calculate the Froude Number. However, different combinations of depth and velocity can give the same value for the Froude number because of overlapping of depth and velocity values between mesohabitats, which makes mesohabitat identification more complex. Nonetheless, it is commonly agreed that distinct combinations of depth and velocity can be used to model the evolution of mesohabitat composition in rivers (Schweizer *et al.*, 2007), rather than the use of the two parameters independently.

In the U.K. the River Habitat Survey provides a description of each type of mesohabitat in order to easily identify them in the field (Newson *et al.*, 1998). Several mesohabitat mapping methods exist to carry out river mapping surveys (Harby *et al.*, 2004).
In Europe:

- MesoCASiMiR (Eisner *et al.*, 2005 ; Mouton *et al.*, 2005 ; Eisner, 2007)

- The Norwegian Mesohabitat Classification Method (Borsanyi *et al.*, 2005; Borsanyi *et al.*, 2006): mesohabitats are identified using codes (thus avoiding confusion with names) and lateral diversity of mesohabitat across channel width is also recorded.
- Rapid habitat mapping method (Maddock *et al.*, 2005): within each mesohabitat one measurement of depth and velocity is taken to characterize them.

In the U.S.:

- MesoHABSIM (North East Instream Habitat Programme, 2003; Parasiewicz, 2007): mesohabitats are identified along and across the reach. Seven points of measurements of depth and velocity are determined randomly to characterize the hydraulic properties of each CGU.

These various methods are based on visual assessment of CGUs in the field. However, differences between them include the number of transects used for the mapping surveys, the number of depth and velocity measurements taken on a transect or in a mesohabitat, the way mesohabitats are referred to (name or code), whether lateral mesohabitat diversity is taken into account or not and in terms of time required for the field surveys. For this study, a MesoHABSIM was chosen with respect to the sampling methodology and the criteria used to identify mesohabitats but was modified in order to make it less time consuming and more easily replicable across the survey season (see Chapter 3).

2.5 FISH BEHAVIOUR AT THE SITE SCALE AND MULTIPLE SCALE INFLUENCES

Unlike other aquatic organisms such as plankton and macro-invertebrates, fish are active swimmers, which should make them less vulnerable to changes in environmental conditions. Moreover their behaviour and distribution is less easily predictable than other organisms within the aquatic community (Lucas *et al.*, 1998). Shirvell and Dungey (1983) already stated that animal distribution, in the absence of man-made physical barriers such as dams, hence in natural, non-regulated rivers, was a function of environmental suitability and social interactions. These factors influence the environmental conditions affecting fish habitats. Hydrological factors affect the structure of fish assemblages, i.e. structure of fish assemblages will be different in a highly variable environment than in a stable environment (Poff and Allan, 1995). Fish react to climatic and morphological features (Alves *et al.*, 2005). Running waters, as opposed to lakes, experience high water level fluctuations, a weak thermal stratification and a longitudinal physicochemical gradient (Irz *et al.*, 2005). Thus fish will respond to these variations by moving longitudinally and laterally in a stream to find the most suitable habitats. However, not one factor alone affects fish habitat use but a combination of factors that interact together, as it was noted for Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*), whose movements are affected by habitat availability (suitable depth and velocity), discharge velocity and water temperature (Cunjak, 1996; Heggenes *et al.*, 1996). Fish movements occur over various temporal and spatial scales depending on the species, population and life stage as well the migratory status of the species considered. For example, Clapp *et al.* (1990) recorded important variations in distances moved within large brown trout (*Salmo trutta*) populations. Factors influencing those movements are numerous and usually interconnected: fish movements are not influenced by one factor at a time but by a combination of factors (Shirvell and Dungey, 1983) *e.g.* seasonal movements are influenced by discharge and temperature, because these factors vary over time. Indeed, Ostrand and Wilde (2001) observed that the abundance and composition of fish assemblages in pools within a prairie stream underwent systematic changes that coincided with changes in environmental conditions, *i.e.* drought. The following sections focus on the main parameters affecting fish behaviour in rivers.

2.5.1. Habitat parameters relevant to the characterization of fish habitat

Accurate characterization of fish habitat involves measurement of both physical and non-physical parameters known to influence habitat variability and availability for living organisms. The influence these parameters have on fish behaviour are further discussed in Section 2.5. Table 2.2 summarizes the various parameters that can be used to describe riverine ecosystems and fish habitat according to scale, from the catchment scale down to the microhabitat scale. Water quality parameters were included as they are relevant to fish studies since they can constitute limiting factors to the presence of certain sensitive fish species, particularly as a result of growing anthropogenic pressure on aquatic ecosystems.

Table 2.2. Riverine habitat physico-chemical descriptors according to scale and their relevance to fish study

Relevant scale	Habitat parameter	Relevance to fish studies	Example Reference
River scale	Historical flow data	Allows the determination of the level of flow variability experienced in the river. As a result, the variability in mesohabitat composition, which affects habitat use by fish in the stream, can be assessed.	Harby *et al.*, 2004; Stewart *et al.*, 2005.
	Slope	Slope influences mesohabitat composition as well as the dynamics of large woody debris. In high gradient streams, large woody debris can induce the formation of pools, which can provide shelter for fish from harsh flow conditions. Slope also influences the type of substrate found on the stream bed, therefore determining the kind of habitat available to fish. In lower Michigan streams for example, stream slope was found to be negatively correlated to species richness and fish average weight.	Beechie and Sibley, 1997; Infante *et al.*, 2006.
	Riparian vegetation	The riparian zone occurs at the interface between terrestrial and aquatic ecosystems and it may, therefore, regulate the transfer of energy and material between these systems, as well as regulating the transmission of solar energy into the aquatic ecosystem. It thus has an impact of the amount of organic matter present in the stream, i.e. food resources, as well as an influence on the amount of overhanging cover present on the reach.	Sagar and Glova, 1995; Pusey and Arthington, 2003.
	pH	Changes in pH can occur a result of natural causes (photosynthesis, organic matter decay, mineral dissolving) or anthropogenic causes such as acid rain and industrial wastes. The pH is an important criterion for water quality because it affects the viability of aquatic life and fish swimming performance, e.g. pH values inferior to 5 appear to be critical for brown trout.	Beaumont *et al.*, 1995; Beaumont *et al.*, 2003; Vehanen *et al.*, 2004.
	Temperature	Temperature is influenced by flow regime as well as seasons. Groundwater input in areas of a stream can explain particular grouping of fish. Temperature affects fish physiology and their swimming performance and behaviour. As a result it can explain changes in habitat use.	Taylor *et al.*, 1996; Lobon-Cervia and Rincon, 1998; Heggenes and Dokk, 2001; Ostrand and Wilde, 2001.
	Dissolved Oxygen	Low D.O. levels are negatively correlated to the survival of salmonid eggs. Changes in D.O. levels can therefore explain a lack of fish recruitment and a drop in fish numbers in a particular part of the stream.	Ostrand and Wilde, 2001; Malcolm *et al.*, 2003.
	Total suspended solids	High concentrations of suspended solids in the water can prevent spawning success for salmonids as the accumulation of fine materials on spawning gravel can smother the eggs.	Norris and Thoms, 1999.

	Conductivity	Conductivity levels in streams influence fish assemblages.	Weigel *et al.*, 2006.
Mesohabitat scale (mesoscale)	Depth	A key descriptor of mesohabitats, it also used to predict fish occurrence as it can be a limiting factor for certain fish species and life stages, e.g. adult salmonids.	Dunbar and Ibbotson, 2001; Pusey *et al.*, 1993; Legalle *et al.*, 2004; Schweitzer *et al.*, 2007.
	Velocity	One of the key parameters that influence fish habitat use through the amount of energy they have to use in order to stay at a particular point. Early fish life stages may not be strong enough swimmers to stand high velocities. It influences densities of fish, e.g. brook trout (*Salvelinus fontinalis*) in Eastern Canada. Velocity is a key descriptor of mesohabitats.	Baran *et al.*, 1995; Dunbar *et al.*, 2001; Garner, 1997; Pedersen, 2003; Deschênes and Rodriguez, 2007.
	Surface flow type	This represents a combination of hydraulic characteristics, e.g. water depth, flow velocity and turbulence. It can constitute therefore a prediction tool to the kind of conditions experienced by fish.	Dyer and Thoms, 2006.
	Channel width	Coefficients of variation and means of river width are used in the determination of the gross river hydraulic conditions. These have an impact on fish habitat use.	Legalle *et al.*, 2004; Stewardson, 2005.
	Bank types	Juvenile salmonids are found in large numbers in the edge areas of streams, i.e. close to the banks, because of the cover and low velocities associated with them.	Clark, 1992; Mulvihill *et al.*, 2003; Beechie *et al.*, 2005.
Meso/microhabitat scale	Substrate composition	Determinant for the completion of parts of the life cycle of certain fish, e.g. salmonids spawn in gravel, which also shelters the development of juveniles.	Power, 1992; Cowx and Welcomme, 1998; Hoover *et al.*, 2006.
Microhabitat scale	Substrate embeddedness	Substrate embeddedness greatly influences fish spawning success. The more embedded a substrate is the less space there is between substrate particles for oxygen, nutrients and water to circulate.	Eastman *et al.*, 2007.
	Shear stress	This parameter cannot be measured directly in the stream as it is a function of water velocity and friction on surfaces such as substrate or wood. However, flow and physical habitat conditions provide estimates of the friction conditions experienced by fish in a particular habitat.	Harby *et al.*, 2004.

Table 2.2 emphasizes that, when characterizing fish habitat, consideration of a wide range of spatial scales is necessary. The mesohabitat (riffle, pool, runs, etc.) scale appears to be the most appropriate to accurately study fish ecology, movements and behaviour (Fausch *et al.*, 2002). The microhabitat scale is useful when studying particular life-stages or behaviour of fish, e.g. spawning. Nevertheless spatial connectivity of habitats has to be considered at the sector/reach scale as fish are mobile animals and use different habitats at different life-stages, different times of day and year and according to their behaviour: spawning, feeding, resting, hiding. These issues are discussed in more detail in the following sections.

2.5.2 Influence of flow (catchment scale)

Discharge is a very important factor that influences fish habitat selection and behaviour (Clapp *et al.*, 1990; Heggenes & Dokk, 2001). Discharge variability and physical habitat parameters are not entirely independent, and flow regime may influence fish habitat use. However, the impact of flow variability on fish habitat use is poorly understood. Extreme events can have marked effects. Young Atlantic salmon (*Salmo salar*) show high sensitivity concerning environmental changes, more particularly flow variability (Kitzler *et al.*, 2005): as a result of increasing discharge, depth and velocity increase, making some areas unsuitable for some fish, because they are too fast flowing or too deep. Jowett and Richardson (1989) demonstrated the impact of a severe flood on trout numbers in seven New Zealand Rivers and observed a sharp decrease in brown trout numbers, particularly those of small size (10-20cm). Discharge has an important effect on stream trout dynamics across biogeographic regions and plays an essential part in fish recruitment (Lobon-Cervia, 2004). However the time scale on which discharge influences fish behaviour is not established precisely as it depends on the river system considered and its flow regime. For example, in the Yorkshire Ouse system, Lucas (2000) found no significant correlation between mean daily discharge and the number of fish to enter a fish pass. This tends to also suggest that discharge alone does not control fish behaviour but most likely interactions between discharge and other environmental parameters.

Flow regime, through its influence on flow variability, has an impact on mesohabitat composition, which implies that fish have to adapt to these changes by moving between more suitable areas. Vegar-Arnekelleiv and Kraabøl (1996) noted that several of the fast-growing brown trout populations in Scandinavia have been negatively affected by river regulation and channelization. This has already been described by Bain *et al.* (1988) who showed that flow regulation induced highly unstable habitats and resulted in the success of some species of fish against others depending on the fish patterns of habitat use. Discharge variability plays a vital role in the health of fish populations. Increasing discharges carry away sediments, nutrients and prey items that are confined upstream at lower discharges, thus favouring development and growth of early fish life-stages.

Availability of habitat types may change considerably depending on discharge and will influence habitat use. With increasing mean flow, areas containing deep waters increased and areas providing low velocities decreased (Heggenes and Dokk, 2001). Varying water discharges not only induce temporal changes in habitat availability, but also affect fish behaviour and the selection of micro-positions (Heggenes *et al.*, 1996). Most studies on the effects of varying water discharges on fish habitat use have been carried out using modelling. Few systematic studies of variability in habitat selection with varying environmental conditions exist and some focus only on summer base flow, which means that our understanding of habitat use between seasons and discharge is incomplete (Heggenes & Dokk, 2001). Changes to river flow characteristics throughout the year, between years, or as a result of regulation alter patterns of fish behaviour and habitat use.

2.5.2.1 Temperature and the influence of seasonality (catchment scale)

Water temperature varies seasonally and is a function of the climate and the biogeographical region considered, as well as the flow regime of the river considered and greatly affects fish behaviour. Heggenes and Dokk (2001) concluded that young salmon and trout changed their habitat depending on water temperature. They observed that when temperature dropped below 8°C, fish would switch to winter behaviour and avoided deeper areas. In the case of salmonids, the choice of deeper areas in winter is explained by the fact that a lesser proportion of the water column will be in contact with external winter temperatures, thus providing fish with appropriate shelter with "warmer" temperatures. Both Atlantic salmon and brown trout display an autumnal habitat shift when water temperature drops below the range 7-13°C (Heggenes *et al.*, 1993). They increase their use of stream areas providing lower water velocities in response to low water temperature. Effects of water temperature on fish behaviour are more likely to be observed in river systems located in regions with sharp diel and seasonal temperature contrasts, e.g. Scandinavia and North America. In temperate regions, *e.g.* Britain, temperature contrasts are less likely to have an influence on fish behaviour, as it was observed in the Yorkshire Ouse system, where the daily numbers of fish going through a fish pass were not significantly correlated to mean daily temperature (Lucas, 2000).

Seasons influence variations in physical parameters through variations in atmospheric and climatic conditions. The increase or decrease in rainfall intensity and frequency affects flow regime and, as a result, instream parameters such as depth and velocity. Increase in day length and temperature occurring over spring and summer will lead to vegetation growth and thus increased cover, as well as a rise in water temperature. Day length and light intensity vary as well between seasons. These variations in habitat parameters between seasons affect fish habitat use and behaviour. For example, large brown trout in a Michigan stream were recorded displaying separate summer and winter range as a result of variations in water temperature (Clapp *et al.*, 1990).

Atlantic salmon and brown trout living in sympatry both change their use of habitat types, depending on season and light (Heggenes & Dokk, 2001), with more habitat segregation between the two species in winter than in summer. For example, at high temperature in summer, the main activity was feeding, whereas at low temperature, fish would hold position on or above substrate. During winter, at low temperatures, a diurnal pattern behaviour was observed with some sheltering during the day and some feeding at night. Brown trout have different behavioural strategies between summer and winter as it was observed by Cunjack (1996) when he studied winter habitat use by salmonids in a temperate-boreal river. In the summer, trout are active during day and night while, in winter, they are active only at night (they must minimize energy expenditure because of the low temperatures). The optimal summer foraging strategy for brown trout is a "sit-and-wait" search strategy. The wintertime strategy consists of a cost –minimizing "shelter-and-move" strategy i.e. the energy allocation is governed by the need to minimise the cost of survival (Heggenes *et al.*, 1993). Lower temperatures in autumn and winter lead to preferences for overhead cover (e.g. surface turbulence, vegetation, substrate).

2.5.2.2 Cover (reach scale)

Numerous studies have identified that fish use different features as cover: vegetation (macrophytes), substrate, undercut banks, woody debris, deep water areas such as pools, tree roots and shade. Pusey *et al.* (1993) have found a significant relationship between species richness and mean cover complexity in streams. Cover provides refuge for fish from direct light, high velocities and from predators. Indeed, Bullhead (*Cottus gobio*) displays a cryptic behaviour by day and is often found underneath stones and may therefore be difficult to detect (Cowx and Harvey, 2003). In the case of bullhead, the use of cover to hide is justified by the fact that bullhead is a small benthic fish, without any swimming bladder, which makes any escape from predators very challenging. Cover allows fish to hide from predators, mostly during the day, or generally during periods of higher light intensity. Langford and Hawkins (1997) reported on the important role large woody debris play in streams as they increase the available refuges for adult brown trout, bullhead and minnow. In the absence of cover or shelter, fish tend to switch to a gregarious behaviour. This is the case for brown trout that usually display a strong preference for cover, and seek shelter in the substrate to move to deeper and slow flowing areas (e.g. pools) (Heggenes and Dokk, 2001).

2.5.2.3 Variations in light intensity (reach scale)

Diel patterns in distribution, habitat use and feeding are characteristic of fish behaviour in freshwaters (Copp, 2004). In European waters, non-salmonid fish undertake diel changes in distribution, abundance and behaviour. In the River Lee (Hertfordshire), Copp (2004) observed the highest densities of fish in mid-channel habitats at dusk. Lucas (2000) recorded a significant positive relationship between day length and the number of fish moving upstream of a fish pass in the Yorkshire Ouse system. From the available evidence, diel variation in fish densities are generally associated with feeding rhythms, e.g. minnows (*Phoxinus phoxinus* L.) are known to forage at dawn and move in shallow, marginal areas to digest their food in more predator-secure habitats (Copp, 2004). Bullhead is also a nocturnal feeder and uses cavities under rocks and other available cover as shelters or resting sites during daytime (Knaepkens *et al.*, 2004). During winter, Heggenes *et al.* (1993) observed differences in behaviour of brown trout between day and night. During daylight, most of the trout were found passively hiding under cover (*e.g.* substrate or submerged vegetation). At night, trout were active and came out as soon as darkness fell and went back to their shelter as the daylight came. When active at night, most of the fish were found in close association to the bottom. Habitats selected by trout at night had much slower water velocities than those selected during daytime.

2.5.2.4 Depth and velocity (sector/reach/mesohabitat scale)

Depth and velocity are probably the most important parameters in terms of habitat choice for fish. Many studies describe fish habitat characteristics and use in terms of combinations of depth and velocity. Different species, and different life-stages of the same species, have different requirements in terms of these parameters. Indeed, young Atlantic salmon (*Salmo salar*) in Norwegian rivers find suitable area between pools and fast flowing shallow areas, where the water velocity is accelerating and the water depth decreasing (Kitzler *et al.*, 2005). The advantage for a fish to hold position in areas of increasing velocities is to facilitate food intake from nutrients, invertebrates and other prey carried downstream by currents. Combinations of depth and velocities are more influential than these two parameters taken separately. Brown trout (*Salmo trutta*) chose position in a stream according to a ranking of depth-velocity combinations (Shirvell and Dungey, 1983). In 1996, Heggenes *et al.* carried out a study on Atlantic salmon and brown trout habitat use over a variety of discharges. In this particular study, Principal Component Analysis suggested water velocity is the most important of the measured physical variables (e.g. substrate size, cover, depth) in determining fish habitat use.

2.5.2.5 Substrate type and size (mesohabitat scale)

Substrate requirements are species-specific, as well as life-stage specific. Atlantic salmon and brown trout mostly use small and medium cobbles all year round, though trout tend to use finer substrate (e.g. gravel) (Heggenes & Dokk, 2001). The latter results from trout favouring slower-flowing habitats. Indeed, substrate type and size is closely related to water velocity, with coarse substrate (cobble, boulder, gravel) found in fast flowing habitats whereas fine substrate such as sand and silt is found in slow flowing habitats. Brown trout and other salmonids spawn in gravel and this substrate is also important for the development of the eggs and fry stage as it provides shelter against predators (Elliot, 1986). DeGraaf and Bain (1986) observed that substrate type had an influence on habitat use by juvenile Atlantic salmon in slow flowing environments but not in riffle-type environments. Substrate can be the critical factor for bullhead because they need coarse, hard substrate, both for spawning grounds and as a refuge from predators (Tomlinson & Perrow, 2003).

2.5.3 Biological parameters influencing fish habitat use

2.5.3.1 Internal or physiological factors

As fish are poikilothermic i.e. their body temperature is not constant and hence is influenced by outside temperature, they have to adapt to any change in environmental conditions, within their range of tolerance, by behaving so as to minimize the impact of environmental conditions on their activity. Fish movements can be seen simplistically as the tool to achieve the best equilibrium possible between the physiology (energy budget) and the environmental conditions. Internal factors include genetic and ontogenetic factors, i.e. "the factors related to the genetic code of an individual as well as to its development and growth (life-cycle)" (Campbell, 1993). They are also linked to the physiology of an individual, for example, energy expenditure. Anderson (2002) described fish behaviour as a reaction to agents such as prey, predators and habitat features that affect fish fitness. Every agent and/ or reaction is analysed by the fish in terms of energy costs and benefits. Fish need to adapt their behaviour in order to minimize energy loss. This behaviour is also known as the optimal foraging theory where a fish, at every given time, acts in order to maximise the energy trade off towards benefits. In winter, specific choice of habitats and the behavioural patterns adopted by brown trout have been suggested to be governed by the need to minimize energy expenditure, i.e. selection of positions in habitats with low velocities and suitable cover and physico-chemical attributes but where energy depletion is minimized (Cunjak, 1996). Internal factors explain the various strategies used by different species to use their habitat. For example, stream fishes use different strategies for over wintering, depending on the species and life-stages. Among salmonids, behavioural movements and habitat use vary between year-classes (Elliot, 1986). Among non-salmonid species, Fox (1978) determined that ontogenic factors were responsible for the switching from larval stages to sedentary, territorial behaviour in bullhead and the resulting choice of habitat where the dominant substrate was of coarse type. Legalle *et al.* (2005) observed that bullhead switched habitat according to their age and body size. This conclusion confirmed that fish habitat occupancy depends on the species and size of individuals

(Heggenes, 1996). Indeed, in Newfoundland Rivers, both habitat use and habitat preference differed between young-of-the-year and parr Atlantic salmon (DeGraff and Bain, 1986).

However, even within the same species and same population, individual variations in habitat use occur, due to an individual own physiological state or energy budget. Greenberg and Giller (2000) observed substantial individual variation in brown trout habitat use on a daily basis with some individuals using the same habitat all day while others switched habitat between day and night.

Internal factors, as described above, play an important role in fish behaviour and constitute the basis for fish adaptation to environmental conditions. However, their influence on the behaviour displayed by fish is also triggered by interactions with external, environment-related factors.

2.5.3.2 External biotic factors

Biotic factors include intra- and inter-specific competition for shared resources such as preys, habitat and refuges, as well as predator-prey interactions. These different types of biotic interactions and their importance for fish habitat use are discussed in further details in the following sections.

2.5.3.2.i Intra-specific competition

Intra-specific competition is linked directly to the density of individuals of a same species in a particular area of the stream for example. (Downhower *et al.*, 1990). In theory, density has an impact on fish distribution and behaviour because as it increases, so does the competition for resources (food, habitat, refuges, cover, etc.). Elliot (1986) concluded that the spatial distribution of brown trout in a Lake District stream in the U.K. was density-dependent and that the behavioural movements of the different life-stages was also a result of intra-specific and life-stage specific competition. On the other hand, in a study on bullhead, Utzinger *et al.* (1998) found there was no significant correlation between population density and fish movements. These observations show that density alone does not appear to be responsible for intra-specific competition. Resource shortage, whether they are food resources, mating partners or suitable habitats can be responsible for intra-specific competition. Elliot (1986) concluded that population density was the chief factor to affect between-year-class variation in spatial distribution for brown trout of similar age. This pattern might result from territoriality and hierarchy, which are key characteristics of trout populations. It thus appears that some species and some life-stages are more sensitive to intra-specific competition than others. Brown trout 0+ density was found in some streams to be regulated by intracohort competition (Cattanéo *et al.*, 2002). Hierarchy and territoriality also play a role in the way fish use available habitat. A study of red spotted masu salmon (*Oncorhyncus masu ishikawai*) in a Japanese mountain stream revealed the existence of size structured dominance hierarchy with the most dominant fish having access to areas of pools allowing them to get primary access to drifting preys (Nakano, 1995).

2.5.3.2.ii Inter-specific competition

This density-dependent factor that occurs when several species have the same diet or the same habitat requirements and that the density of individuals is too high for the available food or habitat resources (Campbell, 1993). Competition between fish species can result in niche segregation for species living in sympatry, e.g. Atlantic salmon (*Salmo salar*) and brown trout. Indeed, brown trout favoured the more slow flowing habitat types while Atlantic salmon preferred more fast flowing habitat. Salmon parr would use a wider range and, in general, deeper (mean=82 cm) habitat, than trout did (mean= 70cm) as well as faster flowing areas. In the absence of brown trout, Atlantic salmon widen their use of depths, but where other pool-dwelling fish species are abundant, the density of salmon in deep-slow water is reduced (Heggenes *et al.*, 1996; Heggenes and Dokk, 2001). Some species can also live in allopatry at a basin scale, i.e. the different species occur in different parts of the catchment with little or no overlap between them. An example of this behaviour could be observed in a stream basin in Utah where cutthroat trout (*Oncorhynchus clarki utah*) dominated reaches at higher altitude while brown trout was the most dominant in lower altitude reaches (de la Hoz Franco and Budy, 2004).

2.5.3.2.iii Predation

Predator-prey interactions play an important role in the regulation of fish populations. Fish are both predators and prey in river and their movements will occur according to their status: predators will use habitats where they can find appropriate prey and prey will tend to move to refuge habitats. Predator-prey interactions often explain the diel patterns of movements observed in streams. Most fish tend to feed at night, first, to increase their chances to catch prey, and secondly to have less risk of being spotted by predators. Bullhead and salmonids are mutual predators: bullhead is known to influence salmonid distribution though predation of the salmonid eggs in locations where there are high densities of adult bullhead (Carter *et al.*, 2004). Bullhead adopt a cryptic behaviour during the day, hiding in refuges, as this species is very vulnerable to predation (Tomlinson & Perrow, 2003) by carnivorous fish such as brown trout, pike (*Esox lucius*) and chub (*Leuciscus cephalus*), and piscivorous birds like the grey heron (*Ardea cinerea*) and kingfisher (*Alcedo atthis*), as well as the introduced North American signal crayfish (*Pacifastacus leniusculus*), the latter predating both on eggs and adults.

2.5.4 PHABSIM and modelling of habitat use

Habitat use differs between species, between populations within a same species, between life stages, between individuals, according to the region where the stream of interest is located and to the flow and physical characteristics of a particular stream. Brown trout that live in Canadian streams do not necessarily have the same behaviour as brown trout in English streams: the climatic region is not the same, nor is the geology or the stream characteristics. Mechanisms of habitat selection among fish are complex and result from the interactions between external factors (both biotic and abiotic) and the physiology and biology of an individual (partly genetically determined) as well as the adaptation ability to environmental variation (Gozlan *et al.*, 1998). Therefore an integrated approach to fish behaviour is needed, taking into account the interactions between the previously described factors.

Over the past decades, global increase in water demands and in river regulation has led to the development of research aiming to assess the requirements of rivers for water. Ads a result numerous methodologies, based on hydraulic rating, hydrology, habitat simulation, hydraulic simulation, have emerged (Tharme, 2003). Using habitat simulation methodologies, substantial progress has been made in trying to predict fish occurrence and habitat use using modelling tools, such as PHABSIM (Physical HABitat SIMulation), (Bovee, 1982). PHABSIM is one of the numerous hydro-ecological methods used in integrated water resource management in order to define environmental flow requirements (i.e. to define the flow regime required in a river to achieve desired ecological objectives) (Acreman and Dunbar, 2004). PHABSIM allows to predict how much suitable physical habitat is available in a river for a target species and/or lifestage depending on changing flows (Spence and Hickley, 2000). By superimposing the total available aquatic habitat for a section of stream (Weighted Usable Areas) determined by field measurements and hydraulic calibration (e.g. use of the River Modelling system, see Heggenes *et al.*, 1996) with Habitat Suitability Curves developed for a particular species or life-stage from data on habitat preference (depth, velocity and substrate) the occurrence of fish in a section can be partly predicted. The use of PhABSIM requires input of field data such as transect depth and velocity data over at least 3 discharges and mesohabitat distribution and ecological preference data (habitat suitability curves). The data us then used for hydraulic modelling and prediction of available habitat (Spence and Hickley, Fig. 2 p.155, 2000). PHABSIM is the most accurate when physical habitat is the main limiting factor for a population. If other factors such as water quality and temperature most affect populations then the use of this technique may not be appropriate. So far, applications of PHABSIM in the U.K. have included abstraction licensing, drought management, habitat improvement and restoration schemes. One main criticism for the use of PHABSIM is that by linking of environmental flows only to habitat preference one gets a very empirical simplified view of the relationships between organisms and river ecosystems (Acreman and Dunbar, 2004). Habitat Suitability Index (HSI) curves have indeed been developed using mostly one factor at a time such as depth or velocity and, as this literature review stresses, several combined factors influence fish movements. Furthermore, HSI curves do not take into account biotic factors responsible for fish behaviour such as predation or inter-specific competition, nor internal factors. When comparing habitat preferences of Atlantic salmon and brown trout with availability (given by Habitat Suitability Curves), Heggenes *et al.* (1996) concluded that spatial variation in habitat use suggests habitat preferences, i.e. usage compared with availability, to be different from HSI curves. Indeed, calculations of habitat preferences demonstrated that the fish selected habitats substantially different from the available habitat. In other words, plenty of suitable habitats, i.e. meeting the habitat requirements of a particular fish species, does not mean that the fish will use those habitats. Research has indeed shown that resident salmonids in streams usually occupy only a small part of the entire habitat available, sometimes less than 15% of the total (Shirvell & Dungey, 1983). Habitat Suitability Curves have mostly been constructed for salmonid species (Heggenes *et al.*, 1996; Dunbar *et al.*, 2001) and they are highly dependent on the local conditions at the stream scale. Lately a consensus has been reached with respect to the advantage that generic curves represent as they can be more easily used on any stream than localised habitat suitability curves. Habitat use curves have also been the subject of much attention (Miller *et al.*, 2007). They are created using the frequency of use by fish of particular values of depth and velocities and categories of substrate. They usually reflect more the reality of fish habitat use than curves based on "suitability". Like Habitat Suitability Index curves, they are usually built for one variable at a time e.g. depth. However, more recently the use of bivariate use curves as opposed to univariate ones, i.e. that they take into account the interactions between depth and velocity in a stream, has been advocated (Miller *et al.*, 2007). Interactions between physical parameters within a stream are being considered more widely in prediction models such as General Additive Models (Jowett, 2007). Another way to predict fish occurrence in a stream has been described by Dedual *et al.* (2007) and consist of using the relationship that exists between food biomass production and flow. This is based on the assumption that fish are most of the time found in the areas of the stream where food biomass (invertebrate and fish) is the most important. Habitat Suitability Index curves and Habitat Use curves, despite the criticism towards their use, constitute a basis for further investigation of fish habitat use in streams according to flow regime. The data collected in this study will allow to test the accuracy and reliability of composite HSI curves already created for other streams (Objective 4, section 1.3.1).

2.6 FISH SPECIES CHOSEN FOR THIS PROJECT: BROWN TROUT AND BULLHEAD

Section 2.5 illustrated that fish exhibit various strategies of habitat use according to the biotic and abiotic factors that characterise the environment they live in. Discharge variability has been identified as a key factor influencing the structure of fish populations and the biological and physical processes taking place in rivers. In order to better understand how different patterns of flow variability affects different fish life history strategies, it was important to select two species that are situated on opposite ends of the range of behavioural traits. On the one hand, brown trout (Section 2.6.2) is a ubiquitous species. This species is composed of both resident and migratory populations. A very mobile fish, they use the whole of the water column. Though the species is characterized by size-related hierarchy, shoaling is often observed particularly in early life stages and during the mating season. On the other hand, bullhead (Section 2.6.1) has not been studied to the same extent as brown trout. This benthic species is characterised by poor swimming mobility due to the absence of swimming bladder, and by high territoriality. It is mainly a solitary species, living on the stream bed under cobbles (Tomlinson and Perrow, 2003).

However both these species have the common feature that they are considered excellent indicators of river health and naturalness. Brown trout require well-oxygenated waters. Bullhead is listed in Annex II of the European Commission Habitat and Species Directive as endangered as a result of the destruction of its physical habitat due to river channelization in continental Europe. The presence of both these species indicates a natural, undisturbed stream with a natural flow regime, which allows the study and determination of flow regime influence on habitats and fish in natural rivers.

2.6.1 Bullhead habitat requirements and use

The study of coarse riverine fish, and of bullhead in particular, has not attracted as much attention as the study of salmonid fish. However, bullhead has become an increasingly important species to study, since its citing in Annex II of the E.C. Habitat and Species Directive in 1992 (EUROPA Environment web site, 2000). Indeed, although widespread in the rivers and streams of England and Wales, bullhead is endangered in several countries of continental Europe (e.g. Belgium, as emphasized by Knaepkens *et al.* in 2004) as a result of the degradation of its habitat. In England and Wales, a potential threat to bullhead is the competition and predation from the American signal crayfish (*Pacifastacus leniusculus*) (Cowx & Harvey, 2003). Therefore, bullhead occurrence can be seen as a very valuable indicator of the health, integrity and naturalness of running waters (Tomlinson & Perrow, 2003). Bullhead life cycle, and in particular the stages in the development of young bullhead as well the potential causes of mortality for this life stage, have been described by Fox (1978). Bullhead ecology was described by Cowx and Harvey (2003): this small fish displays a cryptic behaviour during the day, hiding under coarse substrate and is very territorial. Table 2.3 below summarizes the key information about bullhead habitat use obtained from the literature about studies carried out in France, Belgium, England and Switzerland.

Table 2.3 Summary of bullhead habitat requirements from the literature.

River and location	Flow variability	River size	Pref. Depth	Pref. Velocity	Pref.substrate	Sample size	Reference
Witte Nete, Flanders (Belgium)	Regulated	N/a	No preference	0.2 to 1m.s^{-1}	Stones	40 sites, electrofished once	Knaepkens *et al.* (2002)
River Reppisch, North Central Switzerland	N/a	Mean width: 12.2m; mean steady flow: 1008L.s^{-1}	No preference	N/a	N/a	10 sites	Utzinger *et al.*(1998)
1st order tributary of the River Tillerey, France	Spring fed; $10<Q<15$ L.s^{-1}	400m long; mean width: 1m	No preference	<0.2m.s^{-1}	Cobbles, boulders. Plant occupation seems to be a limiting factor	36 sections; 5 electrofishing surveys	Gaudin and Caillère (1990)
River Hiz system (Great Ouse catchment), England	Width: 4 to 6m; depth: 0.2 to 0.6m.	Small	N/a	N/a	Stones, large pebbles	Fish collection at 3 sites	Copp *et al.* (1994)
Oberer Lunzer Seebach, Austria	Nivo/pluvial flow regime (very flashy)	Catchment size ~20km²; max depth: 0.5m.	$d>0.1$m	N/a	Gravel (juvenile stages)	11 stream sections and 4 surveys (one/season)	Fischer and Kummer (2000)
Glaven, Stiff, Upper Wensum, Whitewater (Norfolk)		Width: 2 to 4m; depth<0.5m	Preference for increasing depth; stony riffles		Stones (nest), gravel	4 surveys/site	Perrow *et al.* (1997)
River Frome, England	Groundwater-fed	Width: 1-2m; depth<0.3m	N/a	N/a	Gravel	5 study reaches; 6 surveys/reach	Welton *et al.* (1983)
Kerledan stream, River Scorff, Brittany, France	Mean Q: 0.18m^3.s^{-1}	Width: 3.11m; slope: 1.3%	$0.2<d<0.4$m	$v>0.4$m.s^{-1}	Gravel	1 site, 4 surveys	Roussel and Bardonnet (1996)
River Saint-Perdoux, France (piedmont stream)	N/a	Length: 13.2 km	$0.15<d<0.3$m	$0.25<v<0.5$m.s^{-1}	Pebbles, cobbles and boulders	32 sampling sites	Legalle *et al.* (2005)
Tributary of the River Tillerey, France	Irregular flow	Reach length: 400m; width<3m	N/a	N/a	N/a	2 sections; 12 surveys	Downhower *et al.* (1990)
River Saint Perdoux (France)	N/a	Length: 525 km; Catchment 57.000 km²	$0.05<d<0.20$m	$V<0.4$m.s^{-1}	Pebbles, cobbles and boulders	554 sampling sites	Legalle *et al.* (2004)
River Avon, Hampshire, England	Groundwater-fed	Length: 100km. Each site ranges between 1 and 2.5 km.	~0.1 to 0.2m	>0.1m.s^{-1}	Large –grained substrata: cobbles and stones.	40 point samples over 200m at each of the 5 sites	Carter *et al.* (2004)
The Highland Water, New Forest, England	Flashy	Width between 2 and 5m	Low (riffles)	High (riffles)	N/a	Several: 5 surveys/site	Langford and Hawkins (1997)
N/a (summary of literature)	N/a	N/a	>0.05m	$0.1<v<0.38$m.s^{-1}	Coarse substrate of clean gravel and stones/cobbles	N/a	Tomlinson and Perrow (2003)

The studies referenced in Table 2.3 were carried out in different kinds of rivers in terms of size and flow regime using different methodologies and numbers of samples. With respect to depth use by bullhead, all studies agreed on the minimum depth required by bullhead, e.g. greater than 0.05–0.10 m. Maximum depth use varied between studies and ranged from 0.2 to 0.4 m. Studies by Langford and Hawkins (1995) and Perrow *et al.* (1997) were very specific about the type of mesohabitat preferred by bullhead, which they found to use mostly riffles, i.e. very shallow and fast hydraulic habitats. The other studies either did not record any favoured depth or either concluded this variable was not important to bullhead location.

Preferred velocity was shown to be above 0.1-0.2 $m.s^{-1}$ for all studies. Maximum values of velocity use were recorded to be around 0.4-0.5 $m.s^{-1}$. Tomlinson and Perrow (2003) added that greater velocities could be sustained if bullhead had access to refuges such as large substrate particles, undercut banks or instream vegetation. Due to the particular ecology of the bullhead, i.e. its cryptic behaviour, it can be concluded that this species can cope with quite a wide range of velocities if suitable refugia are available.

All studies agreed on the type of substrate use and required by bullhead, e.g. gravel, cobble and larger substrate particles.

2.6.2 Brown trout habitat use

Brown trout biology, ecology and habitat requirements have been studied extensively due to this species ubiquity and its economic value.

Habitat use by brown trout has been investigated according to:

- Life-stage (Hayes, 1995; Elliot and Hurley, 1998; Maki-Petays, 1999; Heggenes and Dokk, 2001)
- Sympatry or allopatry with other species (Heggenes, 1996; De la Hoz Franco and Budy, 2005; Olsen and Belk, 2005; Elliot, 2006; Meissner and Muotka, 2006; Riley *et al.*, 2006)
- Discharge (Jowett, 1990 ; Baran *et al.*, 1995 ; Cattanéo *et al.*, 2002 ; Flodmark *et al.*, 2006)
- Season (Cunjak and Power, 1986; Heggenes, 1990; Heggenes and Dokk, 2001)

- Resident/migratory characteristics (Elliot, 1986; Elliot, 1998; Hilderbrand and Kershner, 2000)
- Type of stream (Clapp *et al.*, 1990; Modde *et al.*, 1991; Baran *et al.*, 1997)
- Type of activity (Grost *et al.*, 1990; Beard and Carline, 1991; Zimmer and Power, 2006)

Recent studies have also aimed at establishing this species and its various life stages' habitat preferences in terms of depth, velocity and substrate. Habitat Suitability Index curves have been built using the programme PHABSIM for brown trout. In the UK, for example, this has been developed for fry and parr stages (Dunbar *et al.*, 2001- see Section 2.7.3) in chalk streams, which allow the prediction of fish occurrence in rivers. Heggenes *et al.* (1998) built similar curves as well as Habitat Use curves for brown trout living in sympatry with Atlantic salmon (*Salmo salar*) in streams of the South West of England. Applying those results to the current study would lead to an insight about the applicability of those curves to different types of streams, in another biogeographic region.

2.7 SUMMARY AND RESEARCH QUESTIONS

The critical review above has evaluated current knowledge with respect to flow regime and how it influences instream physico-chemical and habitat parameters. Most of all, it has emphasized the fact that flow regime alone does not account for all the variability within riverine ecosystems. It is the interaction between external drivers such as climate, topography, elevation and geomorphology and instream drivers such as channel geomorphology, sediment input and carrying capacity as well riparian vegetation and floodplain structure, that create a complex ecological response leading to the patterns of variability experienced by instream biota.

Flow regime is a key driver in riverine ecology that influences both physico-chemical characteristics and ecology characteristics, i.e. the number and diversity of taxa using the instream habitat. The hydrological processes and structural character that determine river habitat interact over wide range of spatio-temporal scales. So far, this literature review has identified a number of the factors that the flow regime interacts with as well as some of the processes responsible for the formation and variability of instream habitat structures. This review has also identified the biological and physical factors that influence fish behaviour.

It has emphasized that despite a great deal of research having being carried out on fish behaviour and its interactions with the variable instream environment, there has been limited emphasis on the effect mesohabitat composition and variability, influenced by river flow regime, has on fish behaviour. Within this context, this review has identified a number of research gaps in some aspects of flow regime influence on habitat composition and variability as well as the response fish display in terms of habitat use. In particular, little is known about the influence of differing types of natural flow regimes on instream habitat composition and variability, the effect of flow variability on hydraulic geometry and more particularly mesohabitat physical characteristics such as depth and velocity, the influence of flow regime on fish via the variability of physical factors, the relative influence of flow regime and biological processes on fish behaviour.

As a result, a certain number of research questions have been defined that to be addressed in this thesis:

- RQ_1. Do different types of natural flow regimes result in different types of stream geomorphology and hence in different patterns of mesohabitat composition?
- RQ_2. How does instream mesohabitat composition vary over the range of flows experienced by a river according to its flow regime?
- RQ_3. Is there a pattern of mesohabitat use displayed by the fish populations studied and if so what is it?
- RQ_4. Does mesohabitat use by fish follow the same pattern as mesohabitat variability, i.e. is it influenced only by flow?
- RQ_5. Are other factors involved in fish habitat use?
- RQ_6. What role is played by factors such as seasonality, habitat availability, life-stage and social interactions in the pattern of habitat use displayed by the surveyed population?
- RQ_7. What are the key habitat characteristics that determine fish location?

This study investigates a number of specific physical and biological processes and responses taking place in the river channel, as a multidisciplinary piece of research at the interface between hydrology, geomorphology and ecology to address the main research questions detailed above.

Addressing such fundamental questions may provide a new inside into the hydroecology of natural rivers in the Midlands of England. Indeed, natural rivers in this part of Britain have received far less attention than others like chalk streams in the Southern England or the Ouse system in the East. Understanding the hydroecology of the Midlands natural rivers can provide a model for future research and management of rivers of such scale, as opposed to very large rivers found on the American or Australian continent. The insights gained from the study of brown trout response to flow regime may then be applied to further research at a larger scale, for example across a whole catchment. The insights gained from the study of bullhead behaviour may then be applied to conservation strategies for this species that is endangered in continental Europe and cited in Annex II of the E.U. Habitats and Species Directive. Finally this interdisciplinary research on fish may then be used as a framework for future research into other river systems and other types of flow regimes, for example in order to understand the impact of extreme events such as floods on riverine processes and riverine biotic responses. Overall, the results of this study can help understand the possible impacts of climate change on river flow regimes and how it can affect fish populations. The objectives and research questions identified will be addressed using the methodology described in Chapter 3.

CHAPTER 3

STUDY SITES AND METHODOLOGY

3.1 STUDY SITES

The study reaches were situated in the Upper Severn region, as shown in Figure 3.1. They were chosen to provide sites with a range of flow regimes and with resident populations of the target species, which could allow comparison across the Upper Severn region.

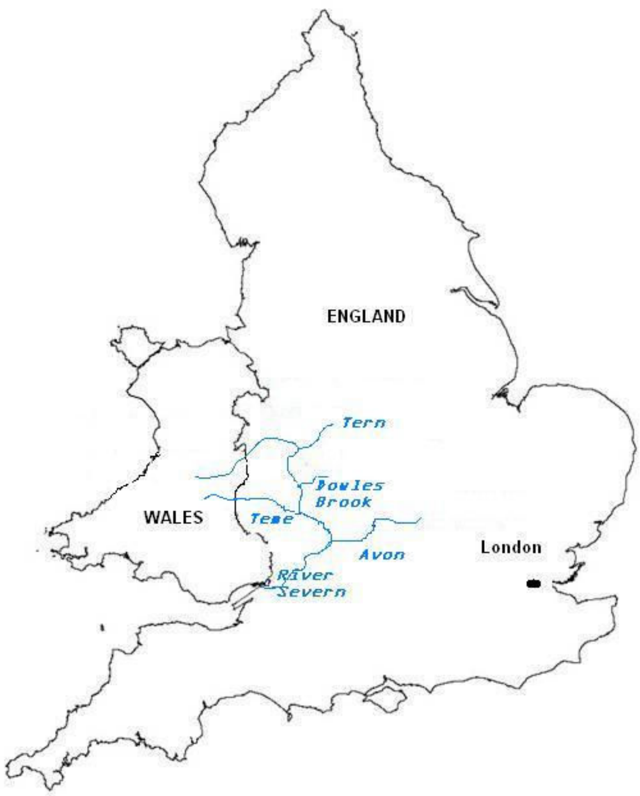


Figure 3.1 Map of the location of the study sites

The Dowles Brook in Worcestershire is a surface runoff influenced stream whereas the River Tern in Shropshire is largely groundwater-fed. Table 3.1 summarizes some characteristics of the two study rivers. The River Tern and the Dowles Brook share very good water quality as well as a similar gradient. Both sites present relatively high diversity in fish species present though fish biomass is dominated by bullhead and brown trout (Pinder *et al.*, 2003; Worcestershire Wildlife Trust online, date unknown).

Table 3.1 Key characteristics of the two river sites chosen for the current study (Natural England online, date unknown; Worcestershire Wildlife Trust online, date unknown)

Characteristics	Dowles Brook	River Tern

The rest of this section describes each site in more detail followed by a comparison of the hydraulic characteristics of the two streams.

3.1.1 River Tern at Norton in Hales, Shropshire

The River Tern (grid reference SJ 707385) flows through pasture land, over a geology of Rhaetic and Liassic clays and Permotriassic sandstone. The 150 metre–long reach at Norton in Hales, Shropshire runs in the middle of a narrow forested wetland, itself located between fields used for cattle grazing. This particular length of reach was chosen because it was already the subject of research as part of the NERC LOCAR programme and as a result, flow gauging equipment was present and data and information on this portion of the reach were already available. Moreover 150-200 metres appeared to be a suitable length in terms of time/work efficiency to study the evolution of mesohabitat composition in a stream. The River Tern is characterised by a high Base Flow Index (for a definition see chapter 2), *i.e.* value of 0.76, indicating a high input of groundwater from the aquifer and typical of groundwater fed streams, which makes it a relatively stable hydraulic and hydrological environment. Substrate consists of fine glacial sand and gravel (Emery *et al.*, 2003).

Figure 3.2 shows the hydrograph for the Norton in Hales site for the years 2004 to 2006. This hydrograph gives an indication of flow variability within the stream. The level of base flow decreased between 2004 and 2005, as a result of low rainfall. Most flows are situated below or around $0.5m^3 s^{-1}$. Only five high flow events ($1m^3. s^{-1}$ and above) occurred during the winter and late spring months. This hydrograph confirms the flow regime described by the BFI value, *i.e.* the River Tern at Norton in Hales is not a very flashy river and the flows over the sampling period did not vary to a great extent.

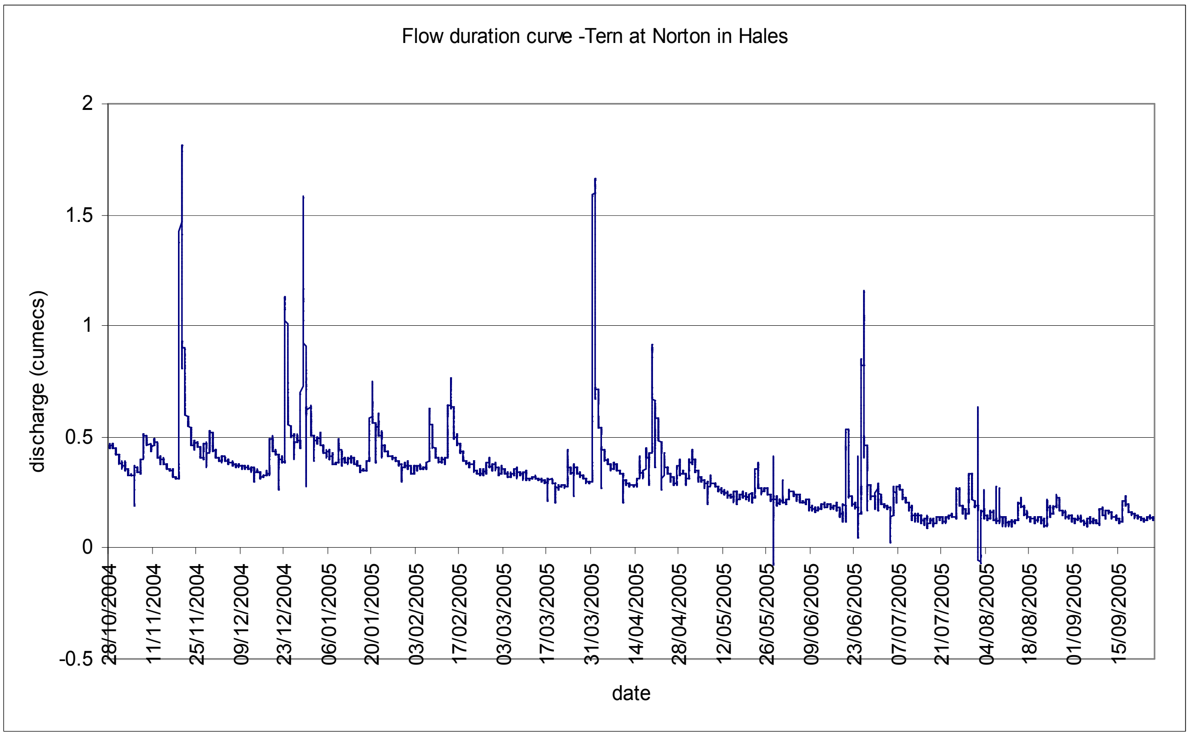


Figure 3. 2 Hydrograph for the River Tern at Norton in Hales, Shropshire for the period 2004-2006

Figure 3.3 View of the River Tern at Norton in Hales, mid reach, looking downstream

3.1.2 Dowles Brook, Wyre Forest, Worcestershire

The Dowles Brook (Figure 3.6), located in the Worcestershire Wildlife Trust Knowles Coppice nature reserve, near Bewdley, Worcestershire (grid reference SO 763765), is characterised by a geology of carboniferous limestone with a Baseflow Index of 0.40 and hence has a flashy hydrological regime. The reach is situated in the middle of a forested area.

Figure 6 shows the hydrograph for the Dowles Brook for the period 2005-2006, drawn from the data provided by the Environment Agency Data Centre. The hydrograph shows high flow variability from the base flow levels as well as higher flows occurring throughout winter and spring. The summer and autumn of 2006 appeared particularly dry compared to those of 2005. Indeed, difficulties in surveying the streams for mesohabitats and fish at higher flows were encountered over this period of time. The hydrograph confirm the “flashy” character of the Dowles Brook and high variability experienced by the flows on this river.

Figure 3.4 Hydrograph for the Dowles Brook for the period of time 2005-2006 (E.A. data centre)

Figure 3.5 Part of the Dowles Brook reach looking upstream

3.1.3 Flow characteristics of the study streams

Table 3.2 below summarizes the flow characteristics of the two streams.

Table 3.2 Flow characteristics of the two study streams for the period of study and for the period of records available

		Q_5	Q_{10}	Q_{25}	Q_{50}	Q_{75}	Q_{90}	Q_{95}	Q_{10}/Q_{90}	BFI	Catchment Area (km^2)
Tern	2005-2006	0.650	0.491	0.367	0.280	0.187	0.139	0.125	3.5	0.76	38.5
	2002-2006	0.719	0.515	0.391	0.299	0.181	0.124	0.108	4.15		
Dowles Brook	2005-2006	0.658	0.445	0.235	0.116	0.044	0.027	0.022	16.5	0.40	41.62
	1995-2006	1.267	0.779	0.325	0.125	0.048	0.028	0.022	35.4		

Table 3.2 shows the flow percentiles calculated for each stream for two periods of time: 2005-2006 is the survey period. For the Tern, 2002-2006 is the period of time for which flow records were available as part of the LOCAR project. For the Dowles Brook, 11 years of flow records were available from the Environment Agency from 1995 to 2006.

