SPATIAL HABITAT USE OF YOUNG-OF-THE-YEAR ATLANTIC SALMON (*SALMO SALAR*) IN RESPONSE TO CHANGING STREAM DISCHARGE AND POPULATON DENSITY: TESTING THE INSTREAM FLOW MODEL CONCEPT IN A CONTROLLED EXPERIMENT

By

Christian Franz Holm

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Abstract:

Many rivers are affected by man-induced regulations of stream-flow. The effects of these on the instream biota have been studied widely and it is generally accepted that assessment tools for the management of regulated rivers are of vital importance. In particular predictive instream habitat models like the Physical Habitat Simulation Model (PHABSIM) have become popular for this purpose with users world-wide. These models predict discharge-related changes in instream habitat availability for target species by modelling the hydraulic geometry of the river reach on the one and the microhabitat preferences of the species on the other side. Despite their popularity, validation studies for this approach have met many difficulties which are mostly related to the biological part of the model, the habitat preference curves. A review of these studies undertaken here reveals that very little information has been published on two main assumptions of the models:

1. The habitat preference of a species is independent of stream discharge
2. The habitat preference of a species is independent of the species population density

Most validation studies are undertaken in field situations. As such they frequently have had problems relating to sampling the microhabitat use consistently, a lack of experimental control and variations in other secondary variables. It was thus decided to conduct controlled experiments in a large indoor flume. Young-of-year Atlantic salmon (*Salmo salar*) caught in a nearby stream were stocked into pool-riffle sequences, landscaped within a natural substrate, in observation areas of 3.6 metres length and 1 metre width. Microhabitat use of fish was recorded at three different discharges within a 15-fold discharge variation.

It was found that the mean column velocity preference of the juvenile salmon, calculated by the standard method, varied largely, mainly due to a shift of preference for low water velocities. "Weighted usable area" (WUA) calculations,

Statement of originality

I hereby confirm that this is an original study written by the undersigned, amd that all research material has been duly referenced and cited.

the final output of instream habitat models, varied up to two-fold due to these differences in preference. Habitat preference also varied with population density. Fish preferred the riffle habitat at low population density and the pool habitat during high population density. Fish used higher mean column velocities during low population density. There are hence fundamental problems related to the approach of using density functions as preference indices as is commonly done for building habitat preference curves, because of a bias for habitat availability. A new approach using Geographic Information Systems (GIS) is taken by comparing the microhabitat conditions fish experience at their chosen positions with the conditions fish would have experienced had they maintained the positions used at the other discharges. It was found that fish adjusted their positions towards significantly different microhabitats between low flow positions and the positions at the other two flows.

This research demonstrates how microhabitat use and preference of wild-caught juvenile salmon varied with discharge and population density in a large near-natural flume. The error introduced by these variations to instream habitat model predictions was large. It confirms that habitat preference curves built as density functions on empirical fish observation data are bound to misrepresent the overall habitat requirements of a species life stage which in the case of juvenile salmon appeared wide and flexible over the range of discharge.

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1. An introduction to river flow regulation in Scotland and its potential ecological effects and management options

1.1. How to run a river?

Since the origin of mankind, rivers have offered us a most beneficial environment. The river and its floodplain has always provided food, water, fertile soils, transport networks, energy and woodlands to name a few vital resources. Many of the human uses stand in conflict either with each other or with the physical and biological elements of the river ecosystem. In order to balance these conflicts of interests and to sustain the valuable river environment, it is necessary to evaluate and control the human activities. Such a management requires a detailed knowledge of all relevant parts and processes of the system as well as the understanding of the interactions of processes across scales of time and space. Built on this knowledge, predictive models are most useful tools for management decisions because they predict the outcome of different management scenarios in the future. Although predictive models are urgently needed, it is important to test the validity, performance and sensitivity of the models before they are used in order to understand the capabilities and limitations of the model.

In the Scottish case, a strong interest has developed for predictive habitat models (i.e., the Physical Habitat Simulation Model, in short PHABSIM, and related models, Stalnaker et al., 1995) to assess and model effects of flow regulation, mostly caused by hydro-electric power generation, on salmonid populations. This research addresses some of the major underlying assumptions of these models, for which very little information has been published yet. It was

decided to conduct controlled experiments in order to investigate the conceptual validity of the assumptions that these models depend on.

1.2. The economic value of salmon fisheries and hydro-electric power generation in Scotland

It is worthwhile to describe the wider context, in which the subject of this research stands. The Atlantic salmon (*Salmo salar*) catches the imagination of fishermen and non-fishermen alike and stands as a symbol for the stereotype of wild Scottish rivers. Its depiction in countless works of art related to Scottish rivers illustrate this romantic notion. From an economic point of view, in particular recreational angling benefits heavily from this species. The economic value of rod fisheries in Scotland by 1995 has been estimated to be between £270 million and £430 million (all figures from The Scottish Office, 1997). Total expenditure by salmon anglers was an estimated £70 million a year in 1995 and an estimated 3,400 full-time equivalent jobs are generated by salmon angling. The net commercial value of net fisheries in Scotland was estimated to lie between £6.2 and £11.4 million, generating a total gross revenue of approximately £2.7 million (including sea trout), providing approximately 650 jobs. The high economic importance of the salmon for Scotland would alone justify the need for a successful management of salmon populations and the currently severely declining catch numbers (The Scottish Office, 1997) emphasise the need for immediate action. The possible reasons of this decline are many and interactions of different factors rather than single elements are to blame. The alteration and degradation of the salmon fresh water habitat by human developments are to the disadvantage of the fish, but these developments too play a significant economic and social role for Scotland. For example, hydro-electric power (HEP) generation is a major source of income for Scotland and plays an important role in providing emission free electricity. Currently, the annual average output of Scottish HEP schemes is 3,226 GWh (all data by Jennifer Paice, Southern Electric plc. pers. comm.), which equates to nearly 10% of Scotland's electricity demand of 35.000

GWh per annum. This output achieves an annual turnover of £79 million at average electricity price. There are currently 220 people employed directly for HEP generation itself, plus there is a number of further jobs in related positions (e.g., Southern Electric head office) not exclusively dealing with HEP generation.

The intrinsic value of rivers, their natural and scenic beauty, their role as ecosystems and as parts of larger ecosystems and the many other important roles they play are acknowledged. However, the apparent conflict in interests between HEP schemes and the conservation of healthy salmon populations can be seen as a prime example that demonstrates the conflicts between natural systems and human development and even more so the necessity to seek solutions to resolve these conflicts. Our understanding of the ecological patterns and principles operating in regulated river systems will determine how well we can manage the impact of human development on this valuable resource. Thus, this thesis examines two major scientific questions concerning the variability of instream habitat for young-of-the-year (YOY) Atlantic salmon taken from a Scottish stream with variations in stream discharge and population density.

1.3.   River flow regulation in Scotland

River flow regulation by man-made structures is a common feature in Scottish river systems. Gilvear (1994) divided them into three sub-groups: HEP schemes, water supply reservoirs and water abstraction points. Control structures are most commonly impoundments, water abstraction points, diversions, and interbasin transfer tunnels. The structures vary in size as well as location with the largest impoundments constructed for HEP schemes on rivers draining from the Highlands to the East Coast. The largest example of this group is the Tummel-Tay system; further ones are the Beauly and the Conon. Water supply reservoirs are predominant in the Central Belt to cater for the industrial and domestic water needs of Edinburgh and Glasgow but can also be found in lower concentrations in the rest of Scotland. Abstraction points are thinly spread over most of

Scotland, principally south of the Great Glen. Taking all the developments together, effectively all catchments of Scotland are subject to flow regulation of one kind or another. Unregulated flow can often only be found on low order streams, whereas larger unregulated rivers are very few, with the River Tilt (Tayside), River Kingie (Invernesshire) and River Feshie (Cairngorms) as the most prominent examples (Gilvear, pers. comm.). For the 950 river systems of Scotland (Smith & Lyle, 1994), Gustard et al. (1987) lists 190 impoundments exceeding 500 million litres or 5 km^2 drainage area. However, the number of small reservoirs is much higher, for Tayside alone 77 reservoirs exceeding 25 million litres are present (Tayside Regional Council, 1991). Of the 190 large reservoirs listed by Gustard et al. (1987), 149 are specified according to type of use. 50 reservoirs are used for hydro-electric schemes and 84 for water supply and the rest for other, often mixed, purposes. Since hydro-power reservoirs tend to be much bigger, they comprise approximately three quarters of the volume of all impounded waters in Scotland.

1.4. The effects of flow regulation on instream ecology and fisheries

River flow regulation affects river ecosystems at a range of spatial and temporal scales. Petts (1984) suggested that the effects of impounding rivers can be understood in a rank order (Fig. 1.1.). Most immediate is the barrier effect of dams, which can obstruct up- and downstream migration of anadromous species like Atlantic salmon and sea trout but also short-range movements of other fish, invertebrate and plankton species. These are followed by first order impacts, like changes in flow regime, sediment load, water quality and plankton. An altered flow regime and sediment load will affect the channel form and substrate composition of the river as second order impacts. Also in this order, the before-mentioned factors plus changes in water quality can affect the macrophyte and periphyton composition which in turn, acting as food source for invertebrates, can alter their species composition. Parallel to these alterations are the effects of channel and flow regime changes to the riparian vegetation. The changes to the

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invertebrate and finally fish communities are labelled as third order impacts and illustrate how the changes to different parts of the river ecosystem can ultimately affect the fish community through a chain of effects rather than direct influence. It also suggests that success in modelling the effect of flow regulation at the fish species level will be unlikely without considerations of the geomorphological, chemical and hydrological aspects of the river ecosystem. Stressing this point, Orth (1987) listed six primary factors that characterise the functional and structural nature of river ecosystems in relation to the abundance and distribution of fish: food, water quality, temperature, physical habitat structure, flow regime and biotic interactions.
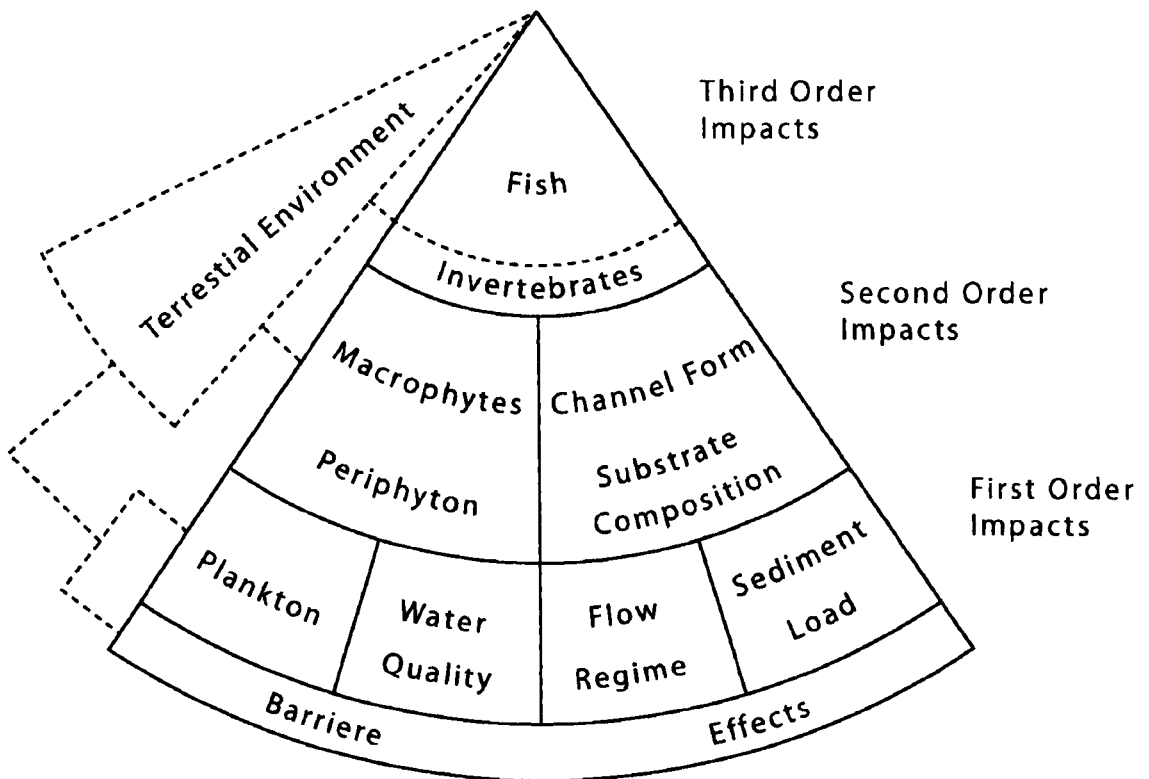
Fig. 1.1.: Order of impacts on stream ecosystem caused by impoundment (after Petts, 1984)

Thus, to a large extent, our present understanding of the effects of river flow regulations are quite basic and the structure and multidimensionality of the river ecosystem is so complex that consequent effects to the system by change to some variables are difficult to predict. This is illustrated, with regard to fish populations by the fact that empirical studies examining the effects of flow reductions and increases often found conflicting results. Aass, Nielsen & Braband (1989) for example found that a brown trout (*Salmo trutta*) population in a Norwegian river reacted very little to a 93% reduction in winter discharge, with only minor changes in fish size and smolt age. Similarly, a 80% reduction in summer flows did not cause any noticeable changes in abundance of brook trout (*Salvelinus fontinalis*) in a stream in Montana (Kraft, 1972). Rimmer (1985) found the population dynamics of young-of-year rainbow trout (*Onchorhynchus mykiss*) in experimental streams largely unrelated in timing and proportionality to permanent flow reductions of up to 60%. Harris, Hubert & Wesche (1991) found the brown trout population to increase only at one of eight sites, 3-4 years after the minimum flow in the stream had been increased by 550%. In contrast, Smith (1976) described a decline in salmonid standing stocks after a 90% reduction in compensation flows in a Californian river. In relation to flow variability, Cowx & Gould (1989) reported the recruitment of Atlantic salmon and brown trout to suffer larger declines in a river with high fluctuations in summer discharge below a regulating reservoir. This contrasted with the findings of Crisp et al. (1983) of enhanced trout populations with similar regulation discharges on the River Tees. In all these cases, the alteration of discharge alone did not explain the changes in the fish populations. These changes were explained instead by the general context of geographic location and stream type and the time and space specific conditions of the ecosystem and species concerned. The following quote may serve to summarise the scientific literature with regard to fish and flow interactions: "The lack of evidence that biota responds to changes in flow and the inability to predict population responses to flow alterations remain frustrations which will persist until intensive long-term research is initiated." (Petts & Maddock, 1994)

1.5. The management of regulated flow

As illustrated above, flow regulation is a most common impact of human development on rivers and the effects for the river ecosystem are often wide ranging. In order to safeguard the ecological characteristics of the river and even the survival of certain species in some cases, it is necessary to optimise the operational practises of existing schemes and predict the impact of newly planned developments. To be able to do this, a detailed knowledge is needed of the factors and processes operating in the river ecosystem, so that the effects of flow regulation can be modelled realistically. Despite this obvious necessity, advances in this field have been slow and methods in use to set compensation flows or to predict the effects of water abstraction are often still purely based on hydrological rather than biological information. More modern methods, most prominently a group of models known as instream flow models (reviewed by Hardy, 1998), which do incorporate biological aspects, are now becoming increasingly popular but their validity, degree of realism and limitations are often still not fully understood.

1.6. Outline of this thesis

The following chapter will briefly review the existing literature for the methods that exist for instream flow assessments and predictions. It will then focus on hydraulic habitat-based models and explain their characteristics and functioning. A summary of the published critiques follows. This firstly examines the models sensitivity, model applicability and limitations. Secondly it examines more fundamental questions concerning the conceptual validity of parts of the models. Based on this assessment of the literature the thesis presents a set of questions designed to improve our understanding of instream habitat modelling and underlying principles of interactions between fish and their habitat in response to

changes in stream discharge and population densities. The experiments to address the questions and consequent working hypotheses are presented in chapter 3, together with a description of all the methods and materials used. The three subsequent chapters present the results to aims I, II and III of the thesis. They all revolve around the main theme of fish habitat use in response to short term changes in hydraulic habitat. Chapter 4 focuses on the question how fish adjust their habitat use in relation to habitat availability when the latter changes. It then examines the relevance of these findings for instream habitat modelling. The experimental results described in chapter 5 add another level of complexity and examine the combined effects of differences in population density on meso- and microhabitat use in a variable environment. Chapter 6 presents a novel modelling approach that overcomes some problems commonly encountered in other studies of animal choice behaviour. Finally, chapter 7 summarises the key findings and discusses these in the context of existing scientific knowledge. The implications for instream flow modelling are discussed and suggestions for further work in this research area are also outlined.

1.7. Study aims and objectives

The overall aim of this thesis is to investigate the spatial habitat use of Atlantic salmon in relation to discharge and population density under controlled experimental conditions and assess the sensitivity of current instream habitat models to these variables.

In particular, the aims are:

<u>Aim I</u>
To investigate the spatial habitat use of YOY Atlantic salmon parr in response to variations in stream discharge.

Sub-aims

1. To identify preferred and avoided water velocity ranges at three different discharges
2. To build and compare three velocity preference curves for the different discharges
3. To test the assumption of PHABSIM-type habitat models, that habitat preference is independent of discharge
4. To model the effects of preference variations on PHABSIM-type habitat predictions

Aim II

To investigate the added effect of variations in population density on spatial habitat use of YOY Atlantic salmon parr at three different stream discharges

Sub-aims

1. To compare the use of mesohabitats (i.e., pool and riffle) at low and high population density
2. To compare the effects of discharge variations on mesohabitat use
3. To compare the use of microhabitats (i.e., water velocity) at low and high population density
4. To compare the effects of discharge variation on microhabitat use
5. To compare microhabitat use within and between the mesohabitats at two densities

Aim III

To analyse microhabitat use of YOY Atlantic salmon with a new method, avoiding the methodical problems of habitat preference, by modelling habitat use within a Geographic Information System (GIS)

<u>Sub-aims</u>

1. To analyse the effects of stream discharge on the site fidelity of fish at the meso- and microhabitat scale
2. To compare microhabitat conditions between newly occupied and vacated positions after discharge changes
3. To compare microhabitat conditions between positions used by fish and random positions

An overview over the experiments addressing the aims given above and stating the working-hypotheses can be found in the methods section in chapter 3.10..

2. A review of instream flow methods and the current state of validation

2.1. An overview of methods to assess and model instream flow needs

Given the fact that current conceptual understanding of the principles and processes involved in the response of rivers to flow regulations is limited, quantitative models of the dynamics of regulated river ecosystems have to be treated with caution. However, the demand for predictive quantitative models for the determination of instream flow needs is high and resource managers and policy makers have to make informed decisions based on best available science and knowledge. It is nonetheless of paramount importance that the aquatic science community rigorously tests the methods used in order to get a realistic idea of their capabilities and limitations. The models are only meaningful to the degree to which we can estimate their performance and know their limitations.

In general, methods to set instream flows can be divided into three groups (Jowett, 1997):
a) historical flow regime methods
b) hydraulic geometry methods
c) habitat methods

Historic flow methods, of which the Tennant (1976) method is the most widely used, define acceptable flows in reference to the natural flow regime of the river in question. Based on physical habitat condition over a range of discharges, Tennant (1976) defined 10% of the average flow as a lower threshold for instream biota and 30% of the average flow as a good to optimum range for rivers of the west coast of the United States. For the UK, Gustard et al. (1987) calculated the average compensation flow to be 18.6% (n= 261) of the average

daily flow. Based on the same data, calculations undertaken as part of this study suggest the average value to be 16% of average daily flow for Scotland for hydro-electric power reservoirs and 23% of average daily flow for supply and compensation reservoirs. As for the methods used to derive the compensation flows however, Gustard et al (1987) concluded: "...local precedents, rules of thumb and bargains struck between interested parties had been the basis of many awards..." (p. 75). Baxter (1961) suggested seasonally variable compensations flows between 12.5- 25 % of average daily flow based on his observations of seasonal fish habitat requirements in 15 UK rivers (Gilvear, 1994).

Hydraulic geometry methods (e.g., Hogan & Church, 1989) focus on the hydraulic geometry of a river, describing the rivers by several hydraulic parameters such as width, depth, velocity and wetted perimeter, based on surveys of actual channel cross-sections. Most often the change in wetted perimeter is being used as a measure in assessing the effects of discharge modifications. Depending on the morphology of the river, a point of inflection can usually be found for the wetted perimeter to discharge relationship which may then serve as a threshold value for compensation flows.

The third and recently most popular category of habitat models is closely related to the hydraulic approach. The models utilise the hydraulic geometry approach, but the hydraulic parameters are consequently weighted for their species-specific habitat values. In doing so, the models takes into account the habitat requirements of aquatic animal and plant species. This group of models will be discussed in more detail below. Excellent reviews of instream flow methods can be found in Estes& Orsborn (1986), Hardy (1998) and Maddock (1999).

2.2. Habitat-based instream flow models

The currently used habitat-based instream flow models (for names and references see Table 2.1.), are also often called ecohydraulic models or micro-habitat models but will here be simply referred to as instream flow models. They all share the same basic approach: they combine a hydraulic simulation model with a biological suitability model (Fig. 2.1). The former provides information on the spatial and temporal distribution of hydraulic variables in the stream and the latter translates those into relevant habitat terms for target species. Modelling is performed for selected animal species and so-called key habitat variables, most commonly water depth, mean column velocity and substrate size as well as instream cover on occasions. Typically based on transect measurements, the hydraulic model quantifies the hydraulic conditions at a given discharge which then are weighted according to habitat suitability criteria (HSC) for the species. These rate the suitability of habitat conditions for a target species between zero, for unsuitable conditions and one, for optimal conditions. The sum of the habitat values for all variables in all cells is the most commonly used measure of habitat quality change with discharge. This, called the "weighted usable area" (WUA) in PHABSIM (e.g., Nehring & Anderson, 1993), is calculated over a range of discharges to obtain a discharge-habitat curve, which in theory shows the changes of habitat availability for the target species of the studied river due to changes of stream discharge (Fig. 2.1.).

Table 2.1.: A list of currently used ecohydraulic models

Name of model	Reference	Main countries of application
CASIMIR	Jorde (1996)	Germany
EVHA	Capra et al. (1995)	France
HABITAT	Harby & Heggenes (1995)	Norway
HAFIMO	Peviani et al. (1996)	Spain
PHABSIM	Stalnaker (1995)	World-wide
other 2-D and 3-D models	- Bovee (1996) - Bartsch et al. (1996) - Boudreau et al. (1996) - Heggenes et al. (1996a)	Canada, France, Norway, USA
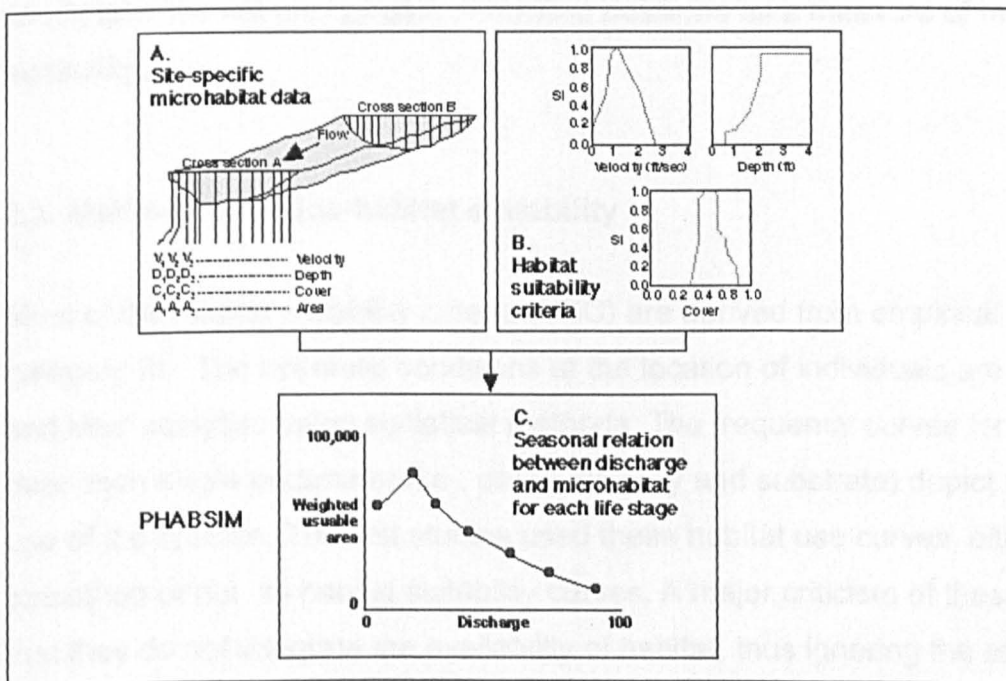
Fig. 2.1.: The concept of instream habitat modelling (e.g., PHABSIM): for a given species and river reach, the microhabitat is modelled for a site (A) and weighted by habitat suitability criteria (B) to obtain a habitat discharge curve (C), (from Stalnaker, 1995)

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The hydraulic model needs to be calibrated with depth, water velocity and substrate data from cross-sections at a minimum of three discharges. More recent models are not transect-dependent but rather resolve a grid, based on independent point measurements. These hydraulic models (e.g., SSIM, Olsen 2000) can model flows in 2D or 3D which allows a higher degree of precision, especially in steeper gravel and boulder rivers with highly turbulent flow. The habitat suitability criteria on the other hand can be derived from different sources and are being classified accordingly. Category 1 criteria are based on expert opinion or literature sources, category 2 criteria are derived from habitat utilisation frequency analysis and category 3 criteria are developed from habitat utilisation frequency data which are corrected for habitat availability (Bovee, 1986). More recently, bioenergetic feeding models have been tested for the development of habitat suitability criteria (e.g., Braaten, Dey & Annear, 1997), which take the net energy gain of feeding positions as a measure of microhabitat suitability.

2.3. Methods to define habitat suitability

Most of the habitat suitability criteria (HSC) are derived from empirical data (i.e., category III). The hydraulic conditions at the location of individuals are recorded and later analysed using statistical methods. The frequency curves for individuals over each single parameter (i.e., depth, velocity and substrate) depict the habitat use of the species. The first studies used these habitat use curves, either smoothed or not, as habitat suitability curves. A major criticism of these curves is, that they do not integrate the availability of habitat, thus ignoring the effects availability must have on habitat use. Habitat use curves would only show habitat preference if all habitat types are equally available. To obtain true habitat preference curves, the habitat use needs to be normalised over habitat availability. Habitat that is used proportionally more than it is available has been considered to be actively selected and is termed "preferred" and habitat being

used proportionally less than available is termed "avoided" (Heggenes & Saltveit, 1990). Methods to sample microhabitat selection by fish are normally snorkelling, bankside observation or electrofishing. Heggenes et al. (1990) compared the three methods and found all of them to be biased in some way. Microhabitat use data can be transformed into binary, univariate or bivariate curves by several methods (see Bovee, 1986, or Baltz, 1990, for details). In most of the studies univariate curves are used.

More often than not curves are transferred to a new study site rather than developed on site. The US Fish and Wildlife Department operates a curve library, which in April 1992 already contained 1900 site-specific curves for 124 species (Thomas and Bovee, 1993). A test of the validity of the imported curves for the study site is crucial and the development of site-specific curves is strongly recommended (Thomas and Bovee, 1993). The transferability of habitat suitability curves is problematic because the microhabitat utilisation between sites varies. Orth (1987) and Lambert (1994) concluded from thorough literature reviews that habitat suitability curves are strongly affected by fish size, season, thermal regime, stream structure, competition, risk of predation and food availability. Seasonal variations in habitat use both between sites as well as rivers has also been documented by Heggenes & Saltveit (1990) for Atlantic salmon and brown trout in Norway. Differences of microhabitat use by Atlantic salmon and brown trout under allo- and sympatry has been found by Kennedy & Strange (1986).

2.4. Critiques of instream flow models

In its early stages, PHABSIM met significant levels of criticism with regard to its conceptual validity and the practical limitations of the model. Table 2.2. gives a summary of the main criticisms raised in papers by Mathur et al. (1985), Scott & Shirvell (1987), Orth (1987), Gore & Nestler (1988) and Bird (1996). Many of the concerns that were initially raised involved technical aspects of the modelling

procedures (e.g., the wrong assumption in the IFG2 and IFG4 hydraulic models that Manning's "n" is independent of discharge, see Scott & Shirvell (1987)) and can be resolved by the use of more recent and sophisticated computer models. Secondly, points were made about the appropriate application and the limitations of the ecohydraulic models, regarding for example appropriate spatial and temporal scales, choice of target species and life stages and transferability of habitat suitability criteria. All the issues mentioned above have either been resolved (or at least improved) over time with of model refinement or by use of discretion and thoroughness by the end-user applying the model. Other criticisms remain, however, and these are with regard to the short-coming of not incorporating biological variables like food abundance, population density and predation pressure (see Orth, 1987). The actual effects of these variables on model performance have still not been formally tested. Fundamental questions regarding some of the underlying assumptions of habitat suitability criteria are also still unresolved and are most frequently related to the question how well HSC can depict a species' actual habitat suitability and if constant HSC can be used across a range of seasonal and biological conditions. In this context, two assumptions are of the highest importance:

a) the suitability of each habitat variable is independent
In all standard models, HSC are designed and applied for each habitat variable separately. This means for example, that velocity preference is assumed constant regardless of water depth and substrate size. This problem is difficult to resolve because depth and velocity and also substrate size are normally closely linked in streams (e.g., in pool-riffle sequences, most high velocity areas are found in shallow depths with coarser substrate and slow flowing water in the deep areas with finer substrate), so that not all combinations of depth and velocity occur against which habitat preference could be tested. Despite this, Pert & Erman (1994) found evidence that adult rainbow trout changed velocity preference between discharges due to overriding effects of depth preference, a finding that contradicts the assumption of independence of the variables.

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b) the suitability of habitat variables is constant over stream discharge

The habitat usage data of a species that HSC are based on are typically collected at only one stream discharge, or are pooled regardless of discharge. The resulting HSC are assumed to apply for any discharge situation consequently modelled. Thus, although fish positions and their microhabitats were recorded during a given discharge, the HSC built on these data are used in the model to interpret habitat conditions at much higher and much lower discharge conditions. Heggenes and Saltveit (1990) were the first to suggest that this might introduce serious error. Studies addressing this issue have come up with conflicting findings. For example, Beecher et al. (1995) reported the assumption of constant preference at two different discharges to be verified, but Pert & Erman (1994) concluded the opposite (see chapter 4.6.2. for a full discussion).

Table 2.2.: A summary of critiques of PHABSIM

Authors	Article	Main points and criticisms
Bird, D.J., 1996	Problems with the use of IFIM for salmonids and guidelines for future UK studies	- PHABSIM inappropriate to use if physical habitat is not the limiting factor - inappropriate choice of species and life stages - inadequate attention given to habitat scale effects - ignorance of the importance of the interactions of habitat variables - sampling errors in habitat variables measurements often high - unrealistic detailed interpretation of HSC - inappropriate transferability of HSC - inappropriate choice of study reach - ignorance of temporal habitat variation
Mathur, Dilip et al, 1985	A critique of the instream flow incremental methodology	- positive relationship between WUA and biomass of fish neither validated nor documented - assumption of independent selection of habitat variables violated without consideration of consequences - WUA values for a cell can be the product of different combinations of habitat suitability (i.e., depth, velocity, substrate) - utilisation, suitability or preference curves should not be treated as probability functions

Table 2.2. (continued): A summary of critiques of PHABSIM

Authors	Article	Main points and criticisms
Scott, D. & Shirvell, C.S., 1987	A critique of the instream flow incremental methodology ad observations on flow determination in New Zealand	• PHABSIM assumes that depth, velocity and substrate are only physical habitat variables determining fish position choice • assumes Manning's N is constant with Q (mean error of velocity calculations in this case 39%, max error 133-200%) • assumes water velocities at 60% of the total depth affect fish preference but many species sit on substrate and velocities there can be very different, especially in deeper rivers (> 1m, mean column and bottom velocity differed for up to 44%) • assumes habitat variables are independent • WUA indifferent to the quality/quantity relationship: lots of mediocre habitat will equal little of good habitat
Orth, D, 1987	Ecological considerations in the development and application of instream flow-habitat models	• six factors control characteristics of stream ecology, PHABSIM only assesses physical habitat changes • above factors can all affect population dynamics, so that WUA is unlikely to correlate strongly with biomass • biotic interactions (food availability, competition, predation) affect populations • selection of target species crucial
Gore, J.A. & Nestler, J.M., 1988	Instream flow studies in perspective	• instream habitat variables are not independent • large sampling errors in developing HSC • WUA is not an estimate of biomass and can not be • niche dimensions vary with environmental conditions • realised niche a population occupies is affected by biological interactions

2.5. Validation of instream flow models

Because of the complex nature of fish population responses to changes in discharge, instream flow models have been designed to model the habitat of a species rather than it's population (Stalnaker, 1995). The quantification of habitat is only meaningful if a population responds to a change in habitat in a consistent manner, otherwise it could be regarded as a concept meaningless in practical terms. After all, river managers are not so much interested in habitat itself but the number of fish it supports in this context. Thus, at the most basic level, attempts have been made to relate "weighted usable area" (WUA) predictions to standing stock or abundance measurements. Scott and Shirvell (1987) summarised the findings of 444 analyses in eleven studies analysing the relationship between standing crop of salmonids and predicted WUA. Some of the reported studies found strong relationships between WUA and fish populations with r-square values between 0.8 to 0.9 (e.g., Stalnaker, 1979; Anderson, 1984). Other studies found correlations variable and often only significant at certain times of the year (e.g., Orth & Maughan, 1982: $r^2=$ 0.47- 0.85, although only in summer). In 74% of all cases, no relationship at all was found (e.g., Anderson, 1984; Loar, 1985). No consistent explanation for this lack of correlation has emerged. Sometimes, good and poor correlation between WUA and standing crop were found within the same study (e.g., Anderson, 1984). Also, no common traits were found for the good or the poorly correlated studies. Thus Scott and Shirvell (1987) concluded in a PHABSIM review, that chance could not be statistically rejected as the source of good correlation found in some of the studies. In another similar review, Fausch et al. (1988) report additional early studies. Of these, Wesche (1980) found good correlations between WUA and standing crop, Nehring (1979) and Nickelson et al. (1979) had variable results with some good and some poor correlations depending on trout species and Annear & Conder (1983) found no significant correlation. Table 2.3. summarises the findings of another eight similar studies conducted since the publication of the reviews cited above. Although these studies cover a range of different river types, salmonid species, life stages and evaluation techniques, only two out of these eight

studies found strong relationships between WUA and population measures. Taking into account all these published results, the vast majority of studies in the scientific literature to date have not found strong relationships between habitat estimates and population measures.

Table 2.3.: A summary of instream flow model validation studies, comparing WUA calculations with population measures

Author	Model	Stream type	Species	HSI source	Validation technique	Results	Comments
Conder & Annear, 1987	PHABSIM	Wyoming, small trout streams	several trout species	imported	statistical analysis of WUA and electrofished population estimates for 5 years	little correlation for WUA and standing crop between streams and within streams between discharges	used imported HSC within stream comparison only between WUA and standing crop *estimates* by habitat quality index (!)
Irvine, Jowett & Scott, 1987	own version for WUA calculation	replicate experimental streams	rainbow fry	imported	WUA calculation versus electrofished population	very poor correlation	high variance in population data, abundance increase despite closed system!
Jowett, 1992	not specified	89 New Zealand streams and rivers	brown trout (> 200mm)	imported	downstream drift diving, count >200mm regressed versus habitat variables (74)	WUA for drift feeding habitat and invertebrate biomass *combined* explained trout abundance by r^2= 0.64	between streams comparison Interesting: WUA for food production HSI develop on trout>450 mm big fish study some rivers stocked?
Bourgeois et al., 1996a	PHABSIM	N Brunswick, Canada MAD 1.23 m³ /s	Atlantic salmon	imported + tested	WUA versus population density at various spatial and temporal scales	correlation very poor on 43 scenarios best possible: 15 day-average flow WUA versus abundance within mesohabitat	extensive study

Table 2.3. (continued): A summary of instream flow model validation studies, comparing WUA calculations with population measures

Author	Model	Stream type	Species	HSI source	Validation technique	Results	Comments
Capra, Breil & Souchon 1995	EVHA	2 streams in France MAD 1.4m³ /s	wild brown trout	imported +modified	"continous under threshold habitat duration" (CUT) for life stages versus relative population density	spawning CUT was related to YOY population density in the following year (r²= 0.37)	
Harris, Hubert & Wesche 1991	PHABSIM	Douglas Creek Wyoming	brown trout 76% + brook trout	developed fry imported	WUA versus populations pre- and post- compensation flow change	no increase in standing stock of trout >4 inch apart from 1 site despite high increase in WUA	possibly limited by physical habitat, lack of instream cover
Nehring & Anderson 1993	PHABSIM	Colorado rivers and streams	rainbow trout	imported	5-11 year trout population record versus WUA by linear regression	10 of 11 correlated with PHABSIM habitat bottleneck WUA (mostly fry emergence) highly important for population	very high correlation
			brown trout	fry developed			
Shirvell, 1989	PHABSIM	river	Chinook salmon	developed	compare redd locations with simulation predictions	poor: 70% of used area were predicted unusable, 87% predicted usable have never been used 210-660% more spawning habitat predicted than used	scale: 50m transect spacing (random) very heterogeneous streambed topography!

2.6. Sources of variation in instream flow model validation

The variations, discussed in the previous section, in the findings of studies examining stream discharge versus fish population data illustrate some of the fundamental problems involved in applying instream flow models as well as estimating fish populations. Boudreau et al. (1996) stress that this does not automatically invalidate instream flow models, reasoning that the large intrinsic uncertainties of both data types as well as common high confidence intervals due to insufficient sampling effort are likely reasons for the low success rate in detecting a relationship between habitat estimates and fish stocks. Examples for the high variability of both WUA (e.g., Gan & McMahon, 1990) and stock estimates (Cowx, 1990) can be found in the literature. Care must also be taken to distinguish between fish abundance for a given study site and temporary redistribution (Mathur et al., 1985). Apart from these methodological problems, which are all too common in the monitoring and modelling of river systems, the likely reasons for poor model performance will either be due to misconceptions of the underlying principles of the stream ecosystem or due to the failure of the model to simulate the relevant processes. It is therefore obvious, that the correspondence of habitat estimates to standing crop can only be apparent to the degree to which instream habitat (represented by depth, velocity and substrate size) is the limiting factor to the population. However, many other factors can potentially limit salmonid standing stocks too and are presented in Table 2.4..

Table 2.4.: Other factors than habitat that can affect fish standing crop

Variable	Examples
Food availability	Ensign & Strange (1990) found brook and rainbow trout populations in streams to be limited by the availability of food during summer
	Wilzbach (1985) reported food availability to be the overriding factor determining emigration rates of brown trout in a flume experiment
Spawning habitat	Beard & Carline (1991) found total densities of brown trout in streams strongly related to spawning habitat but not to instream habitat variables
Predation	Lemly (1985) demonstrated with removal experiments how green sunfish suppressed number and biomass of other fish species
	Anderson (1985) concluded that predation limited sculpin populations in larger streams
Water quality	Harriman et al. (1995) observed that salmonid density was positively related to the acidic neutralising capacity (ANC) in Scottish streams
Water temperature	Egglishaw & Shackley (1985) report temperature to be the main controlling factor for growth of salmon parr in Scottish upland streams
Fishing mortality	Orth (1987) remarks that most of the validation studies are conducted on game fish species which are likely to be limited by exploitation rather than habitat availability. Also, game species are sometimes stocked or subject to other management practises.
Cover	Shirvell (1990) showed that the abundance of coho salmon fry and steelhead trout parr was positively correlated to cover
Turbidity	Sigler et al. (1984) describe how chronic turbidity affected the number of salmonids during emergence and rearing

In all of the studies listed in Table 2.4. (for more examples see Gibson, 1993), factors other than habitat limited the population size, so that it's variation was largely unrelated to WUA. This fact could explain some failed model validation attempts like that of Harris et al. (1991), who suspected a distinct lack of instream and bank side cover (due to timber floating and gold dredging) to be the reason for a lack of population response to instream habitat increases. However, it also illustrates the difficulties in defining whether instream habitat is the major limiting factor and an instream flow model application is appropriate or if other variables or habitat bottlenecks (e.g., droughts) limit the population.