Q_{10}/Q_{90} represents the overall variability of the stream and Table 3.2 shows that the Dowles Brook is the most variable stream in terms of discharge (Q_{10}/Q_{90}=16.5) while the Tern is the least variable (Q_{10}/Q_{90}=3.5) during the study period. The period 2004-2006 was particularly dry and experienced less flow variability than the longer term average, which is shown by the lower values of Q_{10}/Q_{90} for the study period compared to Q_{10}/Q_{90} calculated from the entire flow records. The flow percentiles calculated in Table 1 allowed the flow duration curves for the study sites during the period of study to be drawn and these are shown in Figure 3.8, which shows the flow duration curves for the two study streams for the study period, i.e. 2005-2006. The steepness of the curve taking into account Q_5 shows that the Dowles Brook is the most variable stream, which is confirmed by values of Base Flow Index. Indeed BFI values are 0.40 for the Dowles Brook and 0.76 for the River Tern. The next phase in the study of these streams was to map and monitor their mesohabitat composition to see if it varied at the same pace as flow.

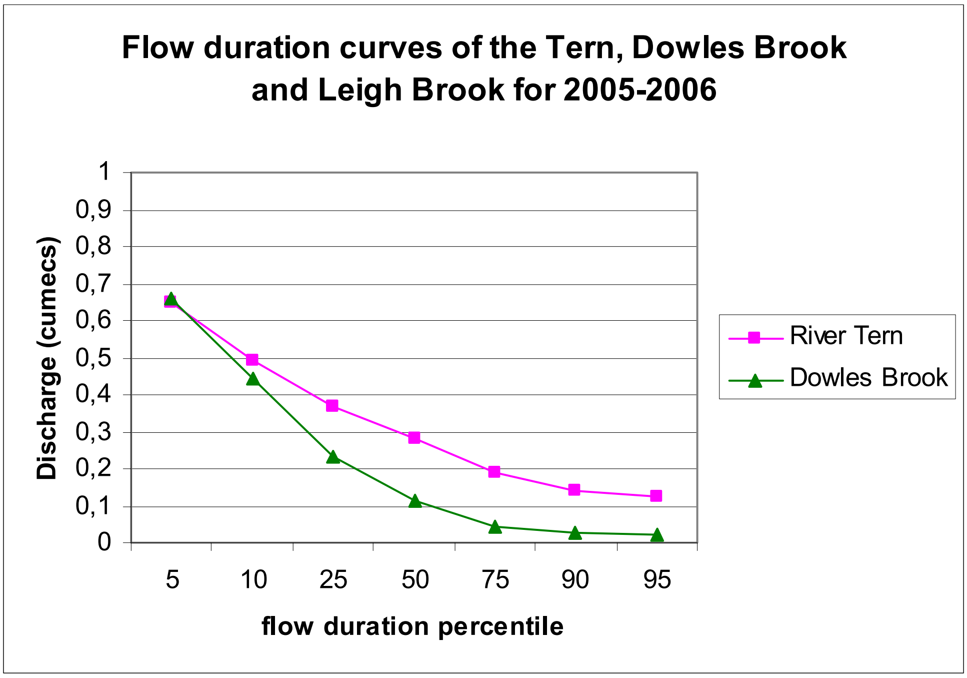


Figure 3.6 Flow duration curves for the two study reaches during the study period

3.2 MESOHABITAT SURVEYS AND MAPPING

3.2.1 Survey method

The 'meso-scale' was chosen as it has been shown to be the scale at which habitat features relevant to fish ecology such as spawning grounds and barriers to movements are visible (Newson *et al.*, 1998; Fausch *et al.*, 2002). Several habitat mapping techniques exist (see chapter 2) that present different levels of precision with respect to the description of instream habitats and the amount of data to collect. For example, MesoHABSIM (Northeast Instream Habitat Program, 2007) used mostly in the U.S.A takes into account instream lateral habitat diversity but requires a very high number of data to be collected and is very time consuming; at the other end of the range is the Rapid Habitat Mapping method (Maddock and Lander, 2002), which is, as indicated by its name a rapid assessment method with the requirements for only one measurement of depth and velocity per habitat. The advantage is it is not time consuming and allows to get an overview of the range of habitat and hydraulic conditions present in a stream. On the other hand it was not considered detailed enough to characterise the habitat variability within units that are available to fish. For the purpose of this study, a method was needed that balanced the needs for a description of instream habitat characteristics as precise as possible with relatively low time-consumption and easy replication of the procedure. During each survey, each mesohabitat was identified according to the nomenclature used in the MesoHABSIM method and surface flow type. Mesohabitats can be defined as habitats at the intermediate scale that result from the interactions of hydrological and geomorphological forces, hence comprising depth, velocity and substrate (Armitage and Cannan, 2000). Newson *et al.* (1998) had previously defined mesohabitats using the term "physical biotopes", which can be identified using flow types. Hence, the relation between flow types and the physical biotopes they are associated with allows identification of mesohabitats from the river banks. This method of identification was used in the present study and the mesohabitats encountered are presented in Table 3.3 together with their associated flow types (according to Newson *et al.*, 1998), the level of turbulence encountered in these habitats and their description according to the MesoHABSIM classification that was simplified for the purpose of this study: only the main mesohabitat types (relevant to the morphology of the study streams were used) and the number of measurements of depth and velocity were reduced.

With the description detailed above, the next phase was to be able to identify the mesohabitats in the field, which required a few surveys to become familiar with the nomenclature. Figure 3.7 shows three examples of mesohabitats and associated surface flow types.

Table 3.3 Description of the mesohabitats encountered during the mesohabitat surveys, according to the MesoHABSIM method (Northeast Instream Habitat Program, 2007). The method and nomenclature were simplified to be used in this study.

Mesohabitat (CGU)	Associated flow type	Turbulence	Brief description
Riffle	Unbroken standing waves	Turbulent & moderately fast	The most common type of turbulent fast water mesohabitats in low gradient alluvial channels. Substrate is finer (usually gravel) than other fast water turbulent mesohabitats, and there is less white water, with some substrate breaking the surface.
Run	Rippled	Non-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	Smooth boundary turbulent	Non turbulent & moderately slow	Smooth "glass-like" surface with visible flow movement along the surface, relatively shallow (compared to pools) depths.
Pool	Scarcely perceptible flow	Non turbulent & slow	Relatively deep and slow flowing, with fine substrate. Usually little surface water movement visible. Can be bounded by shallows (riffles, runs) at the upstream and downstream ends.
Backwater	Scarcely perceptible flow	Non-turbulent and slow	Water is ponded back upstream by an obstruction, e.g. weir, dam, sluice gate, etc.
Chute	Chute/ broken standing waves	Turbulent and fast	Water passes over a break or step in the substrate.

Figure 3.7 Examples of mesohabitats and associated surface flow types (SFP). From left to right: a run (SFP=rippled), a riffle (SFP=unbroken standing waves) and a pool (SFP=scarcely perceptible flow)

Lateral mesohabitat diversity was taken into account, which required the recording of the mesohabitats across the stream width. Each identified habitat was measured in the field using a Bushnell laser range finder (to 0.1 m accuracy) and then sketched onto a map of the reach to be used later under GIS software (MapInfo). Surveys were carried out on each reach every six weeks or at a significantly different flow stage/ discharge in order to be able to study the variation in mesohabitat composition according to flow. After identifying each mesohabitat, its physical characteristics were recorded according to the method described below.

3.2.2 Physical parameters measured

The length and width of each habitat were measured using either a Bushnell laser range finder or a tape measure. This provided the necessary data to subsequently digitise the habitats using GIS software. Parameters measured included depth, velocity, surface flow type, substrate composition, instream vegetation, overhead cover and bank types. Depth and velocity measurements were taken at five points distributed according to a cross pattern within the core of each CGU. Indeed, it was estimated that five points of measurement constituted an appropriate trade-off between the need for accuracy and representation of the mesohabitat conditions and the replication of this method during surveys. The core of each habitat was estimated visually and was used to take the measurements as the values obtained would be more characteristic of each type of mesohabitat and would be less likely to be influenced by other adjacent mesohabitats. Figure 3.10 shows where the measurements of depth and velocity were taken in each mesohabitat along a reach.

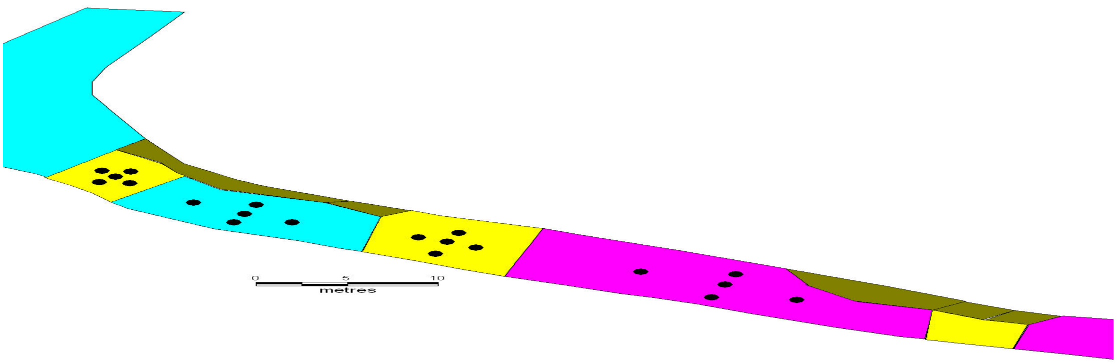


Figure 3.8 Location of depth and velocity measurements with respect to mesohabitat boundaries

Substrate composition was recorded according to a simplified Wentworth scale, as used in the River Habitat Survey protocol (Environment Agency, 2003). The extent (none, some (<50%), much (>50%), 100%) and type (macrophytes, bryophytes, algae, periphyton) of instream vegetation were recorded. Overhead cover was recorded quantitatively in the same way as for instream vegetation. Data for the River Tern were provided by the University of Birmingham for the duration of the LOCAR project and then provided by the LOCAR Data Centre in Wallingford. Discharge data on the Dowles Brook were provided by the Environment Agency Data Centre. Table 3.4 provides a summary of the parameters recorded during the mesohabitat mapping surveys.

These measurements allowed determination of the main physical characteristics of each mesohabitat, which could be later analysed in conjunction with the results of the study of fish mesohabitat use.

Table 3.4 Summary of the physical parameters recorded for each identified mesohabitat

PARAMETER RECORDED/MEASURED	METHOD USED FOR RECORDING	LEVEL OF ACCURACY
Length	Laser range finder	0.1 m
Width	Laser range finder	0.1 m
Depth (5 points/CGU)	Ranging pole	cm
Velocity (5 point/CGU)	Current meter	$m.s^{-1}$
Dominant substrate	Visually (after Wentworth scale)	
Subdominant substrate	Visually (after Wentworth scale)	
Instream vegetation	None/some/much	order
Overhanging vegetation	None/some/much	N/a
Bank types	Environment Agency RHS method	N/a
Surface Flow type	See above	N/a

3.3 STUDY OF FISH HABITAT USE

In order to identify the riverine mesohabitats elected by brown trout and bullhead, direct instream observation by means of snorkelling was identified as the most appropriate method (Heggenes and Saltveit, 1990; Harby *et al.*, 2004): Starting from the downstream end of the reach, the survey involved snorkelling in an upstream direction in a zigzag manner to enable the probability of encountering a fish to be equal whatever the mesohabitat considered. When a fish was spotted in the water column, it was observed at the same location for up to a minute to make sure the fish location was the result of deliberate choice and had not been disturbed into that position by the surveyor. The estimated length of the fish, its position and activity were noted. At the location of each fish observation, a weighted float was positioned on the stream-bed. For this particular project, weighted floats (see Fig. 3.11) were made of a polystyrene table tennis-type ball attached to a wooden cocktail stick and attached to a fishing lead weight with nylon rope. Each weighted float was identified by a number and subsequently located onto a map of the reach using a mapping grade GPS, a quick set level or by drawing directly onto the map.

The two conditions to be fulfilled in order to carry out snorkelling surveys in a reach are: (i) enough depth and (ii) clear water to allow good visibility, i.e. low turbidity.
Direct underwater observations were preferred to electrofishing to study fish habitat use for three main reasons:

i. Direct underwater observations allow assessment of the precise location of a fish, its behaviour/activity as well as to see the surroundings of its location.
ii. Fish behaviour/location could easily be related to a particular mesohabitat thanks to the weighted floats. If electrofishing had been used, stop nets would have been necessary to separate each mesohabitat, which would have been time consuming and information on fish position within mesohabitats could not have been recorded.
iii. Ethical reasons: snorkelling does not involve contact with fish nor the risk of killing them.

Surveys were carried out in each stream at monthly intervals in order to sample as many different hydraulic conditions as possible. However, the dry weather conditions during the winter months forced the last survey on the Dowles Brook to be postponed in order to get the highest flow possible. In May 2007, flow was high enough (Q_{43} = 0.168 $m^3.s^{-1}$) compared to the previous flows surveyed to assess the reach in order to record fish habitat use at higher flows. Both brown trout and bullhead were searched for in the same survey. While looking for trout in the water column, stones on the stream bed were lifted to look for potential presence of bullhead, which are known to be typically hiding under stones.

Figure 3.9 Two weighted floats of the type used during the fish surveys, on site

After completion of the snorkelling surveys, a mesohabitat survey was carried out according to the protocol described in section 3.2. At the location of each weighted float, depth and velocity (at 0.6 depth for brown trout and on the stream bed for bullhead), substrate composition, embeddedness (visually estimated using the method developed by Eastman *et al.* (2007), then quantified between 1= low embeddedness and 4= complete embeddedness), instream vegetation, overhead cover, the mesohabitat in which the weighted float was located as well as the surface flow type were identified or measured. Table 3.5 summarizes the parameters measured during the different types of surveys.

The fish surveys as they were described above were carried out with a dual purpose:

i. They allowed the investigation of the interactions between flow variability, mesohabitat composition and fish behaviour.

ii. They allowed the relevance and accuracy of Habitat Suitability Index curves to be tested in predicting the occurrence of both species of interest. Generalized HSI curves exist for brown trout (see chapter 2). Those for bullhead were drawn as part of this study and the methodology used is described in the next section.

Table 3.5 Summary of the different types of parameters measured during both mesohabitat and fish surveys for this project.

	Fish survey	**Mesohabitat survey**
Fish-related parameters	Species Body length (visually estimated) Life stage Position Activity	N/a
Physical habitat parameters	Depth (m) Velocity (bottom or at 0.6depth) ($m.s^{-1}$) Substrate Embeddedness Surface flow type Mesohabitat type Instream vegetation Overhanging vegetation	Mesohabitat type Length; Width Depth (5 points) (m) Velocity (5 points; 0.6depth) ($m.s^{-1}$) Substrate Instream vegetation Overhanging vegetation Bank types Surface flow type
Other measurements	Flow stage (subsequently converted into discharge) Water temperature Dissolved Oxygen pH Conductivity Turbidity	

3.4 DERIVATION OF HABITAT SUITABILITY INDEX CURVES (HSI) FOR BULLHEAD

The study of coarse riverine fish, and of bullhead in particular, has not attracted as much attention as the study of salmonid fish. However, bullhead has increasingly appeared to be an important species to study, since being cited in Annex II of the E.C. Habitat and Species Directive in 1992 (EUROPA Environment web site, 2006). Indeed, although widespread in the rivers and streams of England and Wales, bullhead is endangered in several countries of continental Europe (e.g. Belgium, as emphasized by Knaepkens *et al.* in 2004) as a result of the degradation of its habitat. In England and Wales, a potential threat to bullhead is the competition and predation from the American signal crayfish (*Pacifastacus leniusculus*) (Cowx & Harvey, 2003). Indeed, American signal crayfish occupy the same ecological niche as adult bullhead. Some cases of predation on bullhead eggs have also been recorded. Therefore, bullhead occurrence can be seen as a very valuable indicator of the health, integrity and naturalness of running waters (Tomlinson & Perrow, 2003).

Though several studies have aimed at identifying the specific physical habitat requirements in terms of depth, velocity, substrate and cover, a review of which is presented in Chapter

2, the data obtained in order to describe what habitat is suitable, if not optimal, for bullhead are still very imprecise.

In particular, habitat suitability curves are lacking. They can help determine which habitat is most likely to host a population of bullhead. Some Habitat Suitability Index curves were constructed for bullhead in the River Garonne system, Southern France, by Legalle *et al.* (2005). Several studies by Knaepkens *et al.* (2004) have aimed to identify the parameters most relevant to the presence of bullhead in rivers and particularly determined that coarse substrate was a requirement for species occurrence. Chaumot *et al.* (2006) started a modelling approach using an artificial neural network to identify the species ecology requirements. However, general habitat suitability curves that could be transferable and applicable to the study sites for the current project, i.e. natural, sinuous, non regulated UK lowland streams, appeared more suitable for the present study.

Therefore the method designed by Franklin (2002) was selected to build Habitat Suitability Curves for bullhead using data from the literature, i.e. papers and reports on studies carried out over the past two decades on several rivers in the UK and continental Europe (see Chapter 2).

In order to build the most reliable habitat suitability curves possible, each study was allocated a weighting factor according to (i) its relevance to the present study (see Table 3.6) in terms of geographical location, with due regard to hydro-climatic and biogeographical regions, and type of study (field or experimental), and its reliability (see Table 3.7) in terms of the number of samples and /or sites used to obtain the data.

Table 3.6 Relevance of the literature to the present study.

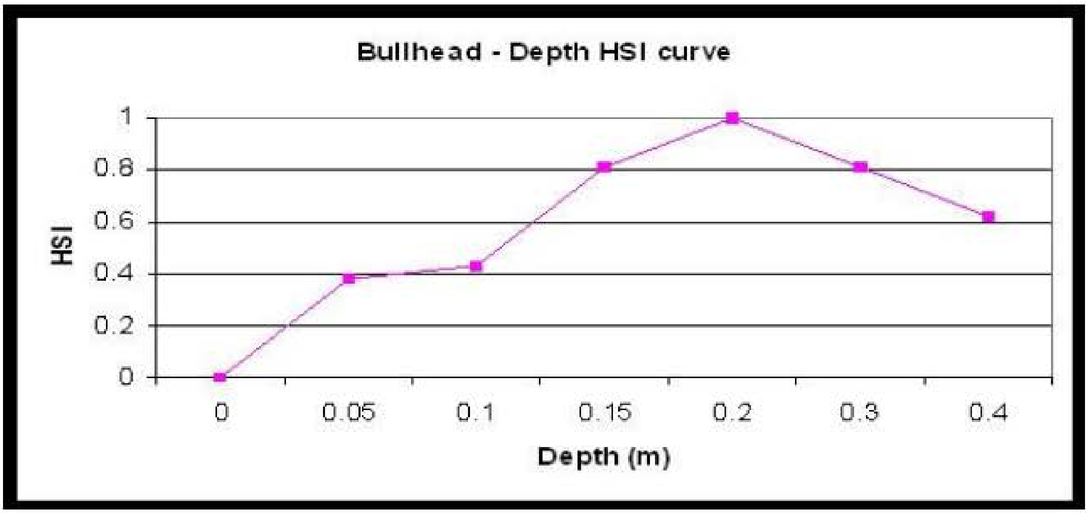
Type of study	N° reports/papers available	Weighting
Study on Midlands lowland river	0	5
Study on other U.K. lowland rivers	6	3
Study on other European rivers	6	3
Study on upland river or artificial stream or tank	2	1

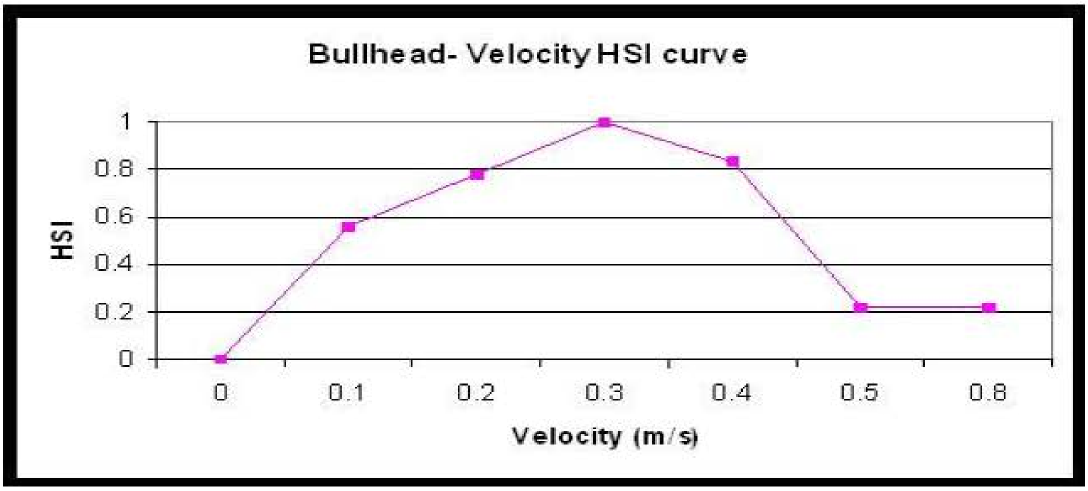
The same value of weighting factor was used for both studies on other UK lowland rivers and studies on other European rivers because their locations were situated within the same biogeographical region, which is the Atlantic biogeographical region, according to the map of biogeographical regions as part of the Natura 2000 network (European Commission, 2006).

Table 3. 7 Reliability of the data from the reviewed literature

Reliability	N° reports/papers	Weighting
Study based on a single sample/site	1	1
Study based on 1-10 samples/sites	2	3
Study based on more than 10 samples	9	5

The highest value of weighting factor was given to studies based on more than 10 samples. Indeed, the higher the number of samples/sites used for a particular project, the more statistically reliable the results of the work. The total weighting factor for each study equals the sum of the relevance factor and the reliability factor. Data on depth, velocity, substrate and cover were put into an excel spreadsheet and allocated the relevant total weighting factor, according to the above tables. The transformed data, i.e. (the original data)*(total weighting factor), were then put in an array equal to the size of the maximum value for each transformed parameter. The last step of this method consisted in normalizing these transformed data into true Habitat Suitability Indices ranging from 0 (unsuitable) to 1 (optimal). The Habitat Suitability Index curves for bullhead, obtained following the above method, are shown in Figure 3.12.





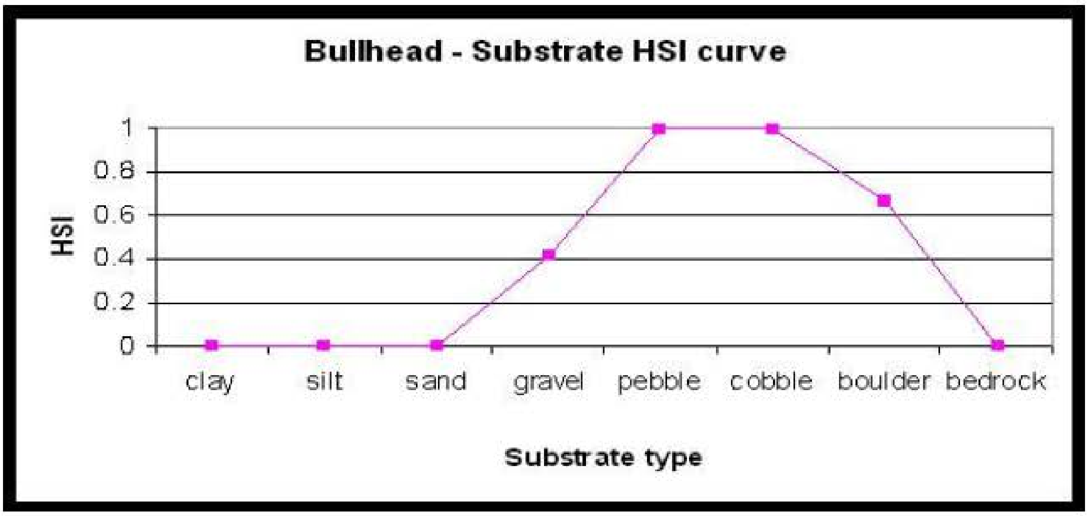


Figure 3.10 Habitat Suitability Index curves (depth, velocity and substrate) for bullhead, built from the literature

These habitat suitability curves show that the optimal habitat characteristics for bullhead would be depth of 0.2 m, velocity of 0.3 $m.s^{-1}$ and presence of coarse substrate such as pebble and cobble. These curves could be tested after the data analysis of fish surveys (see section 3.5.4). Moreover they allowed habitat use prediction maps to be drawn (see section 3.5.3).

3.5 DATA ANALYSIS

3.5.1 Mesohabitat maps using GIS tools

The mesohabitat maps resulting from the habitat surveys were drawn using MapInfo 8.5 Professional for Windows. Maps of the three study sites were obtained through the Ordnance Survey Digimap service. After conversion into the appropriate format, they could be used in MapInfo. Each mesohabitat was digitised on the map from the sketches made during field surveys. MapInfo provides a distance-calculation tool so that each mesohabitat was drawn to the exact dimensions (length and width) measured on site. A specific colour was allocated to each type of habitat for ease of visual assessment.

Glide= “bright pink”
Run= “light pink”
Riffle =”yellow”
Backwater = “navy blue”
Pool = “turquoise”
Cascade = “green”.

Geomorphologic features were also indicated on the maps, such as mid-channel bars and lateral gravel bars at low flows. All the maps created on each survey helped produce a summary map (see chapters 4 and 5) of each reach of the spatial variability in mesohabitat composition together with the location of fish observations, probability of occurrence and information on riparian vegetation.

3.5.2 Flow and mesohabitat data analysis

Mean flow values were provided one each survey occasion and were then used to study the evolution of mesohabitat parameters and fish habitat use according to flow. The long-term flow records allowed the calculation of flow duration percentiles (Table 1) and the determination of flow variability on each study reach. The flow percentiles were used to draw flow duration curves for the three streams for the period of study.

The depth and velocity measurements recorded during the mesohabitat surveys were analysed according to each mesohabitat type to see how the characteristics of each type of mesohabitat (glide, pool, etc.) evolved with discharge. Mean values of depth and velocity for each type of mesohabitat and each discharge were calculated as well as their standard deviation. Statistical comparison was then run on these values to determine any significant influence of flow on mesohabitat characteristics. The number of mesohabitats of each type recorded on the various surveys was used to determine how the mesohabitat composition (in percentage) varied in each stream according to flow, thus helping to understand the influence of flow regime on mesohabitat composition.

3.5.3 Prediction maps of fish habitat use

In order to test the accuracy of HSI curves in indicating the presence/absence of brown trout and bullhead at the reach scale, the curves shown in section 3.4 were used to calculate relative habitat suitability indices for each mesohabitat that was identified during the various surveys. As a result, maps representing the habitats according to their suitability for each of the two species of fish could be drawn using GIS tools.

3.5.3.1 Habitat relative suitability indices

When calculating the indices using bullhead HSI curves, substrate, depth and velocity were considered. Indeed, substrate has to be considered as bullhead are bottom-dwelling fish and thus live permanently on the stream bed. Only depth and velocity were considered when calculating indices for brown trout habitat. Indeed, as opposed to bullhead, brown trout is a “water-column” species. As a result, substrate is not as important variable to their habitat use except during the spawning season. For each mesohabitat, the mean value of depth and velocity from the five measurements taken during habitat surveys were calculated. The obtained values were then plotted onto the relevant Habitat Suitability Curves, which allowed the determination of the corresponding suitability index for each parameter. With respect to substrate, the dominant substrate in each mesohabitat was considered and its suitability index was identified on the relevant curve. The suitability of each habitat was then calculated by multiplying the various relative indices.
For instance, habitat suitability for bullhead would be calculated as follows:
HSI= rHSI (depth) * rHSI (velocity) * rHSI (substrate)

Habitat suitability for brown trout would be:

HSI= rHSI (depth) * rHSI (velocity)

Relative habitat suitability index values typically rank from 0 to 1.The range of values was divided into four categories, each assigned with a degree of suitability. For rHSIs values between 0 and 0.25, the habitat was described as "poorly suitable"; between 0.25 and 0.50, the habitat was said to be "fairly suitable"; for values ranging from 0.5 to 0.75, the habitat was "sub-optimal"; a unit was considered "optimal" for rHSIs values between 0.75 and 1.

3.5.3.2 Fish presence prediction maps

The maps were again drawn using MapInfo 8.5 Professional for Windows from each mesohabitat map produced as a result of the habitat surveys. Each mesohabitat on the map was assigned a colour code according to its calculated relative habitat suitability index.
The adopted colour code is shown in Table 3.8:

Table 3.8 Colour code used to represent habitat suitability

Relative Habitat Suitability Index value	Colour code used
Less than 0.25	Red
Between 0.25 and 0.50	Orange
Between 0.50 and 0.75	Light green
Greater than 0.75	Bright green

The resulting maps allowed the determination of where fish of each species should or should not be at a particular flow stage in the specific stream, in other words to identify the habitats most likely to host fish in each stream, and whether the suitable habitats remained the same or differed over a range of discharges. These maps could then be compared to the results of the fish surveys.

3.5.4 Fish data analysis

The location of fish observations was plotted onto the mesohabitat maps drawn for each reach at each flow surveyed in order to determine the spatial variation in fish observations. The number of observations recorded on each survey was used to study the evolution of the population during the survey period and to relate any variation to physical or biological influence. Fish length measurements were used to study the evolution of length frequency distribution of the observed fish between surveys, according to flow and to seasonality as well as the population structure.

The habitat parameters measured at each fish location were used for statistical analysis to characterize the habitat chosen by fish at different flows, and to see whether those characteristics fitted the habitat suitability curves and prediction maps. It also allowed the study of the potential influences of flow and season as well as biological processes on fish habitat use at the mesoscale. Measurements of depth, velocity and substrate were used in the building of habitat use curves.

3.5.5 Statistics used during the project

The SPSS package was used for all the data analysis in this project. Descriptive statistics such as mean, frequency and standard deviation were calculated. The statistical tests used were non-parametric using k non-related samples (Kruskal-Wallis test) or 2 non- related samples (Mann-Whitney test). These tests do not require normality of the data sets and allow the comparison of data from different surveys with respect to a common parameter. The absence of normality in this study's data sets resulted in the use of these tests instead of using parametric tests such as ANOVA. Kruskal-Wallis tests were used for example to compare the use of glides by bullheads on the 6 surveys that were carried out in the Dowles Brook (See chapter 4). The surveys were independent from one another. Mann-Whitney tests were used when comparing two independent samples, for example habitat use by adult brown trout at two different flows (see chapter 5). The observations at the two different flows were independent, which justified the choice of Mann-Whitney tests as opposed to Kruskal-Wallis tests.

3.5.6 Habitat use curves

Habitat use curves were created in order to compare them to the Habitat suitability curves and determine their value in terms of representation of habitat use by fish. They were built using Excel and the values of depth, velocity and substrate recorded at each fish location during the fish observations surveys. The range of depth and velocity chosen was between 0 and 1m.s^{-1}, divided into 0.1m /0.1m.s^{-1} categories. From the values of depth and velocity measured in the field, the frequency of use of each category of depth/velocity could be determined and then transformed into an array ranging from 0 to 1. With respect to substrate, the same protocol was used but instead of numerical values, the categories chosen corresponded to substrate type such as sand, gravel and cobble. This type of curve was built for all surveys all together, for each flow as well as for each life stage/size category. As a result they allowed the comparison of depth, velocity and substrate use according to flow and to life stage/size and reflected fish mesohabitat use.

3.6 SUMMARY

This chapter presented the methods and materials used in order to carried out the various aspects of this project, namely mesohabitat surveys, fish surveys, derivation of Habitat Suitability Index curves for bullhead and data analysis.

Four key points can be drawn from this chapter:

1. The method used for mesohabitat surveys was derived and adapted from the established MesoHABSIM technique in order to suit the particular needs and conditions of this project.
2. Snorkelling was used to monitor fish habitat use. This method was adapted to the differing ecology of the two fish species studied: 'standard' snorkelling was used for brown trout while survey of bullhead involved lifting of stones.
3. Derivation of Habitat Suitability Index curves for bullhead was carried out from the existing literature using the method developed by Franklin (2002). This was the first time HSI curves were developed this way for this species.
4. Analysis of the data obtained from both mesohabitat and fish surveys aimed at (i) the determination of the effect of flow regime on mesohabitat composition and variability, (ii) the study of the influence of mesohabitat variability and availability on fish habitat use among two species with differing ecology, (iii) testing the validity and reliability of HSI curves for both bullhead (built during this project) and brown trout (built in previous studies).

The results from investigation of habitat use by brown trout in a groundwater-fed stream are presented in Chapter 4.

CHAPTER 4

HABITAT USE BY BROWN TROUT (*SALMO TRUTTA*) IN A GROUNDWATER–FED STREAM

From the extensive literature existing on brown trout ecology (reviewed in Chapter 2), the species behaviour has been shown to be influenced by a variety of biotic and abiotic factors. Though a few studies have focused on the impact of flow variability on trout habitat use, a lot of uncertainties remain with respect to habitat use at the mesoscale and the behavioural patterns displayed by trout in response to flow.

This chapter presents the work carried out in order to achieve the objectives of this project in the River Tern. The 4 objectives, already stated in section 3.1.3 (p.16) are as follow:

1 Characterise the above species' habitat in groundwater and surface run-off influenced streams.
2 Use an intermediate scale (mesohabitat) approach to understand the implications of spatial pattern and habitat connectivity in streams.
3 Evaluate the temporal dynamics of habitat use and species' response to habitat variability in relation to flow regime.
4 Evaluate the accuracy and reliability of HSI curves.

Work in the River Tern involved the identification of the types of mesohabitats in which trout were found, the study of the possible influence of flow and season on the use of a particular type of mesohabitat, the determination of potential life-stage related use and whether other factors, both biotic and abiotic have an effect on the mesohabitat a fish may choose and/or use. Particularly, the study aimed to address the following research questions relating to the River Tern and brown trout (previously identified in generic terms in section 1.3.1).

RQ_2. How does instream mesohabitat composition vary over the range of flows experienced by the River Tern (groundwater influenced flow regime)? (Section 4.1)

RQ_3. Is there a pattern of mesohabitat use displayed by the brown trout population studied and if so what is it? (Section 4.3)

RQ_4. Does mesohabitat use by brown trout follow the same pattern as mesohabitat variability, i.e. is it influenced only by flow? (Sections 4.3.1 and 4.4.2)

RQ_5. Are other factors involved in brown trout habitat use? (Sections 4.3.2, 4.4.3 and 4.4.4)

RQ_6. What role is played by factors such as seasonality, habitat availability, life-stage and social interactions in the pattern of habitat use displayed by the surveyed population? (Sections 4.3.2, 4.4.3 and 4.4.4)

RQ_7. What are the key habitat characteristics that determine brown trout location in the study reach? (Section 4.6)

As a result, work on the data consisted of analysing the possible trends in the population parameters according to both flow and seasonality. In addition, this research examined the possible relationships between the physical factors: flow, mesohabitat availability, depth, velocity, cover and substrate and habitat use displayed by brown trout at the mesoscale in the selected stream. Furthermore it was intended to establish the relationship, if any, between mesohabitat availability and mesohabitat use as well as to study the effect of flow and seasonality on the fish use of particular types of mesohabitats. Finally, the relative influence of flow related factors and biological factors (such as competition and hierarchy) in determining brown trout habitat use were also investigated.

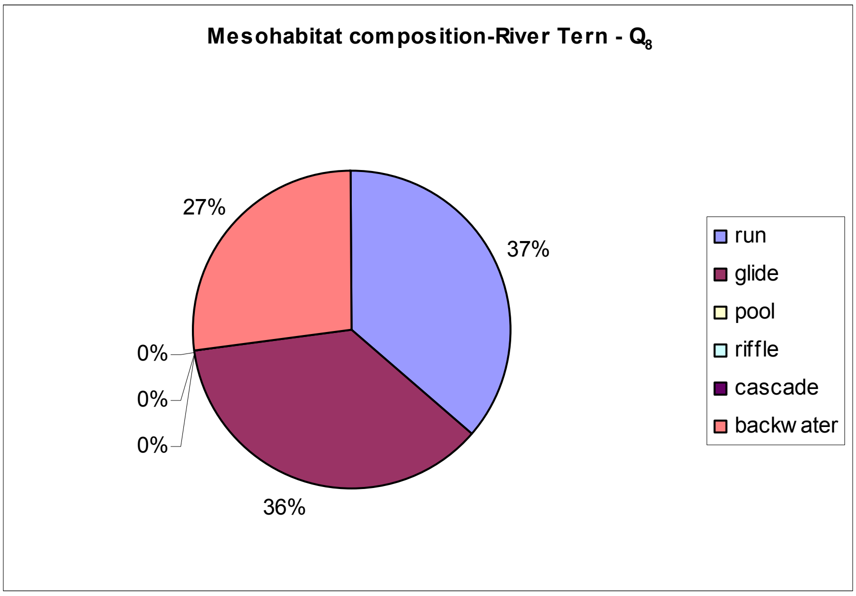
4.1 THE RIVER TERN: A GROUNDWATER-FED RIVER

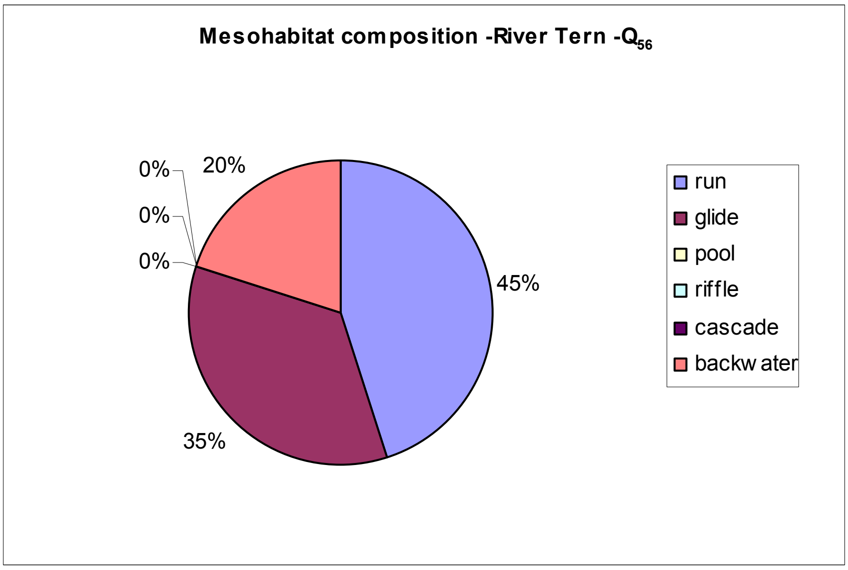
4.1.1 Mesohabitat composition according to flow

RQ_2. How does instream mesohabitat composition vary over the range of flows experienced by the River Tern (groundwater influenced flow regime)?

The River Tern's flow regime is groundwater dominated (Base Flow Index = 0.76; Q_{10}/Q_{90}=3.5) hence it constitutes a relatively stable environment for instream organisms. Indeed, groundwater input in the stream acts as a buffer so as to prevent any drastic changes in riverine variables such as water quality, temperature and physical variables like mesohabitat composition that could affect organisms. Figure 4.1 represents the evolution of mesohabitat composition with decreasing flow in the Tern, described at flows of Q_8 (0.5598 $m^3.s^{-1}$), Q_{56} (0.306 $m^3.s^{-1}$) and Q_{91} (0.139 $m^3.s^{-1}$). Mesohabitat surveys carried out on this stream for 18 months showed no significant change in the mesohabitat composition of the stream. Runs, glides and backwaters were present at all flows with the rare occurrence of a riffle or a pool. The proportion of each mesohabitat type hardly varies between flows. At all flows, glides and runs were the two dominant types of mesohabitats. This pattern of mesohabitat variability (or lack of variability) is characteristic of groundwater-dominated flow regimes (Geoffrey Petts, *pers.comm*.). This is further shown by Figure 4.2, which shows the spatial arrangement of mesohabitats in the River Tern at 3 different flows.

Figure 4.3 shows a summary map of the stream with the location of fish observations at all surveyed flows. To summarize the observations made on the River Tern and to get a broad picture of the interactions existing between fish and their environment, the map of the stream was divided into units of varying lengths representing the variability of mesohabitats occurrence in the reach. For each of the units, the total amount of fish (sum of all observations on all surveys) and their location in the unit (left bank, mid-channel, right bank) were plotted and on the side of the map, qualitative and quantitative information were added with respect to the habitat in the unit, such as the type of mesohabitat and how it evolves in time, cover, substrate, mean depth and mean velocity. Parameters relating to the fish observations e.g. proportion of parr/adult in the unit, mean depth and mean velocity of observations, behaviour (resting, feeding, holding station, etc.) as well as the probability that a fish will be observed in a given unit (calculated dividing the number of surveys where fish were observed in a unit by the total number of surveys) were also noted. The aim was to provide an integrated view of the instream environment-fish interactions in the River Tern.





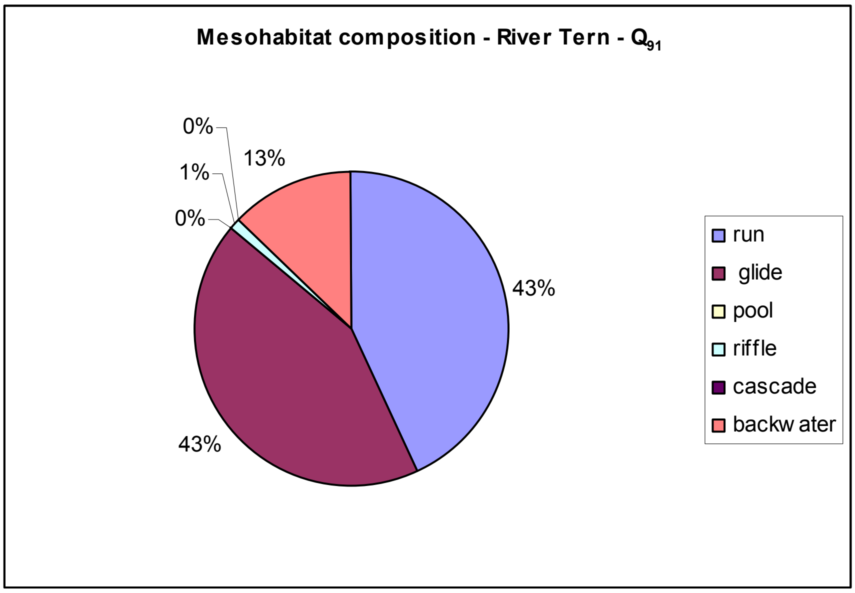


Figure 4.1 Mesohabitat composition at three different flows in the River Tern, Norton in Hales

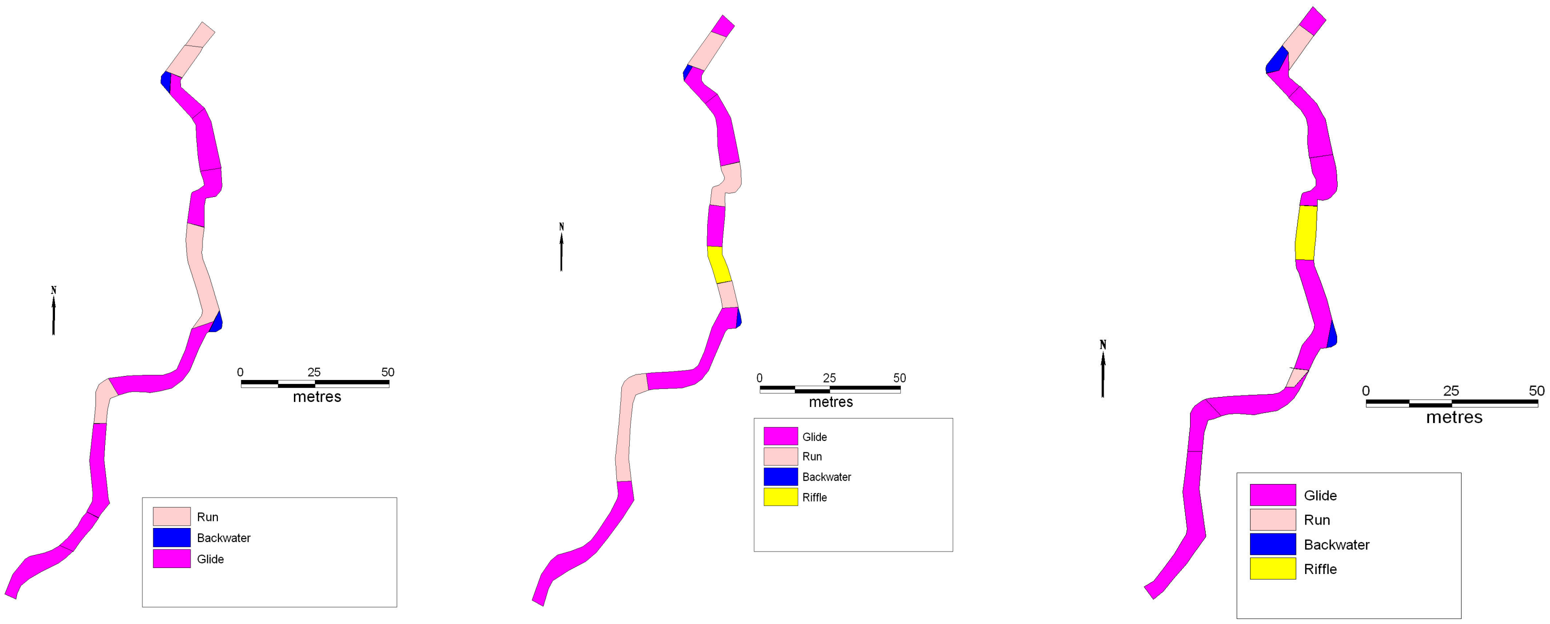


Figure 4.2 Evolution of the spatial arrangement of mesohabitats in the Tern at Norton in Hales at Q_{51}, Q_{61} and Q_{77}

The study reach at Norton in Hales is located between a concrete road bridge at the upstream end and an electric fence at the downstream end. The right bank of the reach (when looking downstream) is surrounded by a riparian wood while the left bank is separated from a cattle grazing field by a small riparian wood that stops around 30 metres before the downstream end of the reach, leaving these last 30 metres of reach without overhead cover. Fourteen units were identified on the map, eight of which are stable in terms of mesohabitat type throughout the flows: four glides, two runs and two backwaters. The wavy lines between the units indicate that the boundaries between the units are not fixed and that the change from a type of mesohabitat to another occurs progressively. The green areas within the stream indicate permanent instream woody debris dams and/or fallen trees across the channel. Finally, the yellow circles at fish locations indicate the probability of fish occurrence in a particular unit, i.e. the ratio of the number of times fish were observed in a particular unit against the number of surveys on the reach.

Figure 4.3 shows that fish observations are scattered along the reach and are not concentrated in a particular area like one of the ends of the reach for example. However, the probability of fish occurrence varied between the fourteen identified units and ranged from 0 for all backwaters to 1 for units 1 and 2 (a glide/run and a run respectively). Thus, not all mesohabitats are equal in their probability of hosting trout. Trout were not observed with the same probability of occurrence even within a particular type of mesohabitat, e.g. run/glide 1 presents a probability of occurrence of 1 whereas the probability of encountering trout in run/glide 9 is only 1/6.

Therefore it can be suggested that not only the type of mesohabitat is important with respect to fish habitat use, i.e. run or glide compared to backwater, but also that the location of the mesohabitat in the stream may have some influence on fish behaviour. Its location can directly affect fish habitat use or indirectly by resulting in different characteristics of the mesohabitat: the type and extent of vegetation, the type of banks and of riparian zone can vary along the stream and according to the time of year and affect habitat suitability from a fish perspective. Moreover, the extent of variability in depth and velocity varied for each type of mesohabitat. This is studied in more detail in the next section.

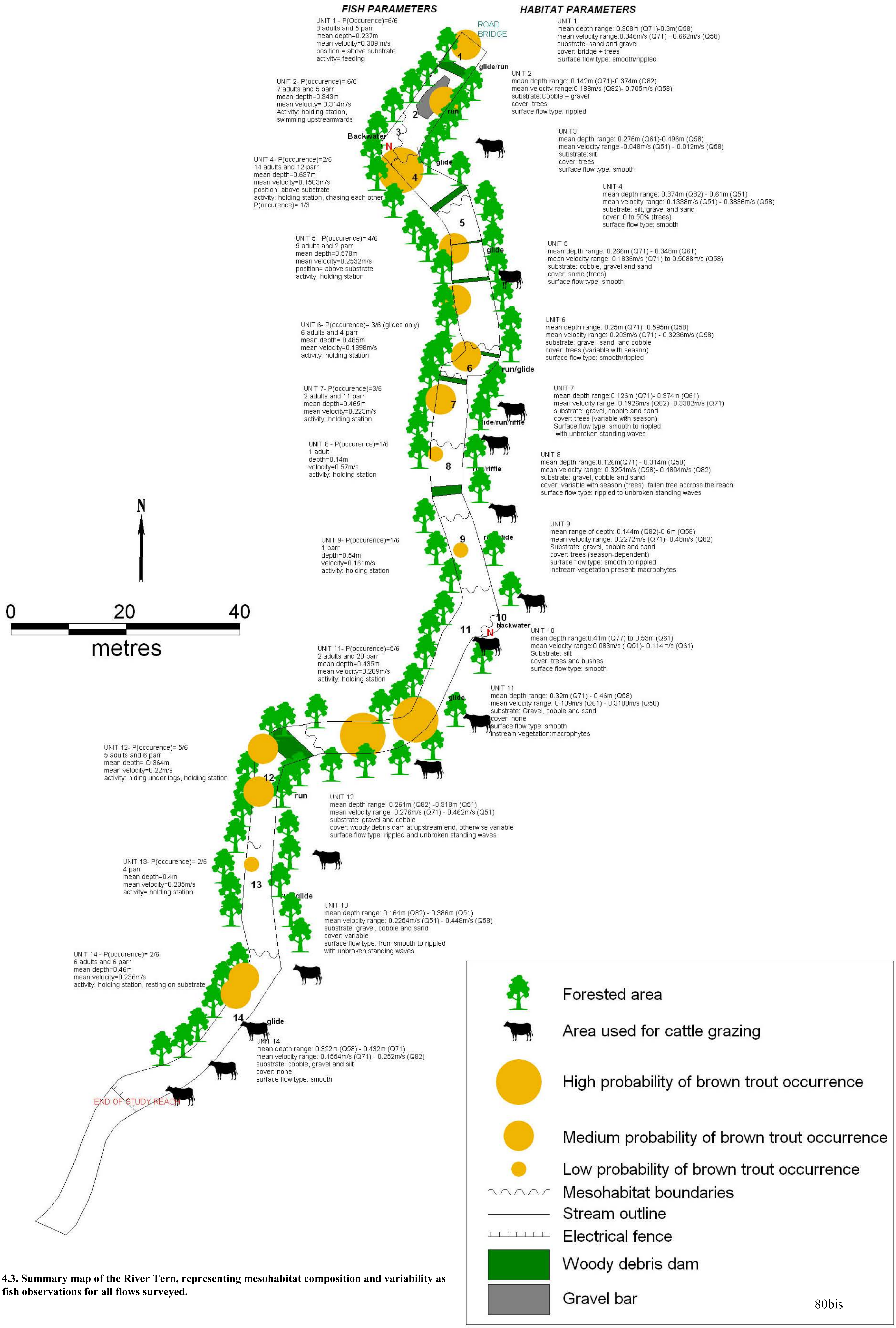


Figure 4.3. Summary map of the River Tern, representing mesohabitat composition and variability as well as fish observations for all flows surveyed.

This section aimed to address RQ_2 (How does instream mesohabitat composition vary over the range of flows experienced by the River Tern (groundwater influenced flow regime)?) by showing the results of mesohabitat mapping surveys carried out over a range of flow. Results show that under a groundwater influenced flow regime, mesohabitat composition shows little variability across flow. The three main types of mesohabitat identified in the reach, i.e. glide, run and backwater, remain present at all flows and the relative amount of each mesohabitat type remains also constant at all flows.

4.1.2 Evolution of mesohabitat characteristics with flow

Physical characteristics such as depth and velocity are influenced by flow. To investigate the influence of flow on hydraulic characteristics, mean depth and mean velocity values and associated standard deviations were calculated according to flow for each major type of mesohabitat present in the River Tern. Tables 4.1, 4.2 and 4.3 below summarize the evolution of runs, glides and backwaters' depth and velocity characteristics according to flow.

Table 4.1 Evolution of run depth and velocity values according to flow, River Tern at Norton-in-Hales.

Flow	Actual discharge ($m^3.s^{-1}$)	Number of measurements	Mean depth (m)	Depth Standard deviation	Mean velocity ($m.s^{-1}$)	Velocity standard deviation
Q_8	0.560	15	0.437	0.140	0.443	0.231
Q_{33}	0.370	25	0.336	0.079	0.435	0.133
Q_{42}	0.345	25	0.465	0.174	0.471	0.173
Q_{51}	0.325	20	0.231	0.092	0.404	0.270
Q_{56}	0.306	45	0.273	0.109	0.452	0.215
Q_{61}	0.260	19	0.275	0.114	0.359	0.112
Q_{72}	0.233	8	0.203	0.106	0.404	0.232
Q_{80}	0.193	40	0.222	0.092	0.367	0.134
Q_{91}	0.139	50	0.201	0.095	0.352	0.171
All discharges	N/A	247	0.281	0.139	0.405	0.186

Table 4.1 shows that variations in flow result in significant variations in run depths (Kruskal-Wallis Chi sq. 83.787, d.f.=8, p=0.000) as well as in run velocities (Kruskal-Wallis Chi sq. 19.785, d.f.=8, p=0.011). Both parameters tend to decrease with lower flows.

Table 4.2 Evolution of glide depth and velocity values according to flow, River Tern at Norton-in-Hales

Flow	Actual discharge ($m^3.s^{-1}$)	Number of measurements	Mean depth (m)	Depth Standard deviation	Mean velocity ($m.s^{-1}$)	Velocity standard deviation
Q_8	0.560	15	0.479	0.125	0.395	0.124
Q_{33}	0.370	30	0.457	0.185	0.290	0.139
Q_{42}	0.345	15	0.648	0.243	0.378	0.138
Q_{51}	0.325	35	0.416	0.167	0.214	0.107
Q_{56}	0.306	35	0.379	0.192	0.242	0.124
Q_{61}	0.260	30	0.391	0.163	0.207	0.149
Q_{72}	0.233	35	0.330	0.142	0.205	0.112
Q_{80}	0.193	40	0.362	0.126	0.209	0.076
Q_{91}	0.139	50	0.315	0.144	0.168	0.090
All discharges	N/A	285	0.393	0.179	0.233	0.129

Table 4.2 shows significant differences in glide depth (Kruskal-Wallis Chi sq. 44.513, d.f.=8, p=0.000) as well as glide velocity (Kruskal-Wallis Chi sq. 57.198, d.f.=8, p=0.000), which both decrease with flow.

Table 4.3 Evolution of backwater depth and velocity values according to flow, River Tern at Norton-in-Hales

Flow	Actual discharge (m3.s-1)	Number of measurements	Mean depth (m)	Depth Standard deviation	Mean velocity (m.s-1)	Velocity standard deviation
Q8	0.560	12	0.538	0.161	-0.053	0.092
Q33	0.370	30	0.350	0.140	0.051	0.078
Q42	0.345	16	0.456	0.210	-0.072	0.082
Q51	0.325	8	0.404	0.170	-0.061	0.033
Q56	0.306	18	0.309	0.166	0.009	0.063
Q61	0.260	7	0.347	0.163	-0.068	0.048
Q72	0.233	8	0.375	0.108	-0.069	0.053
Q80	0.193	25	0.375	0.103	-0.015	0.053
Q91	0.139	15	0.381	0.091	-0.435	0.074
All discharges	N/A	139	0.385	0.155	-0.019	0.081

Likewise, Table 4.3 show significant variations in backwater depth (Kruskal-Wallis Chi sq. 20.422, d.f. =8, p=0.009) and backwater velocity (Kruskal-Wallis Chi sq. 46.281, d.f.=8, p=0.000).

The analysis of the variation in mesohabitat composition in the River Tern and in mesohabitat depth and velocity according to flow reveals that scale is important to consider when studying instream habitat. Though mesohabitat composition in itself is not influenced by variations in flow, depth and velocity values within every mesohabitat is subject to the influence of flow and vary accordingly. For all mesohabitat types, Tables 4.1, 4.2 and 4.3 show that, as flow decreases, mesohabitat depth and velocity values decrease significantly. However, at Q_{42} (0.345 $m^3.s^{-1}$, May 2006) glide and run depths increased compared to values at higher flows. This could be due to the presence of macrophytes in the stream at this time of year which results in a ponding effect and hence an increase in water depth (Armitage and Cannan, 2000).

The following section shows the results from the analysis of data collected during the brown trout surveys that were carried out on the River Tern.

4.2 EVOLUTION OF BROWN TROUT POPULATION PARAMETERS DURING THE SURVEY SEASON

Six fish surveys by direct underwater observations were carried out between June and November 2006 on the River Tern at the Norton-in-Hales site (Shropshire). The flows surveyed ranged from Q_{51}, i.e. 0.2736$m^3.s^{-1}$, in October, to Q_{82}, i.e. 0.165$m^3.s^{-1}$, in late July. The number of brown tout observations ranged from N=10 in June (Q_{58}) to N=38 in September (Q_{77}), which made a total of 139 observed individuals and an average of 23 observations/survey.

Only parr and adults were observed during the surveys: parr have a length between 8 cm and 20cm, as defined by Dunbar *et al.* (2001); adults 'minimum length is 20 cm. No fry (fish with a total length less than 7cm) were observed on any occasion. Figure 4.4 shows the variation in the number of brown trout identified during the underwater surveys between June and November 2006.

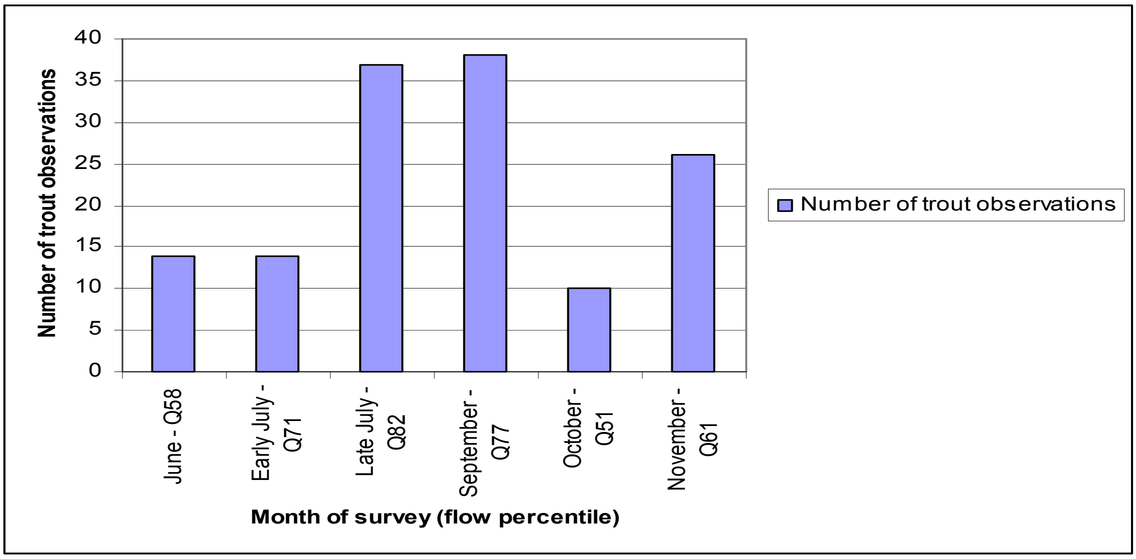


Figure 4.4 Evolution of the number of brown trout observations during the survey season

The number of observations peaked in late July and September (37 observations compared to 14 in June and early July) and then decreased in autumn. The minimum number of observed fish occurred in October (10 fish recorded). More fish were observed in November (25 recorded). Figure 4.5 shows the seasonal evolution of the size structure of the observed brown trout population.

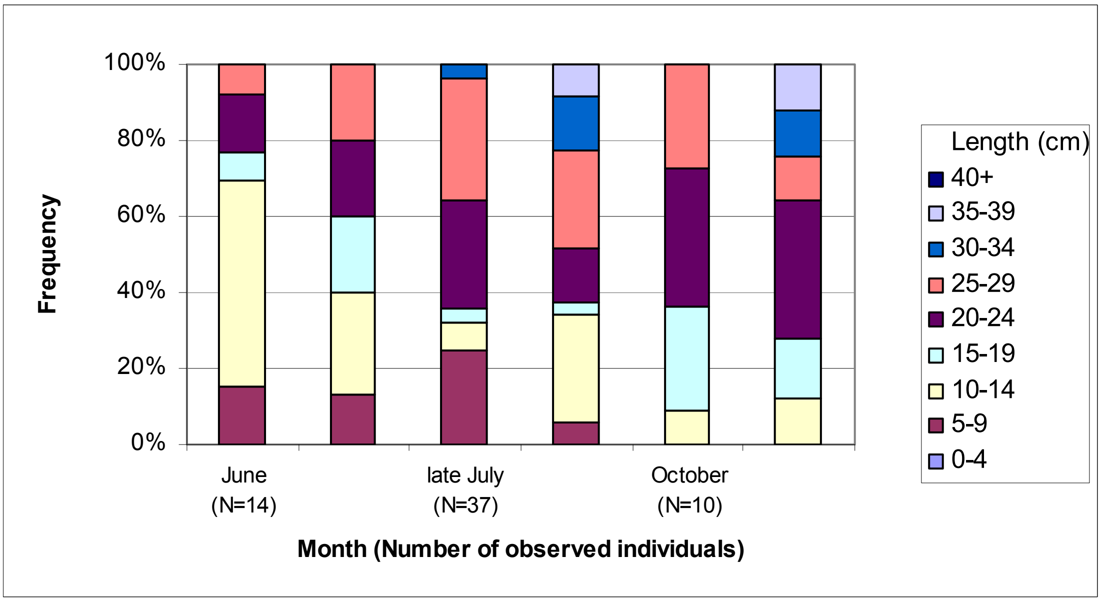


Figure 4.5 Seasonal evolution of the length frequency distribution of brown trout

Figure 4.5 shows a steady decline in the number of individuals with a length up to 19 cm (parr) and at the same time a steady increase in the number of adults (length = 20+ cm).

This reflects the fact that as younger individuals grow and gain in size, the number of individuals in the smaller size classes decreases. Another explanation would be the migration of juvenile individuals to other parts of the river outside the study stream and the migration of larger individuals into the study stream. However it is doubtful that the latter explanation would result in such a regular pattern of increase/decrease in the size of length classes. Figure 4.6 represents the evolution of the proportion of the two life stages identified in the stream (parr and adult).

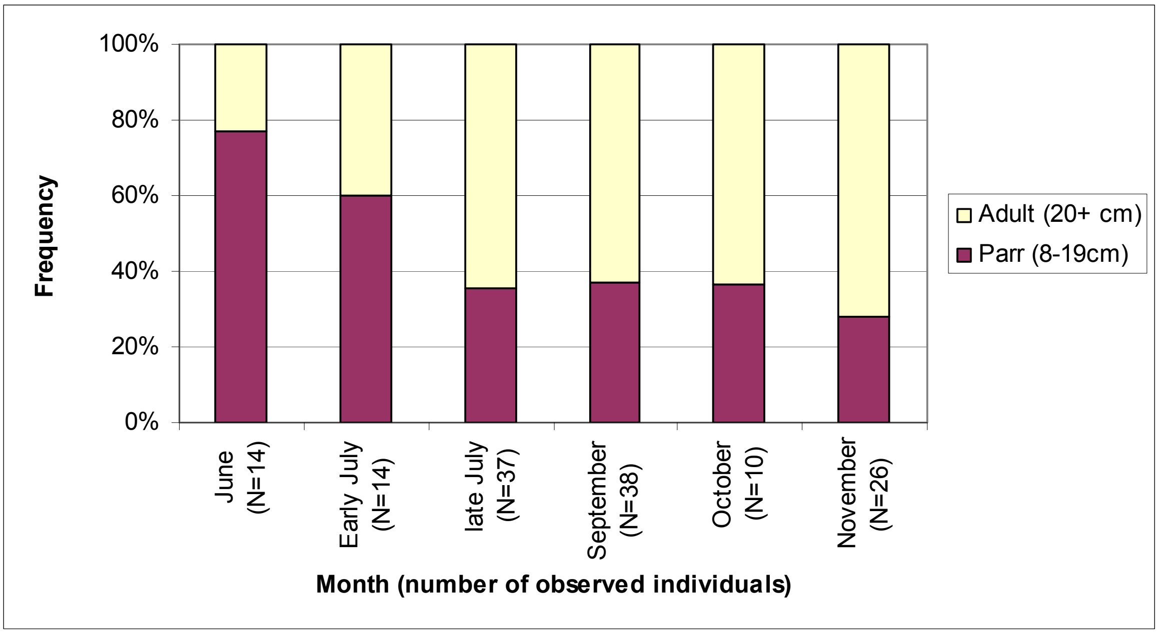


Figure 4.6. Seasonal evolution of the brown trout population structure in the River Tern

Figure 4.6 shows that from June onwards the proportion of parr in the population decreased steadily from accounting for 77% of the observations in June to 28% of the observed individuals in November. Adult individuals represented only 23% of the observations in June but their proportion in the population increased to 72 % in November. This pattern shows that the population consisted mainly of juveniles in late spring (that were fry stages in April-May) that grew during summer and autumn to become adults. Research questions 3, 4 and 5 are investigated in the next section:

RQ_3. Is there a pattern of mesohabitat use displayed by the brown trout population studied and if so what is it? (Section 4.3)

RQ_4. Does mesohabitat use by brown trout follow the same pattern as mesohabitat variability, i.e. is it influenced only by flow? (Section 4.3.1)

RQ_5. Are other factors involved in brown trout habitat use? (Section 4.3.2)

4.3 MESOHABITAT USE BY BROWN TROUT

RQ_3. Is there a pattern of mesohabitat use displayed by the brown trout population studied and if so what is it?

4.3.1 Influence of flow

RQ_4. Does mesohabitat use by brown trout follow the same pattern as mesohabitat variability, i.e. is it influenced only by flow?

At each flow surveyed, the position of brown trout was recorded in the stream and plotted on a mesohabitat map of the reach. These observations are shown in Figure 4.7, according to increasing flow percentile (*i.e.* decreasing discharge).

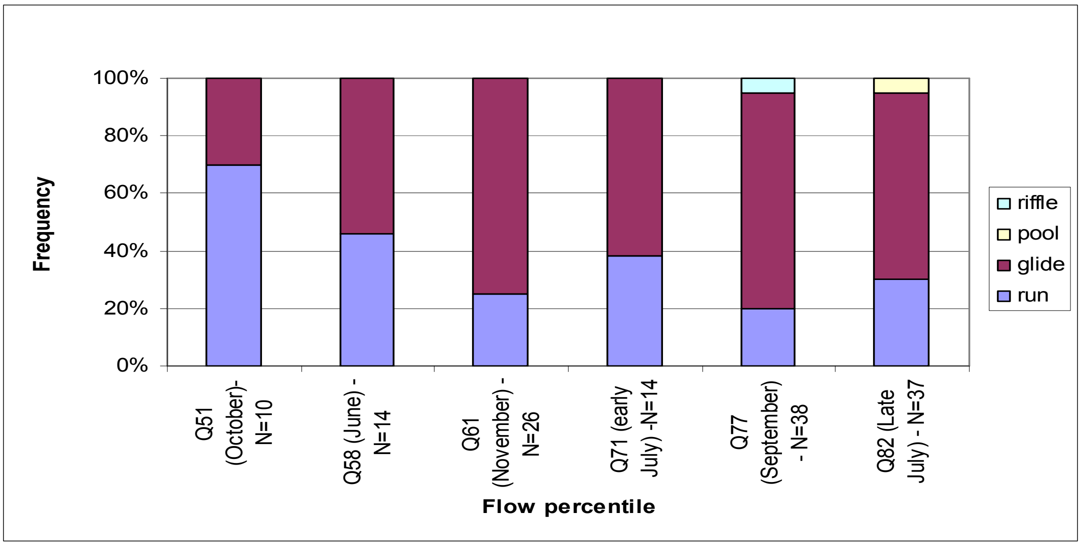


Figure 4.7 Mesohabitat use by brown trout according to decreasing flow in the River Tern

Figure 4.7 shows that the two mostly used mesohabitats are runs and glides, which can be explained by their predominance in the stream. As flow decreased, brown trout in this stream increased their use of glides (slower, deeper mesohabitats) compared to runs (shallower and faster-flowing mesohabitats). This can be the result of either a deliberate choice by the fish (better conditions) or either a decrease in the proportion of runs available in the stream (see Section 4.4.4). At lower discharges (here Q_{77} and Q_{82}) a small percentage of the trout population used riffles and pools, which was not observed at higher discharges. At the same time a higher number of fish could be observed in the stream (37 and 38 compared to an average of 16 individuals at higher flows). Low flows generally result in the loss of usable habitats for the fish - decreasing depth becomes a limiting factor for brown trout (Mike Dunbar, *Pers.comm.*), which can be critical as the number of individuals in the population increases. As a result, most of the population will carry on using the mesohabitat they predominantly use whereas some individuals will have to use other mesohabitats that are suboptimal. Statistical analysis of mesohabitat use according to flow shows no significant influence of flow on brown trout habitat use (Kruskal-Wallis Chi sq. 5.000, d.f.=5, p=0.416).

Two life-stages could be observed during the survey period, i.e. parr (juvenile up to 19 cm long) and adults (20+cm in total body length). The respective habitat uses of these two life stages were analysed as well as the possible influence of seasonality. Mesohabitat use by brown trout parr and adults respectively are shown in Figures 4.8 and 4.9 below. For clarity, the two highest flows surveyed for fish, Q_{51} and Q_{58}, were combined, as well as the two lowest flows surveyed, Q_{77} and Q_{82}.

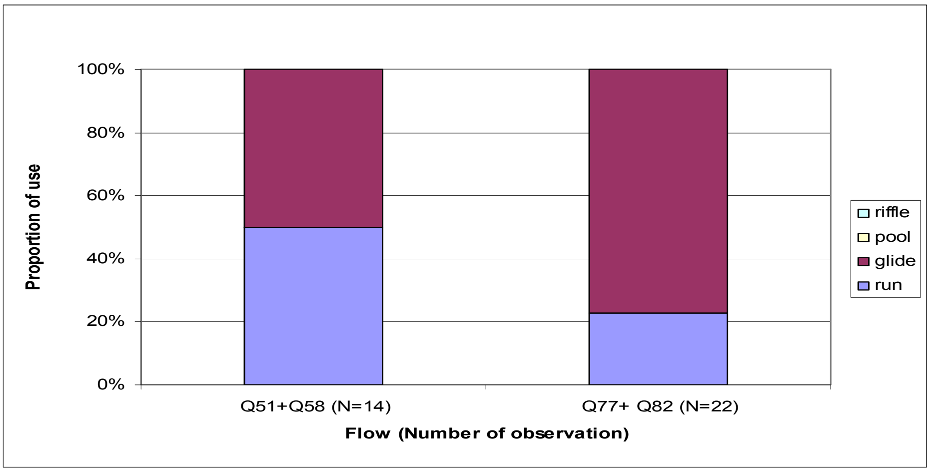


Figure 4.8 Comparison of habitat use by brown trout parr for the two highest and two lowest flows

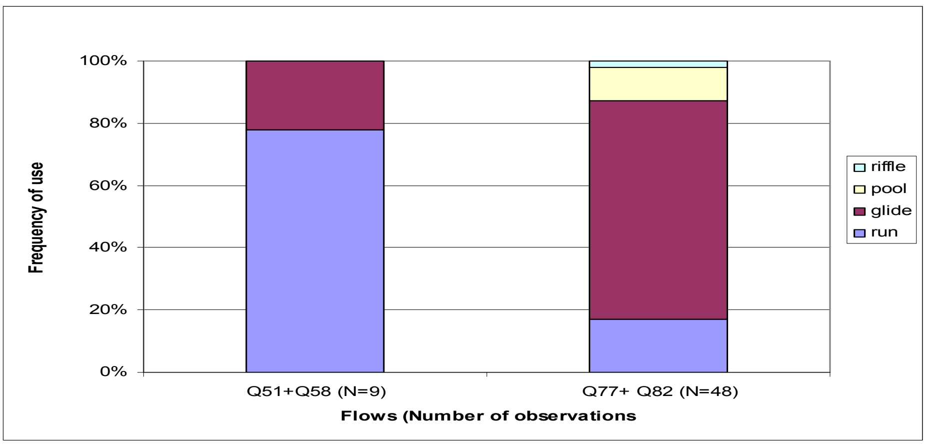


Figure 4.9 Comparison of habitat use by adult brown trout for the two lowest and two highest flows

For both life stages, significant differences in mesohabitat use according to flow are observed, though the sharpest differences are displayed by the adult life stage. Parr habitat use varies significantly from a 50/50 proportion for glides and runs at higher flows to a 80/20 proportion in favour of glides at lower flows (Mann-Whitney U=0). 82% of adult observations were made in runs at higher flows whereas at lower flows runs represented only 18 % of the observations (Mann-Whitney U=0). Adult numbers vary dramatically between the two flows with only 9 observations for the two highest flow surveys and 48 observations at the lowest flows surveyed. Statistical comparison of the two life stages with respect to habitat use show significant differences at the lowest flows surveyed (Mann-Whitney, U=0) with adults displaying a greater use of runs than parr. Similarly, at the highest flows surveyed glide use is significantly different between life stages (Mann-Whitney U=0).

In response to question RQ_4 (Does mesohabitat use by brown trout follow the same pattern as mesohabitat variability, i.e. is it influenced only by flow?), this subsection showed that brown trout were mostly found in glides and runs and that differences in mesohabitat use existed between the highest and lowest flows surveyed as well as between parr and adult trout. However, since statistical analysis of overall mesohabitat use by brown trout did not show any significant influence of flow, the influence of seasonality was hence investigated and the results are shown in section 4.3.2.

4.3.2 Influence of seasonality on behaviour

RQ_5. Are other factors involved in brown trout habitat use?

RQ_6. What role is played by factors such as seasonality, habitat availability, life-stage and social interactions in the pattern of habitat use displayed by the surveyed population?

The variation in levels of precipitation and evaporation (driven by temperature) throughout the year influences river flow. As a result, brown trout may adapt their habitat use seasonally. To investigate this possibility, frequency of habitat use by each observed life stage was plotted against time expressed as months during which surveys took place. Figures 4.10 and 4.11 below show the evolution of habitat use by both parr and adults according to season, i.e. late spring to mid-autumn.

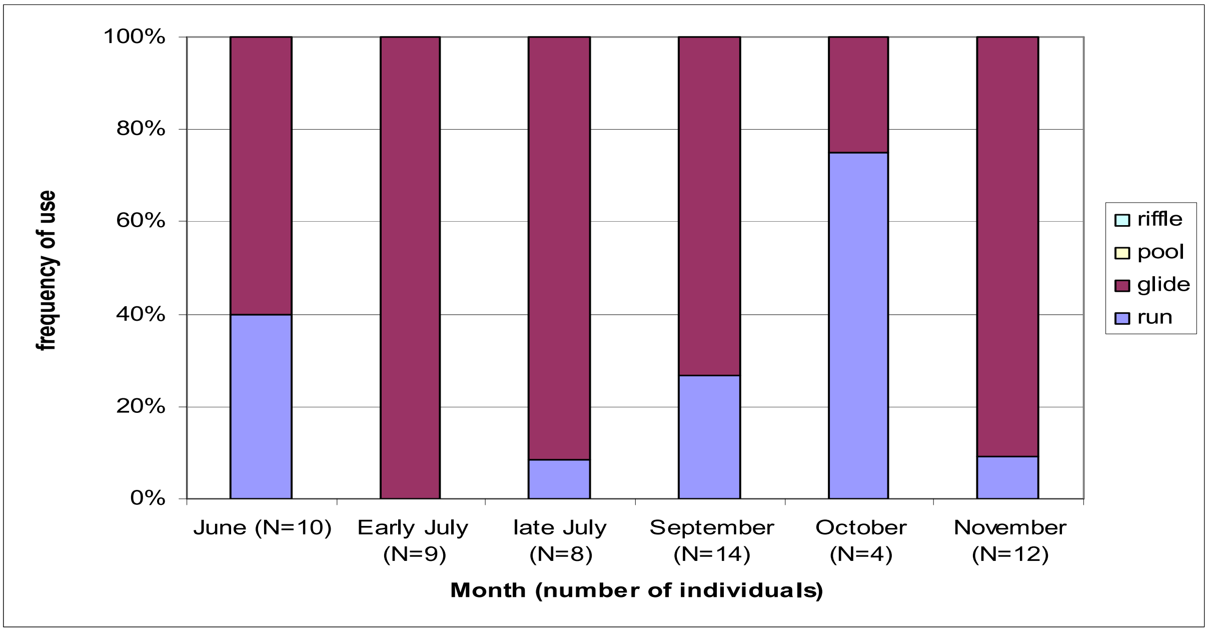


Figure 4.10 Seasonal evolution of mesohabitat use by brown trout parr

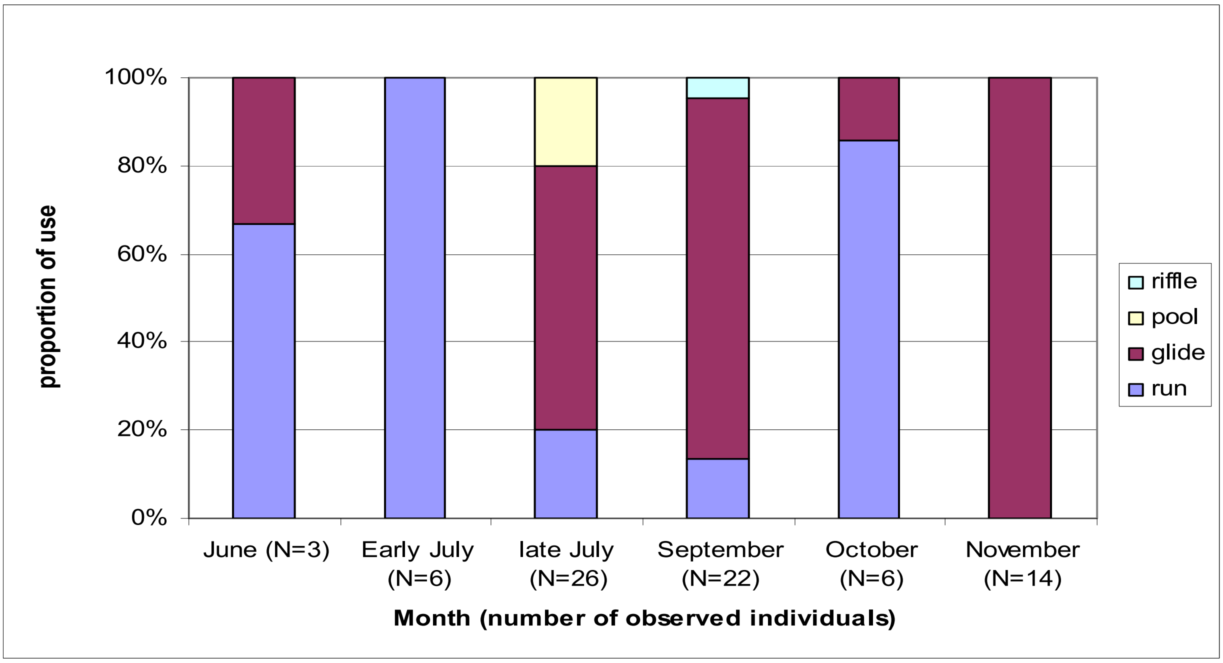


Figure 4.11 Seasonal evolution of mesohabitat use by adult brown trout

When looking at habitat use by both life stages together (Figures 4.10 and 4.11), a pattern can be distinguished. In late spring-early summer (surveys of June and early July), segregation between parr and adults occurred with respect to the mesohabitats where fish were observed. In June 65% of adults used runs and 35% used glides. The proportion is reversed as far as parr are concerned with 60% of them using glides and 40% found in runs. The segregation is even more apparent when considering early July observations. Adults were observed only in runs whereas parr were found only in glides (see section

4.4.3). Statistical analysis show no significant influence of seasonality on brown trout habitat use (Kruskal-Wallis Chi sq. 5.000, d.f.=5, p=0.416), which results from the small size of the study sample. Indeed, the proportions mentioned above are based on uneven numbers of observations: 3 observations in June, 6 in early July compared to 20+ for late July onwards.

This subsection allowed to partly answer research questions RQ_5 and RQ_6. It showed indeed seasonality and life stage influenced brown trout habitat use: parr and adult displayed different patterns of habitat use throughout the survey season. Seasonality influenced habitat use: parr used mostly glides throughout the summer and switched to runs in October before returning to glides in November.

As shown in section 4.1.2, depth and velocity vary within each type of mesohabitat. It thus appeared relevant to study the range of depth and velocity values mostly used by brown trout, as shown in section 4.2.3.

4.3.3 Depth and velocity used by brown trout

To further investigate the physical characteristics, such as depth and velocity that brown trout seek in a mesohabitat, data about mean depth and mean velocity use according to season were analysed and are shown in Figures 4.12 and 4.13 below.

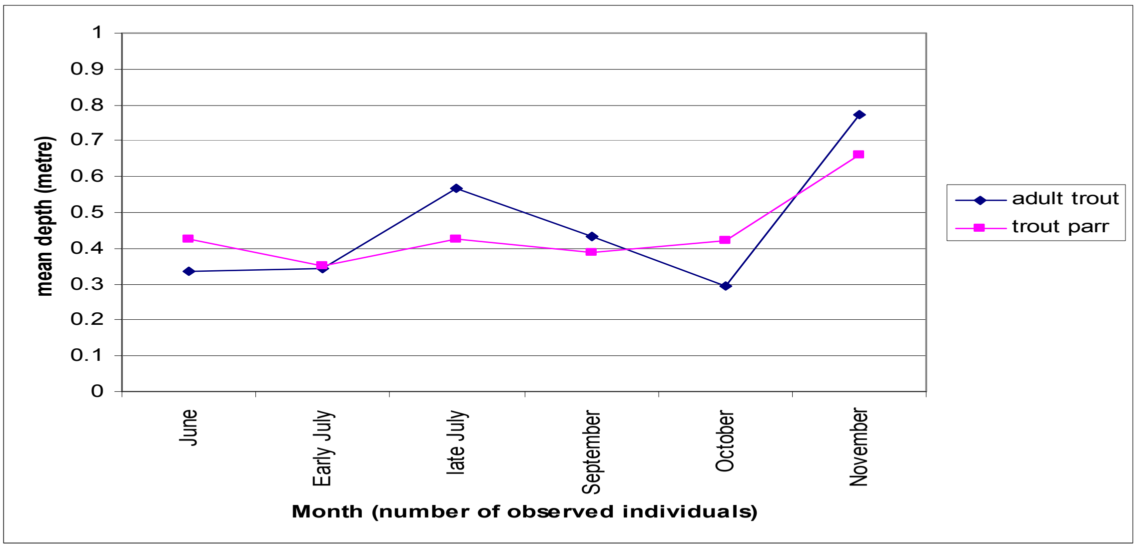


Figure 4.12 Seasonal evolution of the mean depth used by brown trout (all life stages)

Mean depth use by trout parr remained fairly constant at around 0.4 m from late spring to October. Statistical analysis of used depth according to flow shows no significant variation in the depths used by brown trout according to season (Kruskal-Wallis Chi sq. 5.158, d.f.=4, p=0.271). In November, an increase in the mean depth use was observed (0.68 m). With respect to adult brown trout, mean depth use varied from month to month with an increase from late spring to late July (0.58 m) then a decrease though to October (0.3 m) and then a sharp increase in depth used in November (0.78 m).

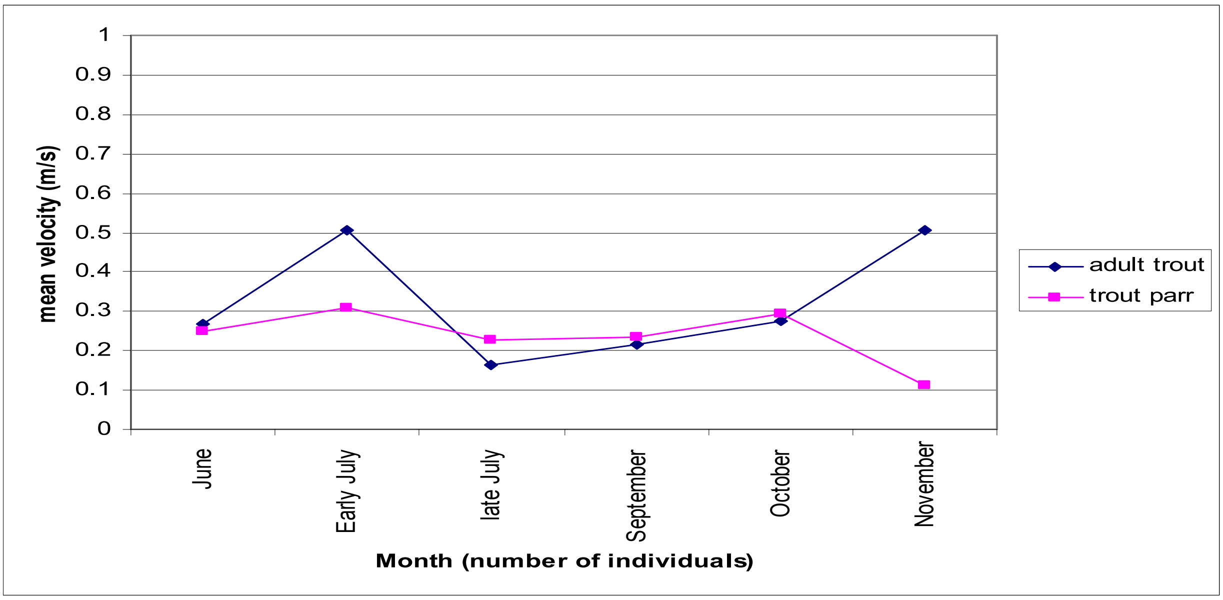


Figure 4.13 Seasonal evolution of the mean velocity used by brown trout (all life stages)

Differences in velocity use can be observed between the two life stages. Parr remained constant in their use of velocity throughout the survey period (between 0.25 and 0.3m.s^{-1}) except between October and November when they used lower velocity (0.1m.s^{-1}). Adult velocity use was more variable. Mean used velocity increased in early July (0.5 m.s^{-1}) and then dropped in late July to 0.16 m.s^{-1} to then steadily increase from late July onwards. Significant variations in used velocities according to season for both life stages were observed (Kruskal-Wallis Chi sq. 14.494, d.f.=4, p=0.006). These differences in terms of velocity use can be explained by the fact that parr mostly used glides throughout the survey period, which are slow flowing habitats. Adults regularly switched from one type of mesohabitat to the other, thus explaining the pattern of velocity used.

The results presented enlighten particular trends in brown trout mesohabitat use, particularly according to seasonality and life stage. However to fully understand these trends, their analysis and interpretation in the context of the stream hydrology and geomorphology and the species ecology is needed, which is presented in section 4.4.

Section 4.3 addressed research question RQ_3 (Is there a pattern of mesohabitat use displayed by the brown trout population studied and if so what is it?): the brown trout population in the River Tern displayed a strong association with runs and glides throughout the year. This pattern of mesohabitat use appeared to be influenced mainly by seasonality and life stage and possibly the stable flow and mesohabitat conditions experienced in the stream.

4.4 ANALYSIS AND INTERPRETATION: FACTORS RESPONSIBLE FOR TROUT HABITAT USE

4.4.1 Variation in the number of observations

Migration events cannot be excluded as a reason for the variation in trout numbers during the survey season. The substantial difference between the numbers of observations (see section 4.2) in late spring-early summer (June and early July with N=14) and the numbers observed in mid-late summer (N=37 and N=38 for late July and September respectively) as well as the decrease, once again, in the number of observations in autumn suggests some fish movements to and from the study stream. It is possible that the instream conditions were not favourable in the early summer, hence the low number of observations. In that case, improvement of the conditions in late summer may have attracted fish from outside the study stream, with subsequent migration outside the reach in autumn. Water quality and environmental conditions in the Norton-in-Hales reach of the River Tern may be more suitable for brown trout compared to other parts of the Tern catchment, which could explain some immigration event and the rise in the numbers of observed fish. Indeed pollution has been recorded in the River Tern downstream of Market Drayton, a few miles from Norton in Hales (Environment Agency, Online). This explanation is offered given that both the survey method and the surveyor have remained the same throughout the survey period. Fish movements can have an influence on fish habitat use. Nonetheless it is necessary to interpret the results with respect to flow variability first, which is presented in section 4.4.2.

4.4.2 Flow influence on mesohabitat use

RQ$_4$. Does mesohabitat use by brown trout follow the same pattern as mesohabitat variability, i.e. is it influenced only by flow?

In section 4.3.1, the variability in habitat use shown in Figure 4.7 can be attributed to several factors. Firstly, the availability in runs decreases with flow therefore brown trout use the next most preferred and available habitat in the stream, which is glide. That would imply that the proportion of glides in the stream increases with decreasing flow. Secondly, the switch in habitat results from a deliberate choice by brown trout, corresponding to the needs of the fish during this particular type of flow. However for the latter, one would need to explain that some fish (both adults and parr) switch mesohabitat whereas others keep on using the same. Thirdly, the number of fish among both life stages increased as discharge decreased. The switch in mesohabitat at lower discharge could be density dependent: fish use the mesohabitats where the density of fish is less.

Parr and adult mesohabitat use for the two highest and two lowest flows surveyed were illustrated in Figures 4.8 and 4.9. These two figures show that parr only used runs and glides whereas adults, though mainly found in these same mesohabitats, also used pools and riffles, but only at lower flows. Comparison of habitat use between the two life stages shows that though parr and adults both use glides and runs, the extent of use of each type of mesohabitat is not the same. At higher discharge, parr were found equally in glides and runs whereas for the same flows, adults were mostly found (78%) in runs with the rest of the observations made in glides. At these flows there are more parr in the population than adults (14 and 9 respectively). This suggests that the difference in the proportion of habitat use between the two life stages could be life stage-related. Indeed, adults, whose numbers are inferior to those of parr, use mainly runs at higher discharge. So either adult first choice of habitat is run while that of parr is glide, or more subtle factors determine habitat use between life stages.

A characteristic of salmonids is the hierarchy that exists within a population with bigger individuals being the dominant ones and the smaller ones at the lower end of the hierarchical scale. Parr are often at the bottom of the hierarchy due to their size hence they do not have as much choice in terms of mesohabitats except if those are free of higher rank trout, i.e. free of fish or used only by similar size/age trout. At the highest flows surveyed, habitat is not limited, mostly with respect to usable depth. As a result, most of adult trout may use runs as their first choice and part of the parr population may still be able to use runs while the remaining parr individuals may have to use alternative locations, e.g. glides.

However at lower flows, habitat use by both life stages was observed to be in similar proportions with a higher use of glides than runs. The only difference resides in the use of other habitats by adults, e.g. riffles and pools. The lack of suitable habitat at low flow can lead to the use of other habitats even though they are less suitable. The fact that parr still only used glides and runs could lead to the following hypotheses: 1.juveniles have less experience in investigating other possible suitable habitats in the stream 2. pools and riffles are characterised by conditions not suitable for juvenile life stages, which is indicated in the Habitat Suitability Index curves for parr developed by Dunbar *et al.* (2001): riffles display velocities too high for juvenile trout. Pools display suitable characteristics but their occupation by adults may prevent their use by juvenile life stages. Also, another possible explanation could be that pools and runs have more value as habitats than glides so that they are used by the higher ranked trout and the rest of the population (both adults and parr) are left with no other alternative than to use glides. Habitat use by brown trout is indeed size-structured (Heggenes *et al.*, 1993) and lower flows, through the decrease in usable areas, enhance intraspecific competition. Several studies on brown trout (Heggenes *et al.*, 1993; Baran *et al.*, 1997; Eklov *et al.*, 1999) stress the key role that size related intraspecific competition plays within salmonid populations in general and brown trout populations in particular. Specifically, Baran *et al.* (1997) record “a strong spatial segregation between fry and adult life stages”, which agrees with the findings of this project. Individual behaviour may also account for the few observations made in pools and riffles and research is needed into the role and importance of individual behaviour in patterns of mesohabitat use.

Flow variability in the Tern (see hydrograph in Chapter 3) is relatively low given the groundwater input in this river. As a result, it is possible that other factors, such as seasonality, play a role in influencing brown trout habitat use (RQ_5 and RQ_6). Research Question 5 (Are other factors involved in brown trout habitat use?) and Research Question 6 (What role is played by factors such as seasonality, habitat availability, life-stage and social interactions in the pattern of habitat use displayed by the surveyed population?) are discussed in section 4.4.3.

4.4.3 Influence of seasonality on mesohabitat use

RQ_6. What role is played by factors such as seasonality, habitat availability, life stage and social interactions in the pattern of habitat use displayed by the surveyed population?

In section 4.3.2, the pattern of mesohabitat use shown by Figures 4.11 and 4.12 shows that other factors are involved in brown trout habitat use that are not linked to flow and mesohabitat variability. The present section investigates the possible roles of life stage-specific requirements (parr are in glides because this type of mesohabitat fits the needs of the fish at this particular life stage and adults use runs because it is the most appropriate habitat for their needs) and social hierarchy (parr are found in glides because all the run-types mesohabitats are already used by higher rank-trout, i.e. adults), in order to answer RQ_6: What role is played by factors such as seasonality, habitat availability, life-stage and social interactions in the pattern of habitat use displayed by the surveyed population?

During the mid/late summer months, i.e. late July and September, there is similarity in habitat use between the two life stages in that glide is the most used type of mesohabitat in both cases. However adult trout also use riffle and pools in a similar proportion as runs whereas parr were only found in glides and runs. As the proportion of run use by adults decreased slightly in September (from 20% to 15%), parr increased their use of run (10 to 25%), suggesting competition for this type of habitat as a result of hierarchy, as previously mentioned. In autumn however, both life stages displayed the same behaviour: a sharp increase in the use of runs (75 % of parr and 85% of adults) and then, in November, a complete switch towards the use of glides (90% of parr and 100% of adults). This time of year corresponds to spawning time for salmonids (Elliot, 1994; Moir *et al.*, 2005) and the sharp increase in run use in October results from fish searching for appropriate spawning grounds, usually found in shallow, quite fast flowing habitats with gravel beds, which are the characteristics of runs in the study site. This gives a good example of how biological factors, here fish ontogeny and physiology, influence fish behaviour, more than discharge or habitat diversity. Glide preference in November could be seen as the aftermath of spawning. Glides might be more appropriate habitats for that time of year.

So far the analysis of fish observations has shown that discharge and seasonality play a role in habitat use. Seasonality is linked to the life cycle of salmonids with spawning taking place in October-November and egg hatching occurring in spring. The various stages in the life cycle of salmonids result in varying habitat requirements, thus explaining the seasonality in habitat use. The Gathering of adult trout in runs in October-November fits with the spawning period, which involves a requirement for shallow habitats with gravel. Biotic factors, which were discussed in Chapter 2, such as competition for resources, are shown to have an effect on fish behaviour, with the example of habitat segregation for parr and adults in early July. In the case of brown trout, competition for habitat and resources results from intra population hierarchy. Trout could also use preferably the mesohabitat type that is the most available in the stream so as to avoid the effects of hierarchical competition for habitat resources. This was investigated in section 4.4.4.

4.4.4 Mesohabitat use and mesohabitat availability

This subsection further addresses research question RQ_6. Figures 4.14 to 4.17 show the influence of habitat availability on habitat use. For both life stages, mesohabitat use was analysed as a function of the increasing availability of the two predominant mesohabitats in the study stream: glides and runs.

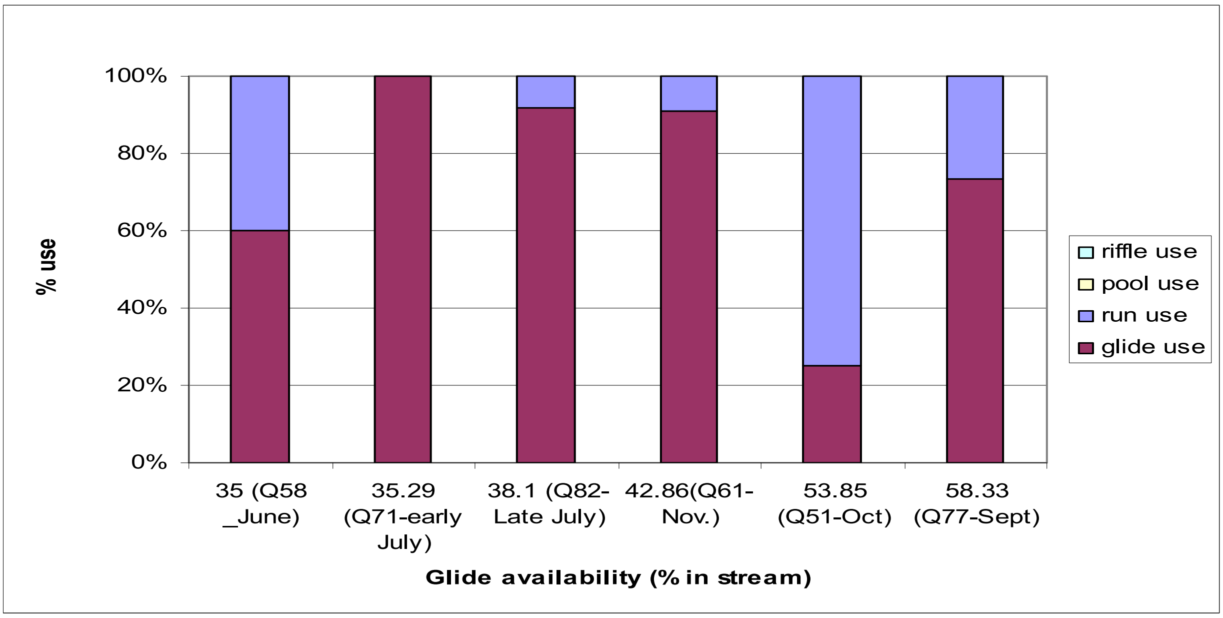


Figure 4.14 Mesohabitat use vs glide availability for brown trout parr

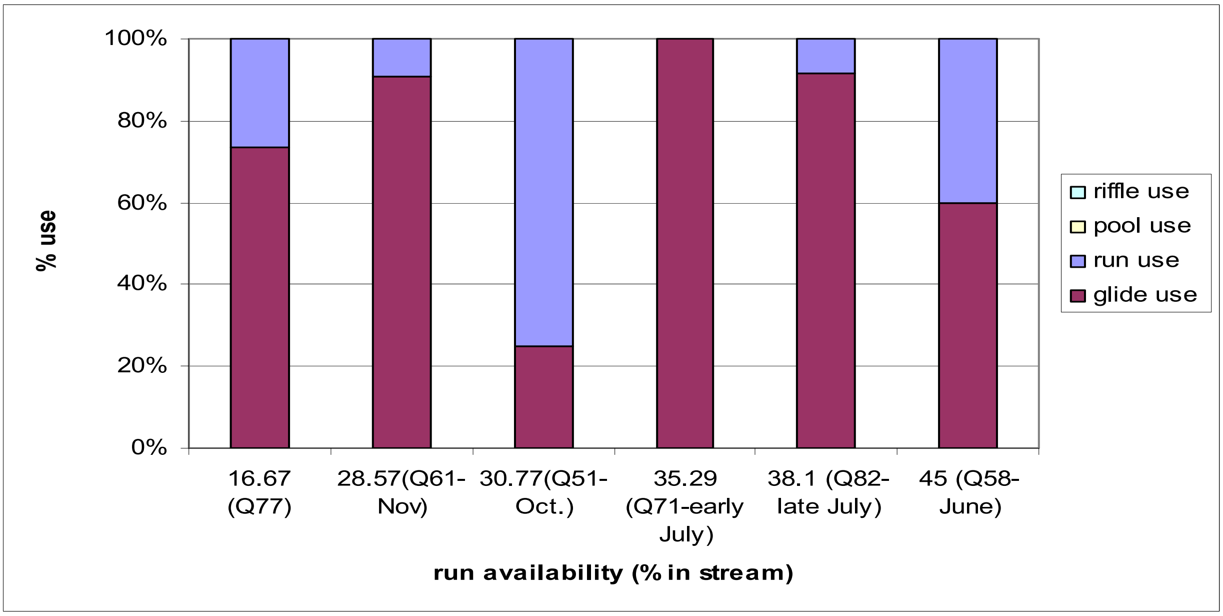


Figure 4.15 Mesohabitat use vs run availability for brown trout parr

Parr use of glides (Figures 4.14 and 4.15) does not appear to be influenced by the availability of this habitat. In other terms, increasing availability of glides does not mean increasing use of glide. Indeed, on the left figure, 100% glide use by parr occurred when glides made 35.29 % of the habitats. Maximum glide availability was 58.33% of the stream and maximum glide use was not achieved at that point. In October, when glide availability was near its maximum value, a sharp increase in run use was observed, possibly due to spawing period, as discussed earlier. Similarly, run availability has no effect on run use. Run availability ranged from 16.67% to 45 %. At intermediate availabilities such as 30.77% (October) and 35.29 % (early July), two opposite behaviours are observed: maximum run use by parr in October, and on the opposite 100% glide use in early July. Mesohabitat availability therefore does not appear to influence parr mesohabitat choice. Below are shown similar charts (Figures 4.16 and 4.17) for adult trout habitat use.

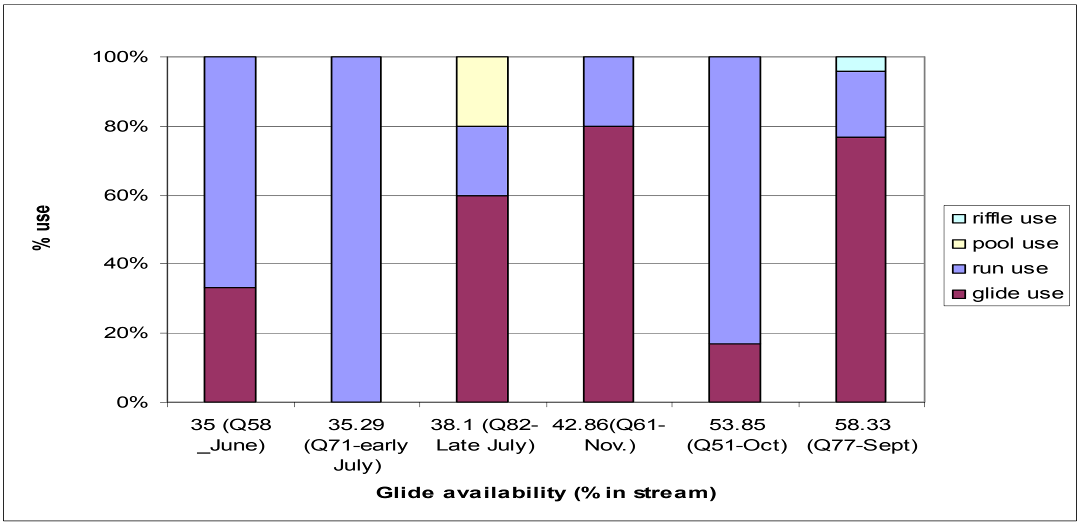


Figure 4.16 Mesohabitat use vs glide availability for adult brown trout

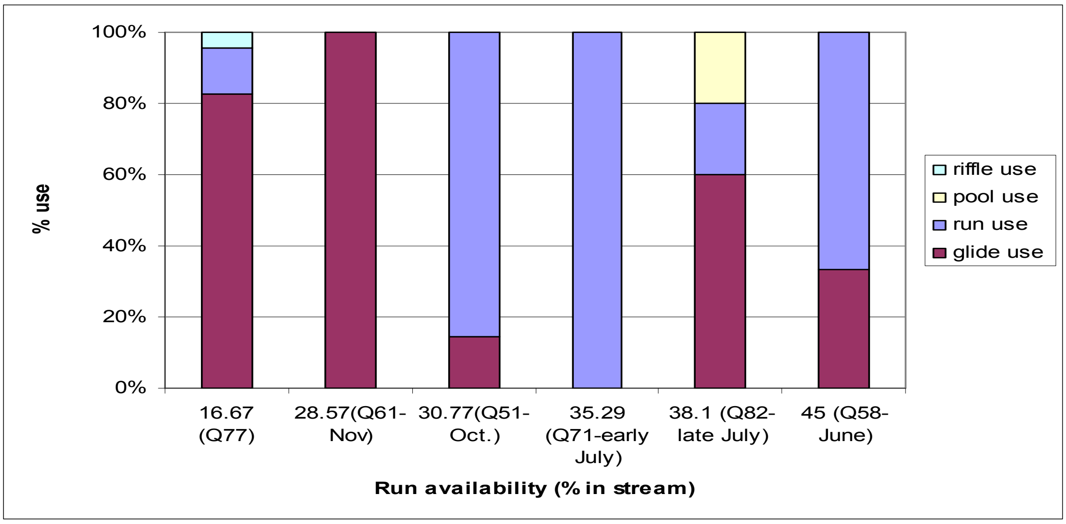


Figure 4.17 Mesohabitat use vs run availability for adult brown trout

Similarly, adults do not appear to be influenced in their habitat use by habitat availability. In early July, when glides represent 35.29% of the stream, they only use runs. In October, when glide availability is 53.85 %, 85% of adults use runs. Run availability does not seem to influence this habitat use either. When run availability is 28.57 % adult trout only glides. At increasing run availability, there is more use of run but the maximum value for run use is not achieved for maximum run availability: 100% run use occurred when runs represented 35.29%. At maximum run availability (45% of the mesohabitats in the stream), 45% of adult trout used runs. In the following section, the main findings discussed in section 4.4.1 to 4.4.4 are summarized.