The definition of the correct temporal scale is another important problem. Stream salmonids are adapted to a life in a highly dynamic environment and can tolerate a wide range of hydraulic conditions (Heggenes, 1994). They can withstand adverse conditions like extreme high flows (Heggenes, 1988) or droughts (Armstrong et al., 1998) over short to medium time periods without having to leave the immediate river reach or possibly even a change in position. Thus, effects of instream flows on immediate abundance can be expected to be minimal, so that the WUA calculation for the day of the stock assessment is of limited meaning. Indeed, testing the standing crop against WUA at different time scales, both Bourgeois et al (1996a) and Gowan (1994) found the best association when calculating the average WUA for the 15 days preceding the sampling date. Furthermore, habitat bottle-necks at any stage of the species' life history could be even more important for the population. For rainbow and brown trout, Bovee (1988) identified early fry habitat to be positively correlated with 1+ standing stock in Colorado rivers in the following year. A similar finding was recorded by Nehring & Anderson (1993). They showed that hydraulic conditions in the first two to four weeks after emergence were critical for fry survival and consequent cohort strengths. Recognising the fact that limiting events sometimes only become effective with a certain duration, Capra et al. (1995) found that the duration of continuous under threshold (CUT) conditions was more successful in explaining brown trout fry numbers than ordinary habitat time series.

The studies quoted so far in this chapter, although all looking at WUA and fish stocks, do so at different temporal and spatial scales. Most importantly, studies were either comparing between-streams or within-streams. Most of the early studies that typically quote high correlations between WUA and standing crop (Stalnaker, 1979; Anderson, 1984; Nehring, 1979) were for standing crop between streams or sites. However, differences in stocks and WUA between streams or sites are very different from differences within streams or sites over time, the situation that instream flow models are actually designed for to cope with. In most cases, both WUA and standing stock will fluctuate less widely within the same stream over time than between different streams so that values along both axes are spread further in the former case. As a result and because between-streams comparison will have more extreme points (i.e., very good habitat with lots of fish and very poor habitat with no fish), the predictive power of WUA at this coarse scale seems higher than in most within stream comparisons, where variations happen on a finer scale.

2.7. Sensitivity of instream flow models and performance of components

The performance of any hydraulic model and the degree of realism achieved is dependent upon the complexity of the system to be modelled and the amount of field data collected for the calibration. The 1-dimensional transect-based water surface profile model used most frequently with PHABSIM was shown to perform poorly in a low-gradient warmwater stream by Osborne et al. (1988). The model was also hard to calibrate and needed large amounts of calibration data. The recent advances in both computer technology and field sampling techniques (e.g., GPS or total station combined with velocity meter and pressure transducer) have made two- and three-dimensional flow models feasible and consequently the standard of hydraulic modelling is currently increasing (Hardy, 1998). The random point sampling techniques associated with these technical advances should help avoid the problem of sensitivity to the number and location choice of transsects that has been demonstrated for PHABSIM (Williams, 1996). Bourgeois et al. (1996b) also found PHABSIM to

be sensitive to transect numbers and location but less to velocity and depth measuring errors. Furthermore, the level of correspondence in scale between sampling and modelling will remain highly important (e.g., Maddock & Bird, 1996). As an example, all mesohabitats (i.e., riffle, pool, run, glide) of the modelled river reach need to be sampled and incorporated in the model to the degree to which they represented in the river.
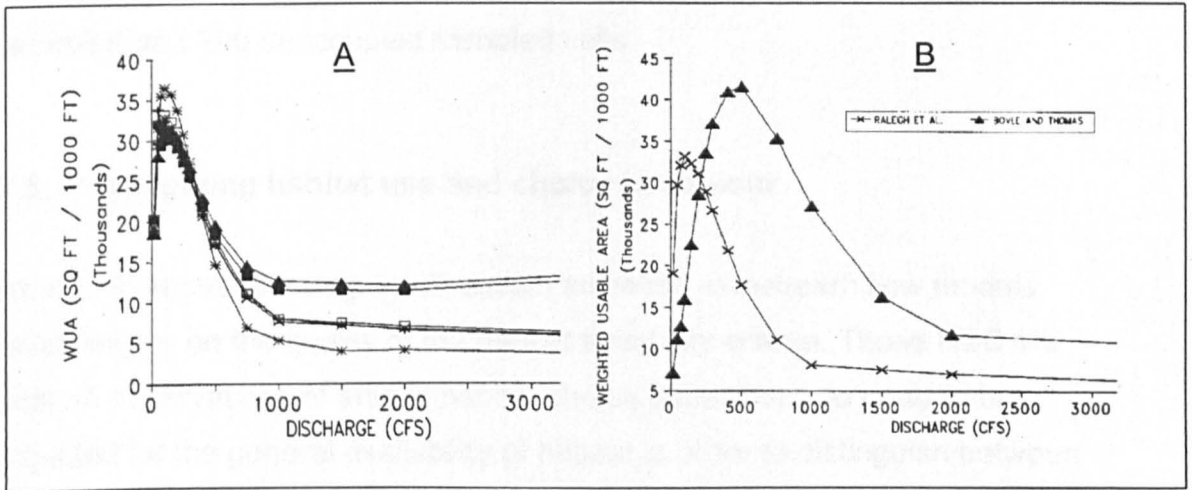
Fig. 2.2.: The sensitivity of WUA output in PHABSIM, using different hydraulic modelling options (A) and different habitat suitability criteria (B), (from Waddle, 1992)

Another source of high variability lies within the various modelling options of the PHABSIM modules. Using different combinations of these, Gan & McMahon (1990) showed that WUA calculations for the same data set varied for up to 1900% which highlights the potential for manipulation and the necessity for discrimination of which modelling option is being used. Waddle (1992) demonstrated in a sensitivity analysis that the output of PHABSIM was much more sensitive to the habitat suitability criteria than the hydraulic model (Fig. 2.2.). Although the different hydraulic models did cause a change in WUA, this was of quantitative rather than qualitative nature with the peak of habitat availability at the same discharge, which would effectively result in the same instream flow recommendations. However, when applying habitat suitability criteria built by two independent researchers for this river,

WUA peaks were located at very different discharges which would result in very different instream flow recommendations and hence illustrates the sensitivity of PHABSIM to the habitat suitability criteria used. Thomas & Bovee (1993) statistically tested the sensitivity of HSC to sample size, in this case to determine required minimum sample sizes to test the transferability of HSC between sites. Testing for non-random use of two classifications (i.e., suitable over unsuitable habitat and optimal over usable habitat) they found type I and type II errors increasing strongly when sample sizes dropped below 55 occupied and 200 unoccupied sampled cells.

2.8. Investigating habitat use and choice behaviour

As shown above, the degree of realism achieved in instream flow models relies largely on the quality of the habitat suitability criteria. Those HSC are built on observations of animal habitat choice behaviour and need to be adjusted for the general availability of habitat in order to distinguish between random and selective habitat use, the latter is normally referred to as "preference". However, the study of habitat use in general and habitat choice behaviour in particular is complicated by several factors. These are discussed below.

1. *the underlying assumption of the optimal foraging theory does not apply*
The habitat suitability concept assumes that fish will utilise their habitat as defined by optimal foraging theory (i.e., an organism chooses the behaviour that optimises the net energy intake, Charnov, 1976) and hence the conditions at the fish position represent the preferred microhabitat. Although the general concept of optimal foraging theory might apply in theory, the effects on microhabitat selection are more complex, because:
   a) position choice must also optimise other variables than those modelled (i.e., velocity, depth and substrate)
   b) positions are optimised in the context of the activity the fish pursues (e.g., feeding, resting, sheltering, reproducing) but HSC are used irrespectively

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2. habitat use and habitat availability are interdependent

Although a fish might *attempt* to occupy an optimal position it is unlikely that it can do so at all times. Not all environments provide the optimal locations and territorial species like salmon compete for the positions available. It is quite possible that optimal preferred habitats are dominated by a few fish and the rest of the population uses relatively poor areas of the stream. The quality and amounts of all habitats in a stream ecosystem are constantly changing over time and space so that many individuals in a population have to cope with sub-optimal conditions for certain periods. In effect, habitat use can only be seen in the context of habitat availability. The availability changes over space (e.g., mesohabitat) and time (e.g., summer droughts, spring floods) as well as in the context of competitive interactions with individuals of their own and other species. Furthermore, the particular conditions at the moment of fish observation may represent an even more limited depiction of the general conditions and can deviate widely from the natural fluctuations that the stream ecosystem experiences over time.

3. preference indices are non-linear

In order to compensate for the fact that habitat use should be seen in relation to habitat availability, electivity indices are used (see chapter 3.8. for details). However, a statistical comparison of preference indices is difficult because they are rescaled and respond non-linearly to variations in the availability of habitat (Lechowisz, 1982). The linear electivity index (L) (Strauss, 1979) can provide a robust statistical comparison of preference indices, but only if habitat availability is constant, which is unrealistic in nearly all cases.

4. the spatial and temporal scales relevant to the animal are often unclear and difficult to identify

In general, river ecosystems function as complex arrays of factors and processes which operate at several different temporal and spatial scales (Petts & Amoros, 1996). It is often difficult to identify the spatial and temporal scales most relevant to the fish because very few, if any, scale boundaries exist. Many of the spatial scales used in river ecology (e.g., river type, river

sector, river reach, mesohabitat, patch; see Maddock, 1999) have no clearly defined boundaries and are traditionally defined mostly on the basis of geomorphological and hydrological characteristics rather than biological ones. Secondly, instream habitat fluctuates over time. Most prominent are short-term fluctuations due to changing stream discharge but long-term changes in channel geometry, riparian vegetation and sediment transport characteristics also occur. The problem for instream flow studies is to know if the modelled habitats encompass all of a species' need and to which moment in time the HSC are applicable to. This is normally done by building HSC based on habitat use samples at "average" conditions (e.g., average daily flow). Although these conditions represent the typical situation for most of the year, the population dynamics of many populations can be largely controlled by bottle-neck situations at very specific moments in time like rainbow trout recruitment in a river which depended largely on high flows in spring (Nehring & Anderson, 1993). Also, the duration of a stream discharge, in particular if very high or low, can determine it's impact on a fish population (Capra, 1995). Regarding the definition of spatial scales, the image that a habitat model can deliver is always that of an average and be sensitive to the number of samples, the dimensionality of the model (i.e., 1-, 2- or 3-D) and the number of cells internally modelled, to name just a few. The habitat model will miss the conditions relevant to the fish, should the model resolution be too coarse or (which will be rarer) too fine.

5. *factors other than instream habitat affect the habitat choice behaviour of the animal*

Habitat choice can, sometimes only temporarily, be affected by other factors than habitat quality, or, to be precise, the importance of certain physical habitats can change because of other environmental variables. Reasons for shifts in habitat choice can be the absence or presence of a predator (e.g., pike caused a habitat shift in trout, see Greenberg, 1994), interspecific competition (e.g., YOY salmon parr chose different habitat in the presence of YOY brown trout, see Kennedy & Strange, 1986), refuge seeking during catastrophic events (i.e., floods and droughts) or in response to time of year and water temperature (e.g., brown trout sheltered in the gravel at

temperatures below 8-10 degrees Celsius, see Cunjak, 1988; Heggenes, 1994).

6. *spatial traits of habitat*

Most of the times, the methods typically used to describe habitat are not spatially explicit. Location of a habitat, habitat patch size, type of neighbouring habitat, distribution of habitat patches and connectivity and isolation of habitat patches are spatial characteristics which can be expected to affect the position choice of a fish. The move from the traditional, mostly numerical, approach towards a spatially referenced landscape approach in many fields of ecology (Farina, 1998) illustrates the change in perception of ecological systems and their description. This has also been due to the wider availability of Geographic Information Systems (GIS). In the past, GIS has been mostly used for data logging and descriptive purposes, but the development and use of truly spatial statistic methods is booming (Farina, 1998).

2.9. The role of water velocity for stream-dwelling salmonids

In the recent past, water velocity has been at the centre of research attention as an important habitat feature for stream-dwelling salmonids. As an example: a search of the "Aquatic Science and Fisheries Database" (ASFA) for journal articles containing the words "salmo*", "habitat" and "velocity" returned 147 publications between the years 1978 and 2000. Several studies have identified water velocity as the single most important habitat variable for salmonids streams (DeGraaf & Bain, 1986; Morantz et al., 1987; Heggenes & Saltveit, 1990). Water velocity is often measured at the water surface or at nose level of the fish (also called focal velocity), but most frequently, in particular in instream flow models, mean column velocity (at 60% of the total depth) is chosen to represent velocity conditions. There are several obvious reasons why water velocity affects habitat suitability for fish in the high energy environment of streams to such a large extent. They are related to aspects of:

1. bioenergetics

At any location in the stream, water velocity strongly affects energy gain and loss of sit-and-wait predators like salmon parr by influencing the delivery of drift food on the one hand and the hydraulic drag force on the fish body on the other. Assuming a constant amount of drift food per volume of water, the amount of drift available to a fish within its feeding range increases directly with discharge, that is, the amount of water that passes the given area in a time unit. Thus, water velocity represents the volume of water (and with it drift food) that passes a fish. Accordingly, studies have found a positive correlation of water velocity and localised drift (e.g., Smith & Li, 1983). The ability of a fish to utilise this increase of food availability is limited though by a parallel increase in energy expenditure related to holding the position and intercepting food items (Hughes & Dill, 1990; Hughes, 1992a) as well as by a decreasing catch efficiency (Hill & Grossman, 1993; Nislow et al., 1999). The optimal foraging theory (Charnov, 1976) leads to the prediction that fish will optimise their net energy uptake by choosing positions where the ratio between energy gain and loss is highest.

2. habitat segregation

The bioenergetically optimal water velocities for each fish species will depend largely on the species' metabolism and hydrodynamics. The latter depend on the shape of the fish and threshold values have been found to apply for each species (Sagnes & Statzner, 1999) above which the hydraulic drag (and thus the resulting energy expenditure) increases exponentially. In effect, different fish species are best adapted to different flow environments and have a competitive advantage over other species in the same ecosystem. Kennedy and Strange (1986), for example, showed, that salmon parr were using deep and slow habitats only in streams where trout were absent. In the presence of trout, salmon were restricted to faster shallower habitats.

3. overhead cover

Riffling of the water surface is a major source of overhead cover from avian and terrestrial predators. Due to the optical distortion of the light by water

surface riffling, fish become much less visible from above. Surface riffling occurs either in areas of convergence and divergence (e.g., boulders sticking out of the water) or where the bottom shear-stress (which depends mostly on the water velocity/depth ratio) exceeds a critical value (Knighton, 1998). In effect, areas of surface riffling will coincide with velocities faster than the local average in a reach.

2.10. Summary and conclusions

As shown above, tools which permit numeric modelling of the effects of changes in stream discharge on instream biota are required for a better management of instream flows in regulated rivers. The most popular methods to date are hydraulic habitat-based models like PHABSIM, which work on the basis of modelling the hydraulic geometry of the stream system and weighing this information for suitability of target species by habitat suitability criteria. The degree of realism achieved has advanced much faster for the hydraulic component of instream flow models than for the biological component. However, the sensitivity of instream flow models to the latter component is high. At the same time, some questions concerning the validity of habitat suitability criteria remain unresolved, in particular regarding the generality of habitat suitability across ranges of other environmental conditions like stream discharge and population density. Also, more fundamentally, the particular relationship between the dynamic instream habitat and population performance, measured as fish abundance, fitness and survival is far from clear due to the multitude of factors operating and the complexity of interactions and scales so that the relevance of habitat modelling to population management remains ambiguous.

Over the past twenty years, critiques of instream flow models have helped to improve and further develop instream flow models. As a result, a better understanding of the applicability and requirements of the models now exists. Nevertheless, all attempts to formally validate the habitat suitability concept and its main assumptions have encountered difficulties and many questions

regarding the generality of habitat suitability criteria remain. These range from fundamental questions regarding the optimal foraging theorem to methodical problems of data collection. Due to the intimate interdependence of habitat availability and habitat use, true microhabitat preference is very difficult to detect. As a result of all these issues, improvements in the field of instream habitat modelling will require advances in the habitat suitability concept. Although the number of applications of PHABSIM is over a thousand, the number of studies that have rigidly tested the underlying principles is low and those conducted in the field often encountered problems regarding the control of the experimental variables (e.g., discharge) and other practical limitations typical of field studies (e.g., sample size and resolution). Thus it was decided that this research project should focus on investigating the sensitivity of habitat suitability for YOY Atlantic salmon parr to changes in stream discharge and population density in a controlled experiment. These two variables were chosen because they are the main factors controlling the amount and availability of physical habitat and food availability as well as the competition for these resources.

2.11. Scope and rational for the research experiments

Detailed information on the methods and materials are presented in chapter 3, but the scope and rationale of the experiments are discussed in brief here. Early in this research, it was decided to conduct the experiments with wild Atlantic salmon parr, because it is arguably the single most important fish species in Scottish rivers, at least from a human point of view. There is a great deal of interest by the fishing lobby and other bodies to utilise instream flow models to improve habitats for salmon. It was decided that a controlled experiment on wild-caught fish in a large near-natural flume would be most suitable to address the aims of this research, because it would give the necessary experimental control over discharge and population density as well as permit repetitive runs and reliable fish observations (see Heggenes et al., 1990, for methodological bias of field observation). Young-of-the-year fish were chosen, because this age class are likely to be most sensitive to flow

(see chapter 2.6.) and because the population density is regulated at this time in the life history (Egglishaw & Shackley, 1977). Also, the small fish with their correspondingly smaller territories resulted in "more habitat per fish" in relative terms within the limited area of the flume, so that population densities could be varied at a fine scale without saturating the habitat. Fish were electrofished from a near-by stream and transferred straight into the flume within one hour of capture. The hydraulic geometry of this stream was surveyed and mirrored in the flume. The flume is fed by river water (in the same catchment as the home stream of the experimental fish) and has a gravel bed; fish fed on naturally-occurring drift food, augmented by some live chironomid larvae. Despite all efforts to keep conditions as natural as possible while having complete control over the main experimental variables, a flume experiment can not be seen as a replicate of the situation in the field, but rather as an artificial set-up in which fish will maintain their instinctive behaviour if the conditions permit. Salmon parr can be found in quite a wide range of stream types and mesohabitats and the behaviour of the fish in the flume appeared normal after 48 hours of acclimatisation.

Because of the possible interactions between water velocity and other variables like depth and substrate, the two latter ones were kept as constant as possible. To achieve this, a lateral and longitudinal gradient of velocities was created over constant depth and substrate in the riffle. The disadvantage of this approach is that an analysis of depth and substrate preference was not possible for the experiments described here. Nevertheless, since water velocity is related to most of the important processes for juvenile stream salmonids (see chapter 2.9.), it justifies the exclusive focus of this study on water velocity. Throughout this thesis, the term microhabitat is used exclusively in reference to water velocity unless stated otherwise.

3. Methods and experimental design

3.1. General outline of the experimental design

A large indoor recirculating flume was used at the experimental facility at Almondbank which belongs to the Fisheries Research Services Freshwater Laboratory. The flume is fed by water from the River Almond and the wild fish were caught a few miles upstream in a small tributary of this river, the Shelligan Burn. The instream physical (i.e., substrate and channel dimensions) and hydraulic (i.e., depth and water velocities) conditions in the flume were specifically designed to resemble those of the Shelligan Burn. Fish were transferred straight from the Shelligan Burn to the flume and resumed natural behaviour (i.e., holding positions and feeding on drift) within less than a day. The fish fed mostly on naturally occurring drift food, dominated by species of mayfly and case-less caddis larvae, which were provided by the constant influx of river water. The physical, biochemical and hydraulic conditions in the flume were thus very similar to those in the source stream. At the same time, use of the flume permitted repeated observations of independent groups of fish under controlled population density and stream discharges at a very high spatial resolution. Stream bed topography as well water surface levels and mean column velocity were mapped in detail at three specific discharges before the advent of the experiments and fish positions within the flume were typically established within a few centimetres. Three discharges were set at Q=2.6, 15 and 46.8 ls^{-1}, referred to as "Q_{low}", "Q_{medium}" and "Q_{high}". Q_{medium} in particular was set to resemble the average flow conditions in the Shelligan Burn and served as the compensation flow when new fish were introduced to the flume. "Q_{low}" was a low flow situation with very low velocities, shallow depths and large areas of no flow. The discharge at "Q_{high}" was set just below the threshold where movement of the implanted substrate occurred. Fish were left to acclimatise for a minimum of two nights

before the first observations were made. Discharge was changed consequently and new observations were made not earlier than the following day. In this way, between July and September 1997; 4 groups of fish at a density of 1.1 fish m^{-2} were observed. 12 groups at a density of 0.55 fish m^{-2} and eight groups at density 4.4 fish m^{-2} were observed in alternating order between June and September 1998. In total, 90 actual observation days of 24 independent groups of fish were achieved during the course of the experiments. All data, fish positions as well as habitat data, was digitised as vector data into GIS software for subsequent analysis.