4.4.5 Summary

From these observations, it can be seen that habitat availability does not influence habitat use by brown trout other than obviously the minimum availability required for fish to be able to use a type of mesohabitat. However, the presence of a particular type of mesohabitat does not always result in its use by fish. A good example during the surveys is illustrated by backwaters. Backwaters were present in the stream on every survey occasion. Nevertheless no fish observation was ever made in this mesohabitat. Moreover, the location of mesohabitats in the stream may have an effect on their use/non-use by brown trout. Not all runs or glides may be used in an equal way as other factors appear to influence fish choice of habitat: as discussed earlier, seasonality, through its influence on brown trout physiology and life cycle, determines the requirements a fish has for certain habitat characteristics. Hierarchy, within the population, results in intrapopulation competition for habitat use, whether for high habitat quality as physical habitat *stricto senso* or for the quantity/quality or food it provides or also the shelter it provides against predators.

Another factor that could influence fish habitat use lies in the instream mesohabitat composition itself, i.e. the sequence of mesohabitats encountered in the stream. One could argue that characteristics of the mesohabitat in which a fish is found matter less than the adjacent channel geomorphic units to which this particular mesohabitat is connected. As it was discussed in Chapter 2, mesohabitats in a stream are often seen as a mosaic that varies with flow. This leads to RQ_7: what are the key habitat characteristics that determine fish location?

This question echoes modelling work by Nestler *et al.* (2002) that show that fish movements and behaviour in a stream are determined by patterns of variations of shear stress and friction, suggesting that fish habitat use results from highly refined cognition processes and interactions of senses with its environment (Nestler *et al.*, 2002; Goodwin *et al.*, 2004). This will be further discussed in Chapter 6.

The data from the fish observations collected during this project hence have helped enlighten several factors responsible for brown trout habitat use. As it was discussed in Chapter 3, the fish observations constituted a mean to test the generic habitat suitability index curves built by Dunbar *et al.* (2001). They also allowed some habitat use curves to be drawn, which are shown and discussed in section 4.5.

4.5 HABITAT USE CURVES

From the depth and velocity measurements made at the fish locations it was possible to derive habitat use curves for depth, velocity and substrate, which are shown below. They represent the values for the variables described above most frequently chosen by brown trout. These are composite curves, i.e. they take into account the values recorded at all six flows surveyed. The curves specific to the highest flow (Q_{51}) and the lowest flow (Q_{82}) surveyed were added in order to indicate which flow had the most influence on the general use of depth, velocity and substrate by both life stages observed in the population.

4.5.1 Brown trout parr

Figures 4.18 and 4.19 show the depth and velocity use curves that were drawn from the data collected during this project for brown trout parr.

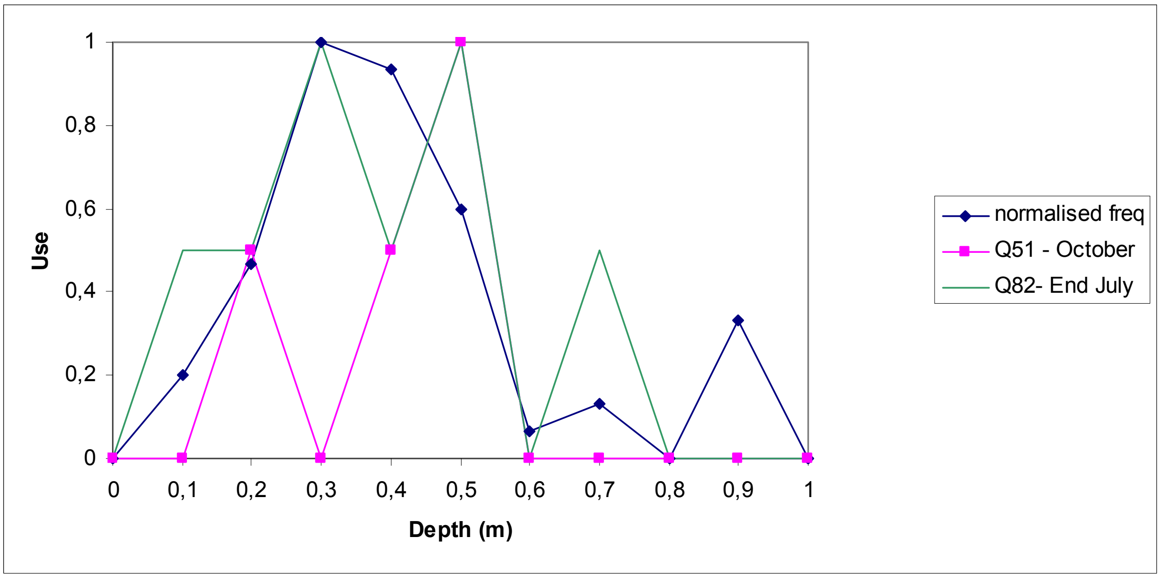


Figure 4.18 Habitat (depth) use curve for brown trout parr

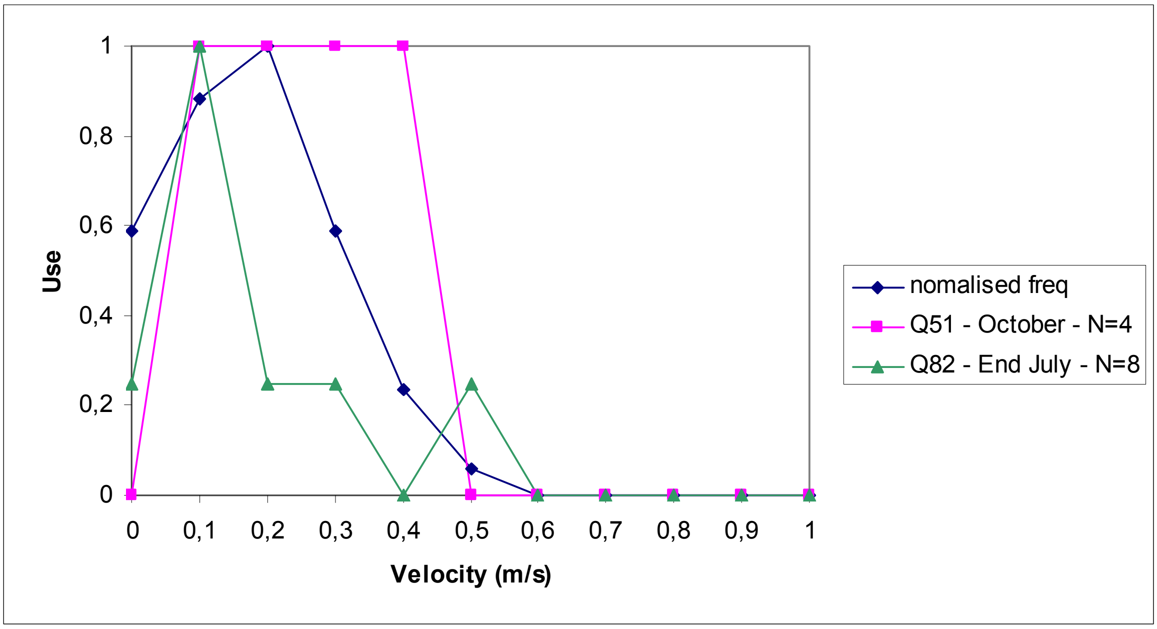


Figure 4.19 Habitat (velocity) use curve for brown trout parr

The depth use curve (Figure 4.18) shows that parr use a broad range of depths but they mostly use depths between 0.2 and 0.6 m (peak of use at 0.3 m) with lower peaks of use for the deepest parts of the stream, e.g. 0.7 and 0.9 m. At the highest flow the range of used depths narrowed with a peak of use at 0.5 m, hence deeper that for the composite curve. At the lowest flow, the use curve is made of two maximum peaks at 0.3 and 0.6 m and a smaller peak at 0.7 m, showing that at lowest flows parr diversify their use of depths, probably because the optimal depth is not always available. From the velocity use curve (Figure 4.19), it can be seen that the maximum velocity used is around 0.5 $m.s^{-1}$ with parr using mostly velocities of 0.2 $m.s^{-1}$. At the highest flow, the curve becomes square-shaped with a maximum use of velocities ranging from 0.1 to 0.45 $m.s^{-1}$. The range of velocities used shifts towards lower velocities (0.1 $m.s^{-1}$) at the lowest flow with small peaks of use at higher velocities up to 0.6 $m.s^{-1}$. This pattern may be the result of the scattering and rarefying of suitable velocities in the stream.

4.5.2 Adult brown trout

Figures 4.20 and 4.21 show the habitat use curves that were drawn from the data collected for adult brown trout.

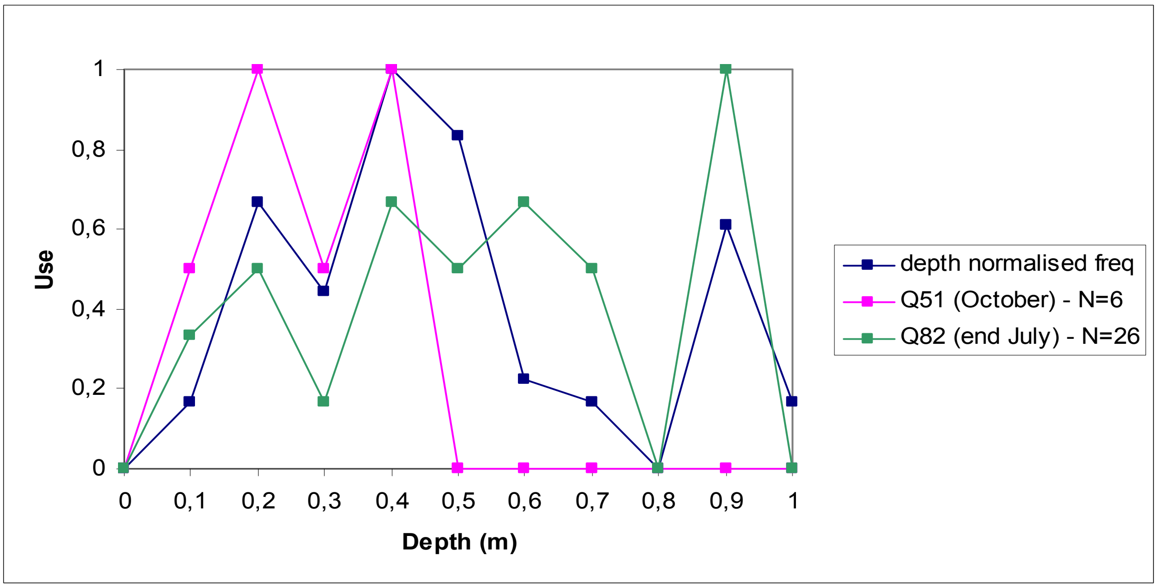


Figure 4.20 Habitat (depth) use curve for adult brown trout

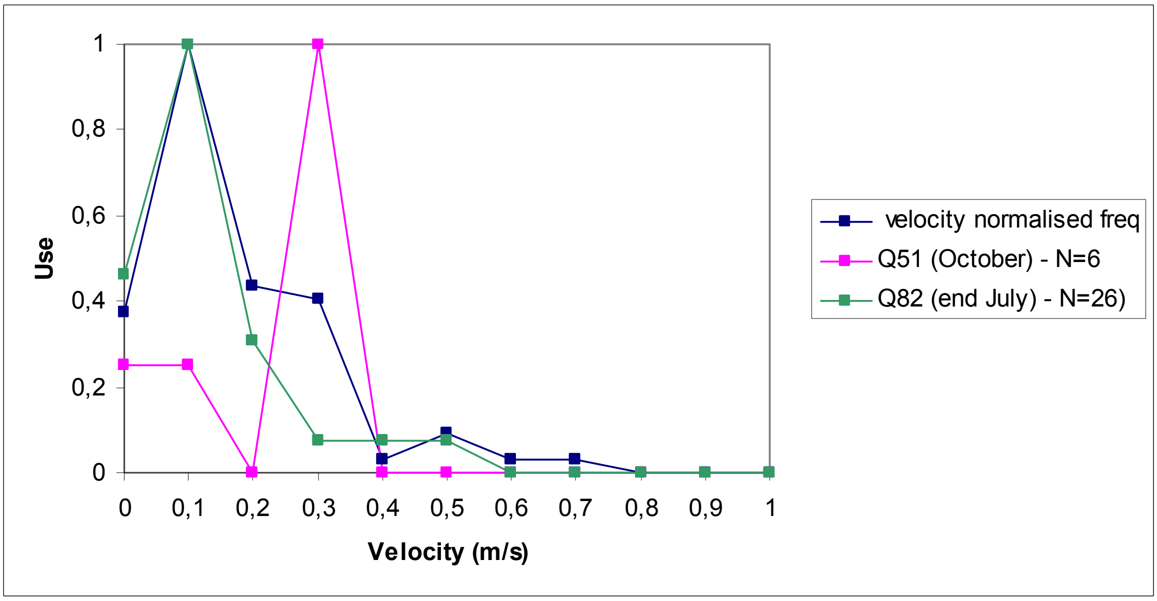


Figure 4.21 Habitat (velocity) use curve for adult brown trout

The depth use curve (Figure 4.20) for adult brown trout shows a complex pattern of depth use. Depths up to 1 m are used with a maximum use of depths ranging from 0.4 to 0.5 m with another but smaller peak at 0.9 m. The highest flow surveyed resulted in a shift of use towards lower depths with maximum use of depths of 0.2 and 0.4 m, probably corresponding to the shift in run use that occurred in October. At the lowest flow adult brown trout extend their use to the whole range of depths available with a maximum use of depths around 0.9 m. This can be explained by the need to hide from predators. At lowest flows deep areas of the reach play the role of cover and shelter for fish.

The velocity use curve (Figure 4.21) presents a similar shape as that for parr though it is much narrower. The most used velocities are around 0.1 $m.s^{-1}$. The highest flow caused a shift in use towards higher velocities (0.2-0.3 $m.s^{-1}$) with a little peak of use for lower values. That can be associated with the fact that all adult observations occurred in runs in October (Q_{51}). At the lowest flow, the velocity use curve is the same shape as the composite one.

4.5.3 Comparison of both life stages

Comparison of habitat use curves for both life stages shows that parr use a narrower range of depths (0.2 to 0.6 m) and are more specific about the values they use most, e.g. 0.3 m, whereas adults appear more tolerant about depths and use the whole range of depths surveyed (0.1 to 0.9 m). This is consistent with the results from other studies (Baran *et al.*, 1997; Maki Petays *et al.*, 1997; Roussel and Bardonnet, 1997) where adult brown trout were found in deeper habitats than juveniles (parr and fry). When considering velocity, the opposite pattern is observed: parr use a broader range of velocities (0 to 0.6 $m.s^{-1}$) than adults (0 to 0.4 $m.s^{-1}$). This can result from the preferred use by adult fish of pools and glides, usually deeper and slower than glides (Heggenes *et al.*, 1993; Baran *et al.*, 1997). The several smaller peaks observed in each curve could be the result of observations of fish in lower hierarchical positions within the population and therefore represent the individual variability resulting from population-related factors, e.g. one individual observed at 0.5 $m.s^{-1}$. Indeed, not all individuals from a population display the same behaviour nor use exactly the same values of depth and velocity. Below is shown the substrate use curve (Figure 4.22) for all life stages and all flow combined.

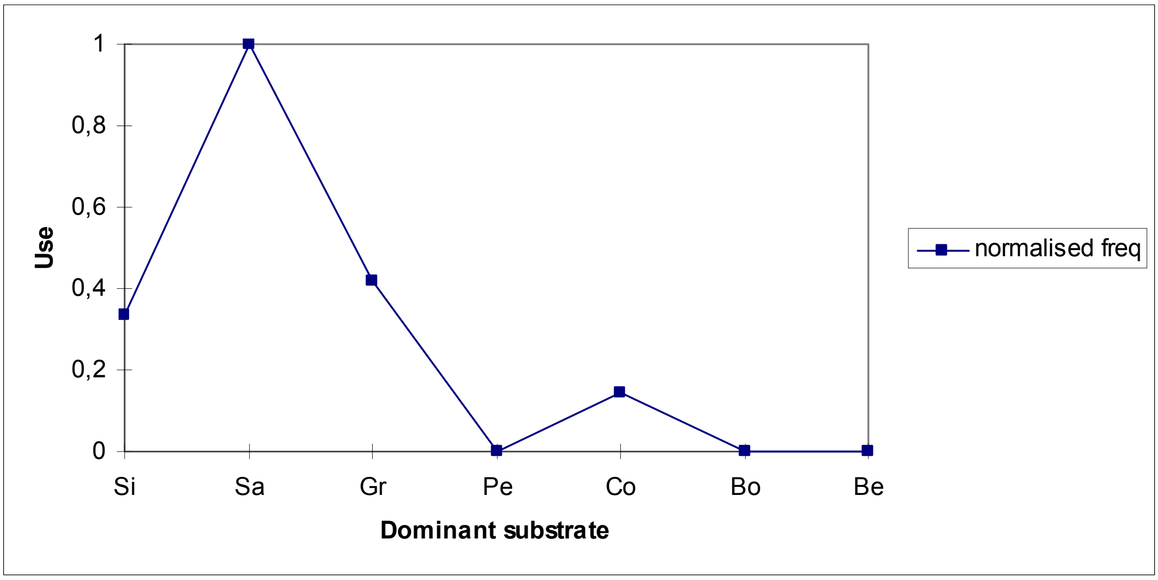


Figure 4.22 Habitat (substrate) use curve for brown trout (all life stages)

All observed brown trout were holding station above the substrate (a minimum of 5 cm above it) so, in itself, substrate does not appear as an important factor in determining trout habitat use as it is for benthic fish for example. However, substrate composition of the stream bed is influenced by habitat geomorphology as well as depth and velocity. Indeed, as it was discussed in Chapter 2, geomorphology and flow partly govern sediment load in the stream and the location of areas with erosion/ deposition of sediments. Therefore substrate constitutes a good indicator of the type of habitat the trout use. Moreover, substrate plays a key role during salmonids spawning season in October, when the fish build redds in gravel beds where they later lay their eggs. The substrate use curve indicates that sand is the substrate selected most frequently: sand makes up stream beds in zones of sediment retention, usually quite deep, slow flowing habitats, which correspond to glides in the study stream. That correlates the results discussed earlier, which show that glide is the mostly used mesohabitat by brown trout in the Tern (see section 4.3). A smaller peak can be observed corresponding to cobbles. Cobbles occur in fast flowing environments (as they are too large to be washed out by fast flowing water), which correspond to runs in the River Tern. Gravel appears to be used as well probably as a result of the high use of runs and subsequently their gravel beds in October during the spawning season. Smaller gravel occurs also in slower flowing environments. The substrate use curve therefore correlates the previous results on mesohabitat use by brown trout, i.e. predominant use of glides and pools (see section 4.3). The next section presents a summary of the results as well as the interpretation of the map shown in Figure 3, section 4.1.1.

4.6 SUMMARY OF RESULTS AT THE REACH SCALE

RQ$_7$. What are the key habitat characteristics that determine brown trout location in the study reach?

The results presented in the previous sections give some insight into the factors responsible for brown trout behaviour in the River Tern. They encompass both biological processes that are linked to the fish species biology and ecology, such as intrapopulation competition and hierarchy, to the fish life cycle with the influence of seasonality, and habitat related factors such as flow, mesohabitat type and availability in the stream, depth, velocity, substrate, cover. The quality and quantity of food resources were not measured in this study, but it is obvious that food biomass plays a role in fish habitat use and constitutes a factor that can be responsible for competition among individuals.

The water quality parameters for this river, e.g. temperature, dissolved oxygen, pH, conductivity, were recorded for every one of the six fish surveys carried out and, as shown in Figure 4.23, do not show any significant variation that could justify a change in trout habitat use.

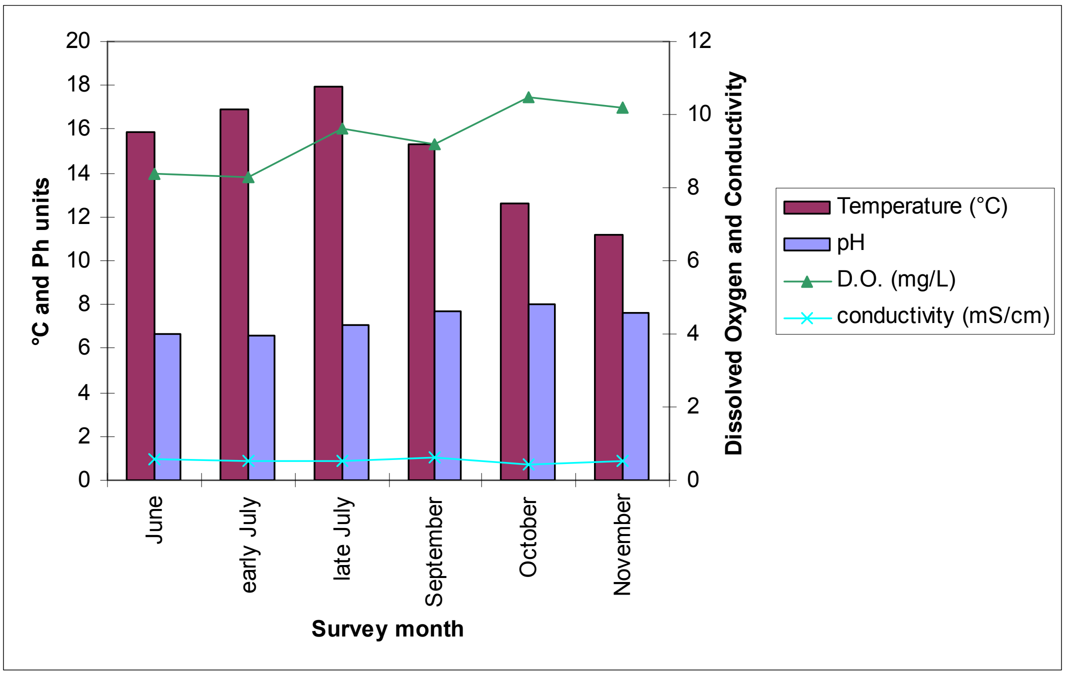


Figure 4.23 Seasonal evolution of water quality parameters in the River Tern at Norton in Hales

Mesohabitat use by brown trout in a groundwater-fed stream appears to be governed by the need for refuge and food resources but also by individual fish choices and positions within the population hierarchy. The lowest ranked individuals will have to use the mesohabitats that remain unused by higher ranked trout. Comparison of the observed pattern of habitat use in the River Tern with the one displayed in a surface runoff influenced stream, by definition more influenced by precipitation and hence displays more mesohabitat variability, would give more insight into fish adaptation to mesohabitat variability. From the results in a groundwater influenced environment, the hypothesis can be made that in a more variable environment, where mesohabitat composition varies to a great extent with flow, habitat use by brown trout will be mostly governed by environment and habitat-related factors and that the biological processes related to the population will have a lesser influence than what was found in a very stable environment.

As previously shown, fish habitat use does not rely only on habitat related factors but on the interactions between various factors, some of which have more influence than others. For example, mesohabitat use was shown to vary greatly between the highest flows surveyed (Q_{51}+Q_{58}) and the lowest flows surveyed (Q_{77}+Q_{82}) for both life stages (section 4.3.1). However when looking at seasonality (section 4.3.2), there appears to be segregation between the two life stages in early July with parr only found in glides and adults observed only in runs. In October, both life stages converged to the same mesohabitat use pattern, e.g. use of runs nearly exclusively. That tends to prove that flow variability cannot explain fish habitat use on its own, nor can seasonality, nor can mesohabitat availability (mesohabitat use does not increase with increasing mesohabitat availability, as shown in section 4.4.4). However, some factors that remain constant among the results are biologically related: interaction, competition and even segregation between the two life stages, the influence of events in the fish life cycle on habitat use (e.g. spawning). These appear to be able to explain most of the observations made during the surveys.

Since the habitat composition in the River Tern does not vary to a great extent and the instream environment remains stable throughout flows thanks to the input of groundwater, one can hypothesise that the dominant factors in determining fish habitat use and behaviour are not so much habitat related factors but biological processes. This would fit with the earlier results that showed that the common factor explaining the observations was population related (section 4.4) and not related to flow or mesohabitat availability.

The absence of trout in backwaters may be the result of different factors: in the River Tern at Norton-in-Hales backwaters are situated inside bends and constitute semi-enclosed areas. This particular location may deter trout as they are difficult habitats to escape from in case of predation. The absence of current and instream vegetation may also not be appealing to fish as they might constitute a poor area in terms of food resources.

Analysis of the map in Figure 4.3, section 4.1.1, confirmed that trout were observed only in glides and runs, as explained previously in this chapter, but it also shows that the observations were more numerous in units where the mesohabitat type remains constant, i.e. either a run or a glide but not switching from one type to another. The only exception is unit 1, where the mesohabitat is usually a glide but on two occasions was a run. Therefore though the consistency in mesohabitat type, i.e. the fact that a mesohabitat remains of the same type through time, seems to be a key factor, other factors have to be taken into account in order to determine what affects trout presence or absence.

The map also shows that except for two units (unit 2 and unit 11) all trout were observed near the right bank of the channel (looking downstream). In unit 2, trout were observed on the right hand side of the channel and in unit 11 trout were found across the whole width of the channel (only 1 or 2 m wide at this point). The reach is orientated north-south so the location of the trout in most units corresponds to the east facing bank, which is sunny during mornings, time during which the surveys were carried out. Hence light appears to be another factor determining trout location as well as cover. However, in unit 14, trout were only observed near the western bank, which, in this part of the reach, is the only one with overhead cover, the eastern bank being on the verge of a field and close to the drinking point for cattle, in an open area.

The detailed analysis of the features specific to each unit on the map reveals links between their presence/absence and that of brown trout. Features providing permanent cover/shelter and/or food resources seem particularly relevant. Unit 1 switches from run to glide and vice- versa with flow and is the only variable mesohabitat within the reach in which trout were observed. The variability in mesohabitat type in this unit does not prevent trout from using it, e.g. P(fish occurrence)=1. Fish are indeed observed in the upstream half of the unit around one metre downstream of the road bridge. The bridge provides persistent refuge against potential predators as well as a source of food as it can be a shelter to macro invertebrates. On a number of occasions trout have been observed feeding in this location. At the downstream end of Unit 1, a fallen tree caused the accumulation of woody debris in that part of the stream and thus constitutes easily accessed shelter. This persistent woody debris dam, which makes the boundary between unit 1 and 2, constitutes a source of organic matter favourable to the occurrence of macroinvertebrates (Goodfrey and Middlebrook, 2007) and provides a food source for trout. As a result, it can also explain the permanent occurrence of trout in unit 2. The variability of depth across unit 2 explains the exclusive location of trout on the right part of the channel between the gravel bar and the right bank. There the channel is narrow (around 2 m wide) with depth of 1 m (compared to 0.2 m on the other side of the gravel bar) and undercut banks that provides permanent shelter to fish. The mid-channel gravel bar hosts macroinvertebrates, which are an easily accessible source of food.

Two units present a probability of trout use of 5/6: unit 11 and 12 are situated towards the downstream end of the stream. Unit 11 remained a glide throughout the surveys and its geomorphology is characterised by a ninety-degrees bent in the channel. The banks are at this point highly vegetated with weeds and grass that grow from the top of the bank down to the water level, which means that the vegetation becomes submerged with increasing flow. Substrate is composed of gravel and cobble and the under banks and the vegetation provide a highly sheltered environment for fish. Moreover during the summer months, three patches of macrophytes occupy most of the width of the channel and its whole depth, which contribute to shelter. Most fish observed in this unit were parr and they were located downstream of the bent. Unit 12 remained a run at all flows and is characterized by an important woody debris dam made of two fallen trees and subsequent accumulation of logs and other woody debris for the whole width of the channel (around 4 m) at the upstream end of the unit (boundary with the downstream end of unit 11). Though the velocity just downstream of the dam was always high (between 0.5 and 0.9 $m.s^{-1}$), the presence below the surface of a large amount of woody debris and logs on the sides of the channel provides shelter for trout while they rest or hold station in order to feed on the macroinvertebrates washed out from the dam.

The other units in the stream are characterized by probabilities of occurrence lower than the ones described above, with probabilities equalling to 2/3, ½, 1/3 and 1/6. Unit 7 hosted trout on half of the surveys. Trout were constantly found under a bushy tree where branches fall into the water. When fish were spotted in this unit they were darting to and from the cover provided by this tree. The probability of trout occurrence of ½ that characterized this unit could result from the variability in the cover provided by the riparian trees throughout the year. The whole study reach is located within a small riparian wood and thus is sheltered by their foliage. The extent of the tree cover above the reach varies from none in the winter as the leaves have fallen to complete cover of the reach in the summer months. The units with probability of trout use less than 2/3 are not characterized by permanent features that can provide shelter and/or source of food at all times and are more subject to the variability of cover from the trees.

The variability in depth and velocity between the units in the reach is not reflected in the location of trout with the exception of units 7 and 8, which were avoided when they are riffles (at other discharges these two units became runs). Indeed riffles were characterized by minimum depth of 0.12 m, which is not suitable for trout. Substrate composition remained constant between the units with cobbles, gravel and sand being the dominant substrate, except in backwaters where the only substrate is silt. It thus appears that the main physical factor influencing trout distribution along the stream is cover in the mean of permanent features providing shelter and also sources of food as they also provide shelter for macro invertebrate populations on which trout feed.

The fish surveys showed another pattern of behaviour. Indeed, from September to November, trout were observed gathering in groups of 8-10 individuals in unit 4, which is a glide. Earlier in this chapter it was discussed that from the end of summer onwards trout used most exclusively runs, which could be linked to spawning and the use of runs to build redds. This gathering behaviour in a glide, of both parr and adults does not fit the above described behaviour and cannot be explained by any territorial or hierarchical behaviour since trout of 35-40 cm in length were also present in these groups. Several factors can explain this behaviour: mating, the presence of a run (unit 2) upstream of unit 4 could provide food by the way of macro invertebrates drifting from the upstream woody debris dams. That would correlate one of the hypotheses discussed in section 4.4.5. Also, since the reach is groundwater influenced, maybe unit 4 could correspond to the location of groundwater input, usually warmer than the instream water thus creating a favourable environment for trout in the autumn months (Heggenes and Saltveit, 1990; Heggenes and Dokk, 2001).

The units with very high numbers of trout observed during the survey period do not necessarily present the highest probability of fish occurrence. In unit 4, for example, 26 fish were observed with only a probability of occurrence of 1/3. In unit 14, 12 fish were observed also with a probability of 1/3. On the opposite, unit 12 presents a probability of occurrence of 5/6 but only 11 fish were observed. That implies that while the most suitable parts of the stream host fish permanently or nearly permanently, other parts, identified above as less suitable, that host fish on a less regular basis still host a relatively high number of fish at a given time. Some habitats are constantly in use while some of them are used only at given time. It is the case of unit 4 where gatherings of trout occurred from September onwards and not at other times during the survey period. Therefore, while habitat characteristics, as shown above, certainly have an effect on trout habitat use, whether permanent or not, seasonality and fish life cycle influence the location of fish at certain times of the year. Trout can choose the same habitat as a permanent location and as a necessary location as specific times in their life cycle.

The scattering of trout observations along the reach (several units presented only one fish observation) suggest that some competition occurs for the location of trout along the reach. Segregation between life stages and within the same life stage has been previously shown in this chapter with respect to mesohabitat use in general (Section 4.4). Since for the same mesohabitat type some units are more suitable than others because of their characteristics, some competition should exist between fish for these highly rated units, with at a given time, the higher ranked individuals in the population occupying the best units in the reach and the lower ranked individuals having to accept less beneficial locations. Example of less appealing units in the reach are units 8 and 9, characterized by a change in mesohabitat type during the survey period, very variable overhead cover and they have been occupied in total by one individual for all of the surveys (one parr for unit 9 and one adult for unit 8).

The above interpretation of results aims at addressing research question RQ_7 and can be summarized as follows. Habitat use by brown trout in the River Tern at Norton in Hales results from complex interaction between the mesohabitat composition of the stream, its stability, the characteristics and features specific to each particular mesohabitat in the stream and their consistency with flow and finally the biological processes governing the species and this particular brown trout population. The above results suggest therefore several habitat-related factors to have an effect on brown trout habitat use.

- Type of mesohabitat: trout favour glides and runs compared to backwaters. Flowing water even with a small velocity appears important, possibly because it allows drift feeding on macroinvertebrates.
- Persistence of mesohabitat type: the highest numbers of trout were observed in units constant in their mesohabitat characteristics (except in backwaters).
- Presence of permanent cover features: the units characterized by a high probability of fish occurrence (1 or 5/6) contain either woody debris dams (unit 2 and unit 12) either a concrete bridge (unit 1) or highly vegetated banks and/or macrophytes (unit 11), which act both as refuge for the fish and food reserve.
- Bank orientation: trout favoured the western bank side of the reach, i.e. the most sun lit. It can also be related to the density of the riparian vegetation on this side of the stream. Does the light have an effect on macro invertebrate presence?
- Environmental stability: the observation of brown trout on all survey occasions suggest that this stream presents the necessary conditions for the establishment of a stable trout population and for the completion, as the results show, of the fish life-cycle.

4.7 FACTORS INVOLVED IN HABITAT USE BY BROWN TROUT

This section presents a summary of the factors influencing brown trout habitat use and allows to bring some answers to research questions RQ_4, RQ_5, RQ_6 and RQ_7. For conservation and management purposes, it is necessary to identify within a given river/ stream which areas are most likely to be used by brown trout throughout the year and over a range of discharges. In a groundwater-fed river, this task is made easier by the nature of this type of river. Groundwater input acts as a buffer against major changes in the environmental parameters and, as it was shown in the case of the River Tern, in the mesohabitat composition. Therefore identifying the mesohabitats along a reach most likely to be used by trout is easier than in the case of a flashy, surface runoff influenced river, because the mesohabitat composition is less subject to variability caused by changes in discharge.

From the results of the fish surveys in the River Tern an organisation chart (Fig. 4.24) was constructed that shows the steps to follow in order to identify the location of brown trout in a groundwater-fed stream.

Such a chart must take into account the time of year at which it is used because of the implications seasonality has on tree overhead cover (see section 4.6) and also on the life cycle of brown trout. Indeed mating involves gathering of fish in relatively deep areas (e.g. in unit 4, depth ranges from 0.36 to 0.61 m) such as glides and pools and during the spawning season (October-November) trout display exclusive use of runs. The use of this chart relies also on the assumption that mesohabitat mapping surveys have been carried out across a range of flows prior to the "fish habitat use survey" in order to gain knowledge about the behaviour of the river according to discharge and the latter has on mesohabitat composition.

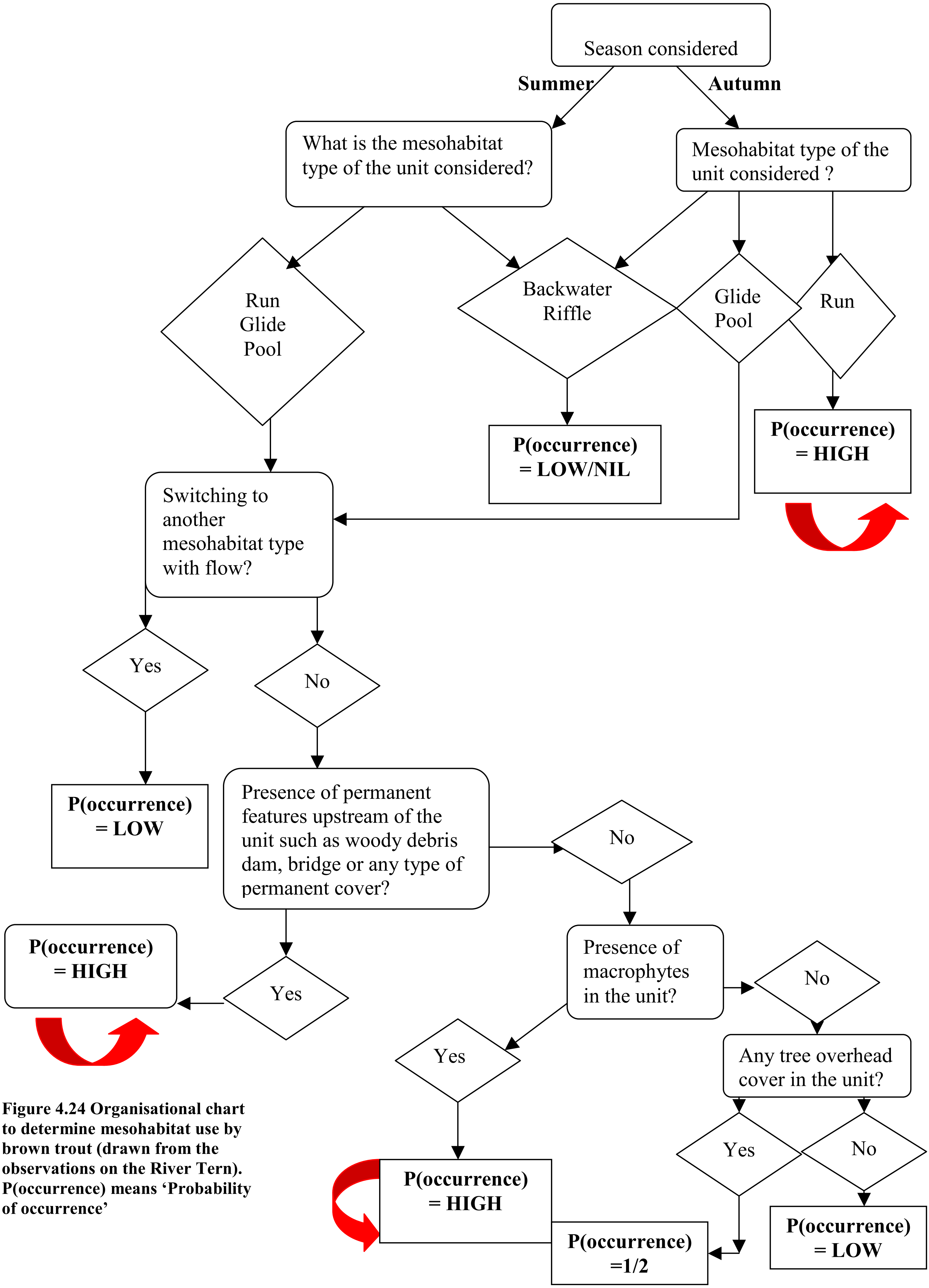


Figure 4.24 Organisational chart to determine mesohabitat use by brown trout (drawn from the observations on the River Tern). P(occurrence) means 'Probability of occurrence'

The first step is to consider the season during which the fish survey is carried out: the fish surveys in the present study focused on summer and autumn and the organizational chart is drawn from the observations made during these two seasons only. For winter and spring, though it can be assumed that the choice of location by trout would hardly change due to the groundwater influence on the river, this remains speculative. Therefore these two seasons were not included into the chart. For both summer and autumn, the type of mesohabitat in the unit has to be determined first. In autumn, if the mesohabitat is a run then the probability of finding trout in it is high, since it was found from the survey observations that trout exclusively use runs in October-November supposedly for spawning. If the mesohabitat is a glide or a pool then the questioning process is the same than for the summer season. For both seasons, backwaters and riffles are not expected to host any fish.

Having identified the mesohabitat type, it is important to know about the behaviour of this unit over a range of flow, in other terms, if the mesohabitat type remains constant over flows or whether it changes to another type of mesohabitat. This appears to be important for trout but whatever the behaviour of the unit considered, one has then to investigate the presence of permanent features upstream (preferably) or even downstream of the unit, such as bridges, instream woody debris or any feature providing permanent cover to the fish. If such features are present then, whatever the evolution of the mesohabitat with flow, the probability it will host brown trout is high. In case of the absence of permanent cover features, the absence/presence of instream macrophytes in the unit has to be recorded. Presence of macrophytes implies that trout will find cover in this mesohabitat; thus the probability of fish occurrence is high. If no macrophytes are present, then the only cover could be provided by trees fallen across the channel or overhead cover from trees situated in the close riparian zone to the stream. If such cover is provided, the probability of finding fish in this part of the stream is considered to be ½. Indeed the survey observations showed that units with only overhead cover from trees were less chosen by trout. As a result, trout can or cannot be there, probably depending on the availability of more suitable units in the stream and on the occupancy of these suitable units by higher ranked individuals in the population. If overhead cover from nearby trees is absent then the probability that fish will use this unit is low. The observations indeed suggest that the most important feature to determine trout choice of a particular location in the stream is cover as it provides refuge and shelter as well as food. The red arrows located near the boxes with high probability of fish occurrence indicate that intraspecific competition is likely to occur for those mesohabitats that are highly suitable. Brown trout is a species characterized by a hierarchical organization of the population with the various individuals within the population occupying various ranks according to their size/age/life stage. The results from the observations on the River Tern show that some segregation exists particularly between parr and adults as they do not use the same mesohabitat during early summer (late June and early July surveys): the adults were found in runs whereas parr occupied glides. This segregation implies some variability to the organizational chart shown above: highest ranked, dominant individuals in the population will have more choice with respect to the most suitable mesohabitats and will occupy them whereas non dominant or lower-ranked individuals will have to use mesohabitats that will constitute the next best available unit. That means for the observations of late June-early July that parr, even if the runs were suitable habitats for them, were confined to glides as suboptimal habitats because adults, i.e. higher ranked individuals, already used the runs. This explanation appears plausible on the River Tern since this stream is groundwater-fed hence provides a stable environment, suitable for a brown trout population to develop and for the biological processes (hierarchy and intraspecific competition) governing this population to take place.

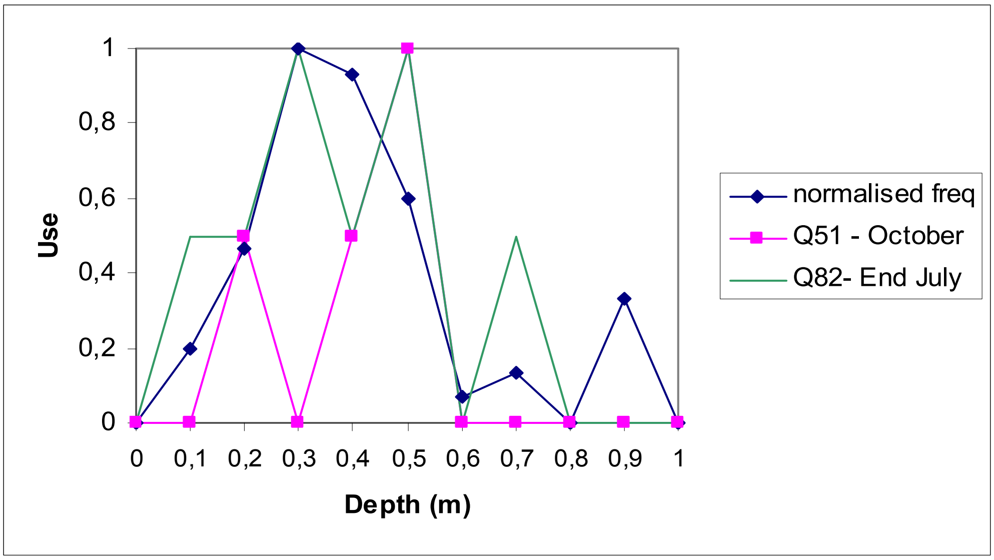
The next section presents the results of the comparison between the observed habitat use pattern for brown trout with existing generic HSI curves. This corresponds to Objective 4 of this thesis.

4.8 RELIABILITY OF HSI CURVES IN PREDICTING TROUT HABITAT USE (OBJECTIVE 4)

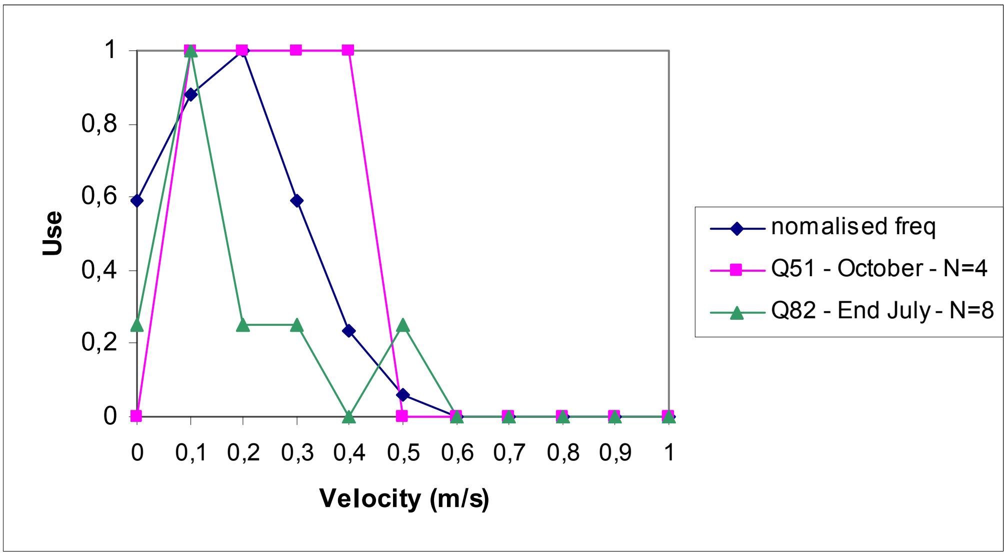
4.8.1 Comparison of Habitat Use Curves with existing HSI curves

<u>4.8.1.1 Brown trout parr</u>

The habitat use curves drawn from parr observations in the River Tern are shown in Figure 4.25 together with the generalised Habitat Suitability curves drawn by Dunbar *et al.* from data in chalk streams in Figure 4.26 (Dunbar *et al.*, 2001).



Use
Depth (m)
normalised freq
Q51 - October
Q82- End July



Use
Velocity (m/s)
nomalised freq
Q51 - October - N=4
Q82 - End July - N=8

With respect to the depth suitability index curve, Dunbar *et al.* (2001) noted that some uncertainty exists as to what the suitability index is for depths greater than 0.5 m. The suitability index of 1 for depths of 0.5 m and above comes is based on the fact that depth is often a limiting factor for salmonids and that with increasing size, fish tend to move to deeper areas (Heggenes, 1996; Heggenes *et al.*, 1998).

Habitat use curves show that trout parr use the whole range of depths between 0.1 and 1m with a peak of use for depths between 0.3 and 0.4 m, which fits with the HSI curves. However, the range of depths varies with flow and increases at lower flows, probably as a result of the decrease in available habitat.

The velocity suitability index curve shows an optimum for velocities between 0.2 and 0.4 $m.s^{-1}$. The composite use curve fits this pattern though the range of velocities mostly used appears more restricted. The range of velocities used also varies with flow. A greater range of velocities is used at higher flows. The use of deeper - slow flowing areas by brown trout parr appears to agree with the findings of Heggenes *et al.* (1998) on sympatric brown trout habitat use in South West England.

The above comparison between Habitat Use curves and the Habitat Suitability Index curves show that the generalised HSI curves obtained from field measurements by Dunbar *et al.* (2001) partly reflect the reality of trout parr habitat use in the River Tern. However, the variability in microhabitat use according to flow is not represented by HSI curves, nor is the habitat available, which is a critical factor particularly in small streams.

Moreover, parr life stage is defined as trout with a total length between 7 and 20 cm (Dunbar *et al.*, 2001; Neary, 2006), the latter length defining the limit between parr and adulthood. As habitat use appears to be size-dependent, that suggests that small differences in fish size and in physiological status (energy budget) for a particular life stage can lead to different patterns of habitat use, which is not represented by HSI curves. Indeed they are often life stage dependent.

4.8.1.2 Adult brown trout

Most of the studies on brown trout behaviour in the UK have focused on the fry and parr life stages, i.e. juvenile stages. However, Neary (2006), as part of his PhD work, reviewed studies on brown trout to establish the range of depths and velocities used by adults both spawners and non spawners (Neary, 2006, unpublished). From his review the range of depths used by adult brown trout is established between 15 cm and 310 cm. The preferred velocity for adult brown trout was determined by Conlan *et al.* (2007) as being within the range 0.15-0.50 $m.s^{-1}$, from studies of brown trout populations in streams in South Wales.

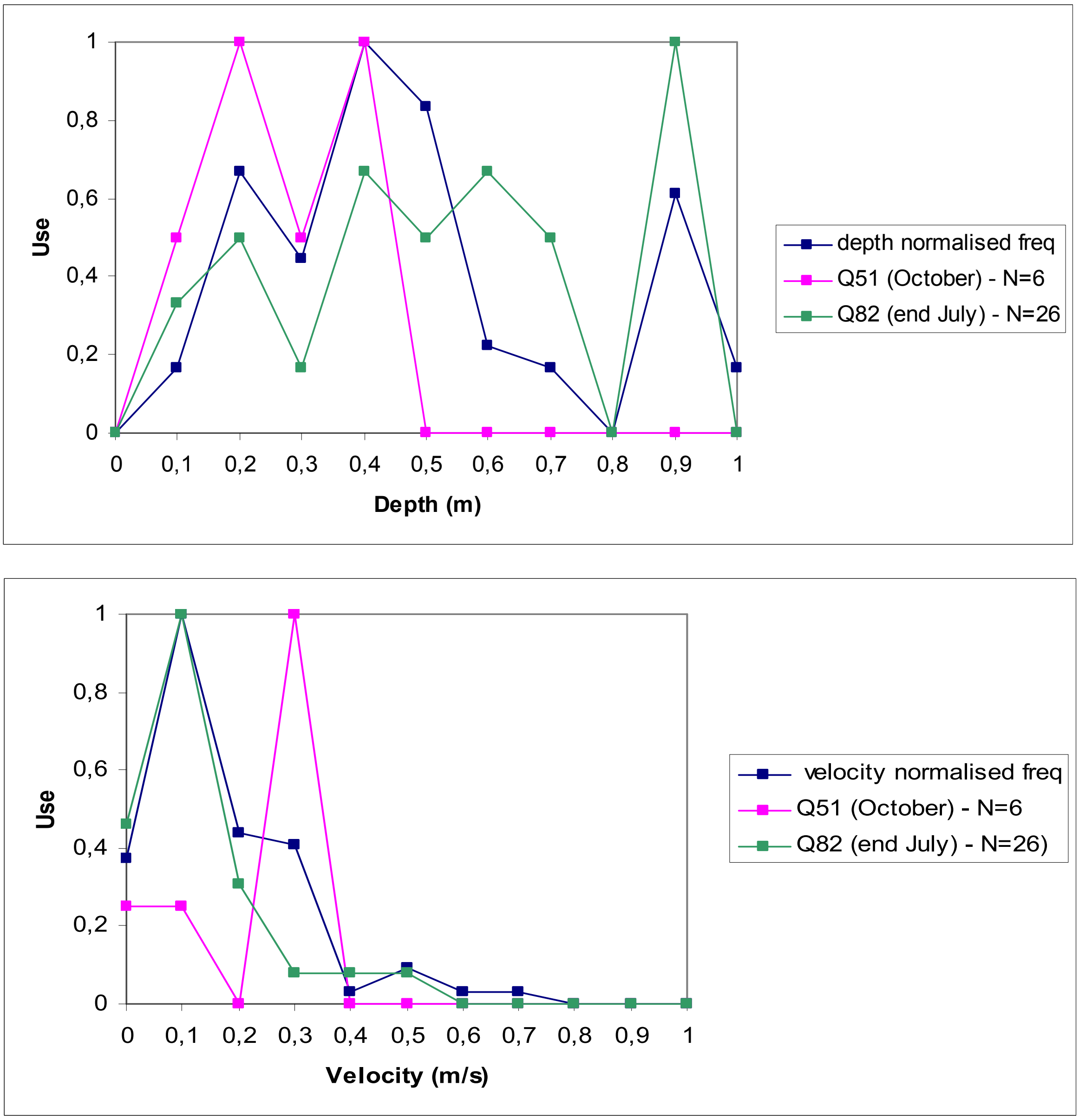


Figure 4.27 Depth and velocity use curves for adult brown trout, drawn from fish observations in the River Tern

The Habitat use curves show that both depth and velocity use are situated within the range of values established by the studies mentioned above. Adult trout use the whole range of depths between 0.1 and 1 m and velocities between 0 and 0.4m.s^{-1} for most individuals. Some individuals were found to use velocities up to 0.8 m.s^{-1}.