3.2. The flume design:

3.2.1. The physical design

The 14 metre long and 1 metre wide channel of the flume has a U-shape in planview (see Fig. 3.1.). The open side of the U is connected by an electric pump which generates the flow of water. The basic channel is rectangular in cross-section and lined with dark rubber with the exception of two observation windows of 2 metre length each. In the current experiment, two separate observation areas of 3.7 metres length and 1 metre width were separated by the use of vertical metal mesh screens.
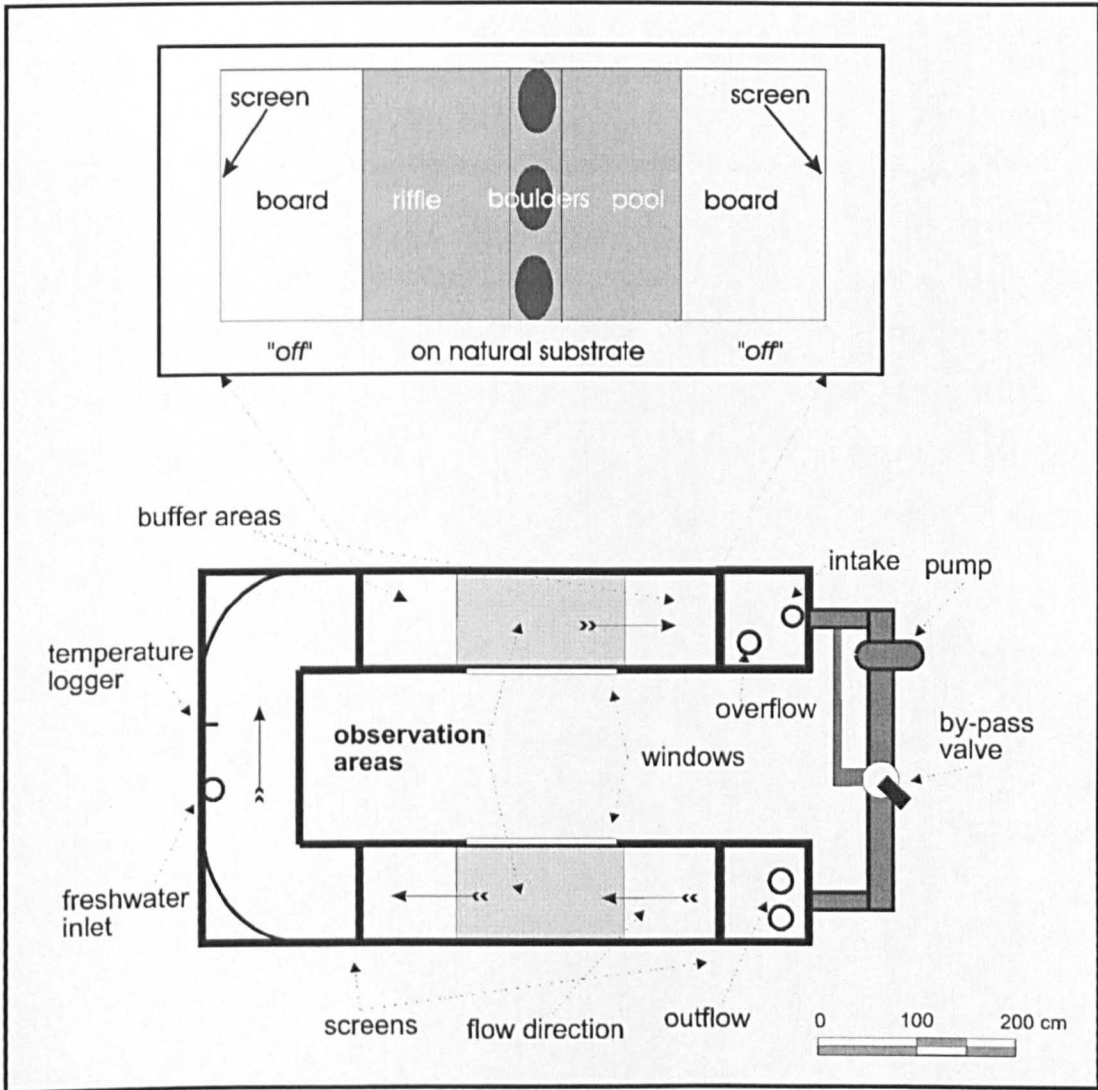
Fig. 3.1: Plan view of the flume used for the experiments; a schematic map of the observation area is shown in the inset.

In order to keep fish away from the mesh screens, which is an unnatural feature, 0. 8 metre long white boards were placed inside the screens restricting the observation area to the central 2 m long area of natural substrate. Fish avoided the boards and kept to the natural gravel, unless stocking densities were high, in which case some use of the boards was observed. In this way, these buffers acted as flexible and temporary over-spill for individuals which did not manage to establish a position within the natural gravel area at any stage in the experiment.

In 1997, Arena 1 was designed to resemble the substrate composition of a typical section in the Shelligan Burn. 39 underwater photographs were taken

at the Shelligan Burn and analysed for substrate measurements. In the section of the burn studied, substrate in sizes of 39-127 mm length made up over 75% of the total stream bottom areas in the photographs (Fig. 3.2.). As a result, the substrate sizes and (small scale) stream bed topography in the observation area was divers (Fig. 3.3.). The spatial occupation of each of 7 substrate size classes was calculated and based on this, a similar amount of gravel, pebbles and boulders of the according sizes was scattered at random in the flume. Due to space constraints, boulders were not included in the stream bed design of Arena 1 in 1997. Fish observations made in 1997 are only used for analysis in Chapter 6.2. of this thesis, all other work is based on data from 1998.

Because water velocity was defined as the main microhabitat variable to investigate after the intial runs in 1997, Arena 1 and Arena 2 were designed into a physically more simple set-up that would provide well-defined gradients of water velocity over constant depth and substrate. In 1998, the gravel in the two observation areas Arena 1 and Arena 2 was landscaped over a length of 2 metres into a pool and riffle sequence (see Fig. 3.4, Fig. 3.5.). An 80 centimetre long oval depression in the stream bed at the upstream end formed a shallow pool, followed by a line of three boulders positioned across the channel, which separated the pool from the flat-bottomed one metre long riffle section at the downstream end. Apart from the boulders (a-axis= 24.6 cm, SD= 1.37), the substrate of the pool and riffle area was composed of homogenous gravel (mean diameter= 2.5 cm, SD= 0.84).

The screens occupied 5% of the total observation area, the boards 40% and the natural gravel 55%. At random use, frequency of use by fish should be proportional to the area. However, a "Goodness-of-fit" test confirmed that fish used the natural gravel much more than could be expected from random, used the screen areas at random and underused the board areas (Table 3.1., Chi-Square= 458.67, df= 2, p< 0.001). This pattern was consistent at both densities (Chi-Square= 3.16, df= 2, p= 0.205) and board avoidance was not affected by discharge at a statistically significant level (Chi-Square= 5.253, df= 4, p= 0.262). Summarising these findings, it has been shown that the boards

were strongly avoided at all stream discharges and fish densities. The screens on the other hand, in particular the upstream screens, did seem to have some attraction as a microhabitat which I believe is due to the fact that they offered some degree of overhead shading and shelter from attacks by other fish by being so far away from the other territories on the natural gravel.

Table 3.1.: Number of fish over substrate type, expected and observed

Substrate type	Observed N	Expected N	Residual
Screen	47	20.4	26.6
Board	9	223.9	-214.9
Gravel	351	162.8	188.2
Total	407		
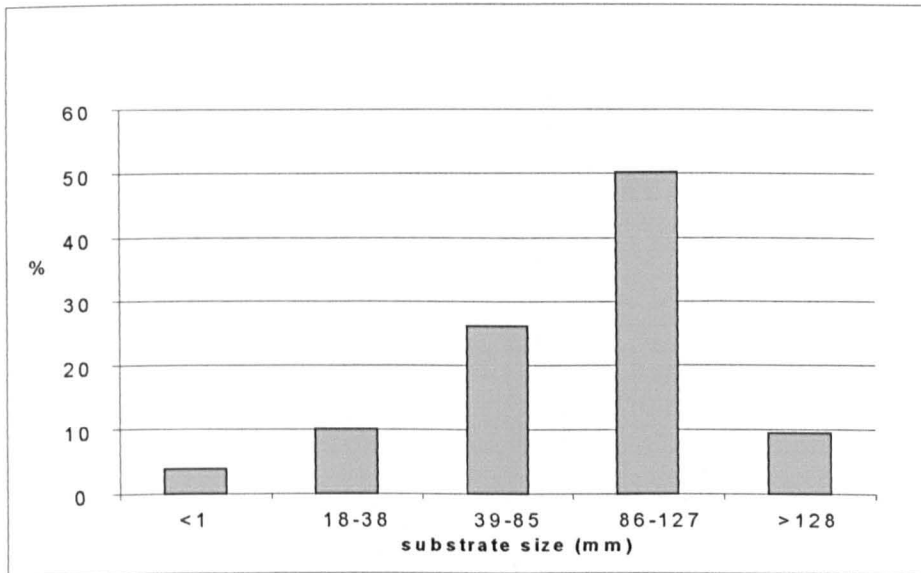
Fig. 3.2.: Proportion of differing particle size classes (a-axis) in the substrate of the Shelligan Burn
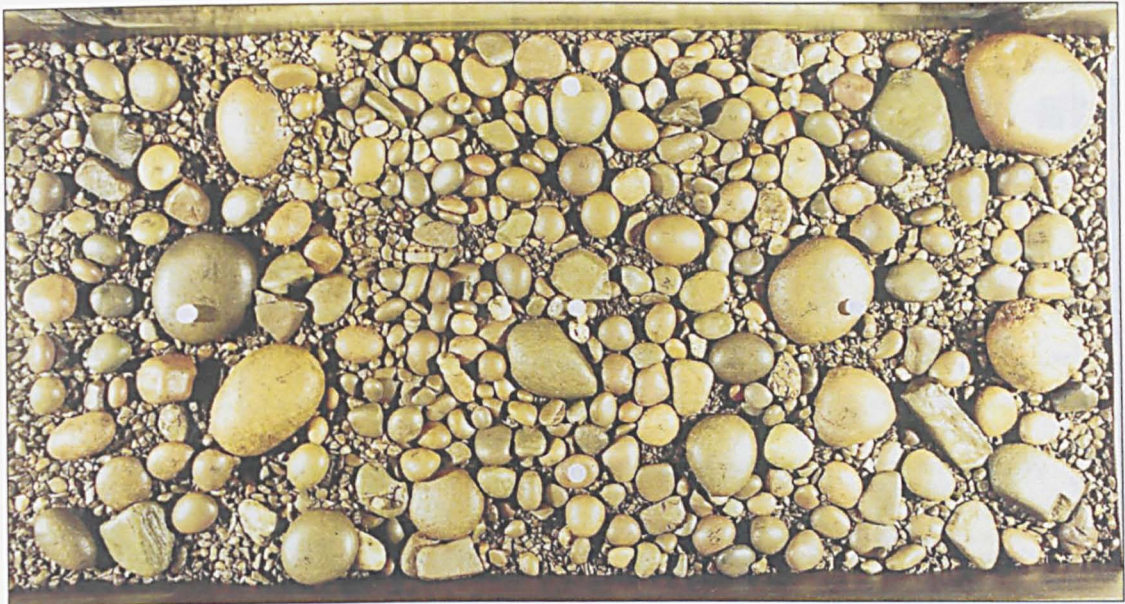
Fig. 3.3: Overhead photograph of Arena 1 in 1997

A

A1-98 Substrate
- [ ] plastic board
- [■] boulder
- [ ] gravel
- [ ] mesh screen

B

A1-98 Topography
Elevation
- [ ] 80.1 - 83
- [ ] 77.2 - 80.1
- [ ] 74.3 - 77.2
- [ ] 71.4 - 74.3
- [ ] 68.6 - 71.4
- [ ] 65.7 - 68.6
- [ ] 62.8 - 65.7
- [ ] 59.9 - 62.8
- [ ] 57 - 59.9

100   0   100   200   Centimeters

C

"Riffle"   "Pool"

← direction of flow

Fig. 3.4: The physical features of Arena 1 in 1998: a schematic map of the substrate (A), the topography of the observation area (elevations in centimetres) (B) and an overhead photograph of the central area of natural gravel (C)
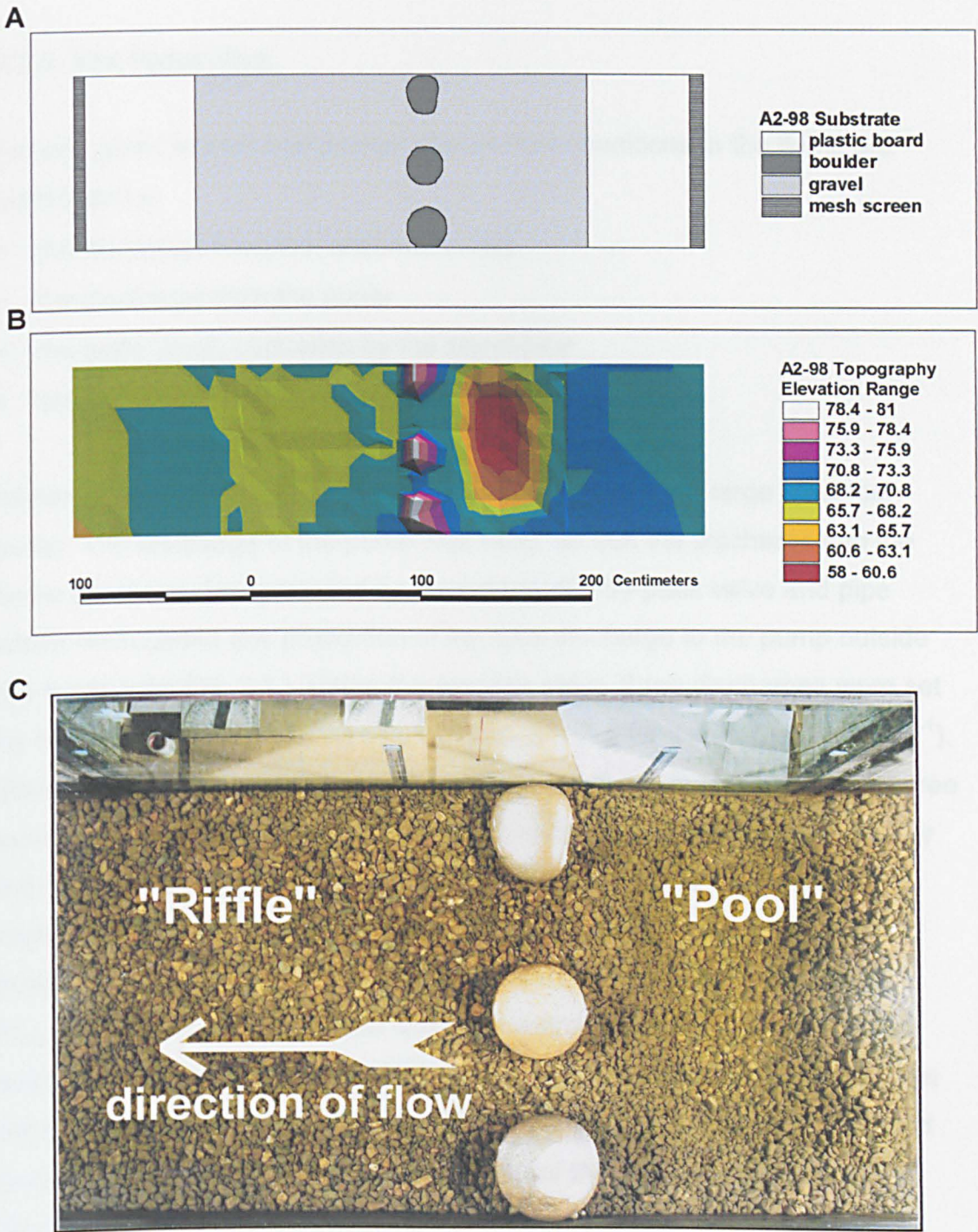
Fig. 3.5.: The physical features of Arena 2 in 1998: a schematic map of the substrate (A), the topography of the observation area (elevations in centimetres) (B) and an overhead photograph of the central area of natural gravel (C) (note the observation window in the top of the picture)

3.2.2. The hydraulics

For any given stream bed design, stream flow conditions in the flume are controlled by:

- the discharge from the freshwater inlet
- the discharge from the pump
- the water level, controlled by the stand-pipe
- the degree of congestion of the mesh screens

Stream discharge in the flume was mostly controlled by a large electrical pump. The discharge of the pump was fixed, so that the discharge into the flume could only be controlled by the means of a by-pass valve and pipe which recirculated any proportion of the total discharge to the pump outside the flume (see Fig. 3.1.). Using the by-pass valve, three discharges were set for the experiment at "Q_{low}" (2.6 I s^{-1}), "Q_{medium}" (15.0 I s^{-1}) and "Q_{high}" (46.8 I s^{-1}). Water velocities, shear stress and turbulence in the flume at each of the three pump discharges were determined by the water surface levels controlled by the stand-pipe (i.e., the lower the water surface level at a discharge, the higher the overall water velocity). Whereas hydraulic conditions were as similar as possible to the Shelligan Burn average flow conditions during Q_{medium}, large areas of very low water velocity and generally low velocities were the target for Q_{low} and as high as possible velocities for Q_{high}. Q_{high} was set just below the threshold stream power where movement of the bed load began, but probably still relates to a flow near the mean annual flow in the Shelligan Burn. For the constant gravel size in the flume, the critical shear-stress at which initial particle movement starts, depends predominantly on water depth and velocity as well as turbulence (Richards, 1982). The overall highest achievable velocities without erosion at Q_{high} were determined experimentally by running the pump at full discharge and gradually lowering the water surface level until the first dislodgement of the gravel was observed. In contrast to natural streams, the flowing water met resistance not only due to bed roughness but also due to the vertical mesh screens which separated the

observation areas. Clogging of the mesh screens with debris slowed down water velocities and increased water surface levels instead. In order to achieve and maintain similar velocities at all times, screens were frequently cleaned in their frame with a coarse brush but not at times of fish observation.

3.3. Water chemistry, turbidity and temperature

Water from the nearby River Almond was permanently supplied to the flume at a rate of approximately 5 litres s^{-1} during Q_{medium} and Q_{high} and a third of that during Q_{low}. The water had a pH of 7.1-8.2, conductivity of 46-122 us/cm and dissolved oxygen content of 91.6 -104% (data supplied by the Scottish Environmental Protection Agency). Water temperatures during the experiments ranged from 9 to 20 degrees Celsius, at a mean of 14.5 degrees (SD= 1.93). Water temperatures during runs in 1998 were cooler than usually in July and August. Turbidity was classified by judgement of eye on a daily basis. Occasional heavy rainfalls and related spates caused high turbidity which sometimes made fish observations impossible. If this occurred during the acclimatisation, the start of the experiment was delayed. In one case, an experiment had to be given up and started again with new fish.

3.4. The fish used in the experiment

All experiments were conducted with young-of-the-year Atlantic salmon (Salmo salar) that had been caught in the Shelligan Burn. Fish were caught by electro-fishing, identified and then transferred to the flume within an hour of capture. Greatest care was taken to minimise the stress for the fish and no fish died after introduction to the flume. A total of 196 fish was used during experiments in 1997 and 1998, with a body length between 30 and 67 mm (mean 44 mm, SD= 9.1) and body weight between 0.2 and 3.32 grams (mean= 0.97 grams, SD= 0.67). Particularly small or big fish were avoided and average sized individuals were selected from the ones caught at the Shelligan Burn. All fish taken out of the flume after the experiments appeared to be healthy. During first runs in 1997, fish were measured and weighed

before and after the experiments and it was found that fish grew well in length and weight. Fish on average gained weight by 2.72% per day (SD= 1.5) and length by 0.65% per day (SD= 0.29) on average (n=39). Despite the obvious statistical advantages of marking fish individually, it was decided against it, because of the loss rates and detrimental health effects expected for fish of this small size which would seriously compromise the quality of the data.

Visual inspection of regularly taken samples of the river water feeding into the flume showed a permanent presence of living invertebrate larvae, dominated by tiny individuals of mayfly, caseless caddis, chironomids and occasional larger stone flies. These invertebrates were too small to be seen through the observation windows, but drift feeding of the salmon parr was observed at all times. Drift feeding attempts of each individual fish (n=61) were recorded for intervals of five minutes and the median value was 2 attempts (range= 0-16, lower quartile= 1, upper quartile= 5). To avoid shortage of food, a constant volume of live chironomid larvae ("blood worms") was fed three times within 24 hours. The chironomids were dropped into a finely meshed net on the outside of the upstream mesh screen from where they gradually entered the water column as drift food. With this set up, timing and spatial concentration of the chironomid drift was simulated semi-naturally. The feeding positions and feeding patterns during the introduction of chironomids did not seem to change, however, fish observations were not conducted during or until 30 minutes after artificial addition of food.

3.5. The techniques used in mapping the microhabitat conditions

Microhabitat conditions were mapped out for the entirety of both observation areas before the commencement of the fish observations. Mean column velocity was measured at the three set discharges at a maximum spacing of 20 centimetres along and 10 centimetres across the channel. Extra samples were taken in areas of complex flow patterns, in particular around the boulders. Water depth was calculated, based on water surface levels and stream bed topography, which had been sampled at a grid spacing of not

more than ten centimetres. Positions of the measurements were determined by the use of a permanent x/y co-ordinate system which was marked on the flume walls. The electro-magnetic current meter was placed on a sliding device which rested on a rectangular metal frame laid across the channel (Fig. 3.6.). The staff holding the probe was fixed by a clamp and lowered down at right angles, controlled by two spirit levels. Using this set-up, all microhabitat data obtained were spatially referenced with a high degree of precision.
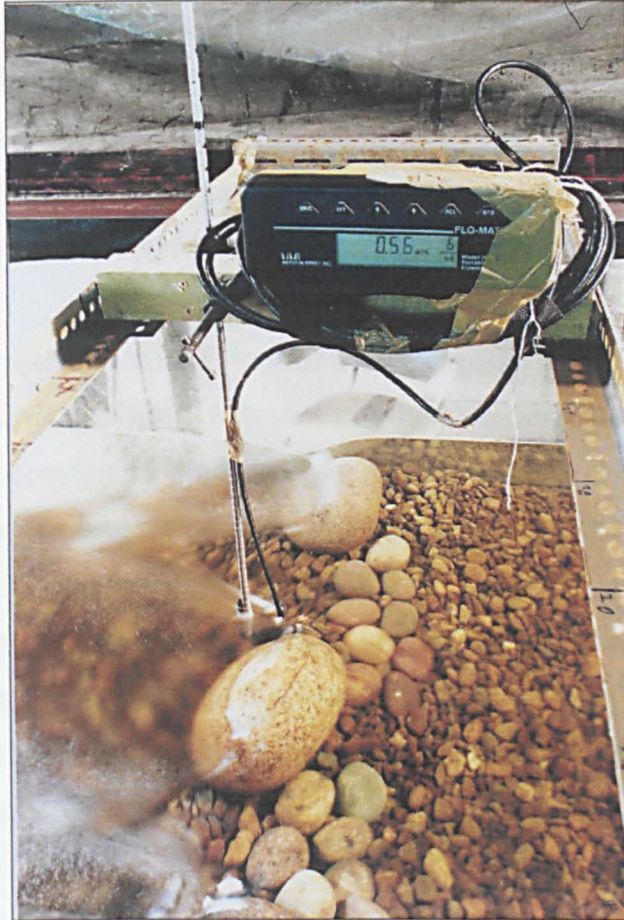
Fig. 3.6.: Photograph of set-up used to measure mean column velocities in the flume

Velocities were measured using a one-axis electro-magnetic current meter (by Marsh-McBirney) and the probe was always positioned at a right angle to the walls in line with the main direction of flow, so that velocities as shown on the map are those along the x-axis. However, the actual direction of flow deviates from the main direction in a number of areas, demonstrated by flow visualisation with milk injections (see Fig. 3.7.). Changes of direction were due

to the stream bed topography which caused convergence and divergence of flow in both horizontal (e.g., around the boulders) and vertical direction (e.g., head and tail of pool). Lateral flows were common at the bottom of the pool and behind the boulders in the riffle. The picture A in Fig. 3.7. indicates some of the flow lines observed when low fat milk was injected into the two gaps between the boulders, the picture B when the milk was injected directly in front of the boulders. Residence time of the milk, and thus any food particle, was prolonged in the turbulent zones behind the boulders and most of the discharge volume was contained in the main currents in line with the two gaps. These areas of highest discharge can also be identified by the distribution of the highest velocities on the velocity maps (Fig. 3.8., Fig. 3.9., Fig. 3.10.). Flow through both gaps converged downstream of the line of boulders at a distance of approximately two boulder lengths.

The flow lines drawn in picture C in Fig. 3.7. show the varied directions of the water currents in the mid-water column. In effect, velocity measurements for the flume will underestimate the true velocities experienced by the fish in areas where local currents flowed in a right angle to the main direction of flow. Areas of reverse flow however, found behind the boulders and along the walls of the flume, were registered as negative water velocities by the flow meter and are displayed accordingly on the velocity maps. However, since the parr always positioned themselves heading into the current, negative velocities relative to the x-axis were converted to absolute velocities when analysed as fish microhabitat.
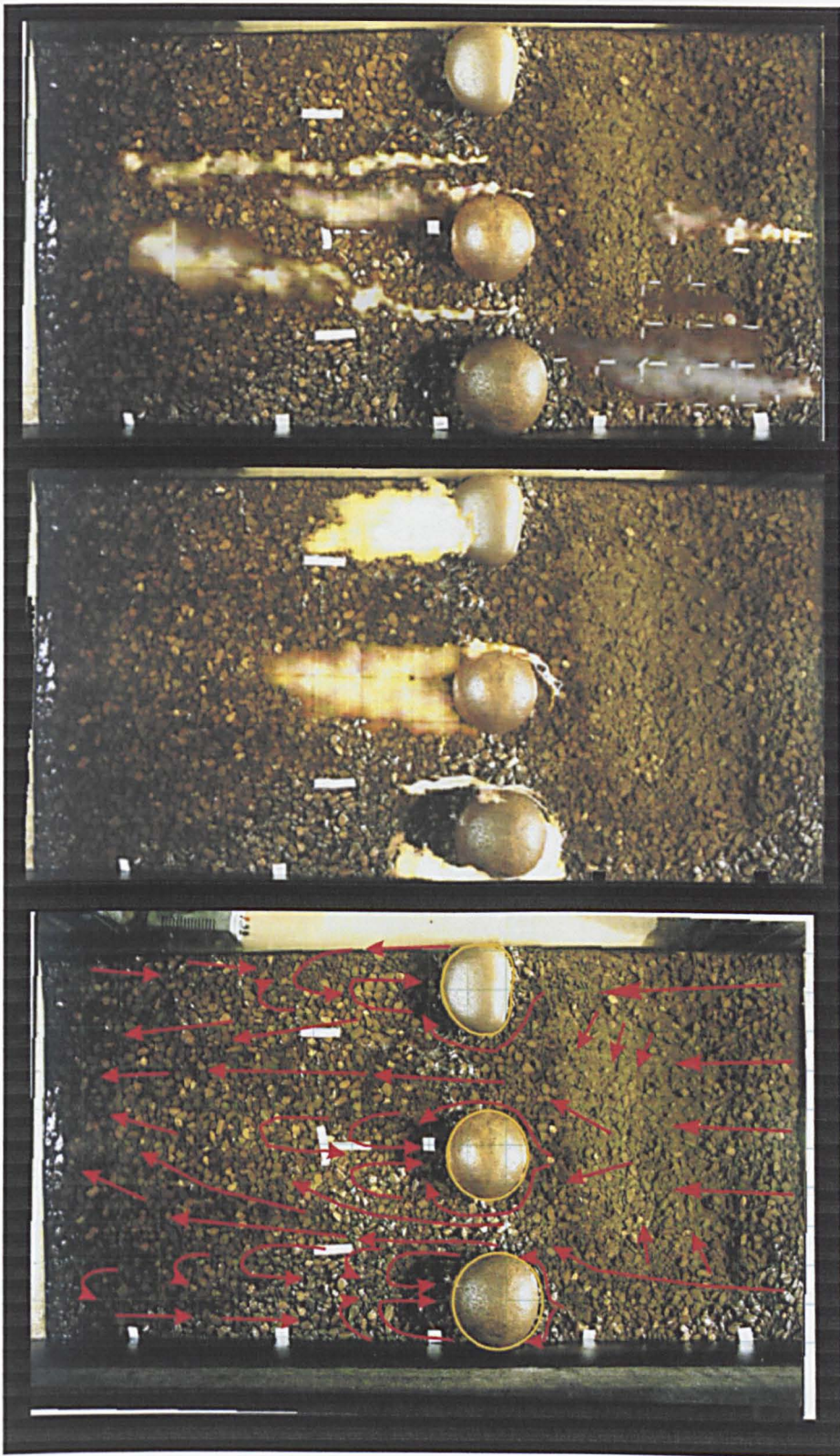
Fig. 3.7.: Examples of flow visualisation with at-a-point milk injection. Video still images of milk injections at various points (A, B) and main flow lines in red (C).

3.6. Determination of fish locations

Due to the small size of the fish and surface turbulence in large parts of the water surface, observation of the fish from above was not feasible. Instead, a glass window along the side of both observation areas was used which permitted observations below the water level. The room for the observer was darkened so that fish did not see the observer. The fish locations were determined by fixing their position using two "eye-sights" and triangulation. The calculation of fish positions by triangulation was more complex than first anticipated and initial errors where as high as 20 cm and more. After conducting lengthy calibration tests, three sources of error were identified:

1. the glass window sat at an angle in its frame and thus was not parallel to the protractors used for reading the angle of sight
2. the orientation of the protractors was offset by approximately 1 degree
3. the two protractors were not on a plane surface but tilted at a slight vertical angle which introduced an error growing in proportion to how much the measured angle deviated from 90 degrees.

After accommodating mathematically for all these factors, the mean error of positions taken by this method was 16.2 mm (SE= 1.2). The error of the triangulation method is highly correlated to the angle alpha at the target (r^2= 0.83) so that the expected error of the calculated fish position can be estimated according to alpha. 95% of the observations used in the later analysis had an alpha value exceeding 20 degrees which was associated with a mean error of 21.6 mm (SE= 2.6) (see Table 3.2.), which equates to approximately half a fish length. Due to the strong refraction of the water/glass surface fixing positions by triangulation was not possible at the near-side edges of the observation windows. In these cases, accurate estimates of fish position were made by direct observation from above in relation to referenced landmarks (e.g., edge of board, prominent stones) instead.

Table 3.2.: Number of fish positions calculated by triangulation. Percentile of observations and the associated mean error of the calculated position for groups of alpha angles (angle at fish)

Alpha (degree)	< 20	25	30	35	40	45	50	55	60-90	n
F fish observations	12	60	43	42	18	16	16	5	15	227
Percentile of observations		95%	68%	49%	31%	23%	16%	9%	7%	
Calibration mean error (mm)	34.5	21.6	15.7	13.8	11.7	6.6	3.1	5.2	4.2	
SE mean error	7.2	2.6	1.7	1.8	1.8	1.5	2	1.5	1.8	

3.7. Data handling

Fish observation and habitat data was processed and analysed with the help of a Geographic Information System (GIS) package. Work started with Arc-Info (Version 7.2.1) running on Unix machines but data were later transferred to Arc-View (version 3.1). Fish positions were registered as x/y co-ordinates and converted to point-coverages. The fish positions were linked to a database, containing all additional information for the observation (e.g., date, flow, temperature, population density). Stream bed topography, water surface level and water velocity data were imported as x/y/z data, with z carrying the actual information on the variable for the spatial reference given by the x/y co-ordinates. Subsequently, digital terrain models (DTM) were constructed to create a complete response surface from which the variable could be estimated for any point in the coverage by interpolation. For most applications DTMs were built as Triangular Irregular Networks (TIN). In order to calculate water depth, stream bed topography and water surface levels were converted to grid format and depth maps created with the help of map algebra (i.e.,

water surface level grid minus stream bed topography grid equals water depth grid). By overlaying the habitat variable tins with the fish point coverages it was possible to obtain information on the microhabitat conditions encountered by each fish. The GIS environment also permitted to generate a range of other spatial data (e.g., distance of fish to the flume side, boulder or nearest neighbour and the precise quantification of habitat conditions like depth and velocity histograms).

All data were stored in MS Access (version 97 SR-2) and handled in MS Excel (version 97 SR-2). Statistical analysis was executed in SPSS (version 9).

3.8. The statistical methods to quantify habitat use

Because habitat use is influenced by habitat availability (see chapter 2.8.), the use of preference indices was necessary. The electivity index commonly used in most instream flow studies is Ivlev's foraging ratio (Ivlev, 1961) which has been adopted by the developers of PHABSIM (Bovee, 1986) to measure habitat electivity, termed habitat preference.

The preference Index P is:

$$P = u/a$$

; where u is the proportion of all fish observed in the habitat class and a is the proportion of the total area represented by the habitat class.

A statistical comparison of preference indices is difficult because they are rescaled and respond non-linearly to variations in the availability of habitat (Lechowisz, 1982). The linear electivity index (L) (Strauss, 1979) can provide a robust statistical comparison of preference indices, but only if habitat availability is constant, which was not the case in the experiments, nor would it be realistic with reference to natural streams. Therefore, goodness-of-fit tests were used, which allowed the distinction between random habitat use (i.e., use equals availability) and choice behaviour (i.e., proportional over- and underutilisation of habitats). Following the recommendation of Jager & Pert (1997), the variation in preference curves was quantified by calculating the

differences in WUA that result from using each curve in turn at each discharge. Microhabitat utilisation between two different population densities and three discharges was analysed by non-parametric comparisons (i.e., 2-sample Mann-Whitney U Test; k-samples Kruskal-Wallis H Test).

3.9. The microhabitat conditions:

3.9.1. Mean column velocity and water depth

The aim of the experimental flume design was to create clearly defined areas of higher and lower velocities at a more or less constant depth and without creating an unnatural environment. This was achieved most effectively in the riffle by placing three boulders at the upstream end which created two bands of high discharge and high velocity downstream of the gaps and three areas of low velocity and backflow downstream of the boulders (see Fig. 3.8., Fig. 3.9., Fig. 3.10.). This lateral zonation of velocity is over a flat bottomed stream bed, thus at a constant water depth (see Fig. 3.4., Fig. 3.5.).

At Q_{low}, hydraulic conditions were similar to those during a natural drought. Water depths were not greater than 9.4 cm (mean= 7.6 cm, SE= 0.08) in the riffle and 21.6 cm in the pool (mean 11.77 cm, SE= 0.33). Mean column velocities were between 0 and 31 cm s^{-1} in the riffle (mean= 8.77 cm s^{-1}, SE= 0.39) and 0 and 28 cm s^{-1} in the pool (mean= 5.55 cm s^{-1}, SE= 0.34) (see Table 3.3. for statistics). The velocity maps (Fig. 3.8., Fig. 3.9., Fig. 3.10.) show large areas of negligible flow with velocities below 5 cm s^{-1} in both arenas during Q_{low}. Velocities were highest around the boulders and downstream of the two gaps between the boulders. Velocities were more variable in the riffle (St.Dev.= 6.85) than the pool (St.Dev.= 4.5).

At Q_{medium}, water depths were between 0 and 14.2 cm in the riffle (mean= 11.2 cm, SE= 0.17) and 5.2 and 25.4 cm in the pool (mean= 16.2 cm, SE= 0.32). The overall velocity range increased to 0-54 cm s-1 (see Table 3.3.). Velocity peaked at 54 cm s^{-1} in the riffle (mean 15.7 cm s^{-1}, SE= 0.75) and 21 cm s^{-1} in the pool (mean= 8.8 cm s^{-1}, SE= 0.35). Variability of flow increased and was much higher in the riffle (St.Dev.= 13.71) than in the pool (St.Dev.= 4.71).