However as it was already described for parr in section 4.3.3.2.1, the range of microhabitat variables values used varies with flow: adults use a wider range of depths at lower flows and lower velocities too. At Q_{51}, the use by adult brown trout of shallower depths and higher velocities than at low flows does not fit with the findings from most studies on salmonids that adult trout use deeper-slower flowing habitats than juvenile life stages.

4.8.2 Prediction maps

Comparison of actual maps of fish observations with prediction maps built using HSI values (see Chapter 3 for description of the methodology used) are shown in Fig. 4.28 and 4.29 for brown trout parr in the River Tern at Q_{51} and Q_{77}.

As for the calculation of relative habitat suitability indices shown in Fig. 4.28 and 4.29, it was carried out using the five values of depth and velocity recorded in each CGU and the HSI curves developed by Dunbar *et al.* (2001).

In Fig. 4.28, the prediction map shows that most of the reach presents optimal habitats for brown trout parr with just two "sub-optimal" mesohabitats (two runs) and two average habitats that are backwaters. According to these maps, fish observations are expected to be located in the optimal mesohabitats. On the actual observation map, fish observations are located both in the "optimal" and "suboptimal" mesohabitats. No fish was observed in the backwaters which were characterised as "average" mesohabitats.

In Fig. 4.29, which represents the River Tern at Q_{77}, the overall suitability of the reach is similar to that in Figure 4.28, i.e. the reach mostly presents optimal habitats with the exception of the mid-reach riffle, which is characterised, by a "fair" suitability for brown trout parr (rHSI value between 0.25 and 0.50). The map drawn from the fish observations in the field shows that all but one trout parr observations are located in optimal mesohabitats. Hence, prediction of brown trout occurrence in the River Tern using the generalised HSIs developed by Dunbar *et al.* (2001) was fairly accurate. Comparison of such prediction on the Dowles Brook would have been very useful, but unfortunately was impossible due to the absence of brown trout in the reach.

Generalised HSI curves can thus accurately predict fish occurrence. However, Moir *et al.* (2005) found they were not as accurate and precise as HSI curves built specifically for a stream/reach. As a result, one can wonder if the accuracy in predicting fish occurrence in the River Tern is not partly due to the stable physical and hydraulic conditions governing the reach. This leads to the conclusions that HSI curves may predict fish occurrence, depending on the method used to develop them, the physical and hydraulic characteristics of the reach considered and the fish species targeted. Nonetheless they only determine fish occurrence as a function of their physical environment and do not take into account the biotic interactions taking place within a population, which can be quite important as it was shown for brown trout in this project for example.

Actual maps of fish observations were compared with prediction maps built using HSI values (see Chapter 3 for description of the methodology used). Fig. 4.28 and 4.29 show the results of this comparison between observations maps and prediction maps for brown trout parr in the River Tern at Q_{51} and Q_{77}.

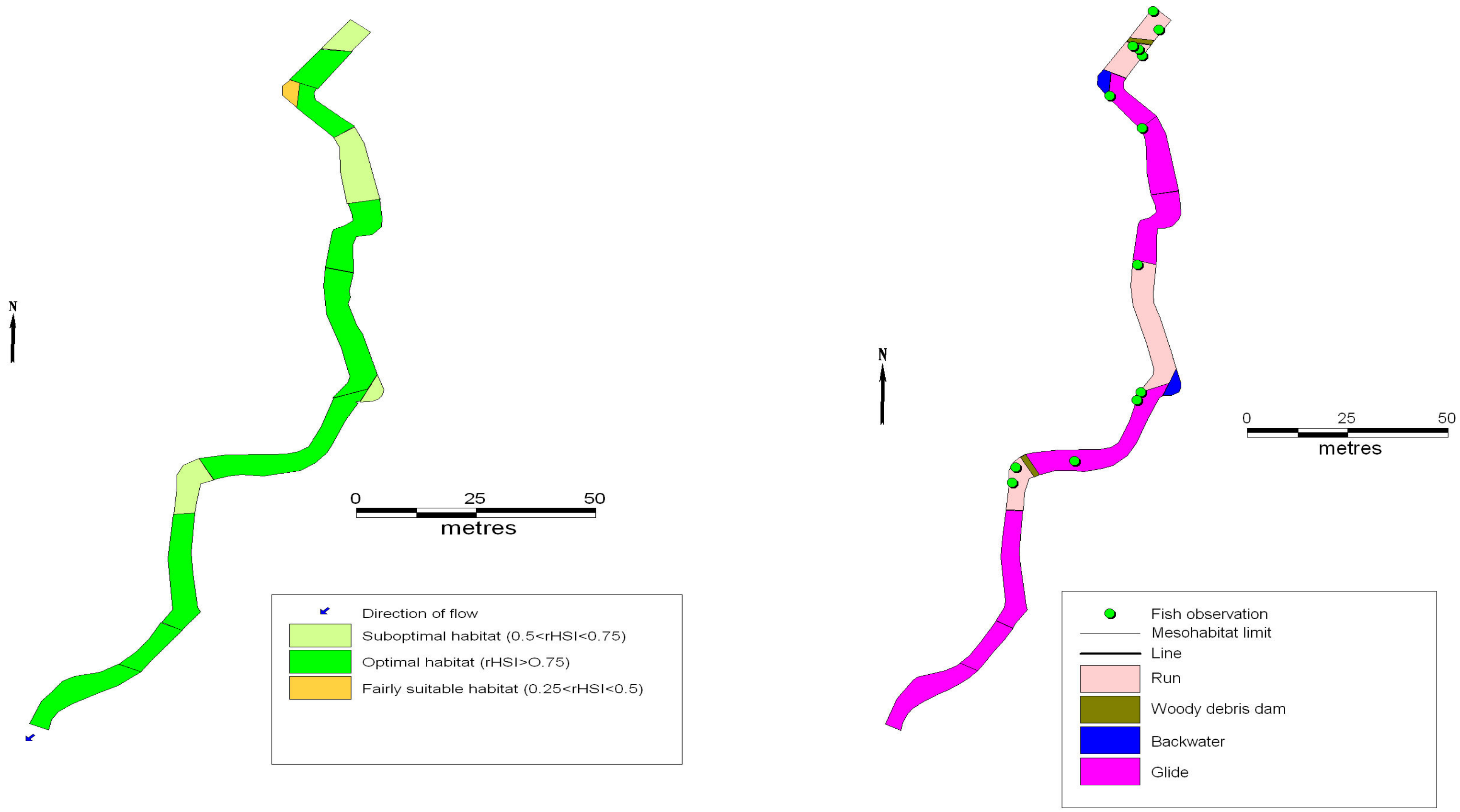


Fig 4.28 Comparison of prediction of brown trout occurrence (left) with actual fish observations (right) at Q_{51}

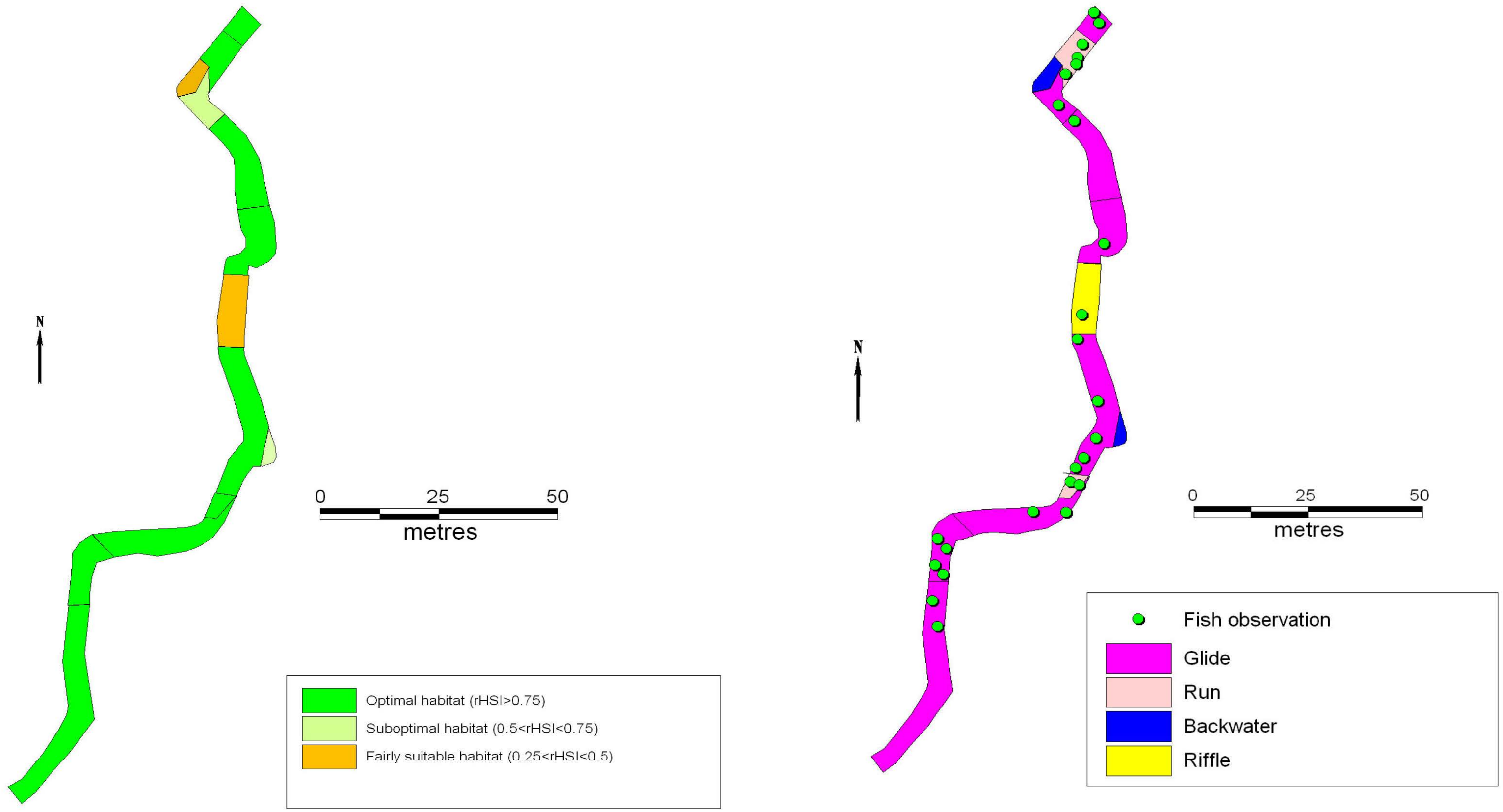


Figure 4. 29 Comparison of prediction of brown trout occurrence (left) with actual fish observations (right) at Q $_{77}$ (September 06)

Suitability of each mesohabitat was calculated using the five values of depth and velocity recorded in each CGU and the HSI curves developed by Dunbar *et al*. (2001). In Fig. 4.28, the prediction map shows that most of the reach presents optimal habitats for brown trout parr with just two “sub-optimal” mesohabitats (two runs) and two average habitats that are backwaters. According to these maps, fish observations are expected to be located in the optimal mesohabitats. On the actual observation map, fish observations are located both in the “optimal” and “suboptimal” mesohabitats. No fish was observed in the backwaters, which were characterised as “average” mesohabitats. In Fig. 4.29, which represents the River Tern at Q_{77}, the overall suitability of the reach is similar to that in Figure 4.28, i.e. the reach mostly presents optimal habitats with the exception of the mid-reach riffle, which is characterised, by a fair suitability for brown trout parr. The map drawn from the fish observations in the field shows that all but one trout parr observations are located in optimal mesohabitats. Hence, prediction of brown trout occurrence in the River Tern using the generalised HSIs developed by Dunbar *et al.* (2001) was accurate with the exceptions of two mesohabitats (see description of figures 4.28 and 4.29).

Generalised HSI curves can thus accurately predict fish occurrence. However, Moir *et al.* (2005) found they were not as accurate and precise as HSI curves built specifically for a stream/reach. As a result, one can wonder if the accuracy in predicting fish occurrence in the River Tern is not partly due to the stable physical and hydraulic conditions governing the reach. This leads to the conclusions that HSI curves may predict fish occurrence, depending on the method used to develop them, the physical and hydraulic characteristics of the reach considered and the fish species targeted. Nonetheless they only determine fish occurrence as a function of their physical environment and do not take into account the biotic interactions taking place within a population, which can be quite important as it was shown for brown trout in this project for example.

Chapter 4 presented the results of the investigations on brown trout habitat use in relation mesohabitat variability in a groundwater-influenced stream. Chapter 5 presents the results of similar investigations, but on bullhead habitat use in a surface-runoff influenced stream.

CHAPTER 5

HABITAT USE BY BULLHEAD (*COTTUS GOBIO*)

Bullhead has received far less attention in terms of research into habitat use and behaviour than brown trout. However, over the last decade interest for this species has grown, possibly as a result of its status as an endangered species and also as an indicator of stream naturalness.

Its ecology and habitat requirements are different from those of brown trout: bullhead are territorial and live a mainly solitary life. They are benthic fish and display a cryptic behaviour during the day, hiding under large substrate particles, which constitute their main habitat requirement. Their ecology and habitat requirements were reviewed in Chapter 2. Differences in ecology and habitat requirements between the two species make the comparative study of their habitat use very interesting.

During this project, bullhead habitat use was recorded in the two streams and flow regimes of interest: the Dowles Brook (surface runoff influenced) and to a lesser extent in the River Tern (groundwater-fed) where the existing population has decreased dramatically over the past 4 years. This will be discussed in more detail at the end of this chapter.

Several studies on bullhead have described the species habitat requirements in rivers in the UK (Perrow *et al.*, 1997) and across continental Europe (Knaepkens *et al.*, 2002; Knaepkens *et al.*, 2004; Legalle *et al.*, 2005; Chaumot *et al.*, 2006). However, flow-induced behaviour has received little if no attention and knowledge on bullhead adaptation to different patterns of flow variability is still lacking.

The present chapter aimed at addressing the following questions relating to bullhead in Dowles Brook and the River Tern (previously identified in generic terms in section 1.3.1).

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RQ_2. How does instream mesohabitat composition vary over the range of flows experienced by the Dowles Brook (surface runoff influenced flow regime)? (Section 5.1)

RQ_3. Is there a pattern of mesohabitat use displayed by the bullhead population studied and if so what is it? (Section 5.3)

RQ_4. Does mesohabitat use by bullhead follow the same pattern as mesohabitat variability, i.e. is it influenced only by flow? (Section 5.3.2)

RQ_5. Are other factors involved in bullhead habitat use? (Section 5.3)

RQ_6. What role is played by factors such as seasonality, habitat availability, life-stage and social interactions in the pattern of habitat use displayed by the surveyed population? (Sections 5.3.3, 5.3.4 and 5.4)

RQ_7. What are the key habitat characteristics that determine bullhead location in the study reach? (Section 5.3.6, 5.5 and 5.6)

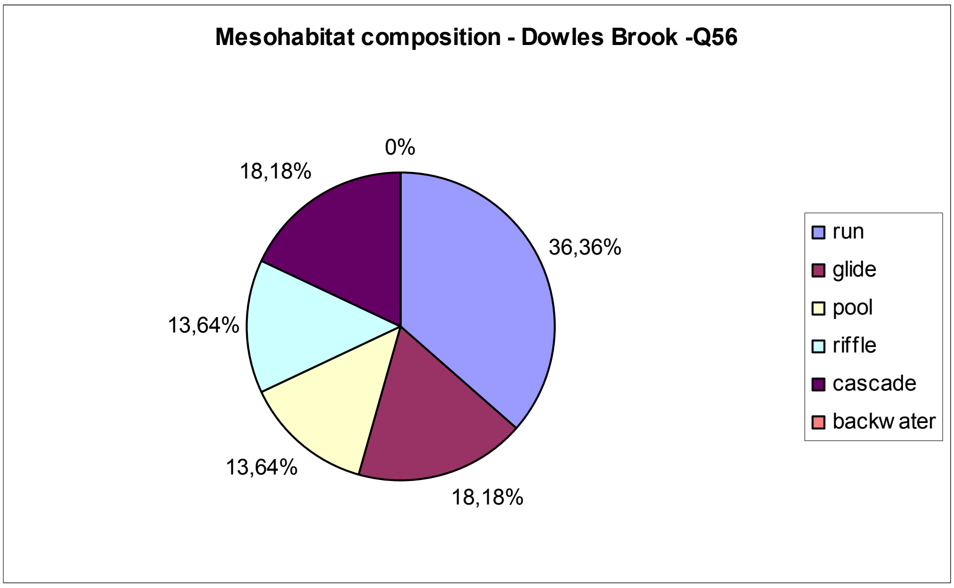
This chapter focuses mainly on the Dowles Brook where bullhead have been observed in fairly constant numbers throughout the survey season. The last section focuses on the River Tern and the few bullhead observations made at this site, with an attempt to compare the species behaviour for the two flow regimes.

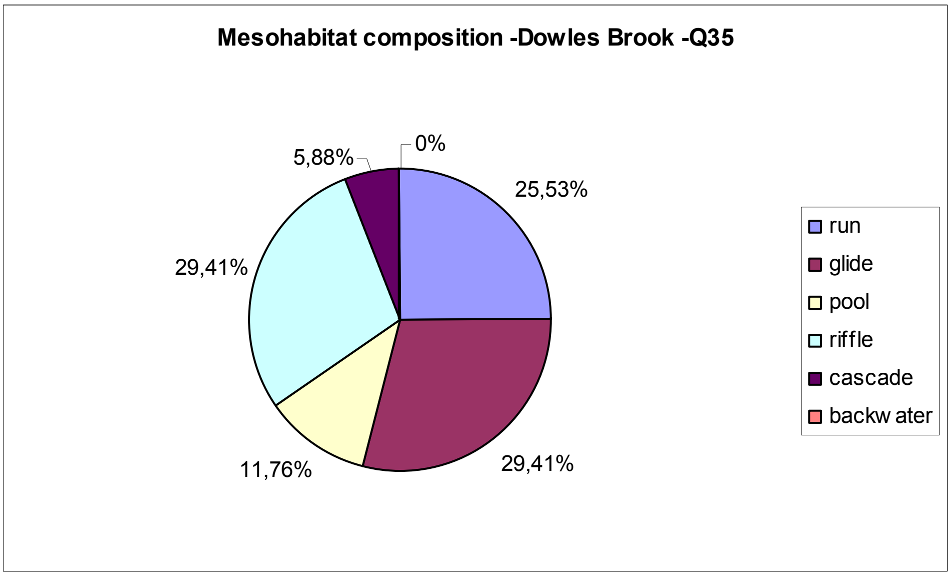
5.1 STREAM CHARACTERISTICS AND MESOHABITAT COMPOSITION ACCORDING TO FLOW VARIABILITY

RQ_2. How does instream mesohabitat composition vary over the range of flows experienced by the Dowles Brook (surface runoff influenced flow regime)?

5.1.1 Variability of mesohabitat composition

The Dowles Brook is a surface runoff influenced stream with a Base Flow Index value of 0.40. Hence it is a river with a ‘flashy’ flow regime that responds relatively quickly to precipitation. Mesohabitat variability is dependent on flow regime and thus a flashy flow regime results in high variability in mesohabitat composition. Fig. 5.1 below shows mesohabitat composition for the Dowles Brook at Q_{35} (0.2163 $m^3.s^{-1}$), Q_{56} (0.1006 $m^3.s^{-1}$) and Q_{96} (0.02119 $m^3.s^{-1}$).





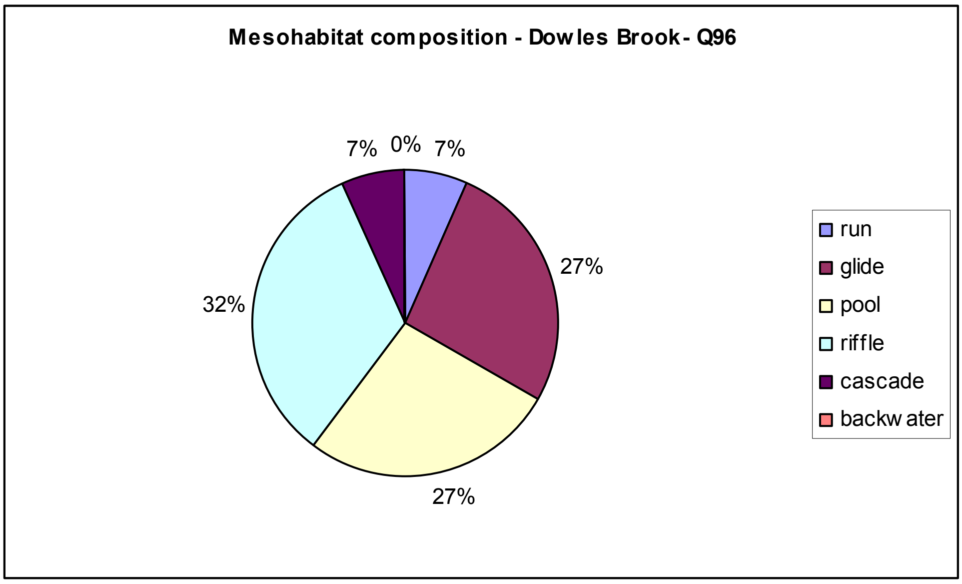


Figure 5.1Evolution of mesohabitat composition (%) in the Dowles Brook for Q_{35}, Q_{56} and Q_{96}

Fig. 5.1 shows a high mesohabitat diversity in this stream, which is characteristic of natural streams (Kemp *et al.*, 1999). Moreover, mesohabitat composition in the Dowles brook varies significantly as flow varies. At Q_{35}, the highest flow surveyed, riffles, runs and glides are the most abundant types of mesohabitats. At approximately the median flow, *i.e.* Q_{56}, runs are the most common type of mesohabitat in the stream with 36.36 % of the reach. At Q_{96}, riffles are the most frequent closely followed by glides and pools. Indeed, as shown by Newson *et al.* (1998), two types of mesohabitat units exist: erosional units such as riffles and depositional units such as pools. These units get transformed as discharge increases due to the increase in deposition and erosion forces linked to higher flows. At low flows, riffles are the most abundant because they are not affected by important erosion forces linked to high flows (they are 'drowned out' at higher flows). Pools get affected by strong depositional forces as discharge increases but at such low flows (Q_{96} here) their geomorphology and hydrological characteristics are not affected (Newson *et al.*, 1998). As flow increases to Q_{56}, the proportion of riffles in the stream decreases while the proportion of runs increases. The increase in flow results in riffles to transform into runs, which are characterised by higher depths than riffles and the emerging substrate in riffles, evident at low flows, becomes completely submerged at higher discharges.

Depositional units such as pools and glides see their proportion decrease with increasing discharge, as they evolve into runs (faster velocities without the loss of depth).

As well as the high variability in mesohabitat composition according to flow Fig. 5.1 also shows that no predictable pattern exists as to which mesohabitat is most abundant according to a particular flow. However the proportion of pools in the stream increases as discharge decreases from 11.76 % at Q_{35} to 26.67 % at Q_{96}.

This shows that flow variability impacts on mesohabitat composition in the Dowles Brook. The hydrology of the stream is characterised by rapid and frequent variations, and these in turn drive similar types of changes in mesohabitat composition. The next section focuses on how flow affects mesohabitat depth and velocity characteristics.

5.1.2. Mesohabitat characteristics and influence of discharge

Mesohabitat surveys included the measurements of depth and velocity parameters at 5 points within each CGU to allow the study of the evolution of these parameters with discharge. Tables 5.1, 5.2 and 5.3 below show for each discharge surveyed the mean depth (d) and mean velocity (v) with the respective standard deviations (S.D.) for the three types of mesohabitats: pools, runs and glides. Only data for these mesohabitat types are analysed as they are also represented in the other study site, *i.e.* River Tern, and allow the comparison of the two streams.

Table 5.1 Evolution of depth and velocity values and their associated standard deviation for runs according to flow. (* SD= Standard Deviation)

Flow	Actual discharge ($m^3.s^{-1}$)	Number of measurements	Mean depth (m)	Depth SD *	Mean velocity ($m.s^{-1}$)	Velocity SD*
Q_{35}	0.216	20	0.209	0.073	0.290	0.194
Q_{38}	0.198	24	0.208	0.073	0.350	0.275
Q_{43}	0.143	35	0.143	0.079	0.249	0.177
Q_{56}	0.101	38	0.104	0.040	0.266	0.183
Q_{72}	0.054	20	0.151	0.513	0.252	0.172
Q_{96}	0.021	5	0.098	0.403	0.156	0.144
Q_{99}	0.016	20	0.094	0.425	0.136	0.115
All discharges	N/a	127	0.146	0.073	0.259	0.202

Table 5.1 shows significant variations in mean depth (Kruskal-Wallis Chi-sq. 59.608, d.f.=6, $p<0.05$) and mean velocity (Kruskal-Wallis Chi-sq. 14.045, d.f.=6, $p<0.05$) according to flow for runs in the Dowles Brook. Study of standard deviation values shows an increase in standard deviation for depth values at very low flows while standard deviations values for velocity increase at higher flows.

Table 5.2 Evolution of depth and velocity values and their associated standard deviations for glides according to flow

Flow	Actual discharge ($m^3.s^{-1}$)	Number of measurements	Mean depth (m)	Depth SD	Mean velocity ($m.s^{-1}$)	Velocity SD
Q_{35}	0.216	127	0.146	0.073	0.259	0.202
Q_{38}	0.198	73	0.2978	0.160	0.163	0.036
Q_{43}	0.143	30	0.255	0.109	0.104	0.085
Q_{56}	0.101	135	0.268	0.101	0.087	0.091
Q_{72}	0.054	20	0.265	0.088	0.071	0.060
Q_{96}	0.021	20	0.243	0.091	0.021	0.035
Q_{99}	0.016	25	0.203	0.099	0.0295	0.030
All discharges	N/a	135	0.268	0.101	0.087	0.091

Table 5.2 shows significant variations in mean depth (Kruskal-Wallis Chi-sq. 19.931, d.f.=6, $p<0.05$) and in mean velocity (Kruskal-Wallis Chi-sq. 59.856, d.f.=6, $p<0.05$) according to flow for glides in the Dowles Brook. Study of standard deviation values lower variability in velocity measurements than in depth measurements. Also mean standard deviation values for glide velocities are less than those for run velocities (0.09111 compared to 0.20232).

Table 5.3 Evolution of depth and velocity values and their associated standard deviations for pools according to flow

Flow	Actual discharge ($m^3.s^{-1}$)	Number of measurements	Mean depth (m)	Depth SD	Mean velocity ($m.s^{-1}$)	Velocity SD
Q_{35}	0.216	5	0.374	0.172	0.004	0.022
Q_{38}	0.198	15	0.359	0.197	0.044	0.059
Q_{43}	0.143	10	0.295	0.159	0.024	0.039
Q_{56}	0.101	8	0.278	0.077	0.009	0.028
Q_{72}	0.054	12	0.361	0.146	0.019	0.022
Q_{96}	0.021	18	0.230	0.127	0.022	0.027
Q_{99}	0.016	15	0.253	0.167	0.007	0.022
All discharges	N/a	73	0.298	0.160	0.020	0.036

Table 5.3 shows no significant variation in mean depth (Kruskal-Wallis Chi-sq. 9.053, d.f.=6, p=0.171) nor in mean velocity (Kruskal-Wallis Chi sq. 7.230, d.f.=6, p=0.300) for pools according to flow in the Dowles brook. Values of standard deviation for depth remain relatively constant at all flows and are higher than for run depths and glide depths.

Very low standard deviation values for pool velocities indicate that within this type of mesohabitat, velocity values are relatively uniform.

The statistical analysis of depth and velocity parameters for pools, runs and glides in a surface-runoff influenced stream shows that while the physical variables for runs and glides are significantly influenced by flow variability, the variables for pools are not subject to such changes. Pools can be therefore considered as stable habitats compared to shallower, faster flowing habitats like glides and runs. This may have some impact on fish habitat use, which will be discussed in section 5.3. The next section focuses on the evolution of population parameters for the observed bullheads.

Section 5.1 addressed research question RQ2 as follows: mesohabitat composition in the Dowles Brookes experienced a high level of variability in response to the flashy nature of the flow regime. Six mesohabitat types were identified in the reach at all flows and their importance in terms of reach area varied to a great extent depending on the discharge level. Depth and velocity characteristics of the main types of mesohabitats also varied with discharge but differences were observed among mesohabitats: pools and glides physical characteristics tend to remain stable across the range of discharge while those of riffles and runs vary a lot.

5.2 EVOLUTION OF POPULATION-RELATED PARAMETERS DURING THE SURVEY SEASON

Five monthly surveys were carried out between May and October 2006 on the River Dowles Brook, a surface runoff influenced (hence flashy) river. The flows surveyed for fish observations ranged from Q_{43} (May) to Q_{99} (August). Bullhead were observed on every occasion and were the only species observed in the stream. The number of observations recorded on each survey varied from 4 fish in May to 22 fish in September with a total number of 79 observations (mean = 15.8).

The River Tern was also surveyed for bullhead (on the same occasions as for brown trout). However, bullhead were only observed on half of the surveys, from September onwards, and the total number of bullhead observed was only 10 for the whole survey period. Hence, comparison of habitat use by this species between the two types of flow regimes is not statistically significant due to the small size of the River Tern sample. Details of the results for the river Tern will be described however in the last part of this chapter. Fig. 5.2 represents the evolution of the number of fish observed during the survey season.

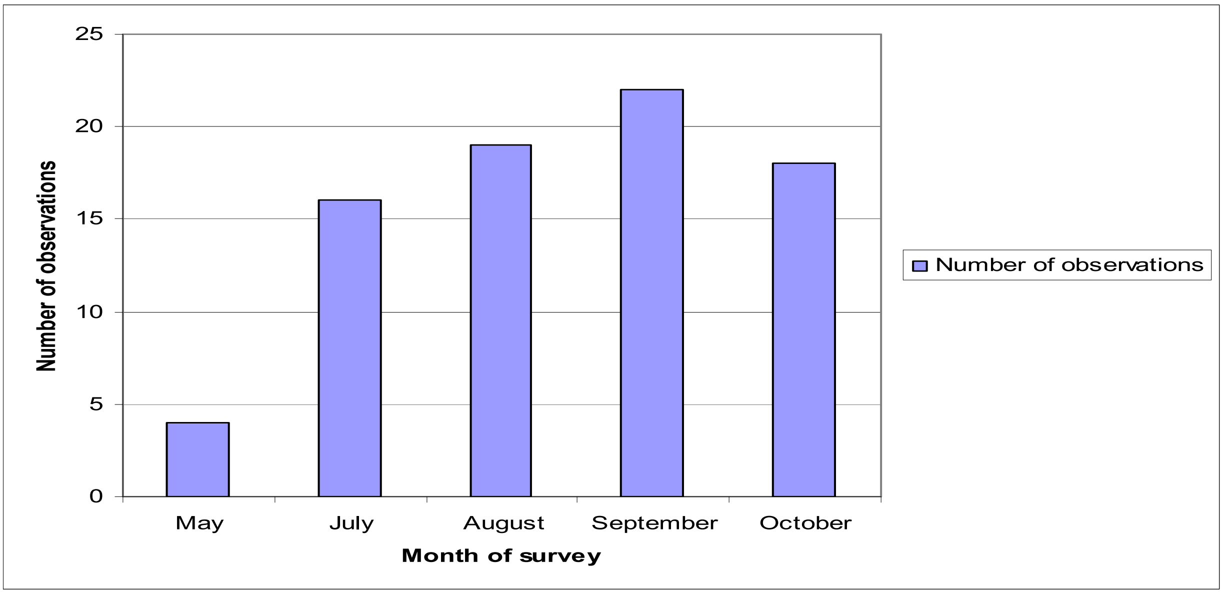


Figure 5.2 Seasonal evolution of the number of bullhead observations in the Dowles Brook

The lowest number of observations occurred in May (only 4 fish) and the highest number of fish was observed in September (N=22). There is still a sharp difference between the numbers of fish spotted in May and July. The number of observations increased to reach its peak in September, which can be due to recruitment.

The total number of bullhead observed was divided into three classes according to the size of the fish and based on information gathered from the literature (Fox, 1978; Cowx and Harvey, 2003). The smallest fish observed was 2cm-long whereas the biggest measured around 15 cm in length. Hence the three classes were:

- Size inferior to 5cm: juvenile and adult-but-not-mature individuals.
- Size from 5cm to less than 10cm: adults of average size
- Size greater than 10cm: large adults.

Bullhead is a territorial species and territoriality appears when the fish become sedentary (around 2-3cm in length, according to Fox (1978)). In this study it was thus assumed that the larger a bullhead was, the more territoriality it would display and thus some size-related habitat choice would be evident. The evolution of the length frequency distribution of bullhead observed in the stream according to season is shown in Fig. 5.3 below.

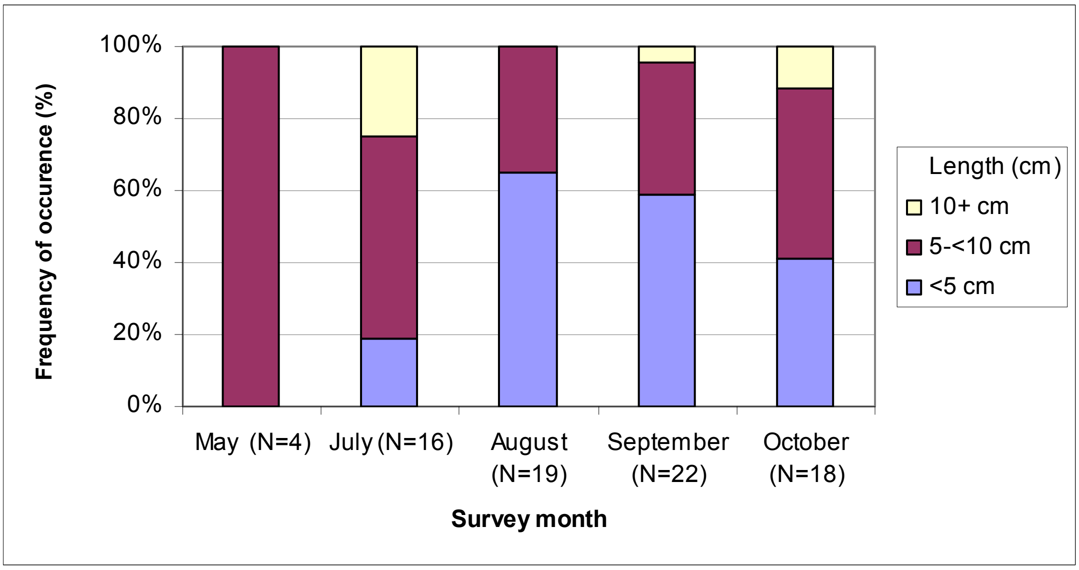
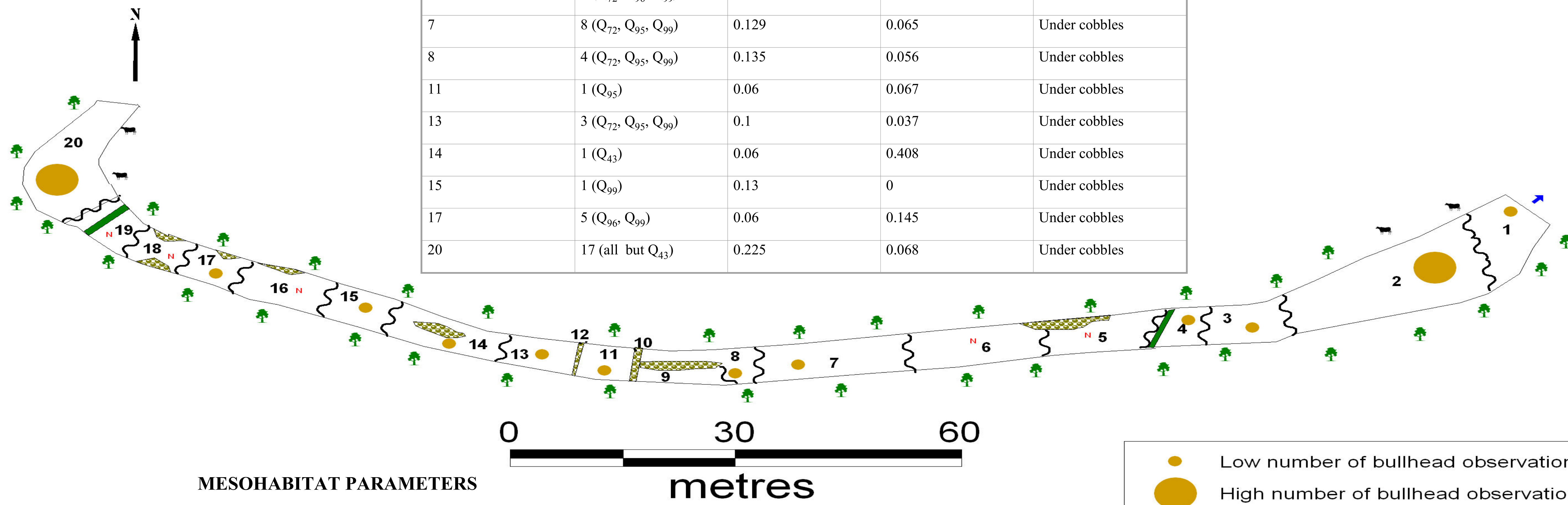


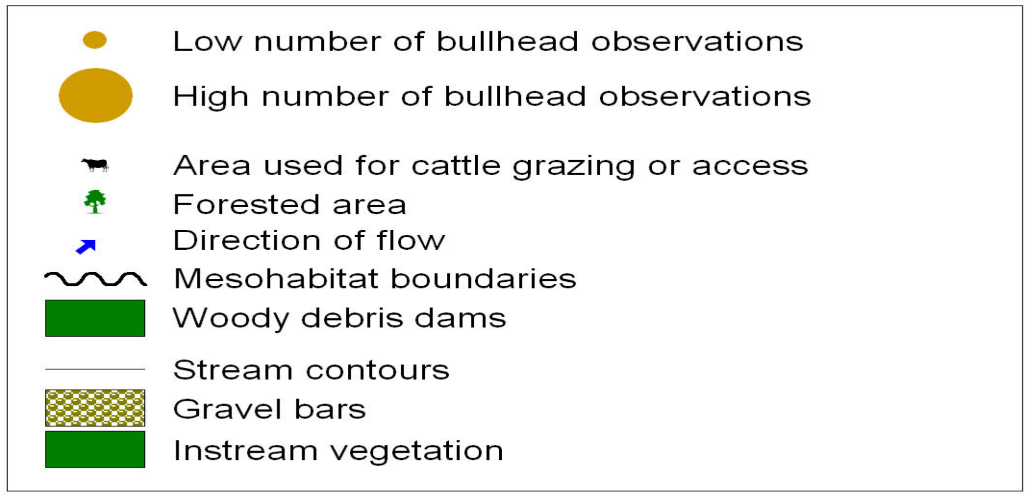
Figure 5. 3 Seasonal evolution of the length frequency distribution of observed bullheads

Fig. 5.3 shows that from July, the number of small sized bullhead (length less than 5 cm) increases to a maximum of 65% of the observations in August and then it steadily decreases. At the same time the proportion of average sized bullhead decrease from May onwards and reaches its minimum in August (35% of the observed population). No particular trend can be distinguished for large bullhead as they were observed in July, then in September and October in small numbers. The rise in the number of small bullhead in July and August could be the result of the larval stages becoming sedentary. Spawning takes place usually in March-April. By July, larval stages have grown and have become sedentary (Fox, 1978). The rise could also result from the migration into the stream, either passive or active, of young bullhead. The decrease in the number of small bullhead in September and October may result either from the growth of these individuals so that they become accounted for in the "average size" class, or from migration of these individuals to other parts of the river outside the study reach. The next section investigates mesohabitat use by bullhead and how size variability affects bullhead location.

FISH PARAMETERS

Unit	N Observations (flow)	Mean depth (m)	Mean velocity ($m.s^{-1}$)	Fish activity
1	2 (Q_{43})	0.04	0.0135	Hiding under cobble
2	25 (all but Q_{99})	0.134	0.065	Under cobbles
3	3 (Q_{72}, Q_{96}, Q_{99})	0.13	0.176	Under cobbles
4	6 (Q_{72}, Q_{96}, Q_{99})	0.15	0.328	Under cobbles
7	8 (Q_{72}, Q_{95}, Q_{99})	0.129	0.065	Under cobbles
8	4 (Q_{72}, Q_{95}, Q_{99})	0.135	0.056	Under cobbles
11	1 (Q_{95})	0.06	0.067	Under cobbles
13	3 (Q_{72}, Q_{95}, Q_{99})	0.1	0.037	Under cobbles
14	1 (Q_{43})	0.06	0.408	Under cobbles
15	1 (Q_{99})	0.13	0	Under cobbles
17	5 (Q_{96}, Q_{99})	0.06	0.145	Under cobbles
20	17 (all but Q_{43})	0.225	0.068	Under cobbles





MESOHABITAT PARAMETERS

Unit/Type	Mean depth range (m)	Mean velocity range ($m.s^{-1}$)	Substrate	Surface flow type
1/riffle	0.07 -0.104	0.1052-0.2424	Cobble+gravel	Rippled
2/Glide	0.168-0.276	0.0134 -0.098	Bedrock, cobble +silt	Smooth
3/run/glide	0.034 –0.268	0.098-0.278	Bedrock, cobble +silt	Smooth to rippled
4/ run	0.096-0.136	0.1556-0.3316	Bedrock, cobble +silt	Rippled
5/run	0.07-0.13	0.075-0.3316	Bedrock, cobble, gravel	Rippled
6/run	0.07-0.13	0.156-0.378	Bedrock, cobble +silt	Rippled
7/glide	0.158-0.22	0.0432-0.474	Cobble,gravel +silt	Smooth
8/glide	0.236-0.322	0.0202-0.0688	Bedrock,cobble, sand	Smooth
11/pool	0.268-0.322	0.0044-0.0688	Bedrock,cobble, sand	Smooth
14/run/riffle	0.046-0.102	0.22-0.3	Cobble, gravel and sand	Rippled
15/glide	0.188-0.322	0.0404-0.102	Cobble, boulder, silt	Smooth
16/run/riffle	0.09-0.18	0.0872-0.3016	Bedrock,cobble and gravel	Rippled
17/glide/pool	0.218-0.262	0.0284-0.1294	Bedrock,gravel	Smooth
19/run/riffle	0.104-0.258	0.0322-0.171	Bedrock, gravel	Rippled,unbroken waves
20/pool	0.294-0.452	0.003-0.028	Bedrock, cobble, silt	smooth

Figure 5.4 Summary map of bullhead observations on the Dowles Brook for all flows surveyed.

5.3 MESOHABITAT USE BY BULLHEAD –OBSERVATIONS AND RESULTS

RQ$_3$. Is there a pattern of mesohabitat use displayed by the bullhead population studied and if so what is it ?

RQ$_5$. Are other factors involved in bullhead habitat use?

5.3.1 Summary of bullhead observations in the Dowles Brook

The map shown in Fig. 5.4 summarises the evolution of the mesohabitat composition as well as bullhead locations and their physical characteristics over the range of surveyed flows in the Dowles Brook, i.e. between Q_{99} (0.0155 $m^3.s^{-1}$) and Q_{43} (0.168 $m^3.s^{-1}$)

The reach was divided into 20 units according to the results of the mesohabitat surveys. Bullhead observations were scattered along the reach in all types of mesohabitats except chutes. The physical characteristics of chutes were not included in the map as usually only one measurement of depth and velocity was taken for these units.

Bullheads were present in 12 units. In 10 of the units the number of observations was less than 10 per unit. However, in 2 units numbers were much higher, e.g. 17 in unit 20 and 25 in unit 2. Unit 20 is a large pool at the upstream end of the reach while unit 2 is a long glide at the downstream end of the reach.

Study of the physical characteristics of these two units show that they present similar conditions, which distinguish them from the other units with less or no observations:

- These locations do not change in terms of mesohabitat type with flow and they remain with the characteristics of a glide ad pool whatever the flow.
- Unit 2 and unit 20 are both deep areas compared to other parts of the reach: in unit 2, depth varied between 0.168 m and 0.276 m while in unit 20, depth varied from 0.294 m to 0.452 m.
- They are slow flowing environments: velocity in unit 20 constantly remained under 0.03 $m.s^{-1}$ while the in unit 20 remained under 0.1 $m.s^{-1}$.
- They are both situated in between two fast flowing units: directly upstream of unit 20 is a run that becomes a riffle at very low flow and is the unit directly

downstream. Unit 2 is situated between a riffle (unit1) and a run/riffle type of unit (unit 3).

- The channel widens at these points, thus enlarging the area available for use.

Substrate composition does not differ from that in the other mesohabitats: bedrock and cobbles are the dominant substrates with presence of silt. The following sections focus on habitat use in relation to flow variability (section 5.3.2), in relation to seasonality (5.3.4) and fish size (5.3.5).

5.3.2 Mesohabitat use in relation to flow variability

RQ$_4$. Does mesohabitat use by bullhead follow the same pattern as mesohabitat variability, i.e. is it influenced only by flow?

Location in terms of mesohabitat was determined for every bullhead that was spotted on the different surveys. The aim was to investigate whether mesohabitat use was determined by flow, by the time of year that was surveyed, or by the size of the fish. Fig.5.5 presents mesohabitat use by the whole observed bullhead population according to flow.

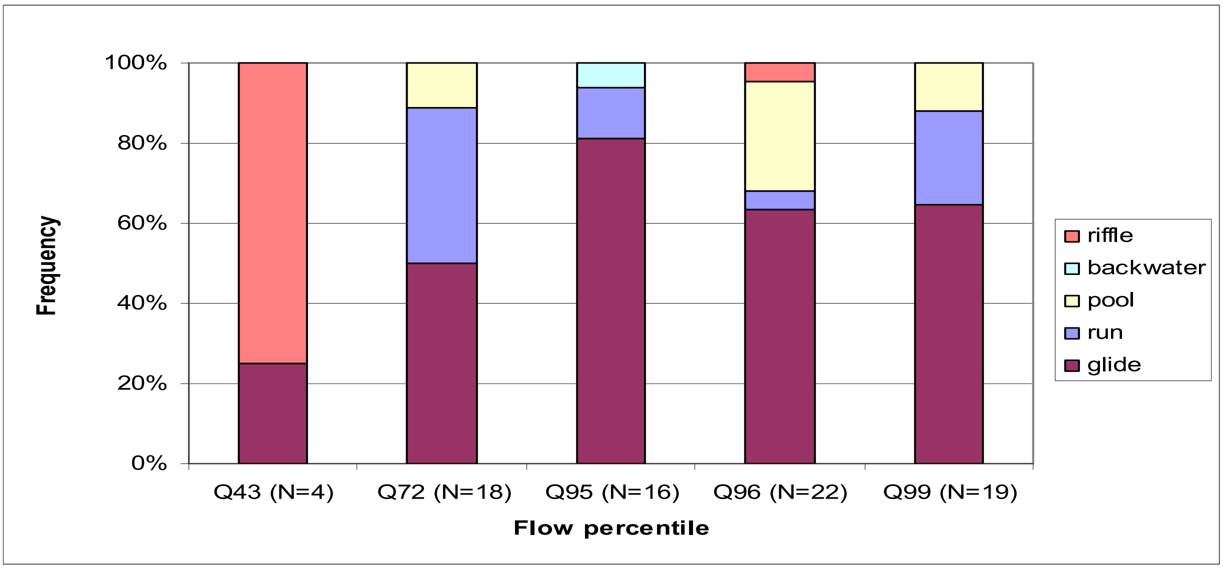


Figure 5.5 Mesohabitat use by bullhead according to flow

Fig. 5.5 shows an increase in glide use with decreasing flow and also an increase in the diversity of mesohabitats where bullhead were found. However, statistical analysis of the results did not show any significant difference in mesohabitat use between flows, probably as a result of the small sample size (Kruskal-Wallis Chi sq. 4, d.f.=4, p=0.406). From Q_{72}, glide becomes the most used mesohabitat. Runs, pools and to a lesser extent backwater and riffles are used at the lowest flows. It is interesting to note the contrast between mesohabitat use at Q_{43}, e.g. 75% of use of riffles and 25% of use of glide and that at Q_{99}, e.g. 65% of use of glide and 35% of use of run and pool. The next section focuses on the influence of seasonality on mesohabitat use by bullhead.

5.3.3 Mesohabitat use in relation to season

RQ_6. What role is played by factors such as seasonality, habitat availability, life stage and social interactions in the pattern of habitat use displayed by the surveyed population?

The evolution of mesohabitat use according to the time of year in the Dowles Brook is shown in Fig.5.6.

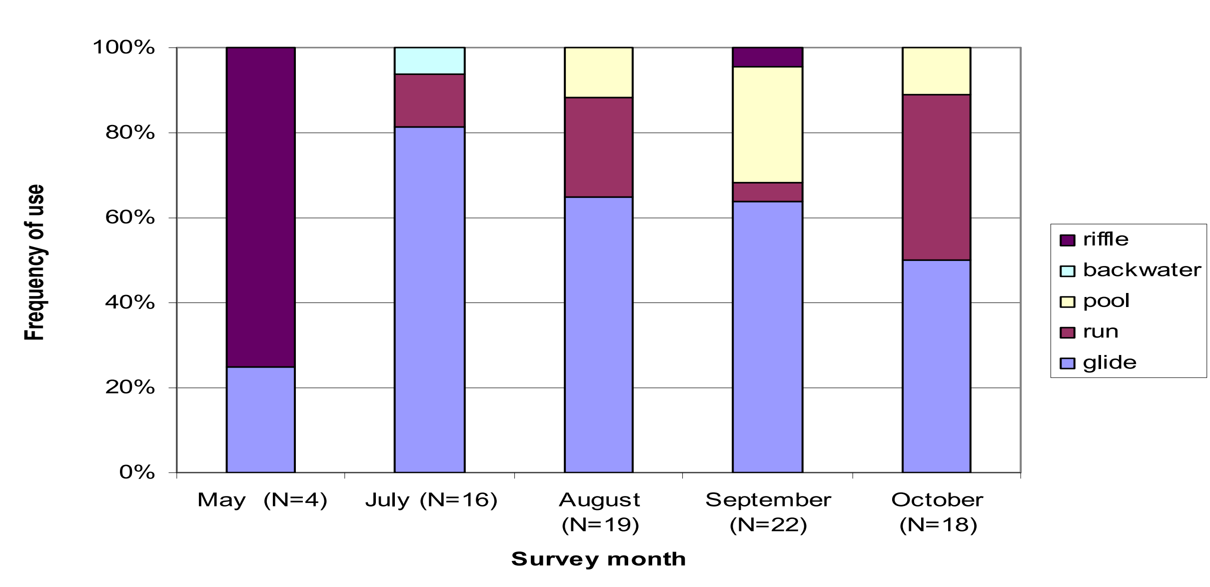


Figure 5.6 Seasonal evolution of mesohabitat use by bullhead. The number of observations for each month surveyed is shown between brackets

Fig. 5.6 shows a great difference between mesohabitat use in May and July onwards. Riffles are the most frequently occupied mesohabitats though the number of observations is very small (N=4) compared to that for other surveys. From July onwards, glide use decreases though glide remains the most used mesohabitat type by bullhead. Statistical analysis revealed no significant difference with respect to mesohabitat use according to seasonality (Kruskal-Wallis Chi-sq. 4, d.f.=4, p=0.406). As an answer to research question RQ_6, seasonality appears to partly influence mesohabitat use by bullhead (constant decrease in glide use from July onwards). At the beginning of this result chapter, three size classes were identified for bullhead. The following section focuses on the possible influence of fish size on mesohabitat use.

5.3.4 Mesohabitat use and bullhead size

RQ_6. What role is played by factors such as seasonality, habitat availability, life stage and social interactions in the pattern of habitat use displayed by the surveyed population?

The above charts showed mesohabitat use by the whole of the observed population. However, when looking at each of the three size classes previously described, some differences appear as shown by Fig. 5.7, 5.8 and 5.9.

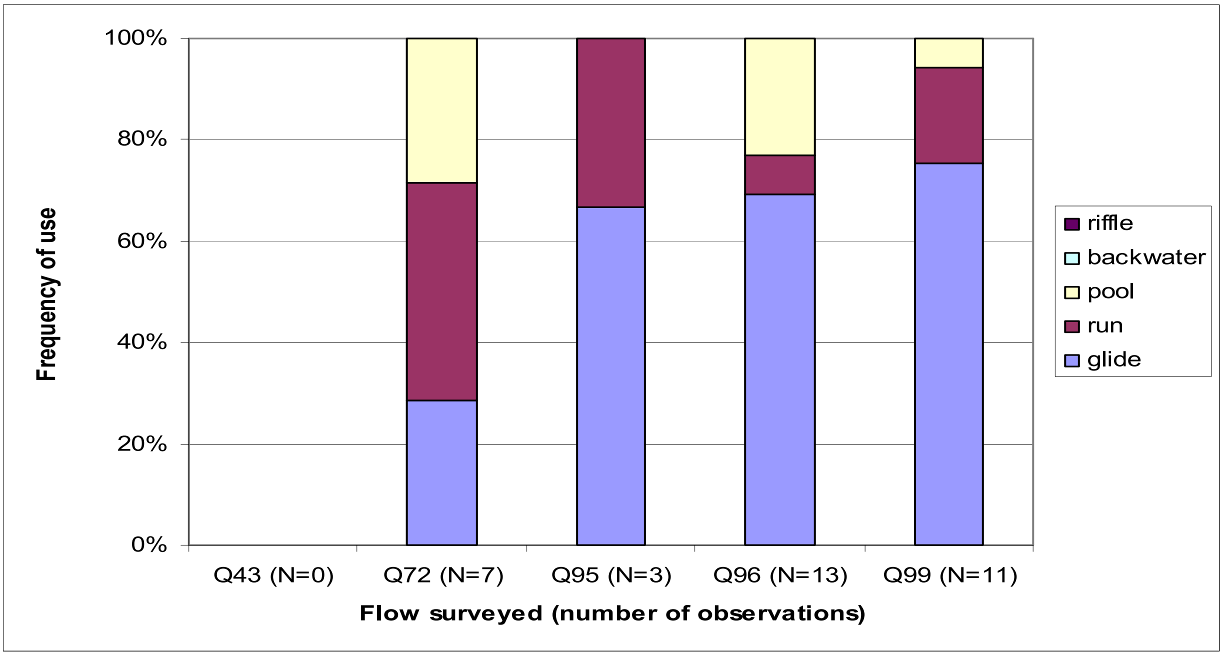


Figure 5.7 Mesohabitat use by small bullhead (length less than 5 cm) according to flow

Fig. 5.7 shows that small bullheads (5cm and less in length) were not observed at Q_{43}. With decreasing discharge, there is an increase in glide use from 28% at Q72 to 75% at Q99. Runs and pools are also used but to a lesser extent and no pattern of use related to flow is apparent for these mesohabitat types.

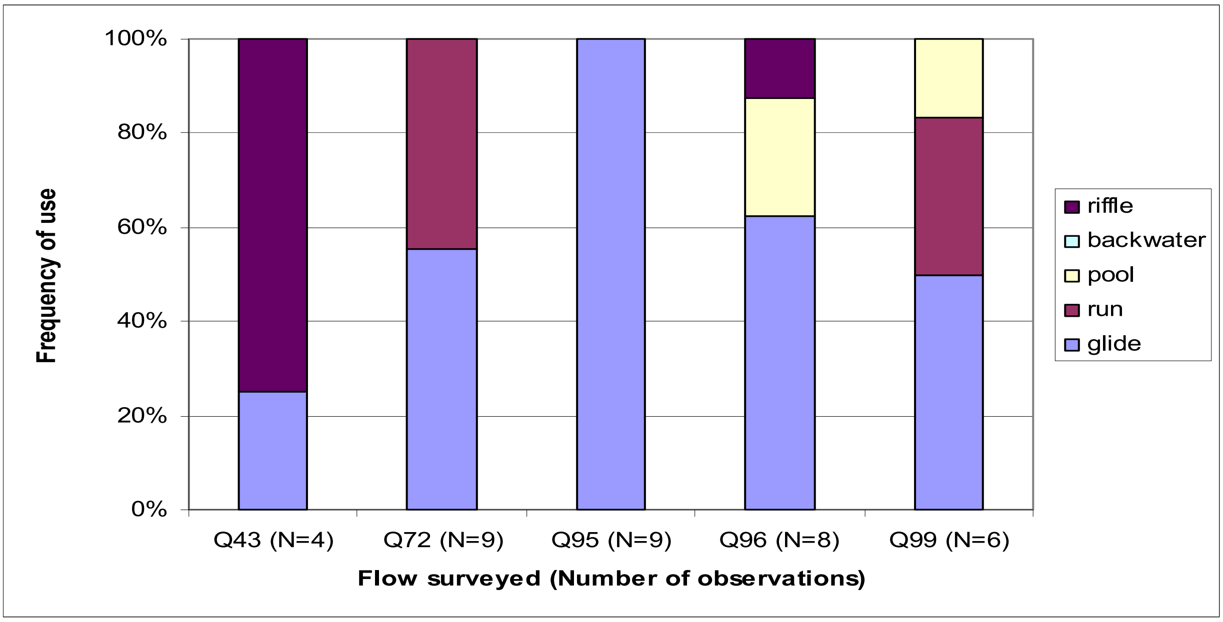


Figure 5.8 Mesohabitat use by medium sized bullhead (length between 5 and 10 cm) according to flow

Fig. 5.8 shows that medium size bullhead (from 5cm to less than 10 cm in length) display a different pattern of mesohabitat use from that of smaller bullhead. Glide use shows a parabolic evolution from Q_{43} with a maximum of 100% of fish using glides at Q_{95}. For all flows except Q_{43} glide is the most used mesohabitat. At Q_{43}, 75 % of fish of this size class use riffles. At lower flows, other mesohabitats used included mainly runs and pools, and riffles at Q_{96}.

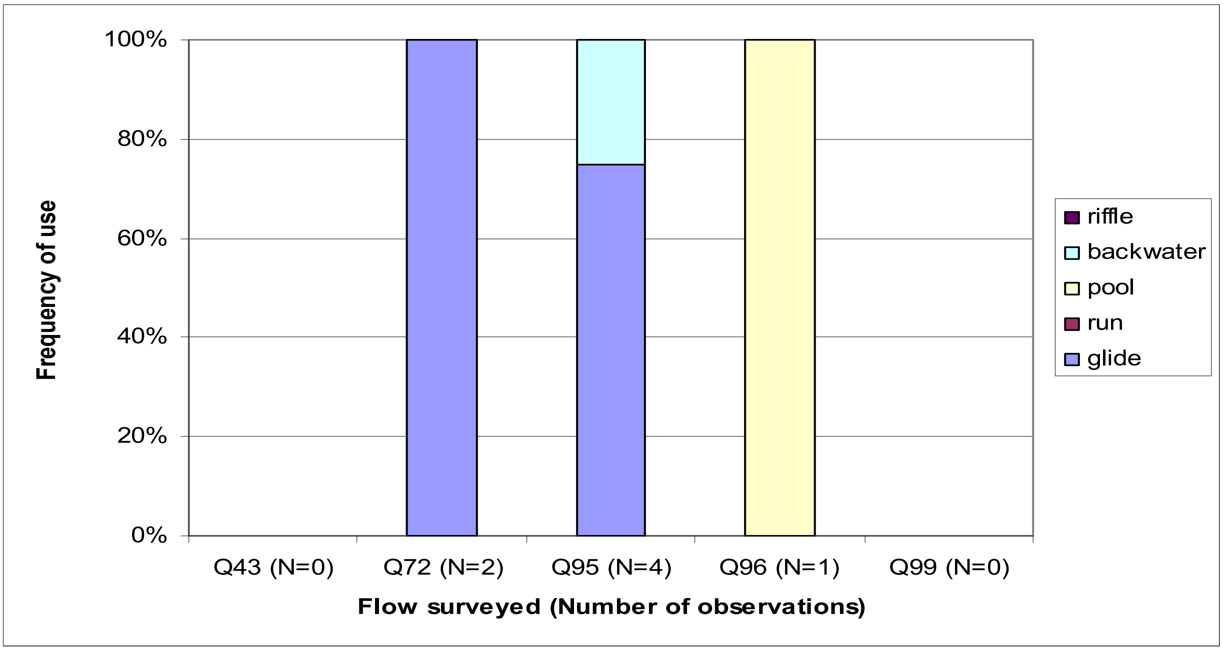


Figure 5.9 Mesohabitat use by large bullheads (length superior to 10 cm) according to flow

Figure 5.9 shows that large bullheads (length of 10 cm and above) were only observed on three survey occasions, Q_{72}, Q_{95} and Q_{96}, and in lower numbers than the two other size classes. They did not display such a variety in habitat use as that of the two other classes. Glide was the only mesohabitat use at Q_{72} and was the most used at Q_{95}. The only large individual observed at Q_{96} was in a pool (unit 20). Large bullhead appear to favour slow flowing mesohabitats, e.g. glide, pool, backwater, compared to fast flowing habitats such as runs and riffles that were used by the smaller individuals. Statistical comparison of mesohabitat use according to bullhead size categories showed no significant difference, between the three size categories (Kruskal-Wallis Chi sq. 4, d.f.=4, p=0.406). This subsection addressed research question RQ_6 and showed that, although differences in location were observed among the three classes of bullhead, they did not appear significant. Hence the effect of fish size on habitat use by bullhead at the meso-scale appears very limited. The study of mesohabitat characteristics in section 5.1 showed that within a type of mesohabitat depth and velocity values varied between flows. As a result it is relevant to study which values of these parameters are chosen by bullhead and this investigated in the following section.

5.3.5 Use of depth and velocity

RQ_7. What are the key habitat characteristics that determine bullhead location in the study reach?

Fig. 5.10 and 5.11 represent the depths and velocities at the locations where bullheads were found and how these vary with flow.

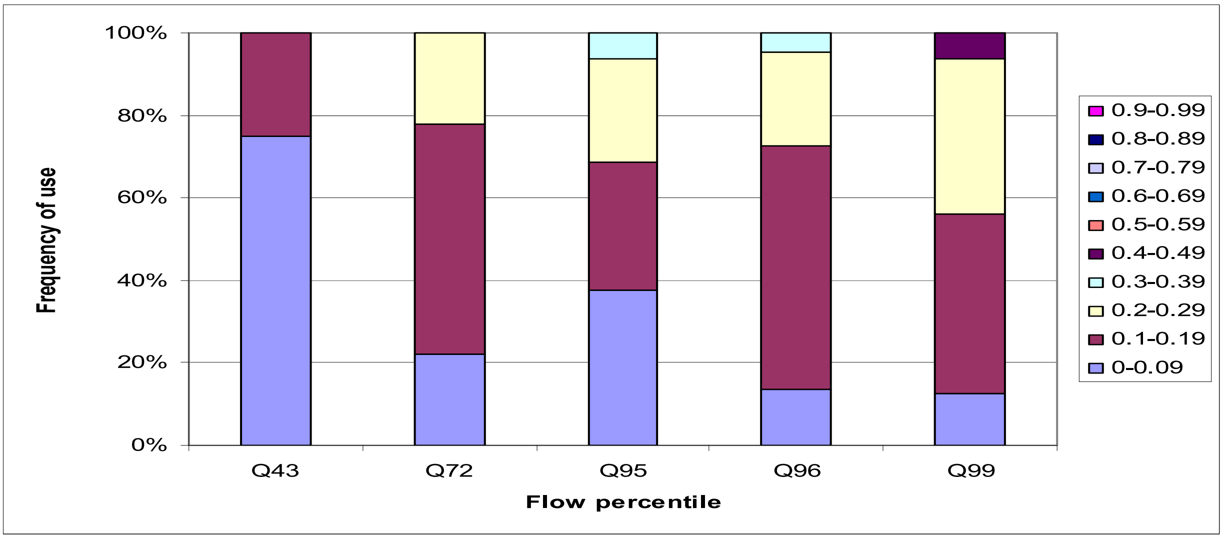


Figure 5.10 Frequency distribution of depths at bullhead locations according to flow

In Fig. 5.10, the frequency distribution of depths used shows a shift from shallow depths (<0.1m) to deeper locations (maximum of 0.49 m) as discharge decreased. However, statistical analysis of used depth distribution between flows shows no significant difference (Kruskal-Wallis Chi sq. 5.158, d.f. 4, $p=0.251$), which means that overall bullhead choice of depth remains stable between flows.

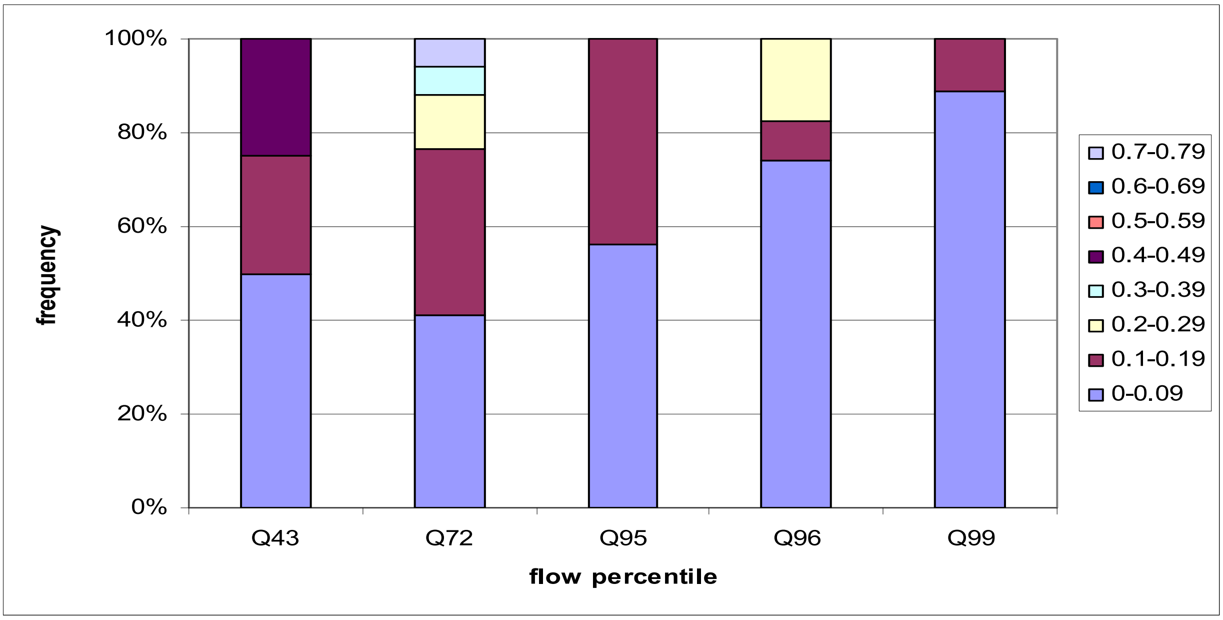


Figure 5.11 Frequency distribution of velocities at bullhead locations according to flow

In Fig. 5.11 the frequency distribution of used velocities shows a significant increase in the use of slow flowing areas (velocity between 0 and 0.09 $m.s^{-1}$) as discharge decreases (Kruskal-Wallis Chi-sq 14.494, d.f.=4, $p<0.05$).

One can note that in the case of Q_{43} ¾ of the velocities used by bullhead have low values, i.e. between 0 and 0.19 $m.s^{-1}$, although the most used habitat was riffle, which is characterised by fast flowing water. This shows that the locations chosen by bullhead not only depend on the mesohabitat in itself, but also at a smaller scale, of the local conditions induced by the presence of stones.

Fig. 5.12 and 5.13 show the evolution of mean depth and mean velocity used by bullhead according to flow. As discharge decreases, bullhead shift to areas of higher depth and lower velocity, which is consistent with the increasing use of glides in the study reach.

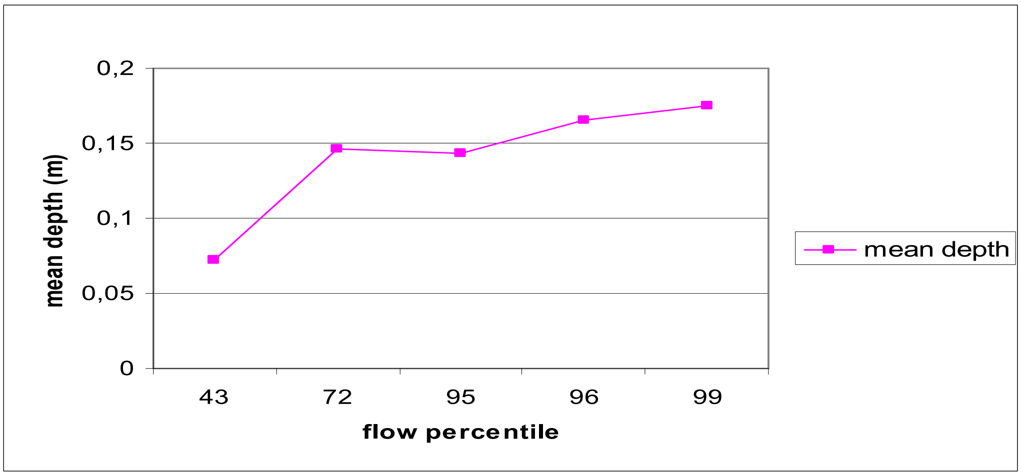


Figure 5.12 Mean depth of bullhead observations according to flow

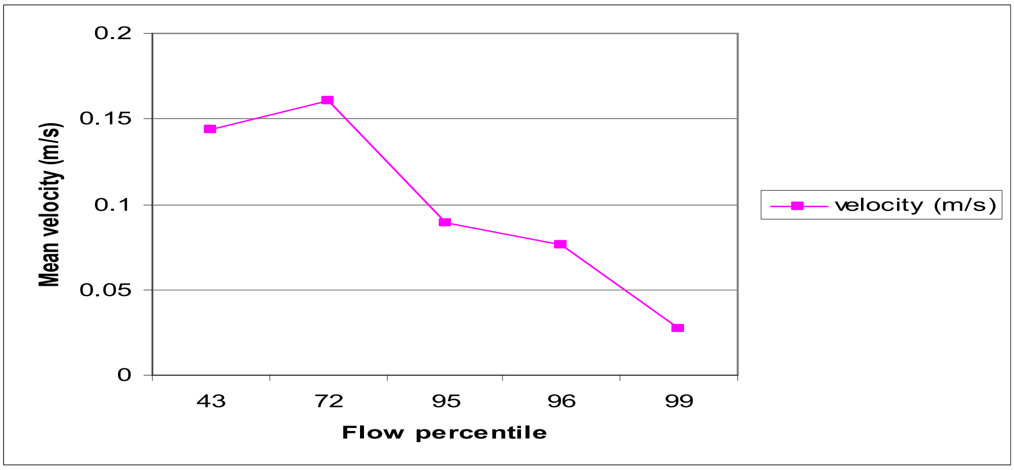


Figure 5.13 Mean velocity at bullhead locations according to flow

In response to research question RQ_7, bullhead were observed at low velocities , i.e. below 0.2 $m.s^{-1}$ and used velocity decreased with a decrease in discharge. The use of depths between 0.1 and 0.2 m increased at lower discharges.

Section 5.3 addressed research questions RQ_3 (is there a pattern of mesohabitat use displayed by the bullhead population studied and if so what is it?) and RQ_5 (are other factors involved in bullhead habitat use?). The results presented in this section showed that a pattern of mesohabitat use was clearly apparent from bullhead observations and that bullhead favoured slow flowing habitats such as glides and pools. Seasonality, habitat availability and fish size appeared to have a limited impact on fish habitat use. However, physical habitat characteristics and their evolution according to discharge affected bullhead location. Section 5.4 presents the analysis of the results shown in section 5.3.

5.4 RESULTS ANALYSIS: FACTORS INFLUENCING BULLHEAD BEHAVIOUR IN A FLASHY STREAM

RQ_6. What role is played by factors such as seasonality, habitat availability, life-stage and social interactions in the pattern of habitat use displayed by the surveyed population?

Some factors to explain the increase in the number of fish in July compared to May are:

- A high flow event caused most of the fish to be washed out downstream of the study reach and the number of observations in July corresponds to a "normal" situation. Indeed, the hydrograph for the survey period shows that flows in July and the following summer months are usually very low while the spring months see higher levels of base flow and flow variability. In the days prior to the May survey, the hydrograph showed a rapid increase in flow following high precipitations.
- The reach usually does not host a great number of fish except in the summer months. Fish migrate into this reach at that time of year for mating and spawning and they start migrating out again in October.
- High numbers in the summer months correspond to the period at which young bullhead shift from the larval stage to a juvenile stage, hence becoming detectable by the surveyor. In May, if there are fish in the stream they may be at the larval stage, hence easily missed, mostly in poor visibility conditions and in deeper water.
- The conditions in the reach during summer are more suitable for bullhead in terms of mesohabitat composition, shelter and food availability. Hence bullhead migrate into that part of the reach in the summer months. May could mark the very beginning of the immigration season for bullhead. The four fish observed in May could have been the first ones to be present in the reach.

The above results show than not only mesohabitat use by bullhead is flow-dependent but also that it is a function of the size of the individuals considered. Some hypotheses that could explain the latter are:

- Bullhead are poor swimmers, hence run the risk of being washed out if located in zones with fast flowing water such as runs and riffles, which explains they are mostly found in glides and pools.
- Riffles and runs do not constitute appropriate mesohabitats for large bullhead so they tend to avoid them.

- Small bullhead, due to their ongoing growth, have increased feeding needs and since they are poor swimmers tend to locate in areas where feeding on drifting macroinvertebrates is easier, hence the use of runs and riffles.
- Territoriality, which is one of the major characteristics of bullhead ecology.

The latter hypothesis appears to be the most relevant in explaining the variability in habitat use among size classes. Bullhead usually hide under substrate particles (cobble, pebble or larger), which constitute their territory. Studies by Knaepkens *et al.* (2002) have shown that the presence of large substrate particles in a river could predict the location of bullhead. Moreover, laboratory studies have shown that bullhead are very faithful to the stone they have chosen as a refuge (Copp *et al.*, 1994).

Large bullheads, because of their size, appear to have more chances of choosing the mesohabitat that suits them best than smaller individuals, hence the fact that they were found only in glides, pools and backwaters, i.e. slow flowing environments and zones of food retention.

Due to the low numbers of large individuals, average sized fish still had a lot of choice with respect to mesohabitats. As a result they chose mostly glides and the parabolic pattern in Fig. 5.8 could be due to flow. The fact that other mesohabitats, i.e. pools and runs, were used could result from competition and territoriality.

At Q_{43} (0.168 $m^3.s^{-1}$), riffle was the most used type of mesohabitat, which could be due to:
- The lack of glides in the stream at that stage;
- Glides, even if in a high proportion, are too deep and silty to provide appropriate habitat;
- Riffles, though they constitute areas of fast flowing waters, are shallow and not silty, hence providing the most appropriate habitat available;
- The poor visibility prevented the spotting of bullhead in deeper areas of the stream by the surveyor.

The use of glides by small bullhead increases as flow decreases. Here glides appear again as the most favoured habitat. The use of runs and pools can be the result of an adaptation to the use of other types of mesohabitats in order to avoid competition from larger individuals. Section 5.4.1 examines the possible influence of mesohabitat availability on mesohabitat use by bullhead.

5.4.1 Mesohabitat use and mesohabitat availability

Another factor that could affect a fish choice of mesohabitat is the availability in a particular type of mesohabitat, which itself is influenced by discharge and the flow regime of the river considered.

Mesohabitat composition varies greatly between discharges. For example, runs make 25.53 % of the mesohabitats in the reach at Q_{35}, then at Q_{56}, nearly median flow, their proportion increases to 36.36 % of the mesohabitats presents while at Q_{96} it is only 6.67 %. The results from the fish surveys showed that bullhead used various habitats at different flows so they have to adapt to these varying conditions.

Fig. 5.14, 5.15 and 5.16 below show how habitat use by bullhead varied according to different mesohabitat types ‘ availability in the stream, i.e. glide, riffle and run.

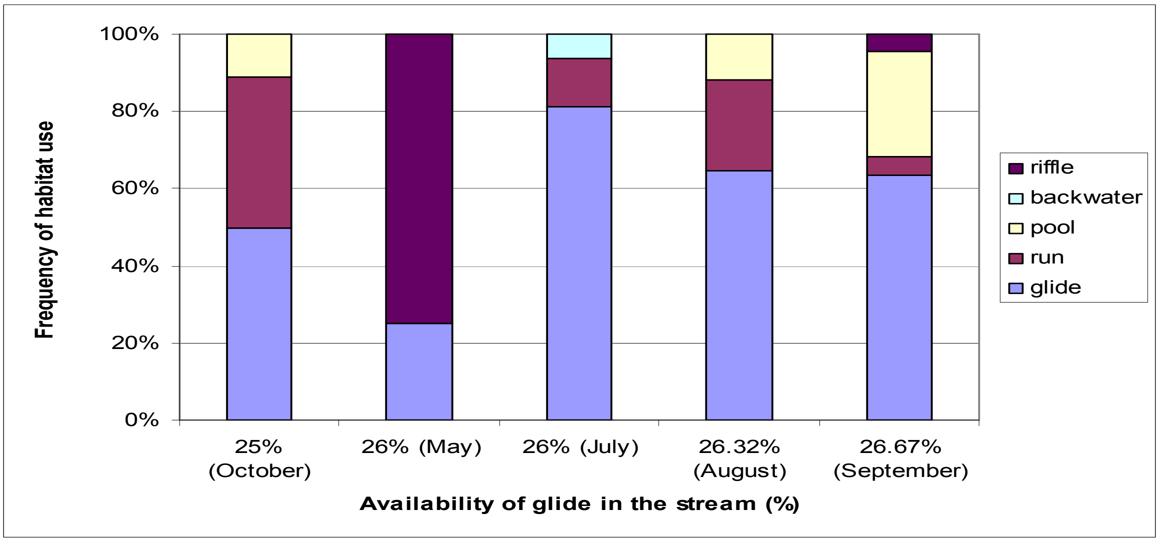


Figure 5.14 Mesohabitat use by bullhead according to glide availability in the Dowles Brook

From Fig. 5.14, the relatively constant proportion in glides (between 25 and 26.67 % of mesohabitats in the stream) does not appear to affect the way in which bullhead use mesohabitats and it certainly does not affect glide use, which varied greatly from one survey to another independently of glide availability.

The possible influence of other mesohabitat availability on mesohabitat use by bullhead is shown in Fig. 5.15 (riffle availability) and Fig. 5.16 (run availability).

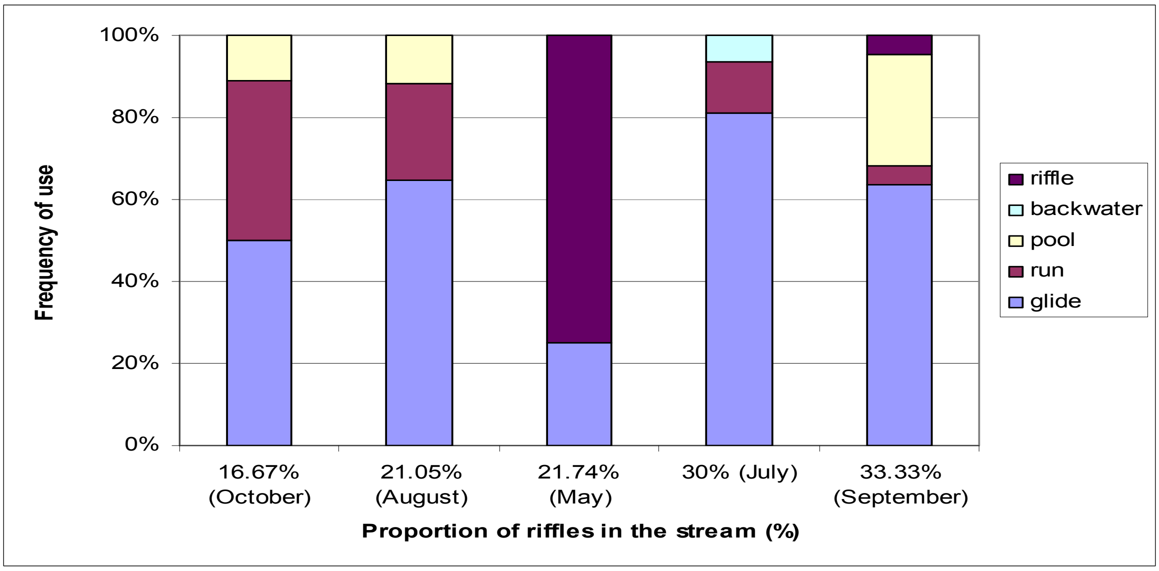


Figure 5.15 Mesohabitat use according to riffle availability in the Dowles Brook

In Fig. 5.15, riffle availability is shown to vary from 16.67 % in October (Q_{72}) to 33.33 % in September (Q_{96}). The growing availability in riffle does not appear to affect mesohabitat use by bullhead. Indeed riffle use occurred only in May (in the middle of the range of availability) and to a lesser extent in September when the proportion is at its highest.

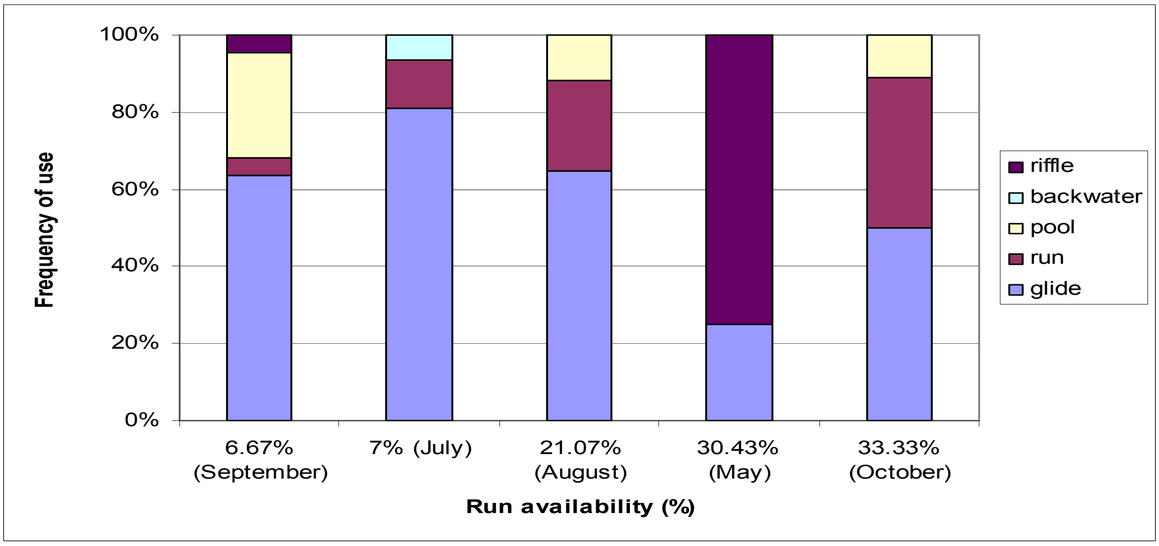


Figure 5.16 Mesohabitat use by bullhead according to run availability in the Dowles Brook

Fig. 5.16 shows that run availability increased from 6.67 % in September (Q_{96}) to a maximum of 33.33 % in October (Q_{72}). The use of runs appears to increase with their availability in the stream except for the month of May when they are not used at all despite a higher availability (this could be due to a lack of observations because of elevated turbidity levels in the stream in May, which may have prevented observations at increasing depths). Runs appear to be used by small and average size bullheads when glides are not accessible, possibly because of territoriality. Thus these results show mesohabitat use is complex and integrates many parameters.

Mesohabitat availability, though influenced by discharge, is not shown to impact on mesohabitat use by bullhead. However, discharge affects mesohabitat use by changing the hydraulic conditions in the stream. The above results suggest that flow is not the only factor affecting mesohabitat use and that territoriality also possibly plays a role.

Moreover, for all observations, bullhead were found hiding under stones (mostly cobbles) and in a few cases they were observed on the stone itself. Bullhead need shelter in the form of coarse substrate and the availability of such features is an absolute requirement for the species to pursue its life cycle (Knaepkens *et al.*, 2004). It thus appears that the availability coarse substrate is one of the critical factors influencing bullhead location. Coarse substrate, like coarse woody debris, provides shelter from predators, competitors and also from particularly harsh hydraulic conditions such as high velocity. Habitat Use Curves drawn from fish observations in the Dowles Brook and presented in section 5.5 allow to investigate bullhead association with coarse substrate.

5.5 HABITAT USE CURVES

RQ$_7$. What are the key habitat characteristics that determine bullhead location in the study reach?

5.5.1 Curves based on all observations

Depth and velocity values as well as substrate characteristics, recorded for all bullhead observations, allowed habitat use curves to be drawn for the Dowles Brook. These curves represent which values of mesohabitat physical parameters, e.g. depth, velocity and substrate, are most frequently used, and hence favoured, by the fish.

The habitat use curves for both the highest and the lowest flow surveyed are represented with the composite curve in order to study their influence on the latter.

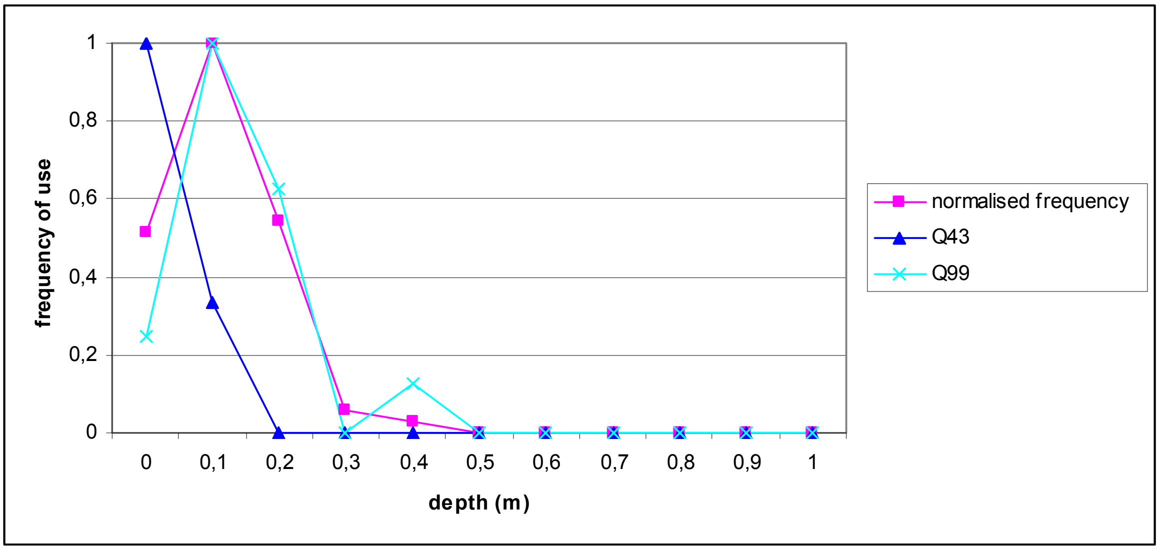


Figure 5.17 Habitat (depth) use curve for bullhead (all sizes) in the Dowles Brook

Fig. 5.17: Depths most frequently used by bullhead are those between 0.1 and 0.2 m. The minimum depth used from all surveys is 0.5 m but it decreases at Q_{99} to 0.23 m. Depths above 0.3 m are not used at all except at Q_{99} where one of two individuals used depths around 0.4 m. With respect to the highest flow surveyed, i.e. Q_{43}, A completely different situation is observed. Depths less than 0.1 m are the most frequently used and depths above 0.2 m are not used at all. The composite curve and the habitat use curve for Q_{99} are similar in shape and peak values.

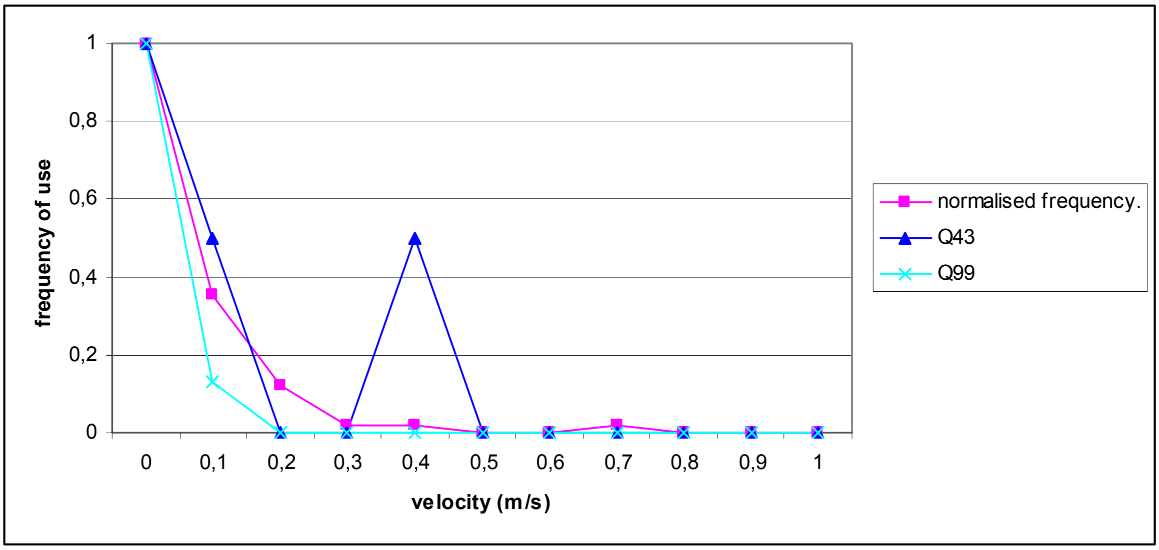


Figure 5.18 Habitat (velocity) use curve for bullhead (all sizes) in the Dowles Brook

Fig. 5.18: Velocities between 0 and 0.1 $m.s^{-1}$ are the most frequently used and bullhead hardly appear to use velocities above 0.3 $m.s^{-1}$. The curve for Q_{43} displays a small peak of use for velocities around 0.4 $m.s^{-1}$ but the results are biased due to the small number (4) of observations for the Q_{43} survey, so that the curve cannot be compared to the other two. The depth and velocity use curves show that bullhead are more likely to be found in shallow, slow flowing areas.

Fig. 5.19 represents the habitat use curve for substrate and is shown below:

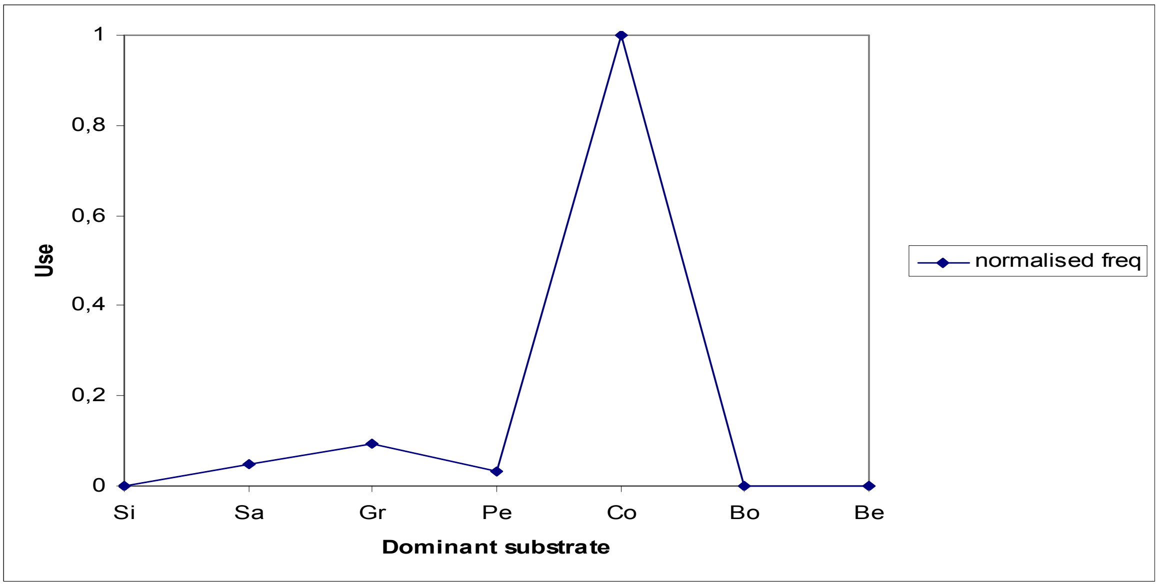


Figure 5.19 Habitat use (substrate) curve for bullhead in the Dowles Brook

The type of substrate considered to draw the above curve (Fig.5.19) was the dominant substrate at each bullhead location. The stream bed in the Dowles Brook is made of a combination of various types of substrate accumulated upon a floor of bedrock. From the substrate use curve shown in Fig. 19 it can be seen that bullhead display a large preference for cobbles, which are coarse enough to provide shelter for the fish. Gravel was used on a few occasions by smaller-size individuals. Underwater observations showed that the presence of finer substrate such as sand and silt with cobbles did not prevent the fish from using cobbles.

5.5.2 Habitat use curves according to fish size

Habitat use curves (Fig. 5.20 and 5.21) were drawn for each of the three size classes of bullhead in order to investigate the influence of fish size on habitat use criteria. The three curves obtained are represented on the same figure below to allow easier comparison.

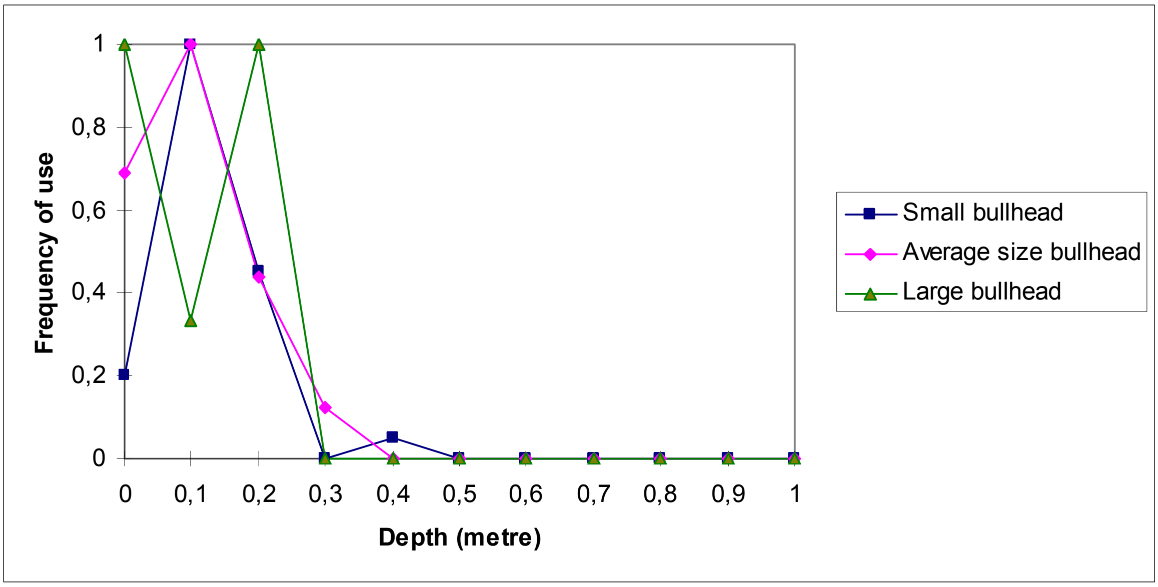


Figure 5. 20 Habitat (depth) use curves for the three size classes of bullhead: small, average size and large.

With respect to depth, it can be seen than small and average size bullhead display the same use of depths, e.g. a peak of use for depth between 0.1 and 0.2 m. However, large bullhead use a broader range of depths, which is indicated by the inverted profile of their depth use curved compared to those of the other two size classes: large bullheads use shallow depths (below 0.1m) to a greater extent than small bullhead (frequency of 0.8 compared to 0.2 for small fish) and the highest depths they use is around 0.4 m. The small peak round 0.4 m on the small fish habitat use curve results from one observation only.

Larger bullhead display a different pattern of habitat use, though the maximum depth used is around 0.3 m for this category as well. Large bullhead are shown to use mostly shallow depths (less than 0.1 m) and depths around 0.2 m. The frequency of use for these two values is 1. However, this last curve relies only on 7 observations in total and as a result appears very much subject to individual variability.

Fig. 5.21 represents the velocity use curve for all three size-classes of bullhead.

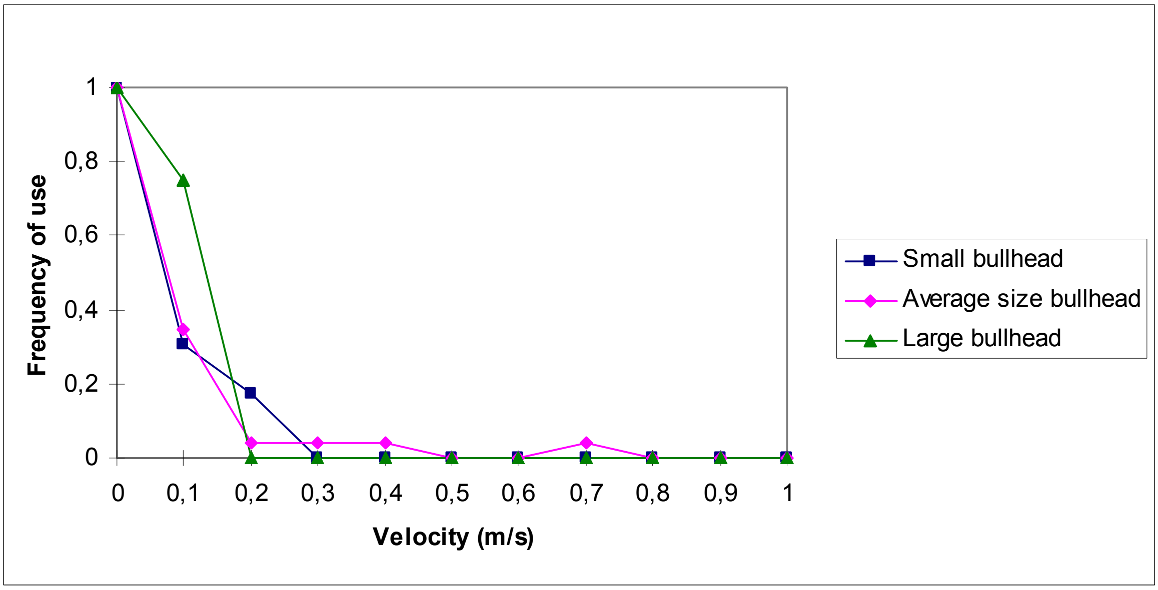


Figure 5.21 Habitat (velocity) use curve for the three size classes of bullhead: small, average size and large.

Fig. 5.21 shows that bullhead use mostly velocities between 0 and 0.2-0.3 $m.s^{-1}$. Small bullhead use only velocities between 0 and 0.3 $m.s^{-1}$ whereas some individuals which length is between 5 and 10 cm use velocities around 0.4 $m.s^{-1}$ and even 0.7 $m.s^{-1}$. But these are individual variations and do not correspond to the majority of observations in this average size class. Large bullhead use a more restricted range of velocities, e.g. between 0 and 0.2 $m.s^{-1}$.

There were no differences between the three size classes with respect to the type of substrate use: cobble was mostly used by all fish and gravel was also used but to a lesser extent. Though some differences are observed between the 3 sizes of bullhead in terms of depth and velocity use, considerable overlap between the frequency use curves exists, which tends to match the statistical analysis carried out on observations of mesohabitat use according to size and shown in section 5.3.5. A summary of the results and their interpretation is presented in section 5.6.

5.6 SUMMARY OF RESULTS

RQ$_7$. What are the key habitat characteristics that determine bullhead location in the study reach?

Bullhead display a pattern of mesohabitat use that is influenced by interactions between abiotic and biotic factors, as it was described in the previous chapter:

- Flow influences mesohabitat use: with decreasing discharge, bullhead tend to use glides more, and in general deeper areas with slow flowing water.
- The nature of mesohabitat is important but so is the local characteristics around the location chosen by bullhead, which explains why even in riffles the velocities at which bullhead were found were low. That means that bullhead tend to consider both the general and local characteristic areas, hence the use of two scales: mesoscale and microscale.
- Fish length by means of territoriality plays a role in determining the locations at which bullhead were found with large individuals always in "low energy" mesohabitats and smaller individuals using both low and high energy areas.

Analysis of bullhead observations in the Dowles Brook enables the following conclusions to be drawn with respect to the ecology of bullhead in this particular river:

- Length frequency distribution of fish is influenced by seasonality through the evolution of the different life stages. The absence of individuals smaller than 5cm in May suggests that larval life stages have not emerged yet at this time of year or, if they have emerged, they are still too small to be spotted during underwater surveys. The continuous increase in the number of individuals less than 5cm throughout the summer months could correspond to the growth of very young life stages. In October, the decrease in numbers in this size class and in parallel the increase in the number of individuals whose size is between 5 and 10 cm would correspond in growth of some individuals that end up being counted as part of another size class.
- The large difference in numbers of observations between May (N=4) and July (N=16) could result from i.) Fish sensitivity to high flow and poor swimming capacity, which means high flows resulted in bullhead being washed out downstream of the study reach. ii.) The presence of bullhead but mostly at the

larval stage or early juvenile stage, which means they are very difficult to observe, being small and perfectly camouflaged in gravel iii.) The turbidity of the water which made the observations more difficult and nearly impossible in very deep areas. However, from the habitat use curves, the probability of finding bullhead in areas deeper than 0.3 $m.s^{-1}$ is nearly nil. Moreover in shallow areas, where bullhead should have been and where the visibility was satisfactory, no observations were made iv.) Bullhead use only this part of the river under certain flow conditions, which were not met in May or at Q_{53}, hence the low number of observations.

- Mesohabitat use by bullhead is more influenced by flow than it is by season. As discharge decreases there is an increase in glide use. Glide is the most used mesohabitat. Runs and pools are also used but to a lesser extent. Riffles and backwaters were use each on two occasions, independently of flow.
- Mesohabitat use does not appear to be dependent on mesohabitat availability. In other terms, the increase in glide use is not correlated to the increase in glide presence in the stream. Analysis of other types of mesohabitat availability in the stream does not show any link to mesohabitat use, with the exception of runs: increasing use of runs looks linked to the increasing presence of runs in the reach.
- Moreover mesohabitat availability in the stream does not appear to be dependent on discharge, but more on the geomorphology of the stream. Predictions of habitat availability and of habitat use are therefore very difficult to make due to the flashy nature of the reach.
- Analysis of depth and velocity uses shows that as discharge decreases, bullhead shift to deeper environments (depths around 0.2-0.3 m) and to slower velocities (between 0 and 0.1$m.s^{-1}$).
- The shift previously described was observed for all three size-classes of bullhead.
- General habitat use curves built from bullhead observations in the Dowles Brook show that this species shows a clear preference for depths in the range of 0.1 to 0.3 m and for velocities between 0 and 0.2 $m.s^{-1}$. The habitat use curve for Q_{43}, i.e. the highest flow surveyed, showed a different pattern of use: shallower depths (0.1m) and some individuals used velocities around 0.4 $m.s^{-1}$. This last curve is however based on only four observations and so the conclusions should be considered with caution.
- Comparison of the habitat use curves for the three size classes of bullhead (<5cm; 5 to less than 10 cm; >10cm) show that overall size does not affect greatly the habitat

used by fish. Small and intermediate individuals show very similar patterns of habitat use whereas large individuals used a broader range of depths and velocities.