Finally, at Q_{high} water depths were between 0.7 and 24.2 cm in the riffle (mean= 19.8 cm, SE= 0.24) and 12.7 and 36.5 cm in the pool (mean= 25.2, SE= 0.37). The patterns of velocity distribution were the same as in the other discharges. Velocities peaked at 88 cm s^{-1} in the riffle (mean= 31.87 cm s^{-1}, SE= 0.92) and 49 cm s^{-1} in the pool (mean= 24.84 cm s^{-1}, SE= 0.63) and variability was much higher in the former (St.Dev.= 16.21) than the latter (St.Dev.= 8.42).
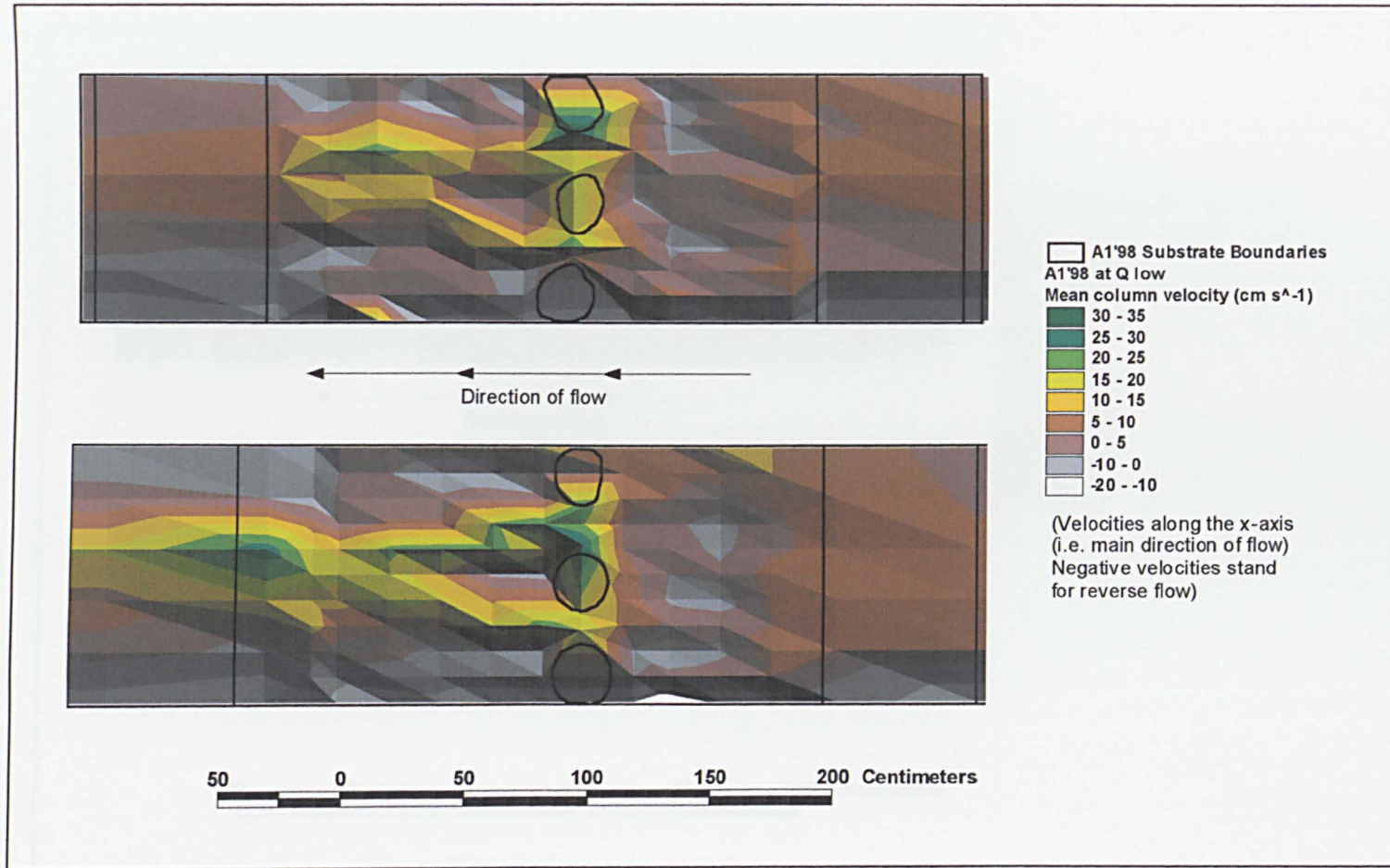
Fig. 3.8.: Mean column velocities in Arena 1 (top) and Arena 2 (bottom) during Q_{low}
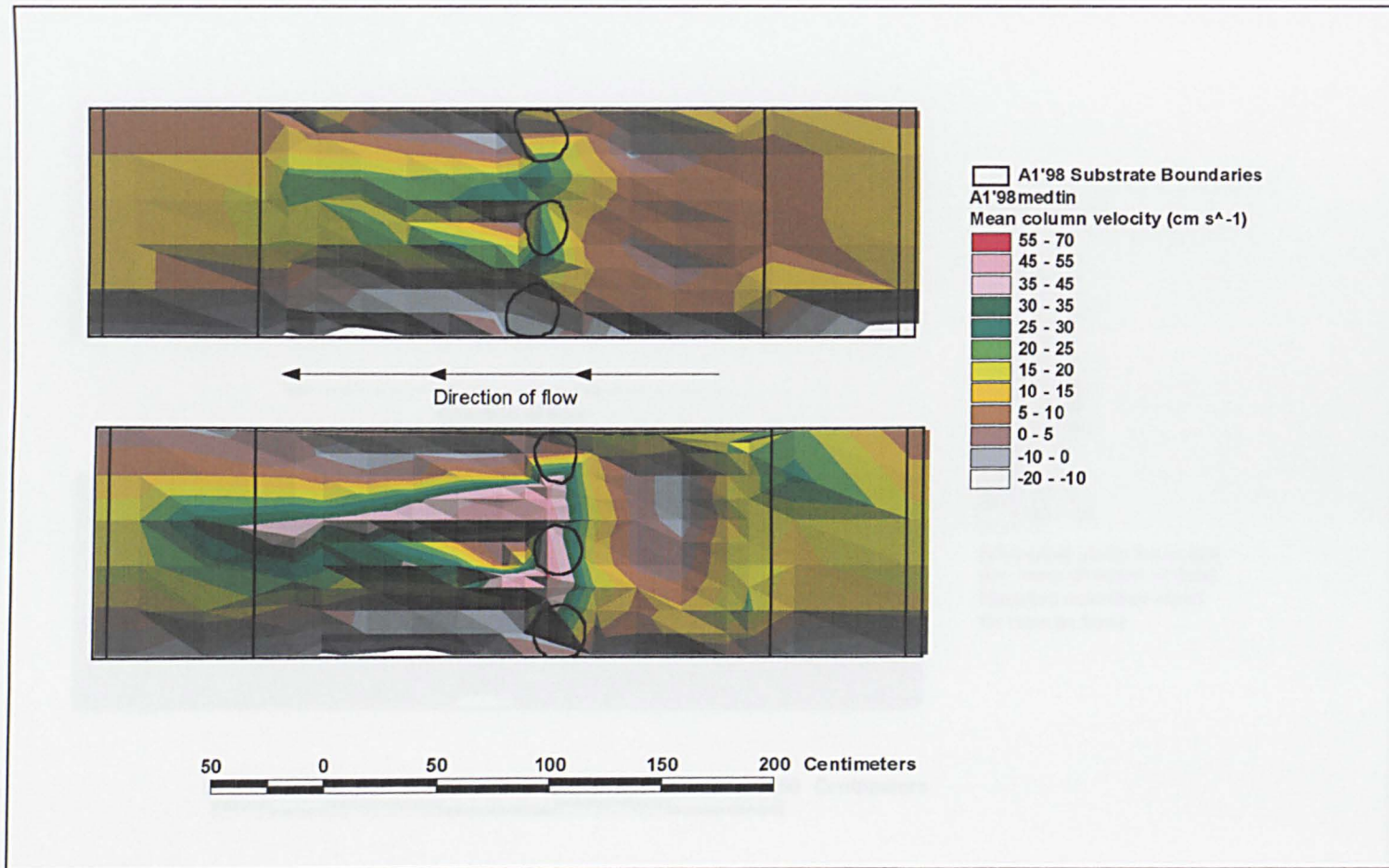
Fig. 3.9.: Mean column velocities in Arena 1 (top) and Arena 2 (bottom) during Q_{medium}

Legend:

A2'98 Substrate Boundaries
A2'98 at Q high
Mean column velocity (cm s^-1)

- 70 - 90
- 55 - 70
- 45 - 55
- 35 - 45
- 30 - 35
- 25 - 30
- 20 - 25
- 15 - 20
- 10 - 15
- 5 - 10
- 0 - 5
- -10 - 0
- -20 - -10

(Velocities along the x-axis
(i.e. main direction of flow)
Negative velocities stand
for reverse flow)

Direction of flow

50   0   50   100   150   200 Centimeters
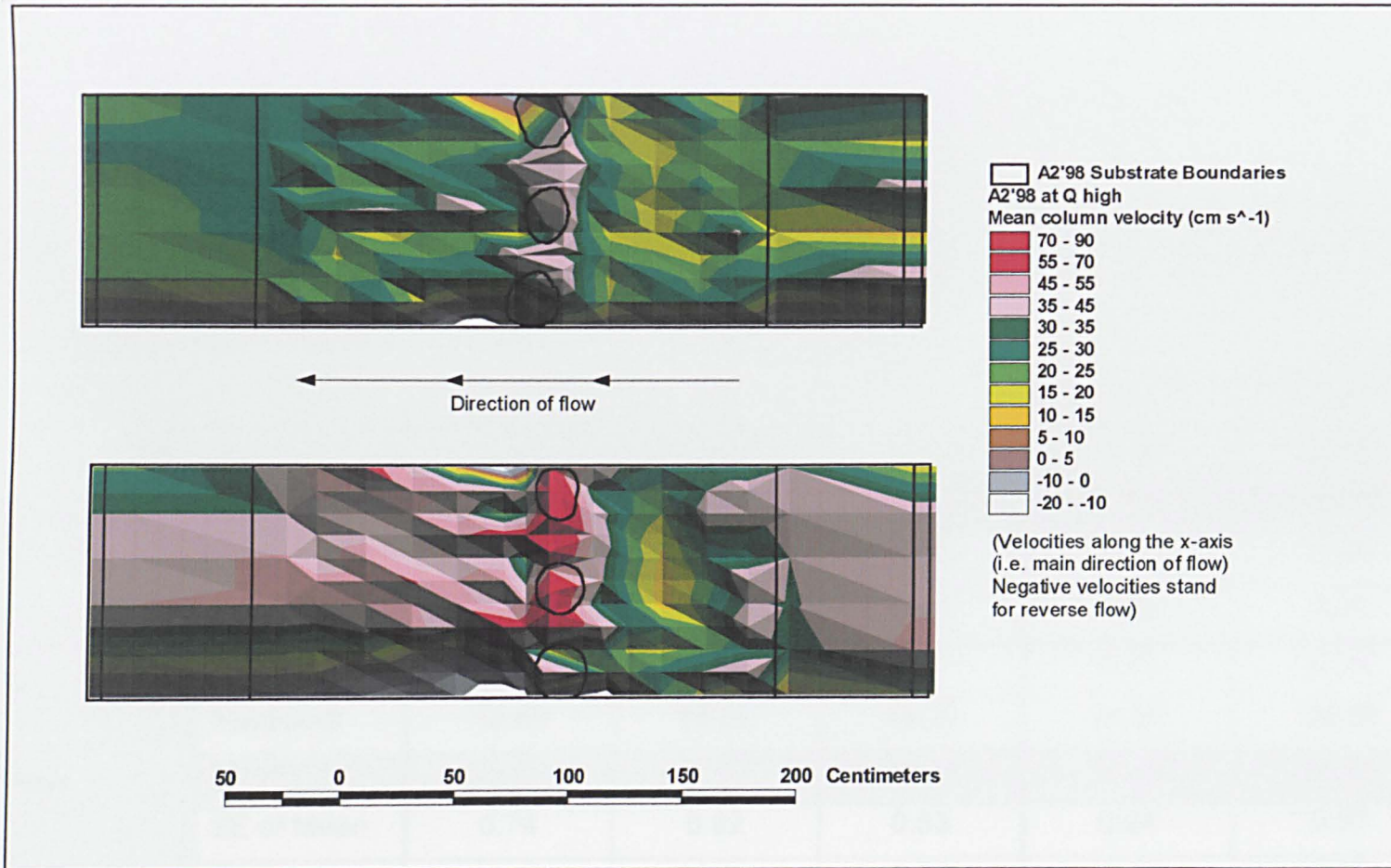
Fig. 3.10.: Mean column velocities in Arena 1 (top) and Arena 2 (bottom) during Q_{high}

Table 3.3.: Mean column velocity and water depth in the flume during three discharges

Discharge		Mean column velocity (cm s^{-1}) in:			Water depth (cm) in:	
		Off	Riffle	Pool	Riffle	Pool
Q_{low}	Minimum	0	0	0	1.00	0.41
	Maximum	19.00	31.00	28.00	9.40	21.60
	Mean	7.40	8.77	5.55	7.62	11.77
	SE of Mean	0.24	0.39	0.34	0.08	0.33
	Std Deviation	4.45	6.85	4.5	1.28	4.37
Q_{medium}	Minimum	0	0	0	0	5.17
	Maximum	36.00	54.00	21.00	14.10	25.40
	Mean	12.74	15.7	8.8	11.15	16.17
	SE of Mean	0.40	0.75	0.35	0.17	0.32
	Std Deviation	7.30	13.17	4.71	2.99	4.31
Q_{high}	Minimum	0	0	0	0.70	12.67
	Maximum	48.00	88.00	49.00	24.20	36.50
	Mean	25.49	31.87	24.84	19.79	25.21
	SE of Mean	0.74	0.92	0.63	0.24	0.37
	Std Deviation	13.47	16.21	8.42	4.18	4.90

3.9.2. Overhead cover:

Overhead cover occurred in the form of

- the margins of the boulders
- shading at the edge of the mesh screens
- overhead riffling of the water surface.

It was planned to minimise the amount of overhead cover available to the fish. However, since the parr were so small (30-67 mm fork length), single fish appeared to utilise the edges of the boulders as overhead cover at stages, in particular when frightened or as refuge to avoid dominant individuals. Furthermore, the only area of shading from above was caused by the mesh screens at the up- and downstream end of the flume. Some fish were observed in these areas right next to the screen, in particular during experiments with high population densities. Surface riffling was the most important kind of overhead cover and the only one available in larger amounts, in particular at Q_{medium} and Q_{high}. Surface riffling occurred mostly in the riffle area of both observation arenas, in particular Arena 2. It was attempted to visualise the amount of surface riffling by photography (Fig. 3.11.). On the photographs, it is possible to identify areas of highest optical distortion which is related to the degree of water surface turbulence and water depth. Optical distortion was classified into four groups, from no distortion (1) to complete distortion (4). In natural situations, areas of high optical distortion offer the parr a high degree of overhead cover in form of visual concealment from avian predators. However, it has to be said that in some cases the camera did produce different images from those observed by the naked eye. Especially at Q_{low}, the photograph suggests a clear water surface and complete visibility of the substrate whereas it was still impossible for the observer to locate fish from above in the areas downstream of the two gaps in the boulders due to some surface riffling. This should be due to the fact that the camera with an electronic flash as the one used takes a picture at a much shorter time interval than the human eye (i.e., the flash operates at a few thousands of a second) so that the surface wave oscillation at low discharge are too slow to greatly affect the camera image.
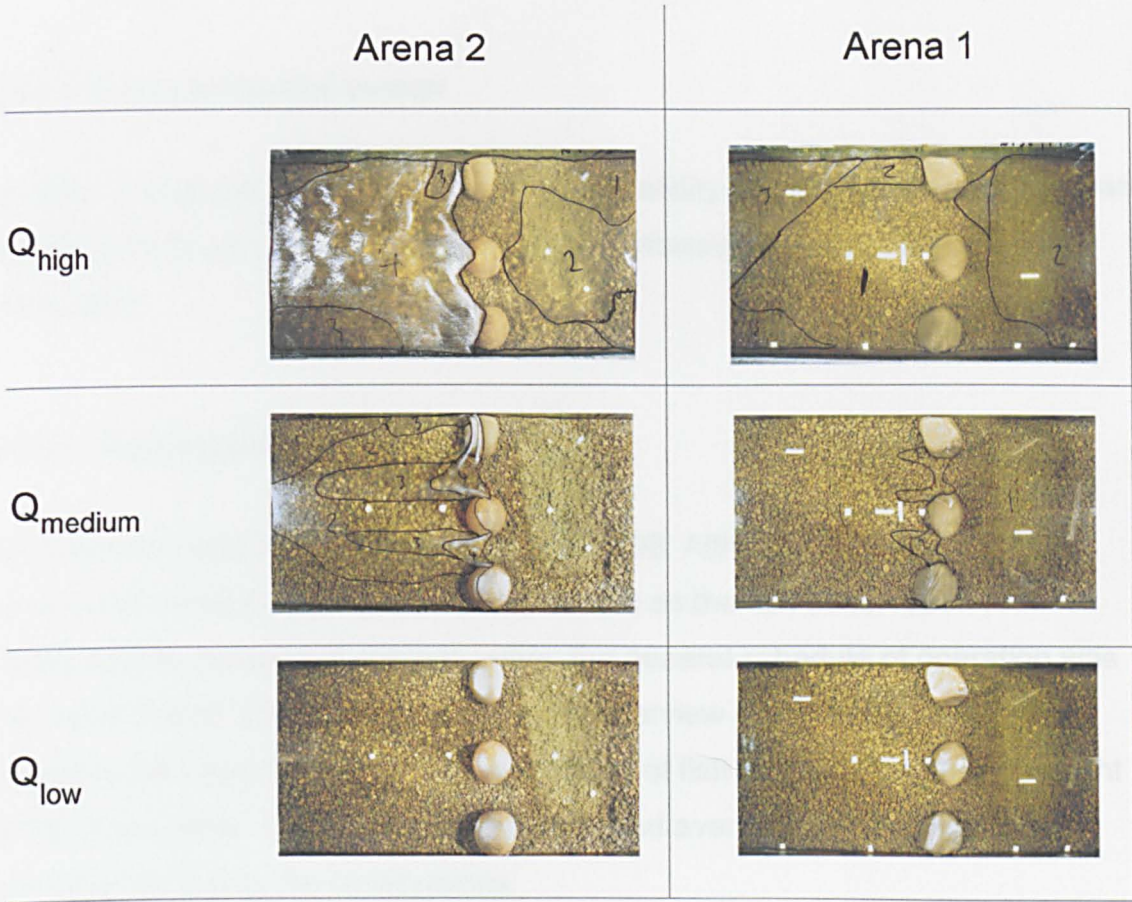
Fig. 3.11.: Overhead cover in both arenas at three discharges. Direction of flow from right to left. Visual distortion was classified into 4 groups from none (1) to complete distortion (4)

3.10. The experimental design

In order to address the issues regarding the validity and performance of instream habitat models as outlined in chapter 2, the following experiments have been conducted:

3.10.1. Experimental schedules:

Experiments were conducted in 1997 and 1998. Although the design of the observation area Arena 1 (see above) as well as the fish observation routines varied slightly between those two years, the general schedule of operation was the same (Table 3.4.). Table 3.5. gives an overview of the timing of all experimental runs, the fish densities, number of fish stocked, length and weight of fish when taken out after the experiment and average day-time water temperature during the observations.

Table 3.4.: Schedule of experimental proceedings

Day	1	2	3	4	5
Discharge	Q_{medium}	Q_{medium}	Q_{medium}	Q_{high} or Q_{low}	Q_{high} or Q_{low}
Phase	fish capture introduction acclimatisation	acclimati-sation	experiment	experiment	experiment

Table 3.5.: Overview of the experiments and the fish (see text for details)

Run	Date of fish observations	Observation arena	Fish density (fish m^{-2})	N=	Mean fork length (mm)	Average weight (grams)	Average water temperature (degree Celsius)
1-97	20.- 24.07.1997	1	1.11	4	47.75	1.12	18.0
		2	1.11	4			
2-97	7.- 11.08.1997	1	1.11	4	56.25	1.9	18.0
		2	1.11	4			
3-97	14.- 18.08.1997	1	1.11	4	53.75	1.67	19.7
		2	1.11	4			
4-97	22.- 26.09.1997	1	1.11	4	62	2.62	11.8
		2	1.11	4			
1-98	16.- 20.06.1998	1	4.44	16	33.06	0.31	13.7
		2	4.44	16	33.56	0.32	
2-98	23.- 27.06.1998	1	0.56	2	33.00	0.34	15.7
		2	0.56	2	34.50	0.37	
3-98	30.06.- 4.07.1998	1	4.44	16	36.69	0.46	14.2
		2	4.44	16	36.81	0.48	
4-98	7.- 11.07.1998	1	0.56	2	41.50	0.66	15.5
		2	0.56	2	40.00	0.60	

Table 3.5. continued: Overview of the experiments and the fish (see text for details)

Run	Date of fish observations	Observation arena	Fish density (fish m^{-2})	N=	Mean fork length (mm)	Average weight (grams)	Average water temperature (degree Celsius)
5-98	13. 17.07.1998	1	4.44	16	40.33	0.61	14.4
		2	4.44	16	41.06	0.67	
6-98	21.- 26.07.1998	1	0.56	2	44.00	0.86	13.9
		2	0.56	2	44.50	0.87	
7-98	30.07.- 3.08.1998	1	0.56	2	52.00	1.41	14.8
		2	0.56	2	49.00	1.18	
8-98	13.- 17.08.1998	1	4.44	16	46.67	1.06	14.8
		2	4.44	16	47.33	1.08	
9-98	19.- 23.08.1998	1	0.56	2	58.00	1.86	13.4
		2	0.56	2	53.50	1.61	
10-98	26.-30.08.1998	1	0.56	2	57.00	1.93	11.6
		2	0.56	2	55.00	1.77	

3.10.2. Experiment 1: "Is microhabitat preference of juvenile Atlantic salmon independent of discharge?"

<u>Objectives:</u>

- to identify microhabitat preference, in particular for water velocity, of YOY Atlantic salmon
- to compare the microhabitat preferences observed at three widely different stream discharges
- to develop preference curves using the data and test how much the performance of PHABSIM is affected by differences in the curves

<u>Working hypotheses:</u>

- fish prefer discrete ranges of microhabitat conditions
- these preferences are constant across different stream discharges

<u>Procedure:</u>

- stocking density 4.4 fish m^{-2}, experimental schedule as described in Table 3.4.
- determination of fish positions at three stream discharges
- overlay of fish positions and habitat maps in GIS
- statistical comparison of habitat use and availability at each discharge and between the discharges
- development of preference curves at each discharge
- comparison of habitat predictions by the PHABSIM method using all three preference curves

3.10.3. Experiment 2: How does population density affect habitat use across different discharges?

Objectives:

- to investigate if the habitat use by YOY Atlantic salmon at three stream discharges is affected by population density
- to assess habitat use at two spatial scales, that of meso- and microscale

Working hypotheses:

- the use of mesohabitat at three stream discharges does not differ between population densities
- the use of microhabitat at three stream discharges is not affected by population density
- the use of microhabitat within each mesohabitat does not vary with discharge and population density

Procedure:

- stocking densities 0.55 fish m^{-2} and 4.4 fish m^{-2}
- experimental schedule as described in Table 3.4.
- determination of fish positions at three stream discharges
- overlay of fish positions and habitat maps in GIS
- comparison of meso- and microhabitat use at different densities and discharges by standard non-parametric test procedures (i.e., Chi-Square Test, Wilcoxon Signed Ranks Test, Kruskall-Wallis Test, Mann-Whitney U Test)

3.10.4. Experiment 3: Site fidelity at different discharges: how different are microhabitats of maintained and vacated positions?