- The substrate use curve shows a clear preference for cobbles and coarse substrate in general by bullhead. To a lesser extent, gravel is also used by smaller individuals. From the notes taken during the fish surveys, cobbles are a clear indicator of bullhead presence as they allow shelter from predators and also from fast flowing water conditions, which are not suitable for bullhead as they are poor swimmers and can be easily washed out.
- Fish size influences habitat use by the territorial behaviour associated with it. Bullhead are very territorial and this explains why bullhead are never observed in groups or close to one another. The observations were always scattered along the reach. The effect of territoriality can also be seen when looking at the mesohabitats used according to flow (section 5.2): while glide is the most used mesohabitat in general, for a same flow value, runs and pools for example are also used. This may result from territoriality, which forces low ranked individuals in other mesohabitats that would be suitable but would constitute the "next best thing".
- Glides are the most used habitat by bullhead because they are slow flowing environments, they vary in depth, i.e. bullhead will use mostly shallow glides, and they also constitute a shelter from predators (because of their depth) as well as a zone of food retention. Indeed, organic matter retained in these channel geomorphic units, constitutes a primary source of food for the macroinvertebrates on which bullhead feed, particularly *Gammarus sp.*
- To be able to observe bullhead during a fish survey, it is necessary to lift cobble on the stream bed; these stones were always shelter to an important biomass of macroinvertebrates, no matter the mesohabitat considered. That would mean that the biomass of prey species is constant throughout the stream, with the exception of chutes where the substrate is only bedrock). As a result food availability would not constitute the main factor of mesohabitat selection by bullhead. Physical habitat conditions *stricto senso* would be predominant, and a result of bullhead poor swimming ability and necessity to shelter from high flows, high velocity conditions as well as predators (the banks of the stream host two nests of kingfishers).

Further analysis of the map of bullhead locations in the Dowles Brook shown in Fig. 5.4 allows the following interpretations to be made. Slow flowing environments constitute zones of retention of organic matter, hence an important food source for macroinvertebrate populations. Their depth and velocity characteristics do not vary significantly with flow, as opposed to runs and glides for example (see section 5.1.2). That may be an explanation for the high abundance of bullhead in these parts of the river such as glides and pools. Indeed, among the 12 units occupied by bullhead, 8 were glides or pools.

From the mesohabitat characteristics it can also be seen that glides and pools are least variable mesohabitats in the stream compared to runs and riffles. It thus appears that in response to high flow and mesohabitat variability, bullhead tend to choose those CGUs that are the most stable in order to minimize the energy expenditure associated with the stress of a constantly varying environment. Bullhead are poor swimmers and they move by hopping on the stream bed. That has implications on the water velocities they can sustain. A mesohabitat that is fast flowing and/or which characteristics are in constant variation imply that bullhead have to constantly adapt to those changes. As a result a fish will either change location (here mesohabitat) in order to get to the conditions closest to its habitat requirements, e.g. move from one habitat to another each time the flow varies, which implies high energy expenditure due to swimming, either it will choose the location that remains the most stable across flows even if this location/mesohabitat is not the most suitable compared to the species requirements and that would minimize the fish energy expenditure.

The fact that some bullhead are nonetheless found in runs and riffles may be the result of competition for space and territories with the most dominant individuals choosing slow flowing environments and the other having to stay in faster flowing locations. Velocity values at bullhead locations show that by hiding under cobbles bullhead can achieve velocity conditions equivalent to those in slow flowing environments. However, a bullhead’s territory is usually limited to the stone the fish is hiding under so that territoriality cannot explain alone the slow number of observations in other units than units 2 and 20.

The bullhead observed in runs and riffles could have also been transient, moving from one habitat to another. Given the cryptic nature of bullhead during the day (they are most active at night), this last hypothesis could not be tested. The scattering of bullhead observations along the reach may also result from the species ecology itself.

Indeed, bullhead ecology can be divided into 2 important periods (Fox, 1978): the larval stage during which young bullhead larvae are subject to passive dispersal and ontogeny, during which larvae become more benthic and more sedentary and most of all start to display territorial behaviour. Passive dispersal can result in larvae drifting to some locations in the reach where they will go through ontogeny and hence settle. Juvenile bullhead may not be experienced or strong enough to go and explore other parts of the river for more suitable locations.

Finally some physical barriers to movement exist in the stream that can prevent bullhead to have access to some parts of the stream: units, 12 and 18 are chutes where the stream bed forms high steps of bedrocks with water flowing at around $1m.s^{-1}$. These appear to be obstacles that bullhead could hardly get through. Hence, depending on where bullheads have settled, some parts of the river are possibly inaccessible.

Finally, the presence of woody debris in the channel and tree roots on the banks does not appear to have attracted bullhead. Observed bullheads were always located in the middle of the channel, despite the survey protocol taking into account the parts of the channel situated near/under the riverbanks.

The analysis of bullhead observations reveals that the factors responsible for the location chosen by bullhead in a surface runoff influenced stream are:

- Flow variability and as a result its effects on mesohabitat composition
- The presence of slow flowing mesohabitats such as glides and pools
- The presence of cobbles on the stream bed, no matter what if other types of substrate are present and what they are.
- Fish size and territoriality associated to it, but to a lesser extent.

It appears therefore that in flashy streams, environmental and physical factors are more determinant in fish location than biological processes. That does not mean that biological processes and population related parameters do not influence fish location but they tend to be of minor effect compared to environmental parameters and flow related factors.

However, the influence of some factors on bullhead mesohabitat use could not be tested because of their absence from the reach. From the literature, it appears that macrophytes can play the same role as cobbles in providing shelter to bullhead (Perrow *et al.*, 1997; Tomlinson and Perrow, 2003) but macrophytes were not present at any flow or on any survey occasion in the stream so that their influence could not be studied. However, in the River Tern, for which the results of bullhead observations will be discussed in section 5.7, macrophytes were present in some parts of the reach and bullheads were found hiding under the macrophyte patch on at least two occasions.

As in Chapter 4, an organisational chart (Fig. 5.22 below) can be drawn in order to provide a step-by-step approach to the identification of potential bullhead habitats in a flashy stream. The use of this diagram implies that the flow regime of the stream is known as well as how mesohabitats vary with flow. Individual variability has to be also taken into account when using such a diagram. Even if the environmental conditions at a particular location are according to the species requirements and indicate a high probability for bullhead occurrence, this occurrence also depends on individual fish requirements, physiology and energy budget. As a result, probabilities on this diagram are described as "high", "low" or "medium" to clearly state that they constitute an indication and not a certainty that fish will/will not be there.

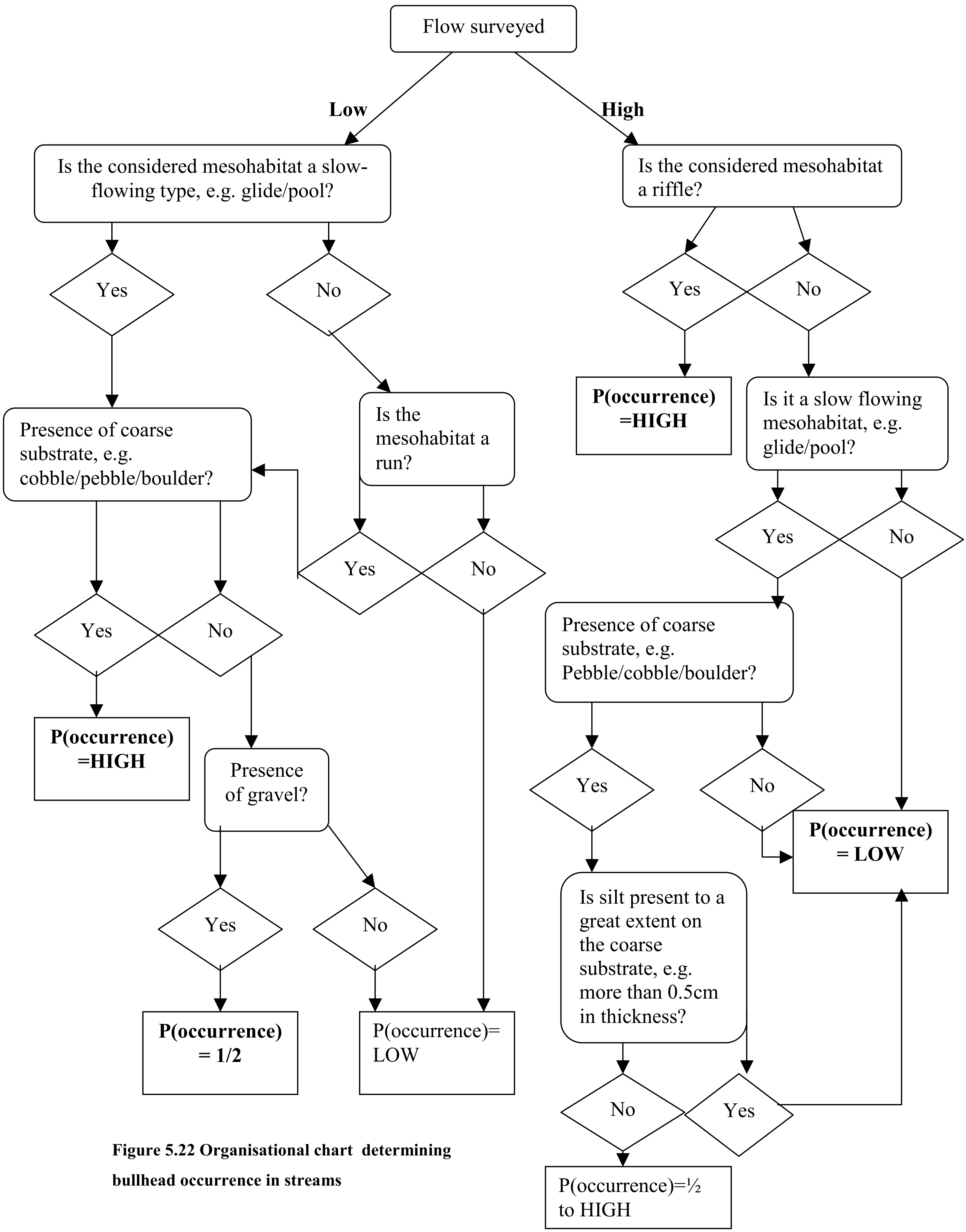


Figure 5.22 Organisational chart determining bullhead occurrence in streams

The first step in order to use this organisational diagram is to consider the flow that is surveyed on the stream. Indeed as the survey results showed habitat use by bullhead is flow-dependent. The limit between differing mesohabitat use was established at the median flow, i.e. Q_{50} .

If the discharge surveyed corresponds to a flow percentile higher than $Q_{50.}$ Bullhead observations on the Dowles Brook showed an increasing use of glides and other slow flowing mesohabitats with decreasing discharge. As a result, if the mesohabitat considered is a glide/pool then the next step is to consider the type of substrate present in this CGU. If coarse substrate such as pebble, cobble or boulder is present then the probability of bullhead occurrence is high. If, instead of the types of coarse substrate previously mentioned, gravel is present, then the probability of occurrence falls to a "medium" level. If no coarse substrate is present at all and instead sand/silt or clay is the only substrate present then the probability that bullhead inhabit this mesohabitat is low if not nil. If the mesohabitat surveyed is not a slow flowing environment but can be characterized as a run, then, by the applying the same selection process with respect to substrate the probability of occurrence of bullhead can be determined. The observations on the Dowles Brook have indeed shown that runs are used to a certain extent at flows lower than Q_{50} and that they are used to the same extent than pools. Their use seems to increase with an increasing availability of runs in the stream.

If the discharge surveyed corresponds to a lower flow percentile than Q_{50}:
If the considered mesohabitat presents the characteristics of a riffle (shallow, fast flowing CGU with boulders/cobbles breaking the surface) then the probability of bullhead occurrence under the substrate is high. It is not necessary to look at the substrate composition of riffles as in this type of CGU the only persistent type of substrate is coarse, *i.e.* size of gravel or above. The finer types of substrate get washed away. If the considered mesohabitat is slow flowing then it is necessary to consider, as for low flows, the type of substrate. The probability of occurrence of bullhead is low if not nil if fine substrate is the only one present. When substrate is fine, another parameter needs to be taken into account at high flows that is siltation. At high flows, pools and glides, due to their geomorphology (they are deeper areas compared to the rest of the stream) constitute retention zones not only for silt and other fine substrate that is washed away from fast flowing CGUs. As a

result silt and sand are likely to accumulate in these mesohabitats and they can smother the stream bed and the fill in all the gaps that exist between coarse substrate. In case of important siltation (roughly a layer of 0.5cm thick on top of cobbles), the presence of coarse substrate does not provide suitable habitat anymore for bullhead as the whole area in their immediate surrounding is smothered. During the spawning period it can also prevent the necessary oxygenation of the eggs that are attached under the stones. As a result, with respect to the organisational diagram, in case of important siltation, the probability of bullhead occurrence is low or nil. If siltation does not occur to a great extent then the probability of bullhead occurrence is medium or high depending on individual variability.

Runs were not considered in Fig. 5.22 at high flows because no observations were made in runs during the surveys. Bullhead may/may not use runs in other streams.

Figure 5.22 does not take into account territoriality, which cannot be quantified as such. It depends on the structure of the population at any given flow, at any given time of the year. To get data on these variables requires extensive study of the population over at least a year and this is not relevant if one needs quick predictions of bullhead occurrence in a newly considered stream. Moreover, as previously mentioned, such a diagram represents a trend with respect to mesohabitat use by the majority of the population but cannot consider individual variability in habitat use that could result from differences in life stage, size, status/rank in the population (resulting in territoriality), sick or malformed individuals.

Figure 5.22 provides with a preliminary study tool that can be useful when considering streams for conservation purposes. Indeed, under the Annex II of the E.C. Habitat and Species Directive, bullhead is listed as an endangered species as a result of the destruction of its physical environment. The presence of bullhead in a stream not only provides an indication of the good physical health of the stream but also adds to its conservation value. This diagram, by helping to identify potential bullhead habitat, can be a useful tool to help implementing this Directive.

As stated at the beginning of this chapter, the focus of the results for bullhead observations was mainly on the Dowles Brook due to the very few observations recorded on the other study site, the River Tern. However, it was judged relevant and useful to nonetheless show the results obtained on the latter river. These are presented in section 5.7.

5.7 BULLHEAD OBSERVATIONS IN THE RIVER TERN

Bullheads were only observed on three out the six surveys carried out on the River Tern and in very low numbers (mean=2 individuals/survey). Observations were made in the last three surveys, i.e. September (Q_{77}), October (Q_{51}) and November (Q_{61}).

The low number of bullhead in the stream goes against a previous survey carried out in 2003 (Pinder *et al*., 2003), which recorded 138 bullheads. At that time electrofishing was used. The difference in numbers between 2003 and the present study surveys can be due for one part to the use of two different techniques (electrofishing versus snorkelling). However, the contrast in numbers between the two surveys is so large that some other factors could have affected the bullhead population in this stream and led to its collapse. Several factors can explain the drop in bullhead numbers:

- A major hydrologic event, such as a flood, has changed the geomorphology as well as the physical characteristics of the stream, making it unsuitable for bullhead. As a result bullhead have migrated. However, continuous monitoring of the stream since 2003 (LOCAR programme) has shown no such major event.
- The presence of an established brown trout population means a high predation risk for bullhead. Brown trout may have predated on bullhead to such an extent that the bullhead population has been depleted. However, the 2003 survey showed that brown trout represented half of the fish population, the other half being bullhead. The two populations have cohabitated in the stream so it seems unlikely that all of the sudden predation by brown trout caused the collapse of the bullhead population.
- During the surveys carried out as part of the present study (both mesohabitat surveys and underwater fish surveys), an important number of American signal crayfish (*Pacifastacus leniusculus*) were observed (around 15 in the whole reach). American signal crayfish were not recorded as present in the stream during the 2003 survey so the infestation of the stream must have occurred between then and 2005, when the mesohabitat surveys on the Tern started. Signal crayfish are known to compete with bullhead for habitat as they have the same habitat requirements and use the same ecological niche. Some cases of predation on young bullhead

have also been recorded in the literature. The invasion of the River Tern by signal crayfish could have resulted in the collapse of the bullhead population whether it be caused by predation or by competition for habitat. During the direct underwater observations surveys, when stones were lifted in search of bullhead, most of the time signal crayfish were found underneath the stones.

The total number of observed bullheads equals 10 and that does not allow conclusions regarding the fish habitat use in the Tern to be drawn as these conclusions may be influenced to a great extent by individual variability. Nevertheless it appears interesting to study the results of the bullhead surveys and to draw some tentative conclusions, if nothing else, on the pattern of habitat use that could be displayed by this species in a groundwater fed stream and to try to compare this with the results previously analysed for bullhead in a surface runoff influenced environment.

All observed bullhead in the Tern measured between 5 and 10 cm in length, which class them in the "medium" or "average" size category, as it was described for bullhead in the Dowles Brook earlier in the chapter. Since all the observations started in September and no bullhead were observed during late spring and early summer, it seems unlikely for reproduction and spawning to take place in this reach. Fig. 5.23 and 5.24 represent mesohabitat use by bullhead according to flow and season respectively.

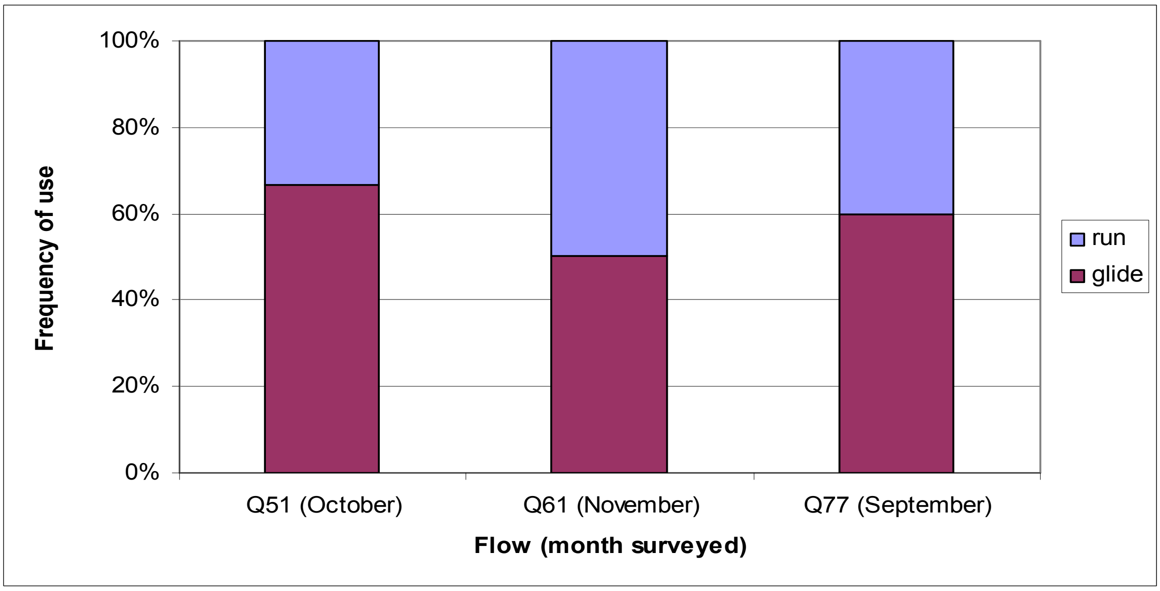


Figure 5.23 Mesohabitat use by bullhead according to flow in the River Tern

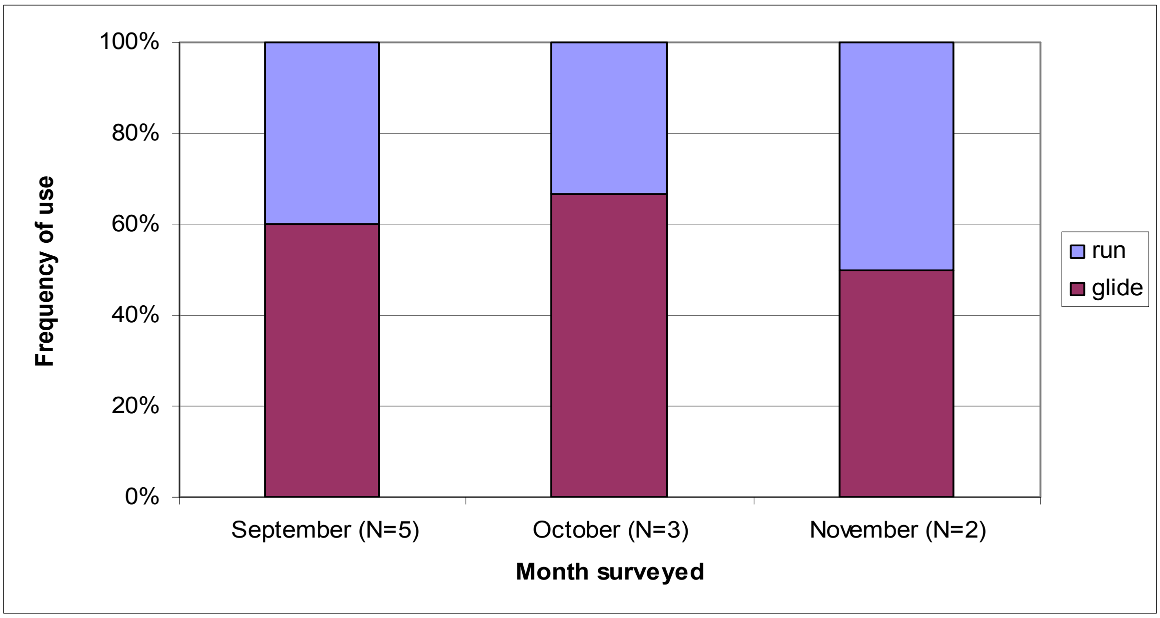


Figure 5.24 Seasonal evolution of mesohabitat use by bullhead in the River Tern

From Fig. 5.23 and 5.24, glide appears to be the most used mesohabitat, which was also a characteristic observed on the Dowles Brook. However, in the River Tern, no particular trend is observed when it comes to how glide and run uses evolve with flow. A similar situation is observed when it comes to mesohabitat use month after month.

This lack of explicit trend is mostly explained by the low fish numbers. The small number of observations makes individual variability more prominent, which mean a trend at the population level cannot be observed. However, the use of glide and runs, though these mesohabitats are the most available type in the River Tern, suggest a particular species requirement for slow flowing environments first and then runs.

The River Tern is a groundwater fed stream and as such constitutes a very stable environment. As a result, biological processes may be more important in determining fish' mesohabitat use than any physical parameters such as flow, as it was demonstrated for brown trout in Chapter 4.

The analysis of the evolution of mean depth and mean velocity according to flow (see Fig. 5.25 and 5.26 below) also show no link between abiotic factors and bullhead habitat use.

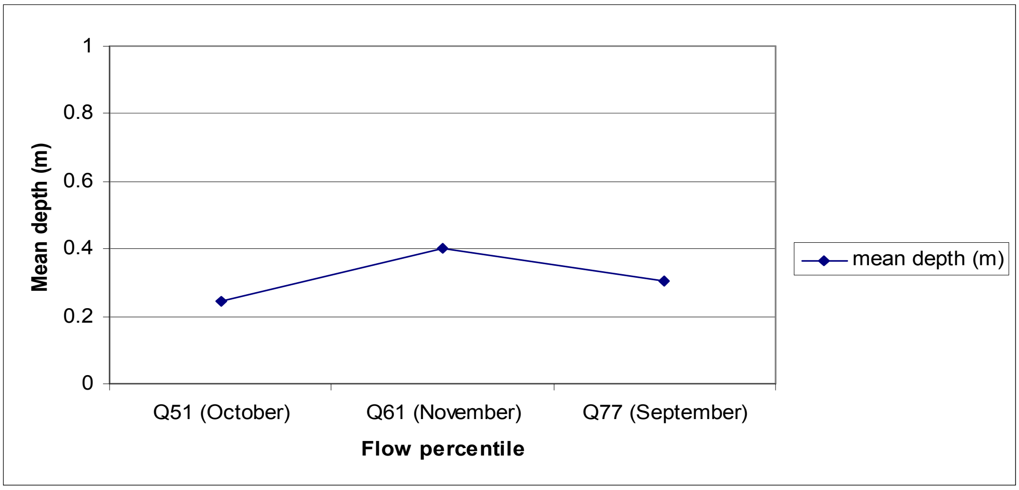


Figure 5. 25 Mean depth used by bullhead according to flow in the River Tern

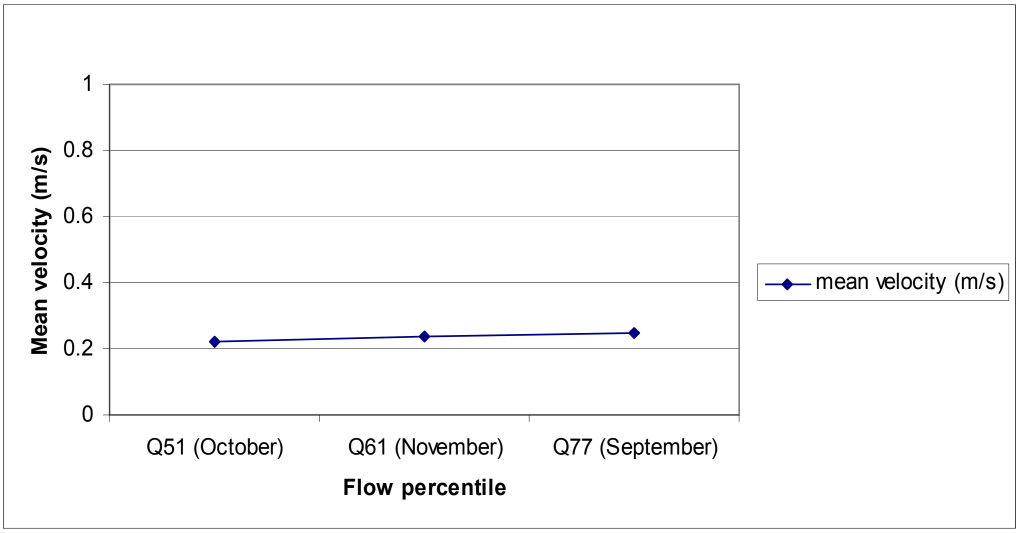


Figure 5.26 Mean velocity used by bullhead according to flow in the River Tern

At all flows, mean used depth remained between 0.2 and 0.4 m with the maximum mean depth used in November. Mean velocity used remained constant throughout the flows, around 0.25 $m.s^{-1}$. Compared with the results for bullhead in the Dowles Brook, in the River Tern bullhead used higher depth for a similar flow percentile (in the Dowles Brook, mean depth remained under 0.2 m for all surveys). Mean velocity was also higher in the Tern than in the Dowles Brook, where it steadily decreased from 0.15 $m.s^{-1}$ with decreasing flow. Fig. 5.27 shows the evolution of bullhead habitat use according to increase glide availability in the stream.

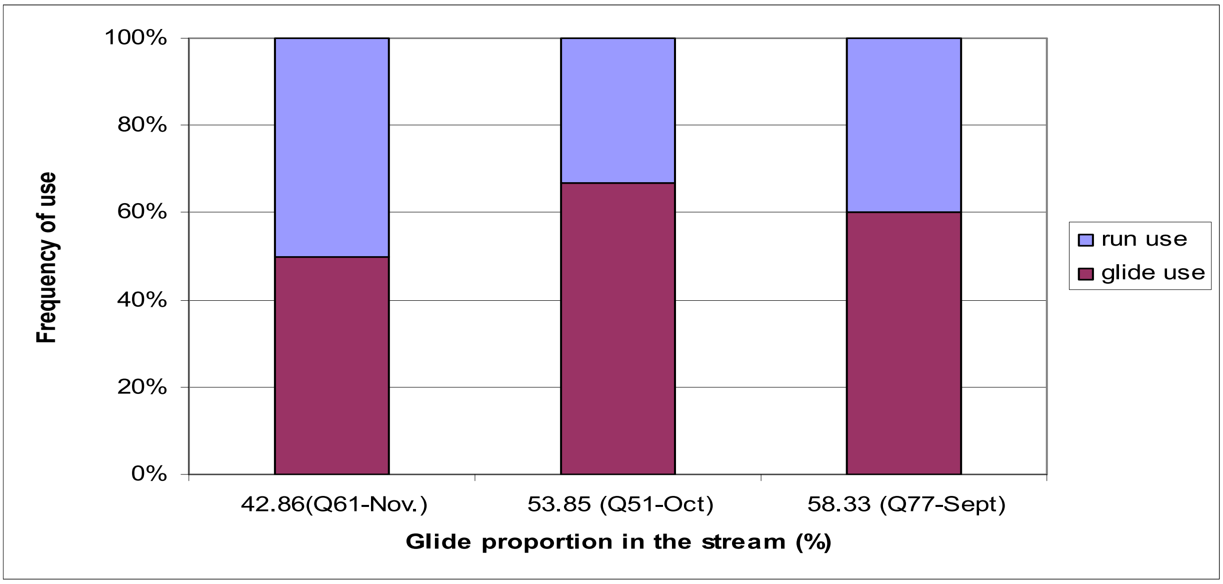


Figure 5.27 Mesohabitat use by bullhead according to glide availability

From Fig 5.27, no relationship can be observed between mesohabitat use and glide availability. This tends to confirm that despite the low number of observations, species requirements in terms of mesohabitat are displayed (similar for bullhead of the two study streams). However, abiotic factors do not seem to be the most influent in determining mesohabitat use.

Bullhead observations in the Tern allowed habitat use curves to be drawn (Fig. 5.28 and Fig. 5.29), which it would be interesting to compare with the ones for the Dowles Brook. For comparison purposes, it is more appropriate to compare these curves with the ones built for the same size class in the Dowles Brook, i.e. the “medium” or “average” size class.

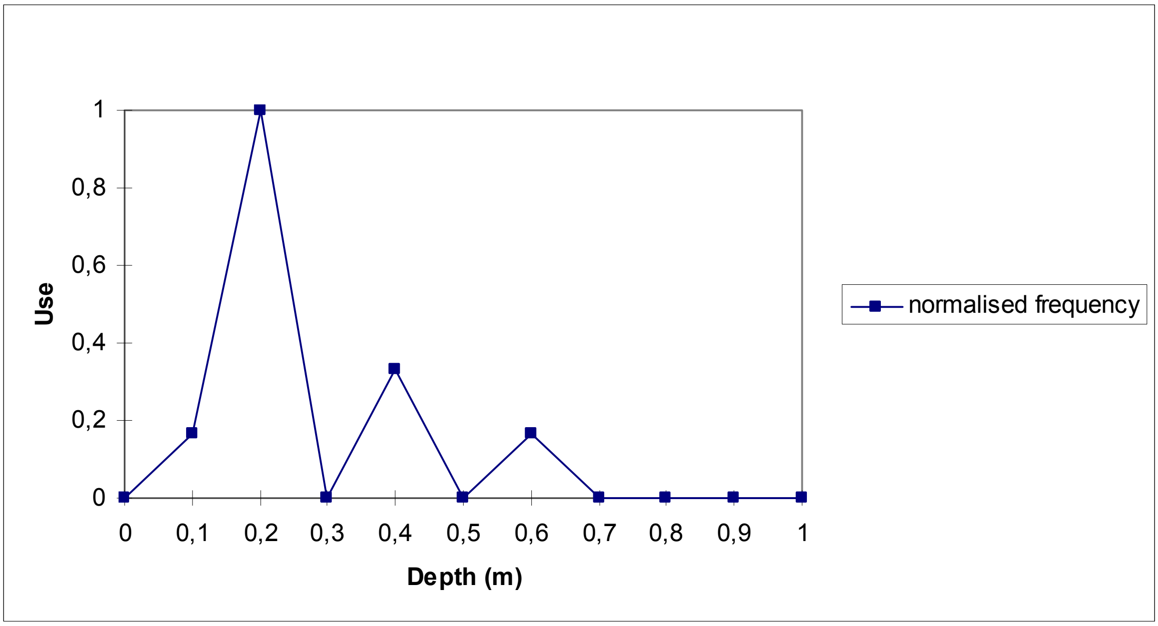


Figure 5.28 Habitat (depth) use curve for bullheads in the River Tern

The depth use curve shown in Fig. 5.28 above presents three peaks of use: a major peak for depths around 0.2 m and two smaller peaks for 0.4 m and 0.6 m. This trend results from the low number of bullheads that could be observed in the Tern during the survey season. These latter two peaks result respectively from 2 and 1 observations so that for comparison purposes it appears more sensible to take into consideration only the major peak.

In the Dowles Brook, bullhead between 5 and 10 cm in length displayed a broader range of used depths and they used very shallow depths: depths around 0.03-0.05 m presented a frequency of use of 0.7. In the Tern, these shallow depths were hardly used. The Tern and the Dowles Brook are very different in terms of geomorphology with the River Tern lacking in very shallow areas.

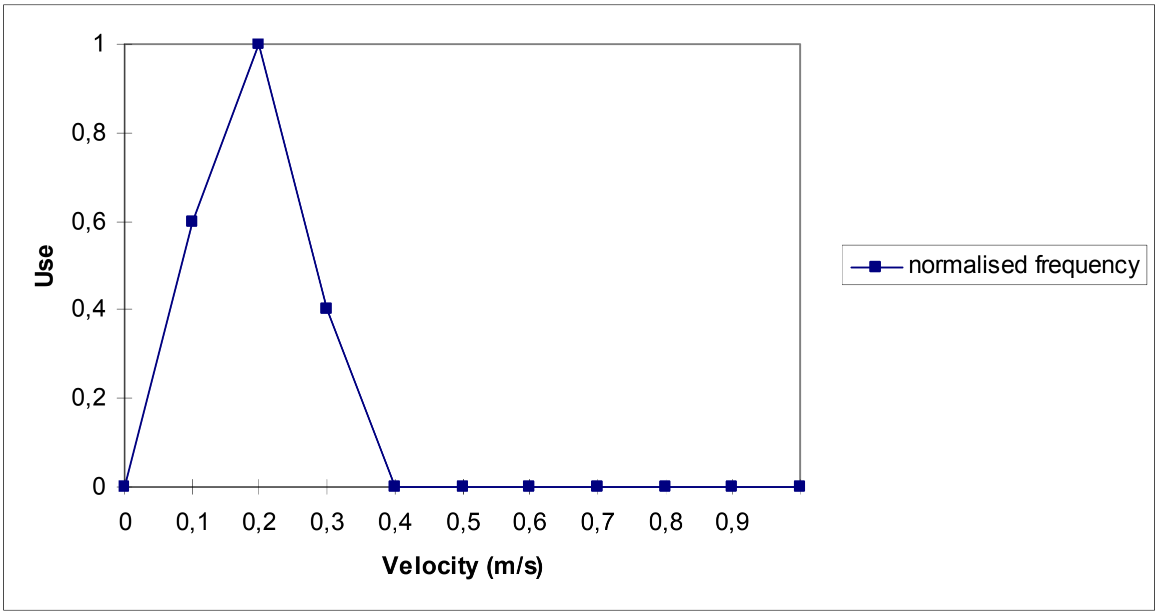


Figure 5.29 Habitat (velocity) use curve for bullheads in the River Tern

The velocity use curve in Fig. 5.29 is made of a single large peak, which encompasses velocities between 0 and 0.4 $m.s^{-1}$. This corresponds to slow to medium flowing environments and is in agreement with the mesohabitat use displayed by bullhead in the Tern, i.e. glide and run.

The curve shape is completely different from that of the medium size bullhead in the Dowles Brook, which shows a clear preference for the use of nil or very low velocities (less than 0.1 $m.s^{-1}$). Frequency of use steadily decreases for velocities above 0. In the River Tern, the most used velocities are that between 0.1 and 0.3 $m.s^{-1}$. These differences are probably due to the differences in the geomorphology of the two streams and obviously to their differing flow regimes. This tends to prove the capacity of adaptation of fish of a same species (so with the same species requirements) to different environmental conditions.

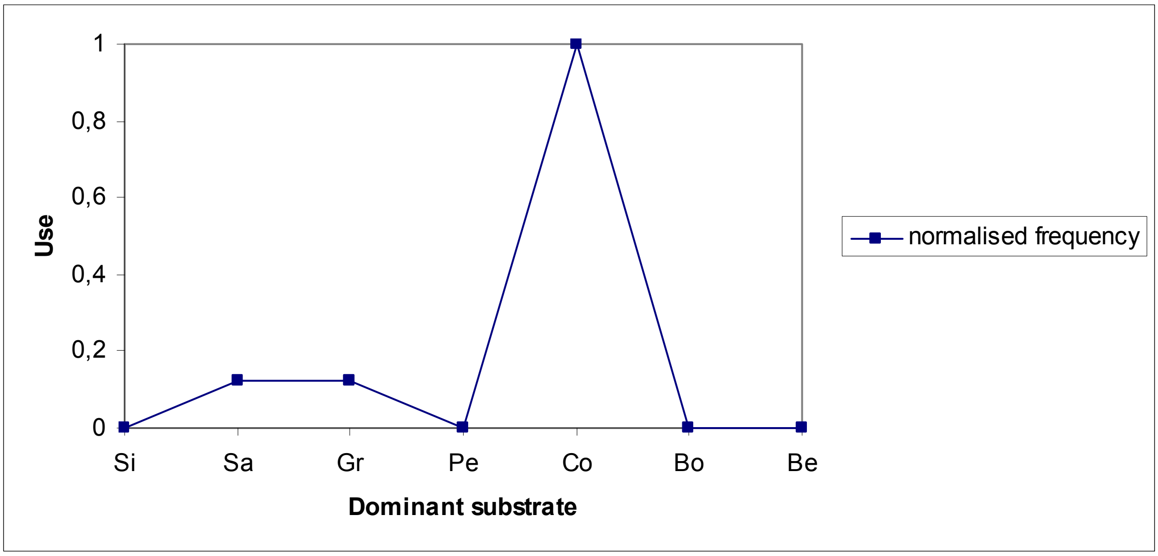


Figure 5.30 Habitat (substrate) use curve for bullheads in the River Tern

In the River tern, bullhead use mostly cobble, as shown by Fig. 5.30 (above), which is in agreement with the finding on the Dowles Brook. Substrate requirements can be considered, as a result, as a species requirement, necessary for the survival of bullhead in a stream as part of its ecology.

Though the number of bullhead observations on the River Tern were too small to be able to draw conclusions about bullhead mesohabitat use in a groundwater influenced stream, they allowed to highlight several characteristics of the species and its ecology.

- Bullhead display a preference for slow flowing environments such as glides. They also use runs, though the reason for such use could not be determined.
- One of the species requirements is the presence of cobbles, which can nearly guaranty to the observer the presence of bullhead in particular mesohabitat. Cobbles and other coarse substrate are necessary as a habitat, for hiding, for the building of the nest by the male and possibly as a source of food since macroinvertebrates are often found underneath.
- The differences in the depth and velocity use curves between the two streams enlighten differences in habitat use at the population level as well as the range of depth and velocity that bullhead are able to sustain. It also shows the ability that fish have to adapt to differing environmental conditions.

- In the River Tern, bullhead mesohabitat use could be influenced by i. predator avoidance (here signal crayfish and brown trout), ii. interspecific competition for habitat with signal crayfish.

However, for the latter, more observations would be needed on a longer period of time as well as experiments to test the extent of the influence of competition and predation on bullhead habitat use.

The relatively high number of bullhead in the Dowles Brook and its consistency survey after survey shows that the environment conditions match this fish habitat requirements. No other fish nor crayfish were observed in this stream at any time which means that instream predation and interspecific competition are nearly non existent. The presence of kingfisher nests along the reach can be a cause for predation nonetheless.

The analysis of bullhead observations shows that flow and its variability and the variation in the stream' physical parameters are the primary driver for bullhead mesohabitat use. At the species level, glides appear necessary for the fish' ecology and life cycle as well as cobbles but flow influences how much this mesohabitat is used. Cobbles provide high value shelter. Glides are an appropriate habitat because they constitute food retention zones as well as velocity conditions suitable for a poor swimmer such as bullhead.

The narrow range of depths and velocity used, as shown by the habitat use curves, may constitute a response to high flow variability: bullhead find a niche of environmental conditions that is suitable and relatively stable in the stream and tend to use it when the flow varies to a great extent.

On the River Tern, despite the low number of observations and the fact that, as a result, the habitat use curves may be biased by individual variability, the majority of the observed bullhead display a broader range of depths and velocities they use. In a groundwater fed stream, environmental conditions are far more stable than in a flashy stream and as a result, fish do not sustain as much physical stress. On the other hand, biological processes such as intra and interspecific competition, predation, lifecycle have far more influence on bullhead mesohabitat use. As a result the fish display a strategy which aims at avoiding competition and predation and which results in having to tolerate and use a wider range of conditions in the stream on a spatial scale.

As a species that is endangered due to the destruction of its physical habitat, bullhead constitutes a very good indicator of the naturalness of a stream. However, other factors such as biotic, as seen on the River Tern, can influence its occurrence, that are not always so easily detectable as a change in hydrologic and physical parameters.

5.8 RELIABILITY OF HSI CURVES

For the purpose of this study, generalized Habitat Suitability Index curves for bullhead were built according to the methodology described in Chapter 3, section 3 from the literature identified in Chapter 2. The depth, velocity and substrate data collected during fish surveys allowed the testing of the drawn HSI curves with respect to their ability to predict the fish location in rivers. To test these curves they were compared (i) with the Habitat Use curves, which were drawn from the field data (section 5.8.1) (ii) relative suitability indices at bullhead locations calculated using the drawn HSI curves (section 5.8.2).

5.8.1 Comparison with Habitat Use Curves

For clarity, the HSI curves and Habitat Use curves for both streams are represented in Fig.5.31, 5.32 and 5.33 next page.

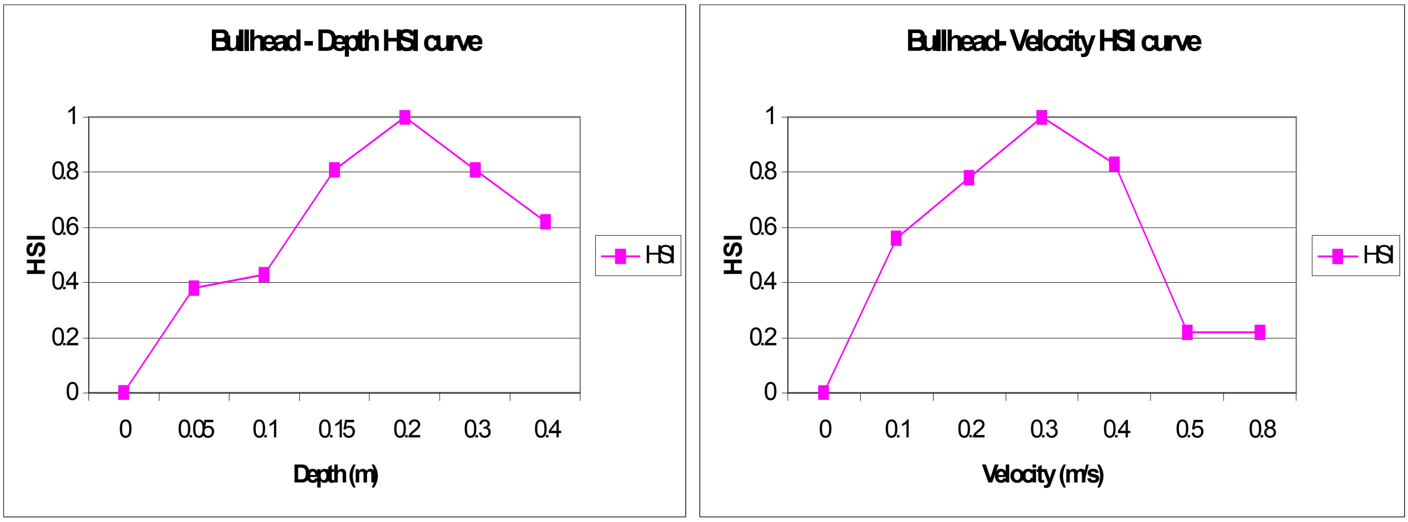


Figure 5.31 Habitat (depth and velocity) curves drawn from the literature for bullhead

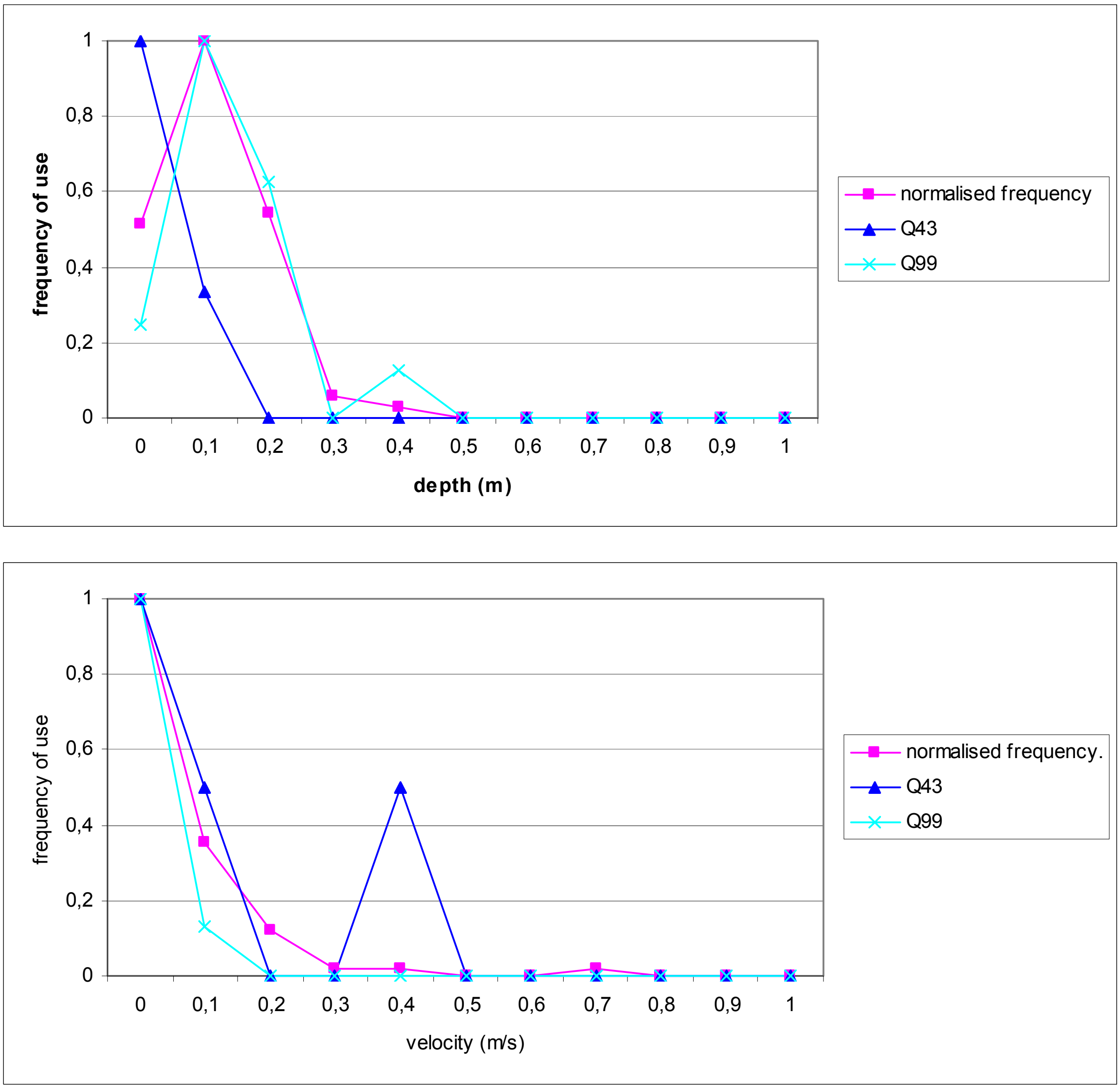


Figure 5.32 Habitat (depth and velocity) use curves drawn from bullhead observations in the Dowles Brook

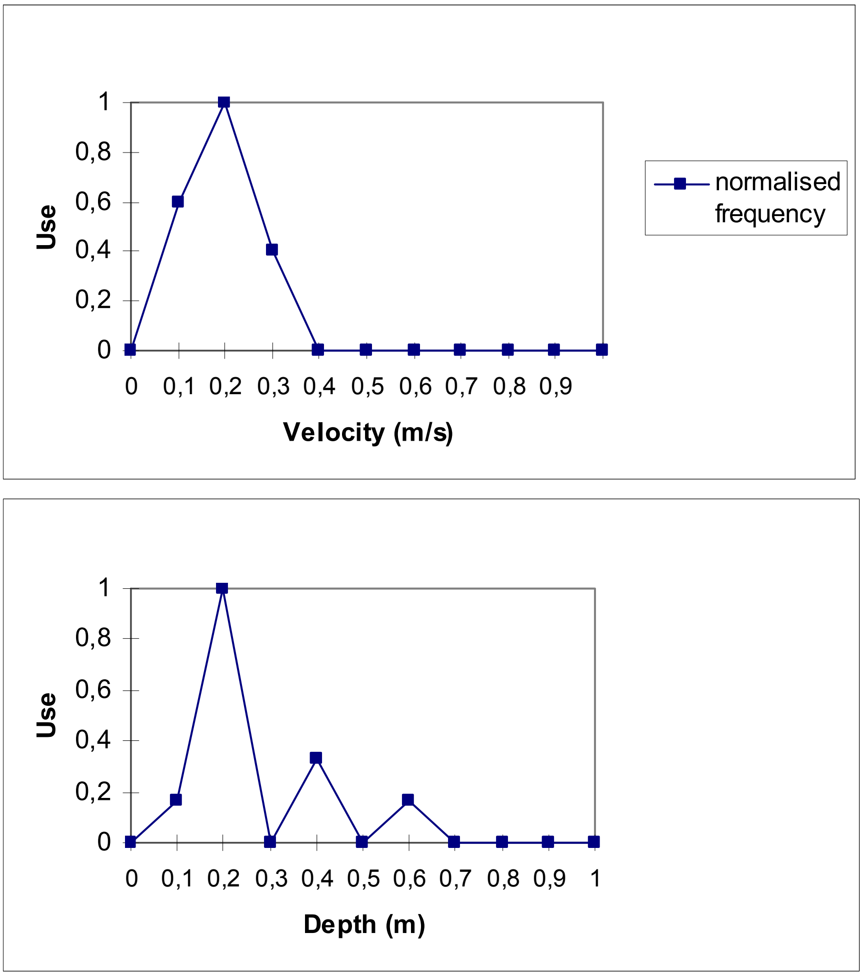


Figure 5.33 Habitat (depth and velocity) use curves drawn from bullhead observations in the River Tern

From the literature, data on depth suitability for bullhead is lacking. The optimal habitat was defined as being 0.2 m deep and with velocity values around 0.3 $m.s^{-1}$. The Habitat Suitability Index curves are characterised by a parabolic shape, which is not the case for the Habitat Use curves obtained from field data. Frequency of use of depth and velocity in the Dowles Brook differ from what would be expected from HSI curves: maximum use occurred at depths around 0.1 m and included all depths between a few centimetres and 0.2–0.3 m while slow/nil velocities were the most frequently used. As a result, HSI curves were more accurate at predicting the depths used than they were at predicting suitability of velocities.

Depth Use curves drawn from fish observations in the River Tern are characterised by three peaks, which correspond to data “noise”, due to the low number of bullhead observations on this study site. Most fish used depths between 0.1 and 0.2 m and velocities around $0.2 m.s^{-1}$. Hence the HSI curves work to a certain extent but are not very accurate, particularly as velocity is concerned. Moreover the range of depths used by bullhead could not be determined from the literature and Habitat use curves show that depths of 0.2 + m are used by this species. The method used to draw these HSI curves (Chapter 3, section 6) relies on studies that differ in terms of location, stream type, methodology and number of samples. Though weighing factors are used to try and counteract those differences, the result is still tentative. Moreover many characteristics related to the location of fish would not have been identified using only the HSI curves, e.g. preference for glides/pools because they are retention zones and the very low numbers of bullheads in the River Tern.

5.8.2 Suitability rating of bullhead locations using the HSI curves

To further show how the use of HSI curves can be misleading or too simplistic representations of a species habitat selection, the characteristics of bullhead locations at the mesoscale were tested for their suitability using relative Suitability Indices. Relative Suitability Indices for each unit of the summary map for the Dowles Brook were calculated to establish each mesohabitat suitability. Suitability Indices at fish locations with each unit were also calculated and are shown in Table 5.4.

Table 5.4 presents a summary of the fish occurrence prediction work carried out using the data collected on the Dowles Brook. The “Depth HSI” and “Velocity HSI” columns represent the range of suitability of each unit identified in the stream and that was calculated using the suitability curves built from the literature (see Chapter 3) and the depth and velocity measurements taken in each unit during mesohabitat surveys. It can be seen from the HSI values for depth and velocity that most of the units in the stream presented a relatively good availability for bullhead. However, calculation of the relative suitability indices for the depths and velocities at bullhead location and the resulting HSI (3 last columns of the table) shows that bullhead were only observed in an optimal microhabitat in unit 4 (rHSI shown in green). Most of the observed bullhead were located in poorly suitable areas (rHSI less than 0.25), particularly those located in pools/glides. These data show that a gap exists between the suitability values determined by the HSI curves and the reality of fish occurrence.

Table 5.4 Relative Habitat Suitability indices calculated for each unit in the Dowles Brook and for each fish location. The colour code used is according to that described in Table 3.8 p.77. Fields marked "N/A" corresponds to units where no fish were observed

Unit n°	CGU type	depth HSI	velocity HSI	fish location depth	fish location velocity	fish location rHSI
1	riffle	0.4 - 0.45	0.6 - 0.9	0.04	0.0135	0
2	glide	0.9	0 - 0.6	0.134	0.065	0.24
3	run/riffle/glide	0.3 - 0.9	0.6 - 0.9	0.13	0.176	0.64
4	run	0.4 - 0.7	0.7 - 0.9	0.15	0.328	0.8
5	run/riffle	0.4 - 0.8	0.4 - 0.9	N/A	N/A	N/A
6	run/riffle	0.4 - 0.8	0.7 - 0.8	N/A	N/A	N/A
7	glide	0.8 - 1	0 - 0.4	0.129	0.065	0.24
8	run	0.4 - 1	0.8 - 0.2	0.135	0.056	0.18
9	pool	0.2 - 0.4	0	N/A	N/A	N/A
10	chute	N/A	N/A	N/A	N/A	N/A
11	glide/pool	0.9 - 0.8	0 - 0.4	0.06	0.067	0.16
12	chute	N/A	N/A	N/A	N/A	N/A
13	glide/pool	0.9 - 0.8	0 - 0.4	0.1	0.037	0.08
14	run/riffle	0.4 - 0.45	0.8 - 1	0.06	0.408	0.32
15	glide	1 - 0.8	0.3 - 0.6	0.13	0	0
16	run/riffle	0.4 - 0.9	0.5 - 1	N/A	N/A	N/A
17	glide/pool	1 - 0.9	0 - 0.6	0.06	0.145	0.28
18	cascade	N/A	N/A	N/A	N/A	N/A
19	run/riffle	0.4-0.9	0	N/A	N/A	N/A
20	pool	0.8 - 0.6	0	0.225	0.068	0.4

Table 5.4 shows further examples of the differences between predicted occurrence and actual occurrence. For instance, the glide/ pool located in unit 11 is an optimal location for bullhead from the HSI curves. However the suitability of the locations at which bullhead were observed in this mesohabitat was calculated as poor. This contrast was observed for other parts of the reach such as units 2, 7 and 13. On the opposite, units where the range of suitability was average or fair, such as unit 4, bullhead were observed in optimal locations (HSI=0.8).

These results confirm that mesohabitats are not uniform features and that the environment conditions such as depth, velocity and substrate vary within a CGU. The data presented in Table 5.4 can result from the following explanations.

1) The stream does not present suitable areas and bullhead adapt and use habitats that are available.
2) As long as cobble is present in the mesohabitat, other physical conditions such as depth and velocity have less importance.
3) Glides and pools are the mesohabitats most appropriate for bullhead habitat requirements, hence, HSI curves are not very accurate and the method used to draw them is not very reliable.
4) HSI curves are only valid and accurate if build for a specific site/ stream and are not generalized ones. This "site-specific versus generalised" HSI curves problematic has been the subject of several studies including those by Ibbotson and Dunbar (2001) and Moir *et al*. (2005).

Chapter 5 presented the results from the investigations on bullhead habitat use according to mesohabitat variability in a surface runoff influenced stream and the results from the few observations made in the groundwater influenced stream. These results as well as those presented in Chapter 4 will be summarized in Chapter 6, where overarching conclusions will be drawn and ideas for future research will be discussed.

CHAPTER 6

DISCUSSION OF RESULTS, CONCLUSIONS AND FURTHER RESEARCH

6.1 INTRODUCTION

This chapter draws together the main findings from the previous chapters in relation to the research questions identified at the beginning of this thesis (Chapter 1 and 2). These research questions, together with the aims and objectives of this work are stated again in section 6.2. Sections 6.2.1 to 6.2.7 summarize the answers brought by this study to the 7 research questions identified. Comparison of these findings with other studies are presented as well as some general conclusions (section 6.3). Finally, section 6.4 will indentify possible further developments in this area of research.

6.2. MAIN FINDINGS AND CONCLUSIONS FROM THE RESEARCH

Table 6.1. Summary of the overall aim, objectives and research questions of the thesis

<table>
<tr><td colspan="4">Overall aim :
To examine the relationship between river flow regime and the spatial and temporal habitat use dynamics for brown trout and bullhead.</td></tr>
<tr><td>Objective 1:
Characterize the above species' habitat in groundwater and surface runoff influenced streams</td><td>Objective 2:
Use an intermediate scale approach to understand the implications of spatial pattern and habitat connectivity in streams</td><td>Objective 3:
Evaluate the temporal dynamics of habitat use and species' response to habitat variability in relation to flow regime</td><td>Objective 4:
Evaluate the accuracy and reliability of HSI curves</td></tr>
<tr><td colspan="2">RQ$_1$: Do different types of flow regimes result in different stream morphology and in different mesohabitat composition?</td><td>RQ$_3$: is there a pattern of mesohabitat use displayed by fish and if so, what is it?</td><td rowspan="6"></td></tr>
<tr><td colspan="2" rowspan="5">RQ$_2$: How does mesohabitat composition vary with flow, depending on the flow regime considered?</td><td>RQ$_4$: Does mesohabitat use follow the same pattern as mesohabitat variability, i.e. is it influenced only by flow?</td></tr>
<tr><td>RQ$_5$: Are other factors involved in fish habitat use and if so, what are they ?</td></tr>
<tr><td>RQ$_6$: What role is played by factors such as seasonality, habitat availability, life-stage and social interactions in the pattern of habitat use displayed by the surveyed population?</td></tr>
<tr><td>RQ$_7$: What are the key habitat characteristics that determine fish location?</td></tr>
<tr></tr>
</table>

Table 6.1 summarizes the overall aim of this work, which was divided into 4 main objectives to address 7 key research questions.

All objectives were achieved and their corresponding research questions answered. No research question was associated to objective 4. A summary of the answers to the research questions is presented in sections to 6.2.1 to 6.2.7 while objective 4 is discussed in section 6.2.8.

6.2.1: Do different types of flow regimes result in different stream morphologies and different mesohabitat composition?

To answer this research question (see also section 6.2.2 below), objectives1 and 2 were achieved, i.e. habitat available for fish was characterized in streams using a mesohabitat approach. Mesohabitat surveys carried out over a range of flows on the River Tern (section 4.1) and on the Dowles Brook (section 5.1) reveal differences in mesohabitat composition between the two types of flow regimes represented by these rivers.

The River Tern reach was composed of mainly 3 types of mesohabitat (run, glide and backwater) at all flows while the Dowles Brook mesohabitat composition was more diverse with 5 mesohabitat types present at all flows.

6.2.2 How does mesohabitat composition vary with flow depending on flow regime?

As presented in sections 4.1 and 5.1, mesohabitat composition variability differs depending on the flow regime considered. On the River Tern (groundwater influenced), mesohabitat composition showed little variation over the range of flows surveyed. On the contrary, the Dowles Brook presented a high variability in mesohabitat composition over the range of flows with some mesohabitats merging at higher flows to form much larger, uniform mesohabitats. Therefore, this suggests that more stable flow regimes may lead to greater stability in mesohabitat composition with varying discharge. However, for both rivers, but particularly true for the Dowles Brook due to the flashiness of its flow regime, the evolution of the number of mesohabitats identified does not follow a simple relationship with flow. For example, some mesohabitats remain constant at all flows, (e.g. in the Dowles Brook the riffle and glide at the downstream end and the pool at the upstream end), whereas others are characterised by variability (e.g. in the middle of the Dowles Brook reach) with some riffles becoming runs at higher flow levels and some pools forming at particular flows depending the presence of woody debris. This shows the relationship between flow and mesohabitat composition is not a simple one, and predicting mesohabitat composition according to flow depends on the local conditions and reach geomorphology at the site.

It is fundamental also to consider the pattern of variability displayed by mesohabitat physical characteristics such as depth and velocities as these partly explain the suitability of mesohabitats for instream biota.

6.2.3 Is there a pattern of mesohabitat use displayed by fish and what is it?

Both species displayed a particular strategy when it comes to habitat use. Brown trout in the River Tern tended to choose runs and glides that remained as such at all flows. The choice of runs and glides appeared to be governed by biotic factors such as social hierarchy and life stage as well as by seasonality: brown trout mostly used glides during the summer, switched to runs in October and used glides again in November. Bullhead displayed a strong preference for slow flowing mesohabitats, *i.e.* glides and pools, whose characteristics remain stable at all discharges and where coarse substrate (gravel, pebble and cobble) is the dominant substrate type. Bullhead were found in glides and pools across the range of discharge surveyed.

6.2.4 Does mesohabitat use follow the same pattern as mesohabitat variability, i.e. is it only influenced by flow?

Flow, although having an influence on fish habitat use is not the only factor affecting their location. In the case of bullhead, flow and mesohabitat variability played a major role in the strategy of habitat use displayed by bullhead, in that results show the fish remain in those habitats with stable physical conditions across the range of flows experienced.

In the case of brown trout, the groundwater influenced flow regime created very stable instream conditions that allow other factors to play a role in influencing fish habitat use. Brown trout used mostly runs and glides across the range of discharges surveyed. Observations showed that glide and run availability according to discharge did not vary to a great extent and did not influence brown trout habitat use. Other factors impacted on brown trout choice of habitat such as variability of mesohabitat physical characteristics (whether at a particular location, the mesohabitat type remains constant or not), the presence of instream features that provide shelter, life-stage (segregation in habitat use was observed between parr and adult) and seasonality.

6.2.5 Are other factors involved in fish habitat use and, if so, what are they?

As already stated in section 6.2.4, the results of the research in both streams showed that other factors are involved in determining fish habitat choice. For bullhead, in the surface-runoff influenced stream, mesohabitat physical characteristics played a major role: bullhead were mostly found in glides and pools, with stable depth and velocity conditions at all flows. The presence of coarse substrate such as cobbles is a key determinant as it constitutes the shelter of choice for bullhead. Food may also play an important role since glides and pools are zones of organic matter retention, and as such constitute a source of food for many macroinvertebrate species which in turn provide a food source for bullhead.

For brown trout, the presence of permanent instream features that provide shelter (large woody debris for example) appears to significantly influence fish location. The results of this study show also the major role played by biological factors such as life-cycle, life-stage and social hierarchy. Food availability obviously plays a role as well although this was not shown directly by the observations carried out.

6.2.6 What role is played by factors such as seasonality, habitat availability, life-stage and social interactions in the pattern of habitat use displayed by the surveyed population?

In the groundwater influenced streams (River Tern) where mesohabitat assemblage does not vary significantly, cover appears to be the environmental factor to influence brown trout habitat use. Biological processes such as intraspecific competition, particularly size-structured competition in the case of brown trout, are dominant in determining fish habitat use. This was particularly emphasized by the observed mesohabitat segregation between brown trout adult and parr.

In the surface runoff influenced stream (Dowles Brook), where mesohabitat assemblage varies, bullhead mostly choose mesohabitat types with constant physical characteristics at all flows, e.g. pools and glides, and remain in those habitats across the range of flows. Three explanations arise for this kind of behaviour: the stability of glide/pool mesohabitat types across flows compared to other types of mesohabitats (e.g. riffles/runs), the presence of cobbles (shelter), and the poor swimming ability of bullhead. This suggests that bioenergetics have to be taken into account when looking at mesohabitat use.

6.2.7 What are the key habitat characteristics that determine fish location?

To answer these questions, two flow charts were created, i.e. for brown trout in the River tern (section 4.7) and bullhead in the Dowles Brook (section 5.6). These summarize the key factors influencing fish location and the two charts are presented again here (figures 6.1 and 6.2). These two charts show that climatic and macroscale factors like seasonality, flow regime and discharge influence fish location. Mesoscale factors such as mesohabitat composition and its variability (influenced by flow regime) are the next factors to play a role in fish habitat use. Cover and shelter in the form of macrophytes, coarse woody debris finally determine fish location.

Such charts show the multiscale nature of the influences on fish habitat use, emphasizing the need for cross-scale studies and management plans when considering fish populations and the rehabilitation of their habitat.

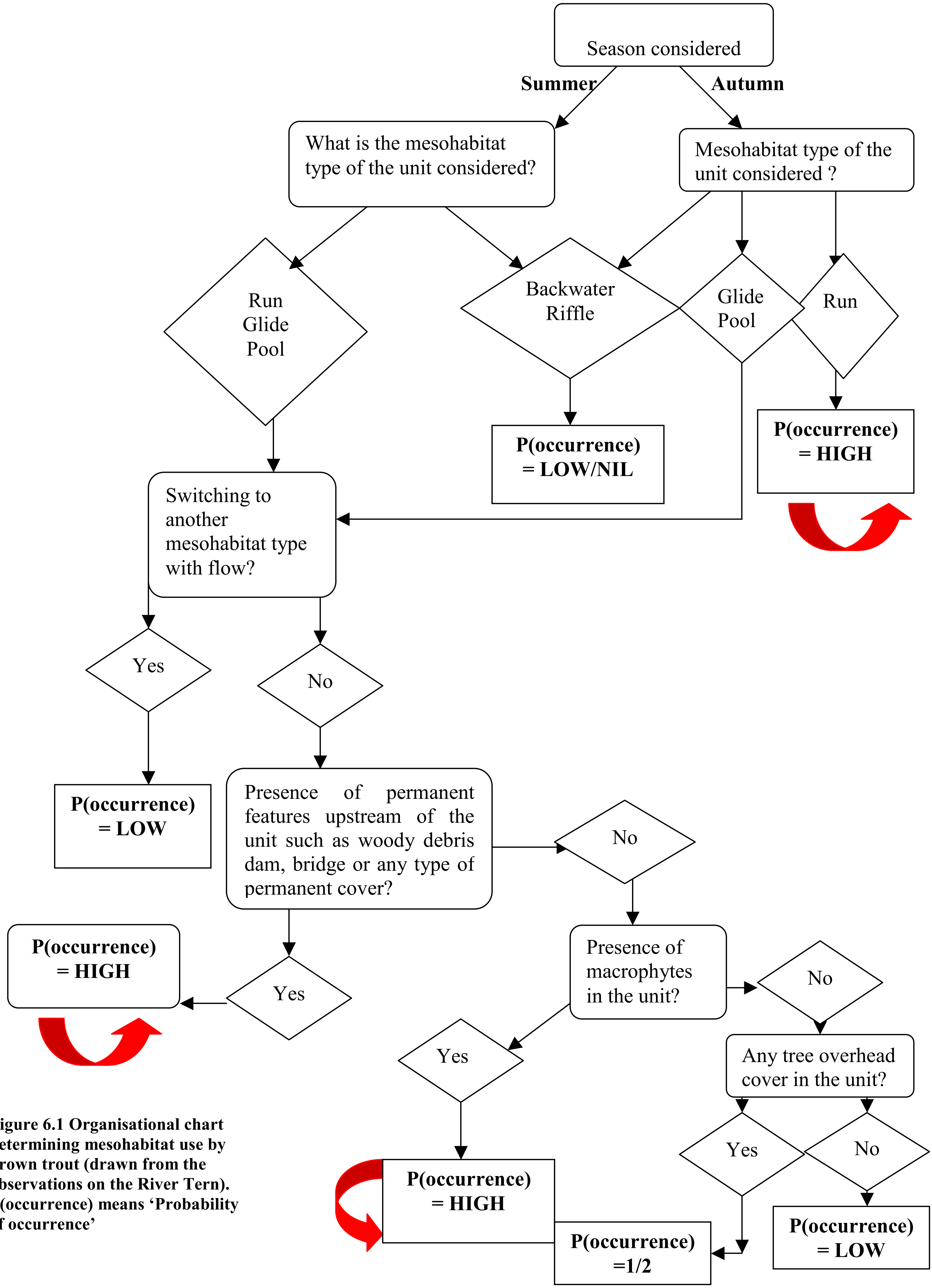


Figure 6.1 Organisational chart determining mesohabitat use by brown trout (drawn from the observations on the River Tern). P(occurrence) means 'Probability of occurrence'

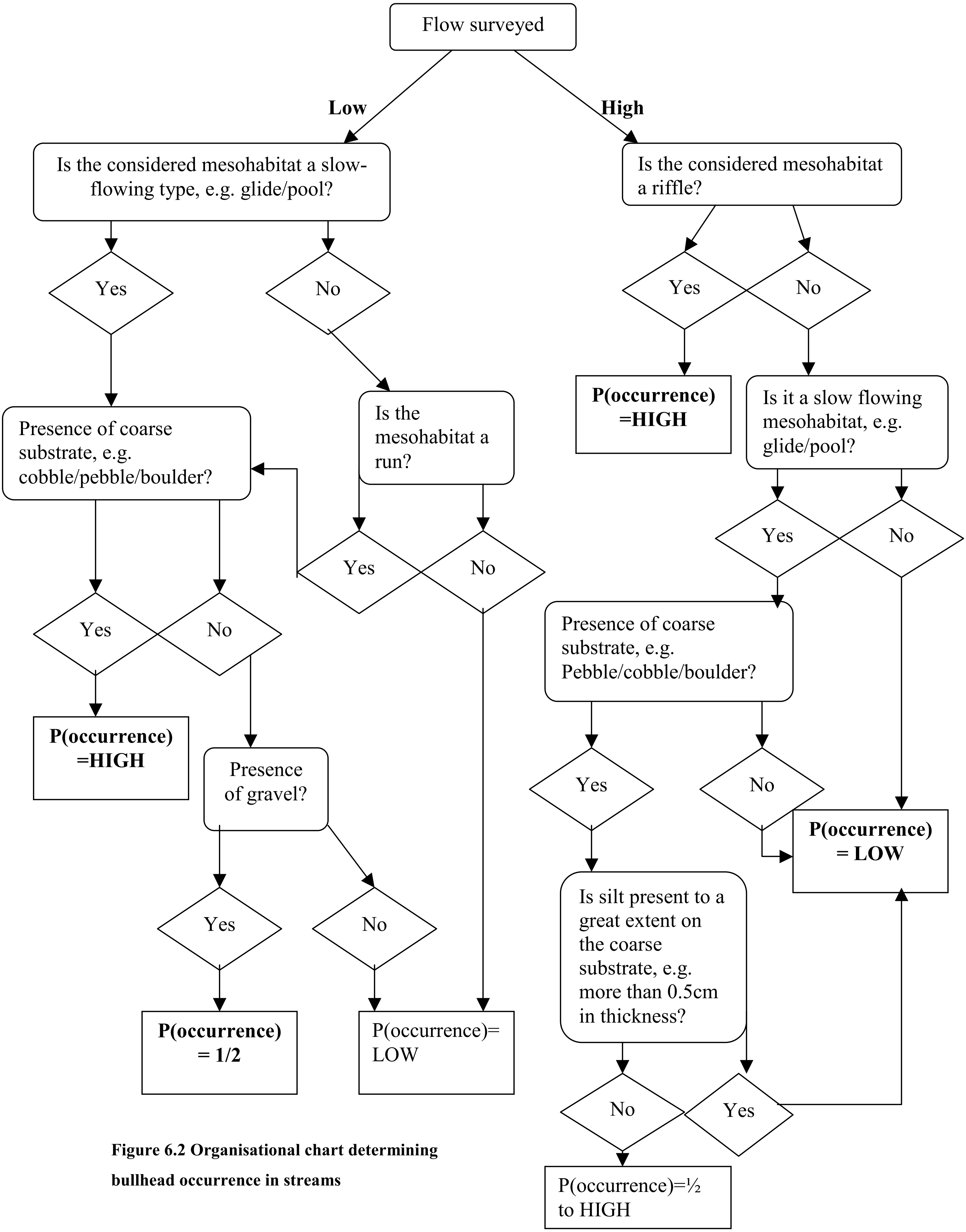


Figure 6.2 Organisational chart determining bullhead occurrence in streams

6.2.8. Objective 4: Evaluate the accuracy and reliability of HSI curves

Two types of HSI curves were evaluated during this study. Literature-based HSI curves were created for bullhead and compared to field observations. There was little agreement between HSI curves and observations, which led to the conclusions that, although literature–based HSI curves can be considered generic due to the number of studies they are based upon, they may not be reliable in predicting bullhead location. This is due to local factors that are key determinants and are more important than depth, velocity and substrate in affecting bullhead habitat use.

Previously published generic HSI curves created from brown trout observations in groundwater-dominated chalk-streams (Dunbar *et al.*, 2001) were compared to actual brown trout observations in the River Tern. Results showed that there is some degree of agreement between these HSI curves and generic habitat use curves drawn from all observations at all flows, which is probably partly due to the stable instream environment resulting from the influence of groundwater input. When comparing flow specific habitat use curves derived from the observations on the River Tern at specific flows to the generic HSI curves, little agreement was found.

The results of these comparisons showed that the use of HSI curves for river ecosystem management is questionable. They are a simple tool that gives a broad indication of the suitability of depth and velocity at a site. However, they do not provide absolutely reliable criteria on fish location because they do not consider other influences on fish ecology and habitat use which depending on the nature of the site, may be the primary determining factors influencing fish distribution and behaviour.

6.3 COMPARISON WITH OTHER STUDIES, DISCUSSION AND GENERAL CONCLUSIONS

6.3.1 Flow regime, stream morphology and mesohabitat composition

Comparison of mesohabitat composition for the surface runoff influenced and groundwater fed streams showed that the groundwater-fed stream (River Tern) displayed less mesohabitat diversity than the Dowles Brook. This agrees with the results from Whiting and Stamm (1995) who found that groundwater-fed rivers display a less diverse geomorphology along their reaches.

The evolution of the number of mesohabitats identified does not follow that of flow particularly in the Dowles Brook. The observed variability according to flow agrees with the findings of Newson *et al* (1998) who emphasise that this variability is the result of interactions between the geomorphology of a river channel (integration of water and sediment transports) and the episodic nature of water discharge and sediment erosion and deposition. The findings of this study also agrees with the observations by Maddock and Lander (2002) on another surface runoff influenced stream (Leigh Brook, Worcestershire) who found that varying discharges resulted in changes in mesohabitat distribution and that subtle differences in distribution occurred particularly at the low flow end of the discharge range. In the case of surface runoff influenced flow regime, the flashy nature of discharges makes the mesohabitat composition quite difficult to predict and further research in this area is needed to try and link a particular flow to a particular mesohabitat composition.

Analysis of the standard deviation of depth and velocity measurements reveals how much a mesohabitat is influenced by discharge variability. In the present study pools and backwaters, both deposition-influenced, were more stable than runs and riffles, which are erosion-influenced. This emphasizes the linkages that exist between flow, geomorphology, sediment transport processes and hydrological parameters in a stream, already described by Poff *et al.* (2006) and Yarnell *et al.* (2006), and these are particularly visible at the mesoscale.

Analysis of depth and velocity measurements also showed a hierarchy in mesohabitats with the fastest mesohabitats being chutes, followed by riffles, runs, glides, and pools. In terms of depth, riffles are the shallowest, followed by chutes, runs, glides and finally pools. These results agree with the description made of these CGUs in MesoHABSIM (Parasiewicz, 2007) and also the River Habitat Survey (Environment Agency, 2003). The range of depths and velocities recorded in the Dowles Brook is similar to that measured in the Leigh Brook, Worcestershire (Maddock and Lander, 2002), a lowland stream within the Severn Catchment that is geomorphologically and hydrologically similar to the Dowles Brook. However, pools in the Dowles Brook are relatively shallow compared to the Leigh Brook, where pool depth reached 0.94 m. The latter stream presented a similar pattern in terms of persistence of mesohabitats according to flow, in that the same mesohabitats were present at all flows but their proportion varied from one flow to the other.

6.3.2 Fish response to flow regime and mesohabitat variability

First the findings of this study confirm snorkelling is an appropriate and viable survey technique (Cunjak and Power, 1986; Heggenes *et al.*, 1998; Heggenes and Dokk, 2001) when trying to link fish habitat use to habitat composition and variability at the mesohabitat scale. Indeed snorkelling allows underwater observations of the fish environment, which can further explain fish location and that would not be possible using electrofishing nor bank-based observations.

Observations confirmed that mesohabitat variability impacted on fish behaviour but that depending on the degree of variability of mesohabitat composition, other factors both physical and biological influenced fish location.

This was particularly emphasized in the groundwater fed stream, where the very low mesohabitat variability allowed the impact of biological factors, in particular life stage and social hierarchy, to be observed within the brown trout populations: of particular interest was the segregation in mesohabitat use that occurred between adult and parr; as shown by figure 6.1, seasonality and the presence of woody debris were also important. Glide use by trout in the River Tern agrees with direct underwater observations conducted by Heggenes *et al*. (1998) that found brown trout parr in streams in South-West England to more frequently use slow pool-glide habitats although in these streams trout were in sympatry with Atlantic Salmon. Moreover, Heggenes *et al.* (1998) concluded that the use of more slow-flowing/deep mesohabitats increased with fish increasing size.

In the surface runoff flow regime, the habitat use strategy developed by bullhead was in direct response to high mesohabitat variability, which consists in a high association with hydrologically stables mesohabitats such as glides in which coarse substrate was present. The strong association with glides conflicts with observations by Roussel and Bardonnet (1996), Langford and Hawkins (1997) and Legalle *et al* (2005) who found bullhead associated with the low depth, high velocity environment of riffles, possibly as a consequence of the presence of gravel in these habitats. However, their definition of riffles differs in terms of depth since they define such habitats with depths ranging from 0.15 to 0.4 m. However, Perrow *et al* (1997) observed on several occasions and in the four rivers of their study the strong selection of woody debris by bullhead leading to a strong association with increased depth and leaf litter, which correlates our results showing strong association between bullhead and increased depth and slow velocity.

Observations also emphasized the importance of microscale variable such as local depth, velocity, and substrate which explains in the case of bullhead while the velocities at which the fish were found even in riffles, were very low and why bullhead are also always associated with coarse substrate such as cobble and gravel. The latter agrees with observations by Knaepkens *et al.* (2004).

6.3.3. Instream habitat quality and population health

This study confirms both fish species as good indicators of the stream naturalness. The dynamics of the brown trout population could be observed during the whole survey season, which confirms the good ecological status of the study reach. However, bullhead observations are a cause for concern: a sharp decline in the numbers of bullheads in the River Tern reach was observed in comparison to the previous survey by Pinder *et al.* (2003). At the time in one survey 128 fish were recorded while during the whole survey season of the study only 10 fish were observed. It is doubtful that the difference in survey method (electrofishing versus snorkelling) does not alone account for the difference in numbers recorded. The River Tern at Norton-in-Hales presented very high numbers of American Signal Crayfish (*Pacifastacus leniusculus*) known to present a potential threat to bullhead via predation and competition (Cowx & Harvey, 2003). This may explain the low numbers of bullhead observed in this study compared to historical data.

In the Dowles Brook, densities of bullhead were very low (0.07 fish /m²) compared to what would be expected for populations living in headwater streams. Perrow *et al* (1997) discussed the densities of bullhead in the headwaters of some Norfolk rivers and defined as low the densities < 0.15 individuals/m² and as high densities those >0.6 individuals/m². Possible causes for such low densities include the absence of woody debris (Perrow *et al.*, 1997) noted the high rate of association of bullhead with woody debris), the high levels of siltation occurring in the stream and invasion of the stream by American Signal Crayfish (*Pacifastacus leniusculus*).

6.3.4. General conclusions

The overall aim of this study was to examine the relationship between river flow regime and the spatial and temporal habitat use dynamics for brown trout and bullhead. This was achieved and the study showed that different patterns of discharge variability resulted in different habitat use strategies by brown trout and bullhead. Brown trout, under more stable flow conditions, displayed a pattern of habitat use greatly influenced by seasonality and biological factors such as social hierarchy. On the other hand, under highly variable discharge conditions bullhead habitat use dynamics were mostly influenced by the geomorphology of the stream and the variability of instream physical conditions at particular locations in the stream.

This study was among the first to try and link natural flow regime, mesohabitat variability and fish habitat use. It confirms that the mesoscale is very appropriate to study fish habitat use at the sector scale as it allows to link specific instream features to fish location. However, microscale parameters are also important in influencing fish habitat use and as such should be included together with mesoscale parameters. The mesohabitat mapping method developed for this study allowed mesohabitat surveys to be easily completed and repeated other the study periods.

Both fish species were of conservation interest: brown trout as key indicator of good instream water quality and bullhead a key indicator of undamaged instream physical habitat.

The flow charts developed based on the fish and mesohabitat surveyed constitute a reliable and appropriate tool to be applied in management plans in order to identify key habitats for fish. As they are based both on fish observations and mesohabitat surveys, they allow the user to link fish to particular instream conditions. Moreover they do not rely only on physical microscale parameters (depth, velocity and substrate) but also on mesohabitats, seasonality, discharge and instream features, which makes them more widely applicable in terms of association between fish and instream habitat. They also emphasize the need for a multiple scale (macro-, micro- and meso-scale) approach in order to fully understand the factors influencing fish habitat use. There is clearly a need for integrated approaches in order to understand how various parameters can influence fish community survival. Fish are situated at the top of riverine food webs, hence they are very good indicators of the health of these ecosystems. Understanding what factors most influence their ecology and survival can contribute to a better understanding of the other parts of the ecosystem they depend on. The tools developed in this study and a multiscale approach are clearly needed in order to achieve the conservation and the monitoring objectives set in the context of the E.U. Water Framework Directive.

6.4 Further Research

As is often the case in studies and research of this nature, while carrying out the investigations to answer to initial research questions identified in the literature review, many more new research questions and gaps were identified during this research project. There were also situations where the research design could have been improved and different methods used to adapt to the variability of the conditions in the study sites. Particularly, the impossibility to study brown trout and bullhead behaviour habitat use in the same stream (apart from few bullhead observations in the River Tern) under similar conditions of flow and habitat variability could have partly been prevented by electrofishing surveys in potential study reaches at the outset to confirm the presence of both species together.

As a result, testing the above results in rivers where both species are present would allow to determine the factors that are species-specific and those that are environmental-related. Indeed the results of this research show that while some fish behaviours are clearly a result of flow variability, different fish species may display different behaviours. Particularly in the case of the Dowles Brook, it would have been relevant to be able to study brown trout strategy of habitat use according to flow variability and see whether the pattern of habitat use displayed is the same or different to that of bullhead.

Modelling of habitat availability and variability according to flow would allow the study of the effect of flow variability on the distribution of depths and velocity in the target rivers. Using the depths and velocity measurements taken in each identified mesohabitat would further allow 2-D modelling of the evolution of instream physical parameters at the mesoscale. Topographic measurements of the variations in the stream bed profile would add a third dimension to the modelling and would provide a valuable and dynamic tool to study instream environment variability with flow. Stream bed topographic measurements were started in 2006 but the lack of time prevented further work to be carried out in this direction. However, it would be interesting to attempt modelling of mesohabitats depth and velocity variations using the mesohabitat data that were collected on the three study reaches.

The mesohabitat mapping method developed for this research (Chapter 3, section 3.2.1) provided detailed information on instream and riparian physical conditions. It was user-friendly, time-efficient and easily replicable over a wider range of flows and the three study sites. Similar sampling could be carried out on different types of streams and flow regimes, e.g. upland streams, chalk streams across the U.K. to get an overview of the various patterns of mesohabitat distribution and variability across different regions of the country. As a result, since mesohabitat diversity can be an indicator of stream naturalness, this survey method could be used in monitoring plans as part of the Water Framework Directive implementation programme.

Depth, velocity and substrate variability across the reach according to flow and in general data on instream environmental conditions such as vegetation, presence of woody debris, would allow to evaluate shear stress levels experienced by fish in the stream and as a result help to understand their strategy of movements and habitat use.

Marking of bullhead and brown trout using a PIT-tag or an external marker could allow to study individual strategy according to flow and mesohabitat variability. Particularly continuous monitoring of fish movements using telemetry or PIT-tagging over a range of flows could provide valuable data on fish adaptation to instream variability (Ombredane et al., 1998; Greenberg and Giller, 2000; Bruyndoncx et al., 2002). As a result, studies on marked fish could be carried out on their fat content to study if and how particular flow conditions affect their fat reserves and energy budget (Persson and Greenberg, 1990). High energy reserves and/or mechanisms to release energy quickly into the body to allow rapid and frequent movements in response to high flow variability could be characterising fish living in flashy rivers. These investigations could allow a bioenergetics-based approach to be used to further study adaptive strategies of fish to varying flow conditions.

These research gaps and questions present a common theme, which is the need for integrated, multidisciplinary approaches to be used in studies of riverine ecosystems. This view has been expressed in many publications in the past 20 years (Hannah et al., 2004; Newman et al., 2006; Fisher et al., 2007). Studies in hydroecology, of which this particular research is a component, require not only to investigate processes taking place in the river itself but also to take into account, as first suggested by the River Continuum Concept and the Flood Pulse concept, how external factors to the stream affect instream biota and instream physical environment and how important longitudinal and lateral connectivity is. An example of these interactions was provided by the study of the brown trout habitat use in the River Tern (Chapter 4) in which large woody debris, originating from the riparian zone, affected trout habitat use providing them shelter and food resources.

This research provides an example of the principles and philosophy of hydroecological research: a multidisciplinary and multi-scale approach investigation of interactions and biological and physical processes occurring in rivers. This study has emphasized that flow variability and flow regime affect fish populations and that in natural conditions fish display a range of strategies to best adapt to changes in their environment. The study stressed the importance of natural variability of habitats and flow for instream biota and it is critical to further understand the interactions between biota and their environment in the context of increasing human pressures on rivers such as river regulation and global climate change.

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APPENDIX A

DRAFT JOURNAL ARTICLE

“Meso-habitat use by bullhead (*Cottus gobio*)”

(removed for copyright reasons)

Table 1. Distribution of CGUs in the Dowles Brook with changing flow (expressed as flow percentiles). The units are numbered from the downstream end of the reach onwards (Figure 1). Locations of fish observations given in bold italics.

Q (%'ile)	Q_{99}	Q_{96}	Q_{95}	Q_{72}	Q_{56}	Q_{43}	Q_{38}	Q_{35}
$Q_{(m^3s^{-1})}$	0.016	0.021	0.030	0.054	0.101	0.143	0.198	0.216
1	Riffle	Riffle	Riffle	Riffle	Run	Riffle	Riffle	Riffle
2							Run	Run
3	***Glide***	***Glide***	***Glide***	***Glide***	Glide	Glide	Glide	Glide
4	Riffle	***Run***	***Run***	***Run***	Riffle	Run	Run	Run
5	***Run***				Run	***Glide***		
6	Riffle				Riffle	Riffle	Riffle	Riffle
7					Run	Run		
8	Glide	Glide	***Glide***	***Glide***	Glide	Riffle	Glide	Glide
9					Run	Run		Run
10					Chute	Glide		Run
11	Pool	Pool	***Backwater***	Pool	Pool	Pool	Pool	Pool
12	Pool			Backwater			Pool	
13	Run	***Riffle***	Riffle	***Run***	Run	Run	Run	Glide
14	Pool	***Pool***	Pool	Pool	Pool		Backwater	
15	Chute	Chute	Chute	Chute	Chute	Chute	Chute	
16	Glide	***Glide***	Glide	***Glide***	Run	Run	Run	
17							Glide	
18	Riffle	Riffle	Riffle	Riffle		Chute	Riffle	Riffle
19	Glide	Glide	Glide	***Run***	Glide	Glide	Glide	Glide
20	***Run***	Riffle	Riffle		Run	Riffle	Run	Riffle
21						Glide		
22						Riffle		
23						Run		
24	Glide	Pool	Pool	Glide	Glide	Glide	Glide	Glide
25	Chute				Chute	Chute	Chute	Chute
26	Run	***Riffle***	Riffle	Run	Run	Run	Riffle	Riffle
27	***Pool***	***Pool***	***Pool***	***Pool***	Pool	Pool	Pool	Pool
N_{CGU}	19	15	15	15	20	23	20	17

Table 2. Changing patterns of velocities and depths within the CGUs including hydraulic geometry relationships based on log 10 transformed data of the hydraulic variable and discharge.

CGU	**N**	**Hydraulic variable**	**Mean (std.dev.)**	**Regression exponent**	**Regression constant**	**R^2**
Chutes	25	velocity	0.652 (0.28)	0.109	-0.097	0.19
		depth	0.142 (0.087)	0.266	-0.683	0.37
Riffles	126	velocity	0.292 (0.175)	0.319	-0.266	0.79
		depth	0.107 (0.046)	0.288	-0.701	0.54
Runs	162	velocity	0.259 (0.202)	0.244	-0.439	0.27
		depth	0.146 (0.073)	0.256	-0.628	0.43
Glides	226	velocity	0.087 (0.091)	0.461	-0.646	0.94
		depth	0.268 (0.101)	0.143	-0.456	0.85
Pools	83	velocity	0.020 (0.036)	0.188	-0.389	0.91
		depth	0.298 (0.160)	0.169	-1.573	0.64

Table 3. Bullhead occurrences in relation to flow, CGU and micro-habitat characteristics.

Flow	**CGU (see Figure 1)**	**CGU type**	**Bullhead observations**	**Mean velocity ($m.s^{-1}$)**	**Mean depth (m)**	**Dominant substrate**
Q_{43}	1-2	riffle	3	0.15	0.05	cobble
	5	glide	1	0.06	0.10	cobble
Q_{72}	3	glide	6	0.11	0.16	cobble
	4-7	run	4	0.40	0.14	cobble
	8-10	glide	2	0.06	0.11	cobble
	13	run	2	0.14	0.13	cobble
	16-17	glide	1	0.09	0.04	cobble
	19	run	1	0.00	0.03	cobble
	27	pool	2	0.06	0.23	cobble
Q_{95}	3	glide	5	0.04	0.06	cobble
	4-7	run	1	0.17	0.10	cobble
	8-10	glide	1	0.07	0.06	cobble
	11-12	backwater	1	0.00	0.08	cobble
	27	pool	8	0.20	0.22	cobble
Q_{96}	3	glide	10	0.04	0.17	cobble
	4-7	run	1	0.27	0.15	cobble
	13	riffle	1	0.06	0.2	cobble
	14	pool	1	0.02	0.18	cobble
	16-17	glide	1	0.06	0.15	cobble
	26	riffle	3	0.13	0.18	cobble
	27	pool	4	0.00	0.26	cobble
Q_{99}	3	glide	5	0.03	0.17	cobble
	5	run	3	0.03	0.10	cobble
	19	glide	6	0.06	0.20	cobble
	20-23	run	1	0.00	0.13	bedrock
	27	pool	2	0.01	0.21	bedrock

Table 4. Bullhead habitat characteristics as described in the literature.

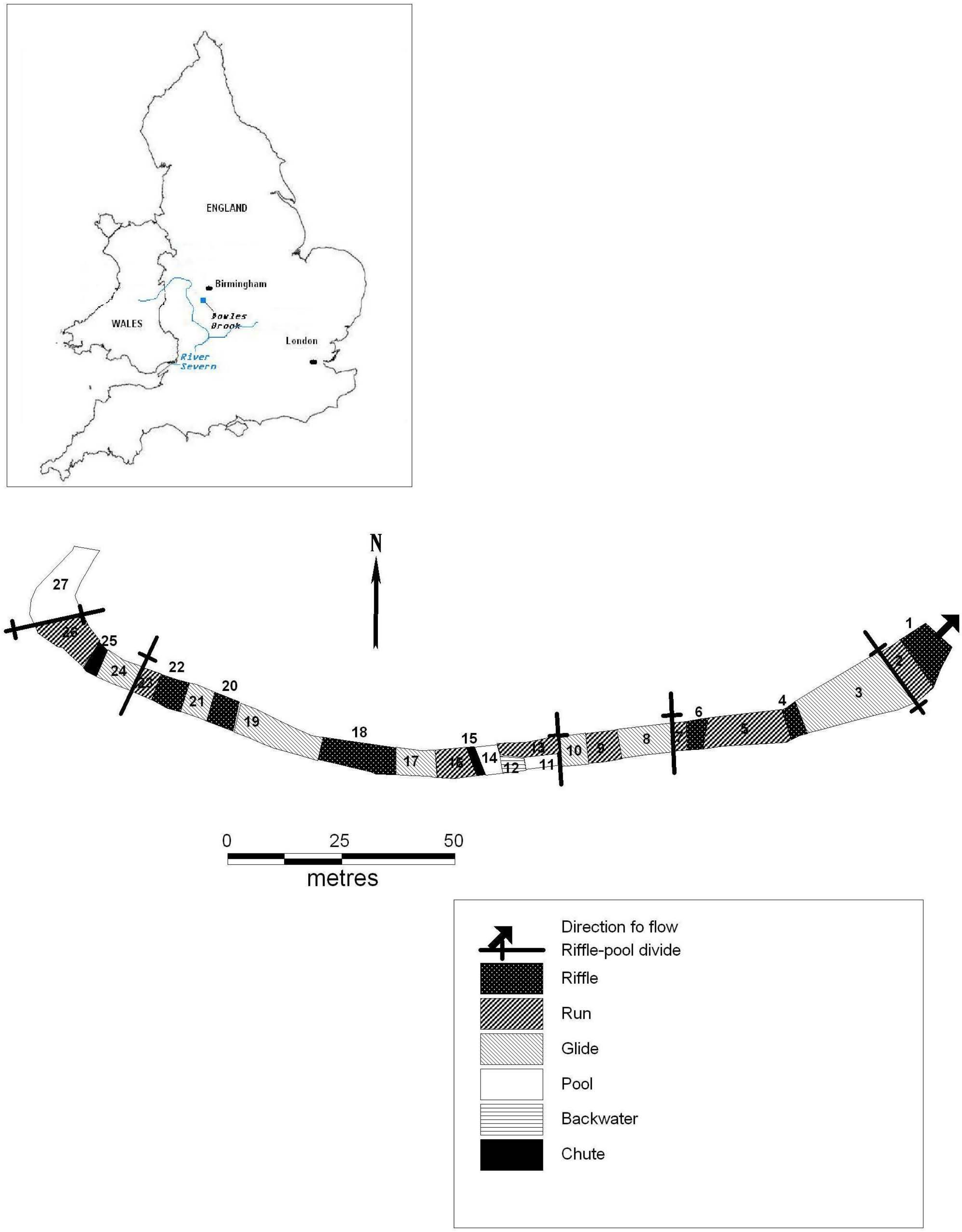
Authors	**River name**	**Channel width**	**Substratum**	**Mean or median discharge**	**Preferred depth**	**Preferred velocity**
Perrow *et al* (1997)	Glaven, Stiff, Upper Wensum, and Whitewater (Norfolk)	1.5 – 4 m	Silt, gravel and coarser substrate	0.15-0.35 $m^3.s^{-1}$	Both shallow (riffles) and deeper depths (associated with pools downstream of woody debris dams)	Not indicated
Carter *et al* (2004)	Avon (Hampshire)	4-6 m	Silt and gravel	Not indicated	~0.1 to 0.2 m	>0.1m.s^{-1}
Legalle *et al* (2005)	Saint Perdoux, Garonne catchment, France	6 m	Pebble, cobble, sand	0.33 $m^3.s^{-1}$	0.15-0.3 m	0.25-0.5m.s^{-1}
Legalle *et al* (2004)	Saint Perdoux, Garonne catchment	6 m	Pebble, cobble, sand	0.33 $m^3.s^{-1}$	0.05-0.2 m	<0.4 m.s^{-1}
Roussel and Bardonnet (1996)	Kerledan, Scorff catchment, France	3.11 m	Not indicated	0.18 $m^3.s^{-1}$	0.2-0.4 m	> 0.4 m.s^{-1}
Knaepkens *et al* (2002)	Witte Nete (Belgium)	Not indicated	Not indicated	Not indicated	Not indicated	0.2-1 m.s^{-1}

Figure 1.Map of the study reach at the lowest flow surveyed showing location of CGUs and, insert, location of the study reach.

Figure 2. Variation of the length frequency distribution of observed bullheads (a) from May to October and (b) their association with mesohabitats. S= small bullhead (length<5cm); M=medium-sized bullhead (length between 5 and 10 cm); L= Large bullhead (length above 10cm).

Figure 3. Habitat Use Curves built for bullhead in the Dowles Brook. (A. depth; B. velocity, and C. substrate).

Figure 1


ENGLAND
WALES
Birmingham
Bowles Brook
London
River Severn
N
27
26
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23
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18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
25
50
metres
Direction fo flow
Riffle-pool divide
Riffle
Run
Glide
Pool
Backwater
Chute

Figure 2a.

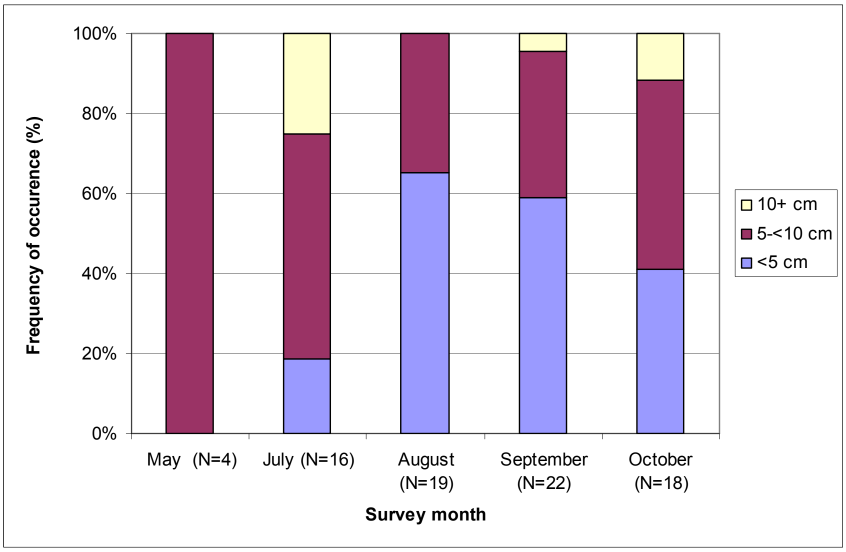


Figure 2b

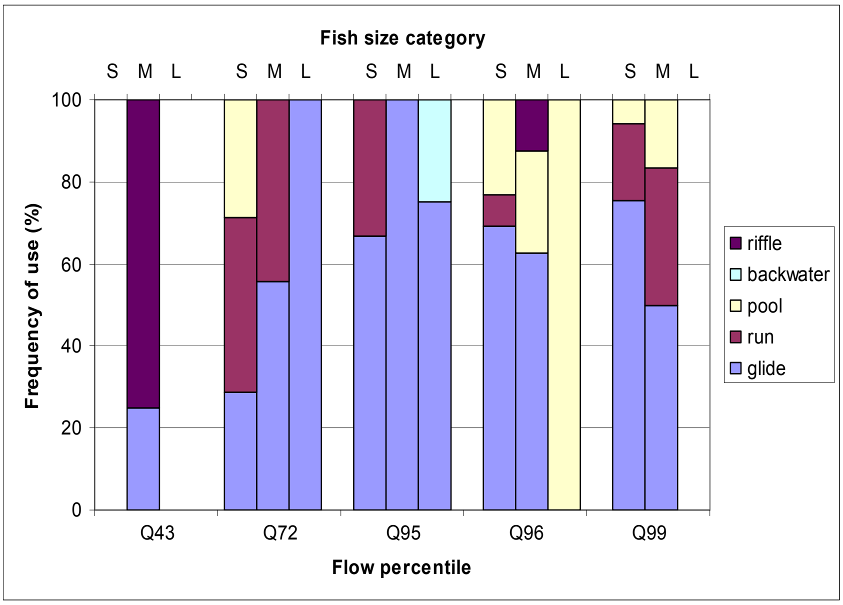
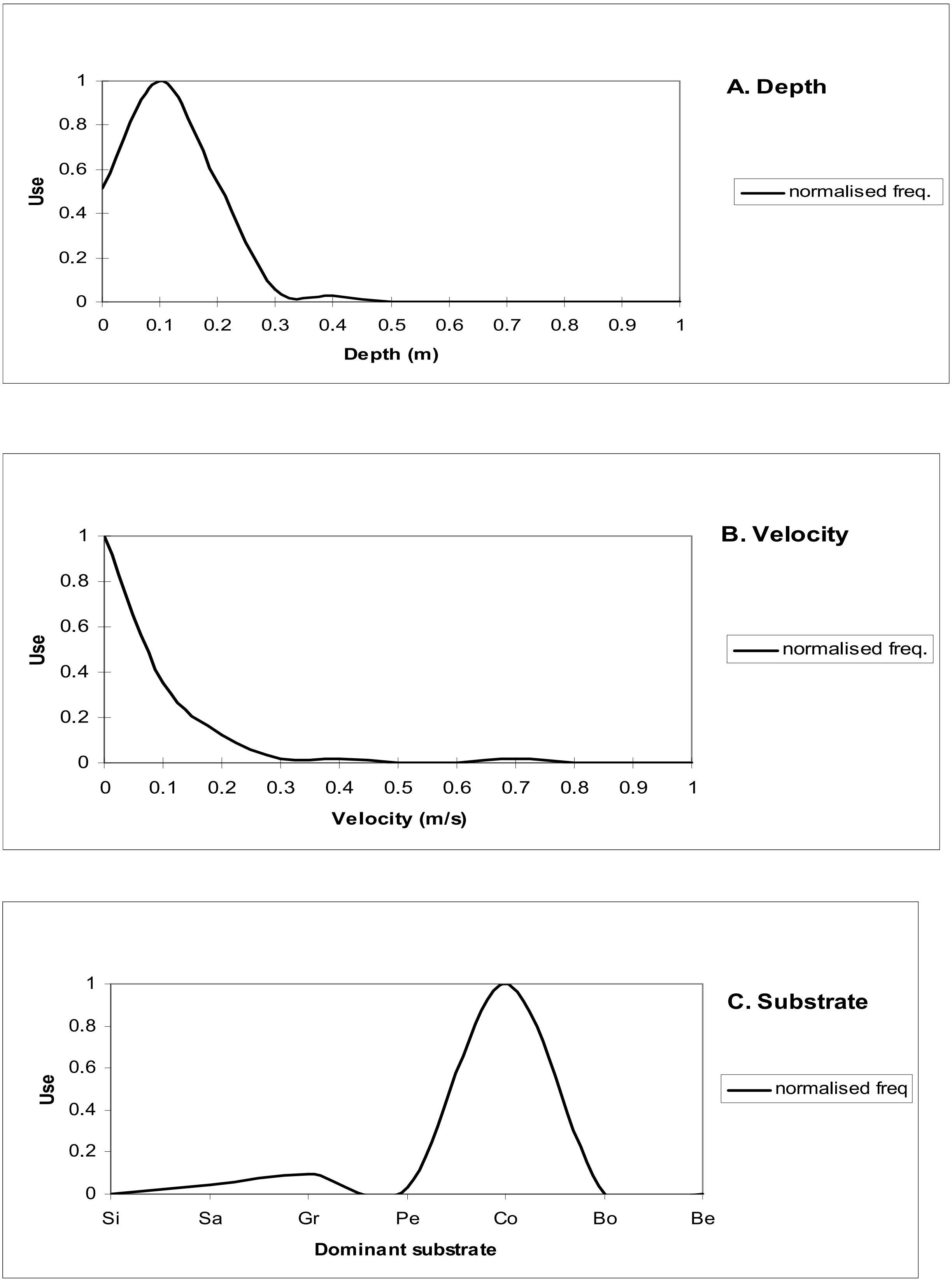


Figure 3.


A. Depth
Use
Depth (m)
normalised freq.
B. Velocity
Use
Velocity (m/s)
normalised freq.
C. Substrate
Use
Si
Sa
Gr
Pe
Co
Bo
Be
Dominant substrate
normalised freq