Objectives:

- to assess the mobility and site fidelity of YOY Atlantic salmon in relation to stream discharge
- to compare the microhabitat conditions between positions that fish maintained and vacated after a change in discharge
- to compare the microhabitat conditions at chosen fish positions with random positions

Working hypotheses:

- fish vacate and maintain positions in the same way at all discharges
- there is no difference in microhabitat conditions between positions fish maintained and vacated after discharge changes

Procedure:

Part 1:

- the flume was stocked with groups of four fish (density 1.1 fish m^{-2}) and each fish was observed for five minutes continuously once at each discharge. Positions were fixed every minute
- experimental schedule as described in Table 3.4.
- overlay of fish positions and habitat maps in GIS
- comparison of frequency of positions changes and distances moved at different discharges and in relation to other variables (e.g., water temperature, mesohabitat) with standard statistical methods.

Part 2:

- the flume was stocked with groups of 16 fish (density 4.4 fish m^{-2}) and fish positions were fixed only once for each fish at each discharge

- experimental schedule as described in Table 3.4.

- overlay of fish positions and habitat maps in GIS

- comparison of microhabitat conditions of maintained and vacated positions after a change in discharge

- comparison of water velocities at fish positions and random positions at each discharge

4. Is microhabitat preference of juvenile Atlantic salmon independent of discharge?

4.1. Introduction

Two of the basic underlying assumptions of instream flow models are:

- fish prefer discrete ranges of microhabitat conditions
- the preferred conditions are independent of discharge

In order to investigate the validity of these two assumption, a flume experiment was carried out with populations of YOY salmon parr which were subjected to three widely different discharges. The exact set-up of experiment 1 is described in chapter 3.10.2.. To avoid possible confusion, it is appropriate here to clarify the meaning and context in which the term "preference" stands. True behavioural preference for any isolated microhabitat variable is very difficult to identify, because the choice behaviour of every individual fish is controlled by interactions of a multitude of factors (e.g., season, water temperature, food abundance, resource competition, predation pressure; see chapter 2.8.). However, in the application of instream flow models, preference is seen as a simple density function, ascribing the highest preference to the habitat with the highest relative use per unit area (Fig. 4.1.). In this chapter, the term preference is used according to the terminology of instream habitat models.

One way of identifying preference and avoidance behaviour more realistically, is to test if the use of a habitat type occurs more or less frequently than could be expected from random. This analysis formed the basis of experiment 1 and was repeated for each of the three discharges. Using the data, preference curves were built by the standard methods used in instream flow modelling (Bovee, 1986; Baltz, 1990) for each discharge. Because a direct comparison of

preference curves is problematic (see chapter 2.8.), the practical implications for the model output were analysed instead by applying the different preference curves to a PHABSIM method model for the flume and comparing the habitat predictions of available habitat expressed as "weighted usable area" (WUA)
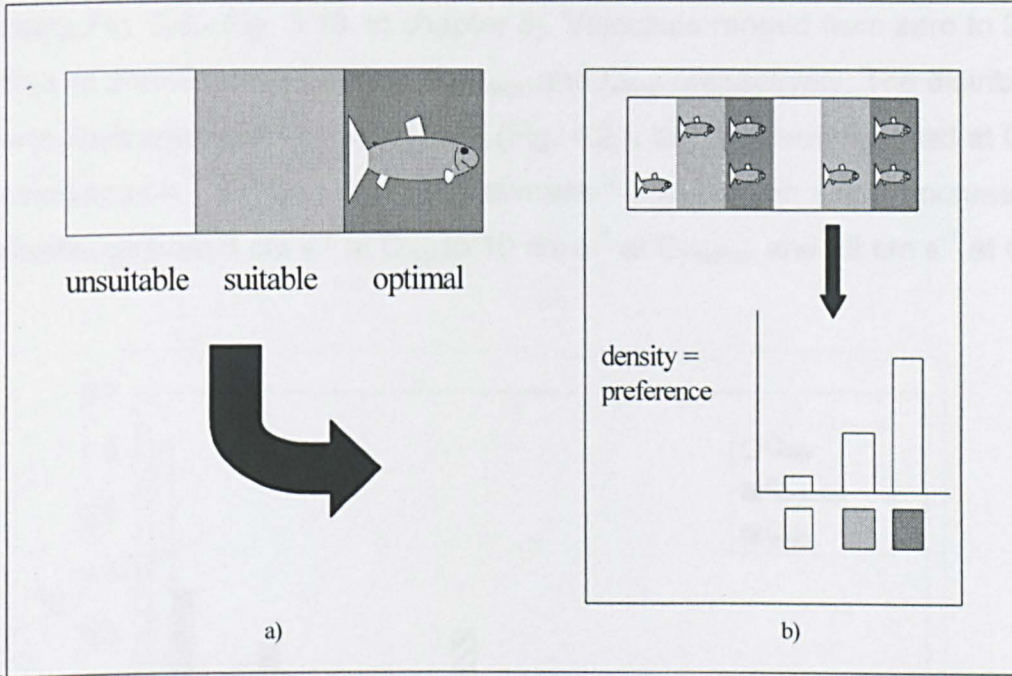
Fig. 4.1.: Concept of habitat preference: fish choose preferred habitat (a) and densities are highest in preferred habitat (b)

Experiment 1 was specifically focused on the following questions:
1. Do fish experience different velocities at their holding positions at different discharges?
2. Do fish prefer discrete ranges of velocities at any discharge?
3. If so, does this velocity preference stay constant over discharge?
4. If not, how does this shift in preference affect WUA calculations?

4.2. The distribution of mean column velocities in the flume and at fish positions

Mean column water velocities in the flume changed significantly with discharge (Pearson Chi-Sq. 718.4, d.f.= 16, P<0.0001) (also, see Table 3.2. A and velocity maps Fig. 3.8.- Fig. 3.10. in chapter 3). Velocities ranged from zero to 31, zero to 54 and zero 81 cm s^{-1} at Q_{low}, Q_{medium} and Q_{high} respectively. The distribution of velocities was near normal at Q_{high} (Fig. 4.2.), but positively skewed at Q_{low} (skewness = 1.31) and Q_{medium} (skewness 1.35). Median values increased with discharge from 6 cm s^{-1} at Q_{low} to 10 cm s^{-1} at Q_{medium} and 28 cm s^{-1} at Q_{high}.
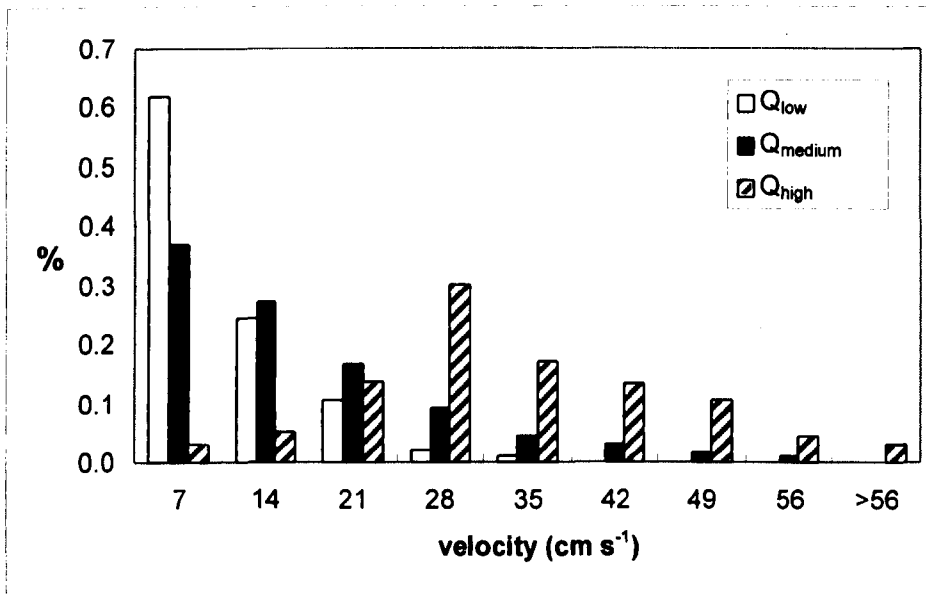
Fig. 4.2.: Velocity availability (as percentages of the total area) at three discharges

The velocities that fish experienced at their holding positions were also significantly different at all three discharges (Pearson Chi-Sq. 117.4, d.f.= 10, P<0.001). Median velocities at fish positions were 8, 10 and 24 cm s^{-1} at Q_{low}, Q_{medium} and Q_{high} respectively. Velocities at fish positions ranged from zero to 26, zero to 48 and zero to 56 cm s^{-1} at Q_{low}, Q_{medium} and Q_{high} and the overall

distribution of velocity use was similar in shape to that of velocity availability (Fig. 4.2., Fig. 4.3.).
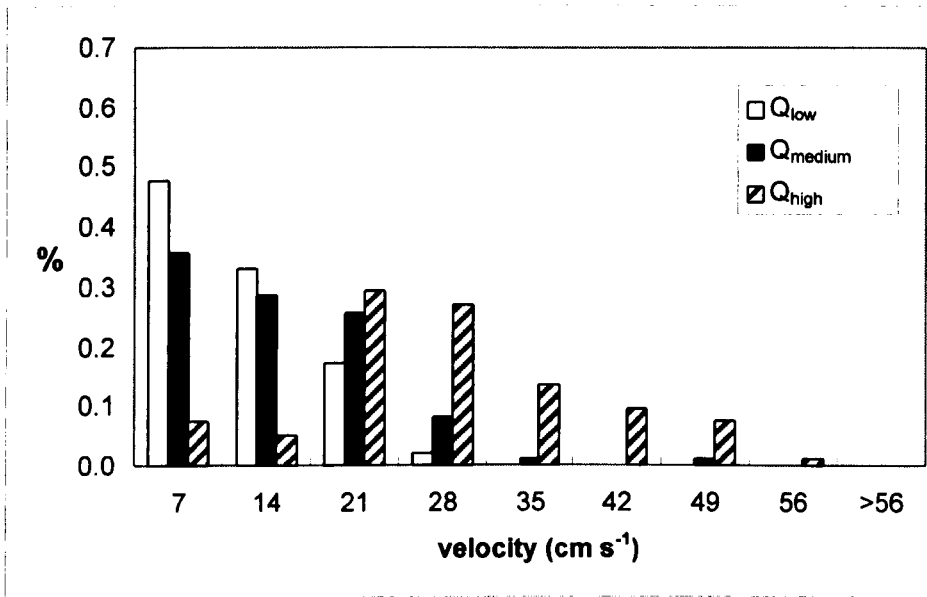
Fig. 4.3.: Velocity use (as a percentage of all fish) at three discharges.

With respect to mean column velocity, fish chose positions in a significant non-random manner in two of the three observed discharges. Figure 4.4. compares use and availability for every velocity interval at the three discharges. Habitat use differed significantly from availability at both Q_{low} (Chi-Sq.= 18.6, d.f.= 4, p=0.001) and Q_{high} (Chi-Sq.= 19.8, d.f.= 5, p=0.001) and bordered on statistical significance at Q_{medium} (Chi-Sq.= 10.5, d.f.= 5, P=0.06).

The only velocity class notably overused at Q_{medium} was between 14 and 21 cm s^{-1}, while areas with velocities exceeding 28 cm s^{-1} were markedly underused. During Q_{low}, velocities below 10 cm s^{-1} were underutilised and velocities between 10 and 20 cm s-1 were overutilised in comparison to availability. Similar velocities between 14 and 21 cm s^{-1} were preferred during Q_{medium}. At Q_{high}, there was a marked overuse of areas with velocities below 20 cm s^{-1} and underuse of those areas with velocities between 40 and 81 cm s^{-1}.
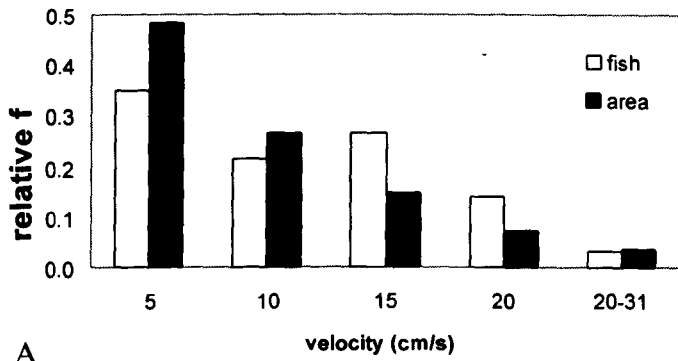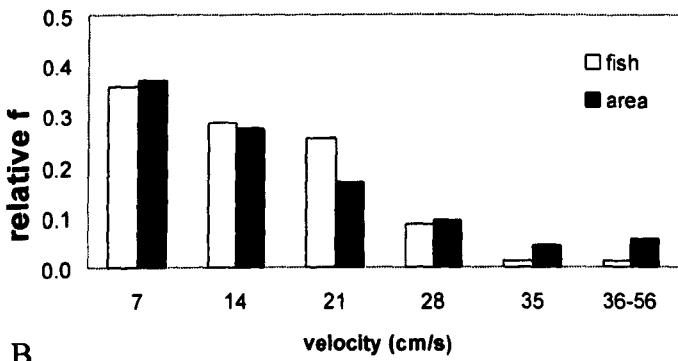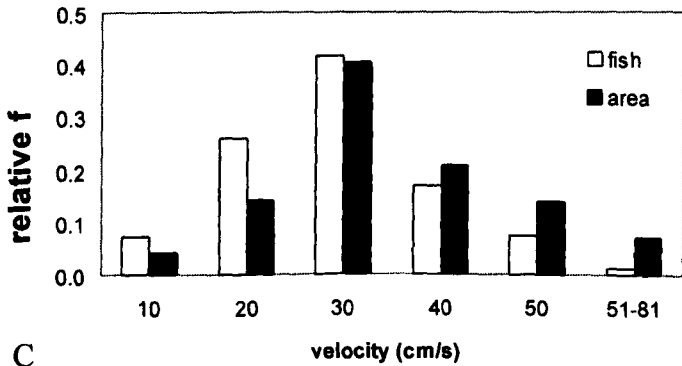
Fig. 4.4. Velocity use and availability at Q_{low} (A), Q_{medium} (B), Q_{high} (C), (see text for details)

4.3. Mean column velocity preference curves

Three velocity preference curves (called P_{low}, P_{medium} and P_{high}) were developed for the fish observation data at discharges Q_{low}, Q_{medium} and Q_{high} (Fig. 4.5.). Preference indices (scaled 0 to 1) of all three curves were greater than 0.75 at velocities between 15 and 20 cm s^{-1} and declined rapidly between 20 and approximately 35 cm s^{-1}. All three curves fell below a preference of 0.5 for velocities exceeding 35 cm s^{-1}. The preference curves were markedly different at velocities lower than 15 cm s^{-1}. The preference indices for low velocities were inversely related to discharge. The shape of the preference curves also differed markedly. P_{low} showed a narrow maxima around 15 cm s^{-1}, P_{medium} a less pronounced maxima at 20 cm s^{-1}, but preference declined constantly with increasing velocity for P_{high} (see Fig. 4.5.).
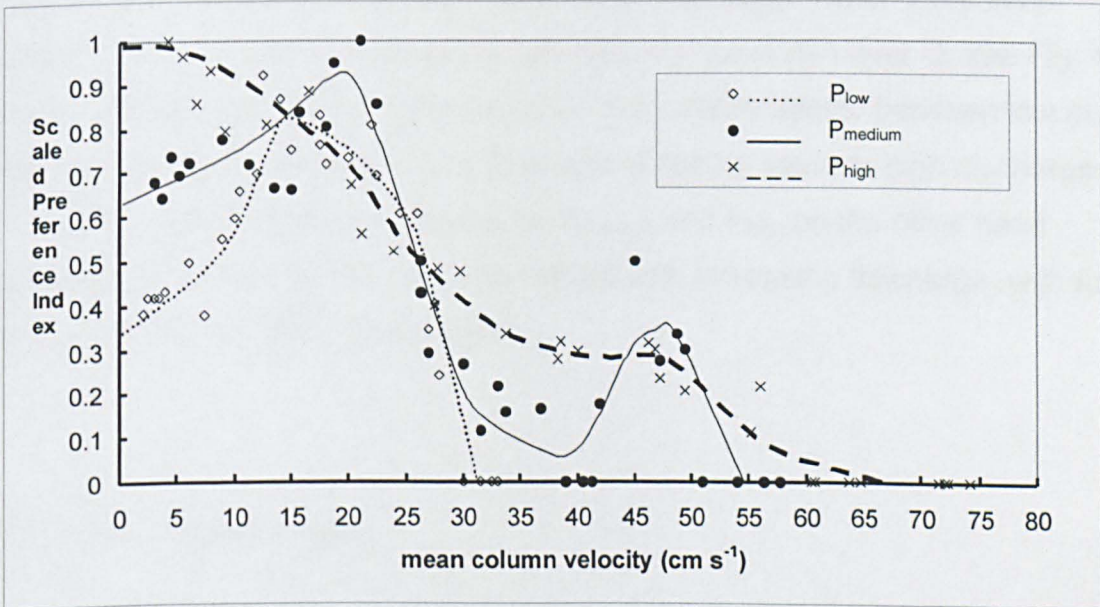
Fig. 4.5. Mean column velocity preference curves derived from observations at three discharges. Curves were fitted by eye

4.4. The effect of preference variation on the performance of an instream habitat model

To assess the effects of the differences in velocity preference curves derived at different discharges (Fig. 4.5.) on the application of PHABSIM, the three preference curves were used to calculate WUA at each of the three set discharges for the flume environment (Fig. 4.6.). Firstly, the habitat predictions were compared by using WUA calculated by P_{medium} as a reference datum. WUA sums of P_{low} were 28%, 24% and 26% lower but WUA sums of P_{high} were 30%, 19% and 1% higher than the reference for Q_{low}, Q_{medium} and Q_{high} respectively. Variation in WUA was also very high when measured against the actual unweighted area (see Fig. 4.6.), with WUA values for Q_{low} as high as 91% of total area calculated by P_{high} but only 50% when using P_{low}.

In terms of instream flow recommendations however, the most important factor is the rate and direction of change in WUA with discharge. These were very different for the three habitat discharge relationships (WUA over Q, see Fig. 4.6.). For P_{low}, there was a slight increase (2%) in available habitat between low and medium discharge, followed by a 28% loss of habitat towards high discharge. The habitat discharge relationships for P_{medium} and P_{high} on the other hand suggest immediate loss of available habitat with increasing discharge, with total losses of 29% and 45% respectively.

4.5. Summary of results:

Salmon parr were exposed to a velocity range of zero to 81 cm s^{-1} and utilised velocities between zero and 56 cm s^{-1}. Velocities used were distributed approximately in proportion to the availability of velocities at medium discharge. Fish were found to select the low end of the velocity range during high discharge and the high end of the velocity range during low discharge.

The velocity preference curves differed between the three discharges. There were also differences in the shapes of the curves in particular at low velocities as there was strong selection for areas of lowest velocities at high discharge. As a result, WUA sums calculated by PHABSIM using the three different preference curves varied up to two-fold. More importantly, habitat discharge relationships predicted by the model varied between preference curves, suggesting a slight increase in habitat for one curve but a large loss of habitat for another.
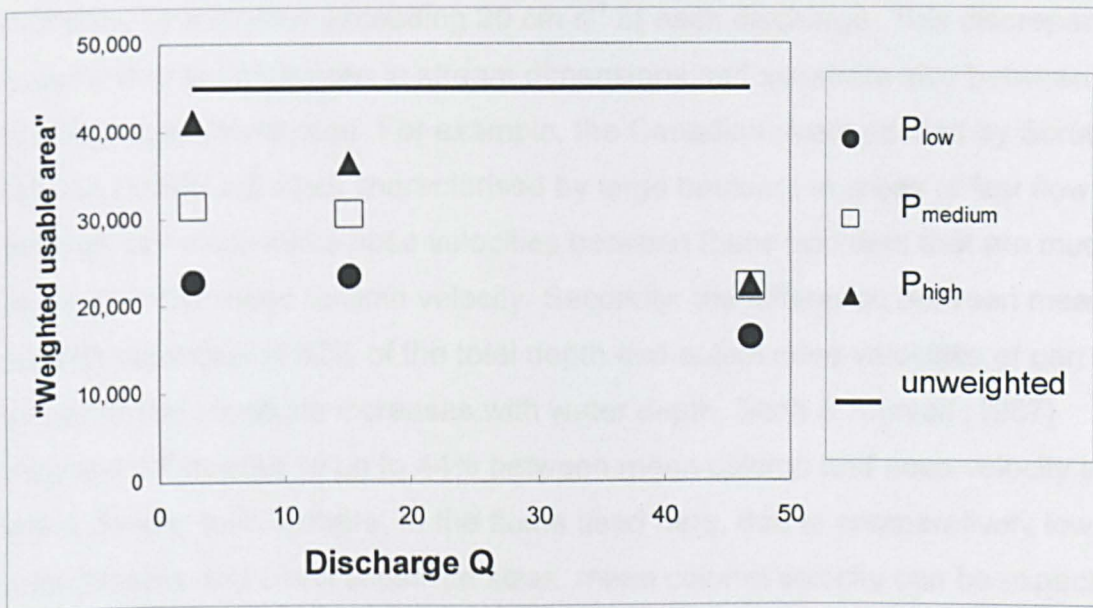
Fig. 4.6.: Weighted usable area, the output of PHABSIM, calculated using preference curves from three discharges

4.6. Discussion:

4.6.1. General velocity preference

In the experimental results reported above, salmon parr were distributed approximately in proportion to the availability of velocities at medium discharge, but tended to select the low end of the velocity range during high discharge and the high end of the velocity range during low discharge. The velocity preference

curves differed between the three discharges. In part, these differences were due to between-discharge variation in the range of velocities available.

At all three discharges, the velocity preference indices of the fish observed were high between 15 to 20 cm s^{-1} and lay within the preferred range for mean column velocity observed for YOY salmon by other workers (e.g., Heggenes, 1994; Scruton & Gibson, 1993; DeGraaf & Bain, 1986; Morantz et al., 1987). These studies also reported high preference indices at velocities as high as 80 cm s^{-1} (Scruton & Gibson, 1993) whereas the preference indices I calculated decreased markedly at velocities exceeding 20 cm s^{-1} at each discharge. This discrepancy may be due to differences in stream dimensions and substrate size between the different systems studied. For example, the Canadian rivers studied by Scruton & Gibson (1993) are often characterised by large boulders in areas of fast flow. Salmon can experience nose velocities between these boulders that are much lower than the mean column velocity. Secondly, the difference between mean column velocities at 60% of the total depth and actual nose velocities of parr sitting on the substrate increases with water depth. Scott & Shirvell (1987) reported differences of up to 44% between mean column and nose velocity in rivers deeper than 1 metre. In the flume used here, due to comparatively low water depths and small substrate sizes, mean column velocity can be expected to be much more similar to the focal velocity experienced by the fish on the substrate. Indeed, the preference curves for mean column velocity in this study are similar to those for nose velocity derived by DeGraaf & Bain (1986) and Morantz et al. (1987), in which the preference indices decreased rapidly at velocities less than 15 cm s^{-1}. The occupation of positions at relatively high velocities at low discharge is consistent with a strategy of maximising feeding opportunities because food availability is proportional to velocity (Fausch, 1984), within the limits of the hydrodynamic potential of the species (Sagnes & Statzner, 1999) and prey catch efficiency, which is inversely related to velocity (Hill & Grossman, 1993; Nislow et al., 1999). Conversely, the occupation of positions of relatively low velocities at high discharge may reflect sheltering behaviour. It is also possible that the shears between high and low flows vary with discharge

such that fish can conserve energy by occupying regions of very low velocity and harvesting prey from nearby areas of high velocity.

4.6.2. Velocity preference with changing discharge

A number of other studies have explored how habitat suitability criteria of salmonids change with discharge (e.g., Heggenes & Saltveit, 1990; Shirvell, 1994; Beecher et al., 1995; Pert & Erman, 1994), but to my knowledge none has controlled environmental variables to the extent that was achieved in this study. Contrary to the results found here, habitat preference was independent of discharge for brown trout, *Salmo trutta* L., at the mesohabitat (Heggenes, 1988) and rainbow trout *Onchorhynchus mykiss* at the scale microhabitat (Beecher et al., 1995). Williams (1997) and Jager & Pert (1997) criticised the work of Beecher *et al.* (1995), on the grounds of methodological and statistical concerns, concerning sample size (n= 21), appropriateness of the statistical tests chosen and the inappropriate comparison of habitat use data at one discharge with habitat preference data at the other. Shirvell (1994), although looking at habitat use (i.e., irrespective of habitat availability) rather than preference found significant differences in microhabitat use of juvenile coho salmon (*Oncorhynus kisutch*) but not for juvenile chinook salmon (*O. tshawytscha*) at three different discharges. Conversely, although not explicitly deriving suitability curves, Armstrong et al. (1998) found that Atlantic salmon parr studied in a pool-riffle sequence of a Scottish river remained in areas which were clearly highly unsuitable (i.e., drying up) during abstraction. Pert & Erman (1994), also studying rainbow trout, found velocity preference to be dependent on discharge, but contrary to observations here, the fish preferred the lowest velocities at low rather than high discharges. They linked this change in velocity preference to the effects of depth, hypothesising that some fish utilised the deepest parts of their observation arena regardless of velocity. The same reasoning could be applied to explain observed changes of velocity preference with discharge in populations of minnows (*Phoxinus phoxinus*) (Garner, 1997), in which some popular positions

were held despite considerable changes in velocity. In my experiment however, most fish did not maintain the same position between discharges (see chapter 6) and other habitat variables were constant or varied little. For example, depth was uniform over most of the area of the flume and fluctuated by only a few centimetres between discharges because water surface levels were controlled by a stand-pipe. Therefore, confidence in the findings which show that velocity preference shifted with discharge is assured.

The ranges of velocities used by the fish in the flume increased with discharge and paralleled the increase in the velocities available. This result is consistent with observations that Atlantic salmon parr use a wide range of velocities in the wild (Heggenes *et al.*, 1996b). An interdependence of velocity availability and preference has been recorded in studies comparing rivers (DeGraaf & Bain, 1986), pools, riffles and runs within a river (Vondracek & Longanecker, 1993), seasons (Rincón & Lobón-Cerviá, 1993) and now, with this study, between different discharges. The implications of this finding is of direct relevance to instream flow modelling.

4.6.3. Relevance of findings to the application of PHABSIM

The PHABSIM method attempts to accommodate variation in velocity availability by calculating a use/availability index, the preference index **P**, (Bovee, 1986). However, it is clear that when availability is zero, **P** must be zero, and suitability indices derived at one discharge will not apply when changes in discharge make additional velocities become available and these are used by fish. In my study, this problem of limited habitat availability would affect the prediction of WUA using preference curves derived at lower discharges and then applied to higher discharges. However, the effect of this was only slight, considering that WUA predictions varied the least when calculated for the high discharge (Fig. 4.6.). WUA variations were the highest at low discharge, which illustrates that the main source of error originates from the low velocities, which were common to all

discharges. The small effect of between-discharge variation in use of high velocities is due to two factors. First, the preference for high velocities was low at all discharges. Secondly, high velocities make up only small proportions of the total area. In contrast, preferences for low velocities varied greatly between discharges and these velocities were also abundant, especially at low discharge, at which variations in WUA were most pronounced (nearly two-fold).

In typical applications of PHABSIM, a preference curve is derived at a single discharge and is then used to test how WUA changes at other discharges. Used in this way, P low predicts a slight gain in habitat with increasing discharge and a subsequent loss between medium and high discharge, whereas P medium and P high predict pronounced habitat losses with increasing discharge (Fig. 4.6.). Therefore, recommended instream flows for salmon parr based on P low would be much higher than those based on P high. This observation shows that PHABSIM is likely to be seriously misleading as a management tool.

These data relates to variations in flow, such as may be experienced by fish during water abstraction and when water is discharged from reservoirs. It is difficult to interpret exactly what the suitability curves mean in terms of the fitness (survival chances and growth) of individual fish. The difficulty of interpreting the ecological significance of suitability curves is a serious shortcoming of the PHABSIM method irrespective of whether the curves themselves are robust predictors of habitat preference, or more accurately, habitat use.

5. How does population density affect habitat use across different discharges?

5.1. Introduction

Chapter 4 has demonstrated how changes in habitat availability due to stream discharge variation can affect the habitat use of salmon parr. The total range as well as the distribution of water velocities changed with stream discharge and fish experienced different velocities at their feeding positions and displayed different choice and avoidance behaviour. However, stream discharge is not the only major factor determining the amount and quality of microhabitat available to individuals of a population. For territorial species like juvenile Atlantic salmon, the accessibility of a suitable feeding position is also highly dependent on the degree of competition for the resource. Fausch (1984) reported the mean potential profit of feeding positions of juvenile coho salmon (*Oncorhynchus kisutch*), brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) to be directly related to the social dominance rank of the individual. Thus, the most dominant fish occupied the positions offering the highest net energetic gain. Hughes (1992b) found the same for arctic grayling (*Thymallus arcticus*) and showed by removal experiments that fish moved to better microhabitats, once a competitor was removed from it. The findings of these studies suggest that the spatial distribution of these stream salmonids follows the theory of Ideal Despotic Distribution (IDD) rather than Ideal Free Distribution (IFD) (Fretwell, 1972). IFD assumes that all individuals of a population utilise the same amount of resources so that patch fish density depends on habitat quality. Preference indices used in chapter 4 and by instream flow studies (e.g., Bovee, 1986) are based on the same logic of IFD in that they assign the highest preference to the habitat with the highest density. However, since IDD is the more appropriate theory of distribution for many

animals, preference indices for stream salmonids might be highly biased by overall population density. It was therefore decided to conduct a direct comparison of microhabitat utilisation at two population densities.

Secondly, it is important to illuminate the patterns of microhabitat availability and choice at different spatial scales. The types and amount of microhabitat prevalent in different mesohabitats (e.g., riffle, run, pool) differ at any discharge and change at different rates with stream discharge due to differences in their hydraulic geometry (i.e., slope, width/depth, cross-sectional profile, see Richards, 1982). In effect, the amount of suitable habitat for a fish will change at different rates and possibly direction (i.e., a gain in suitable habitat in the riffle coincides with a loss of habitat in the riffle), causing shifts between mesohabitats. In the flume, mean column velocities differed between the riffle and the pool at all discharges (Table 5.1., also see velocity maps chapter 3). In this experiment, analysis was conducted not only at the microscale as in experiment 1, but at the mesoscale too (i.e., pool and riffle).

One of the main challenges in the study of habitat choice behaviour of mobile species is the distinction between "preference", "random use" and "avoidance". In particular, if the system is spatially confined as well as constantly changing and the organism is confined to it, like in the case of salmon parr in small spawning burns. To identify choice, it is necessary to filter out the effects of quantitative availability: how much of each habitat is there to be used? Unfortunately, the indices typically devised to compensate for differences in availability (i.e., based on Ivlev's Electivity Index (Ivlev, 1961)) suffer from statistical flaws (see chapter 3., Lechowicz, 1982; Strauss, 1979), which make comparisons really only meaningful as effects to the applied instream flow model as has been shown in chapter 4. For this reason, the use of electivity indices has been avoided in this analysis. Instead, habitat use was taken "in the raw", regardless of habitat availability, for this analysis which centres around the effects of population densities. This is appropriate, because fish experienced precisely the same

physical habitat availability at both population densities since runs were conducted in the same observation areas at the same discharges. Fish densities used in this experiment (0.55 fish m^{-2} and 4.4 fish m^{-2}) should be well below carrying capacity, because natural densities reported for the Shelligan Burn, from where the fish used in this experiment were obtained, range from 2 to 12 fish m^{-2} (see Egglishaw & Shackley 1977)

It follows from the above that microhabitat availability for the individual fish is the result of a complex array of factors operating at several spatial and temporal scales and centring around the physical (e.g., stream bed topography), hydraulic (e.g., stream discharge) and biological (e.g., population density) characteristics of the stream ecosystem. By looking at habitat choice of fish at two different population densities across three widely different stream discharges and two spatial scales, the experiment focused on the following issues:

1. How does mesohabitat use of salmon parr vary with discharge and between population densities?
2. How does microhabitat use of salmon parr vary with discharge and between population densities?
3. How does microhabitat use within mesohabitats vary with discharge and between population densities?

5.2. Mesohabitat use in relation to population density and stream discharge

Mesohabitat use, defined as the use of "pool", "riffle" and "off" habitat, was highly dependent on population density at all three discharges. (Q_{low}: Chi-Square= 13.8, d.f.= 2, p= 0.001; Q_{medium}: Chi-Square= 12.1, d.f.= 2, p= 0.002; Q_{high}: Chi-Square= 11.9, d.f.= 2, p= 0.002). Riffle habitat was selected most at low density of 0.55 fish m^{-2}, used by 73-82% of the total population at the three discharges (Fig. 5.1.), but more fish used the pool than the riffle at a density of 4.4 fish m^{-2}, with 43-53% of all fish in the pool. The use of riffle habitat was consistently much lower and the use of pool habitat consistently much higher at the high fish density

at all three discharges. The use of "off" habitat was highest at density 4.4 fish m^{-2} with 17%, 15% and 13% of all fish using "off" habitat at Q_{low}, Q_{medium} and Q_{high} respectively. At density 0.55 fish m^{-2} fish were seen off the natural substrate at Q_{low} (9%) and Q_{medium} (14%) but not Q_{high}. Apparently, the use of "off" habitat slightly decreased with increasing discharge at density 4.4 fish m^{-2}, an observation that coincides with Q_{high} being the only discharge with no fish on "off" habitat during density 0.55 fish m^{-2}. (For a more detailed analysis regarding "off" habitat use see chapter 3.10.) The flume area split up into 42% "off", 37% riffle and 21% pool habitat. Habitat use was analysed in relation to this habitat availability. Fish used the habitats at non-random both at the density of 0.55 fish m^{-2} (Goodness-of-fit Test, χ^2= 46, df= 2, p< 0.001) and density 4.4 fish m^{-2} (Goodness–of-fit Test, χ^2= 186.52, df= 2, p< 0.001). "Off" habitat was strongly avoided in all cases but preference switched from the riffle at low population density to pool during high population density (Table 5.1.).

Table 5.1.: Number of fish observed and expected in comparison to the amount of available habitat area at low and high population density

Habitat	Area	Population density 0.55 fish m^{-2}			Population density 4.4 fish m^{-2}		
		Observed	Expected	Residual	Observed	Expected	Residual
Off	42%	5	27.7	-22.7	51	143.2	-92.2
Riffle	37%	50	24.4	**25.6**	123	126.2	-3.2
Pool	21%	11	13.9	-2.9	167	71.6	**95.4**
Total	100%	66			341		
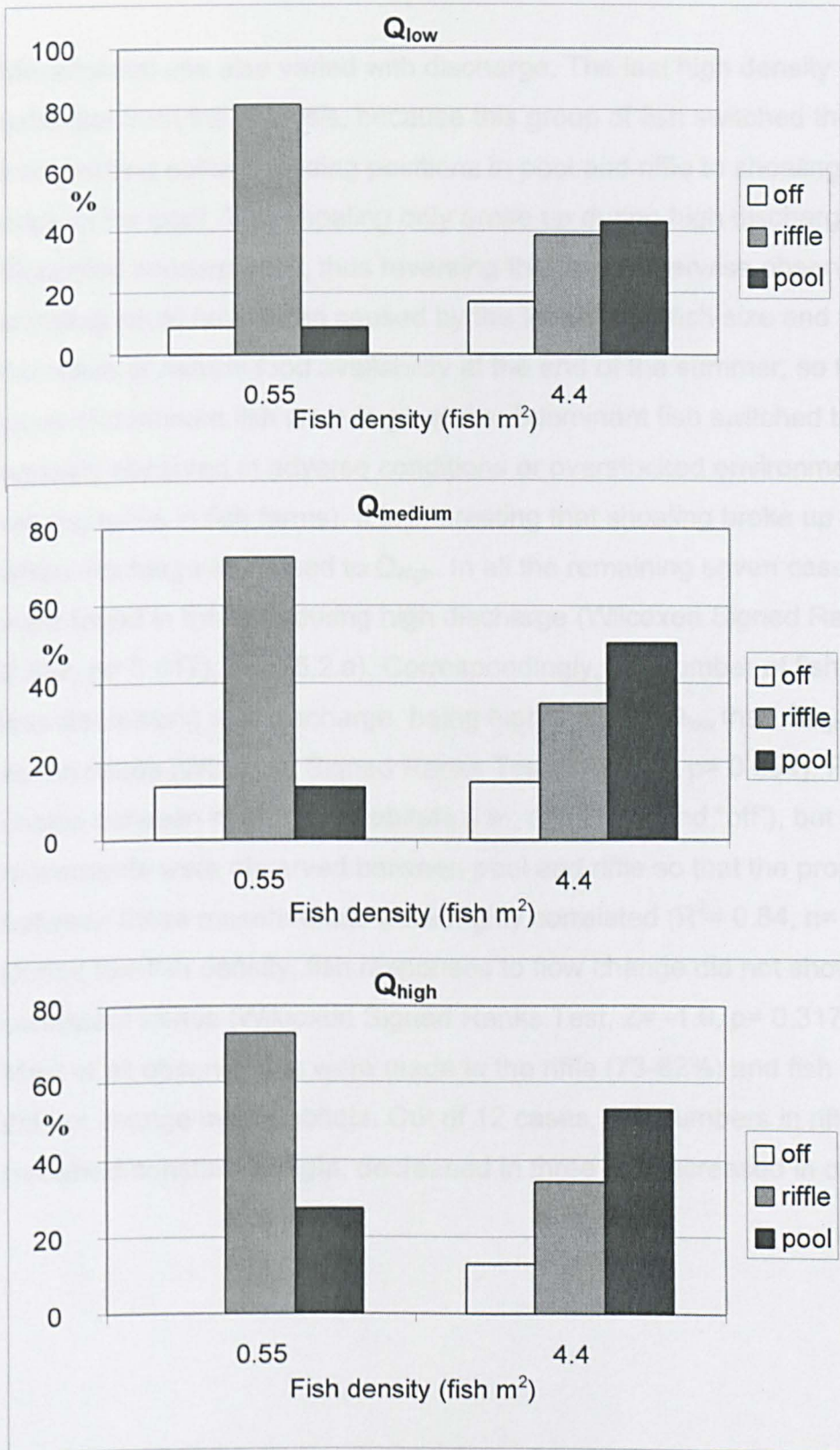
Fig. 5.1.: Proportional use of mesohabitat at two population densities over three discharges

Mesohabitat use also varied with discharge. The last high density run was excluded from the analysis, because this group of fish switched their behaviour from holding solitary feeding positions in pool and riffle to shoaling at the front edge of the pool. This shoaling only broke up during high discharge and fish dispersed consequently, thus reversing the trend otherwise observed. The shoaling could have been caused by the increase in fish size and the suspected decrease of natural food availability at the end of the summer, so that territory sizes of dominant fish were large and subdominant fish switched to a behaviour typically observed in adverse conditions or overstocked environments (e.g., rearing tanks in fish farms). It is interesting that shoaling broke up repeatedly when discharge increased to Q_{high}. In all the remaining seven cases, more fish were found in the pool during high discharge (Wilcoxon Signed Ranks Test, Z= -2.392, p= 0.017), (Fig. 5.2.a). Correspondingly, the number of fish in the riffle was decreasing with discharge, being higher during Q_{low} than Q_{high}, in six out of seven cases (Wilcoxon Signed Ranks Test, Z= -1.93, p= 0.054). Fish had the choice between three mesohabitats (i.e., riffle, pool and "off"), but most fish movements were observed between pool and riffle so that the proportions between these mesohabitats were highly correlated (R^2= 0.84, n= 24) During low fish density, fish responses to flow change did not show any consistent trends (Wilcoxon Signed Ranks Test, Z= -1.0, p= 0.317) (Fig. 5.2.b) Most of all observations were made in the riffle (73-82%) and fish most frequently did not change mesohabitats. Out of 12 cases, fish numbers in riffle at Q_{high} remained constant in eight, decreased in three and increased in one case.
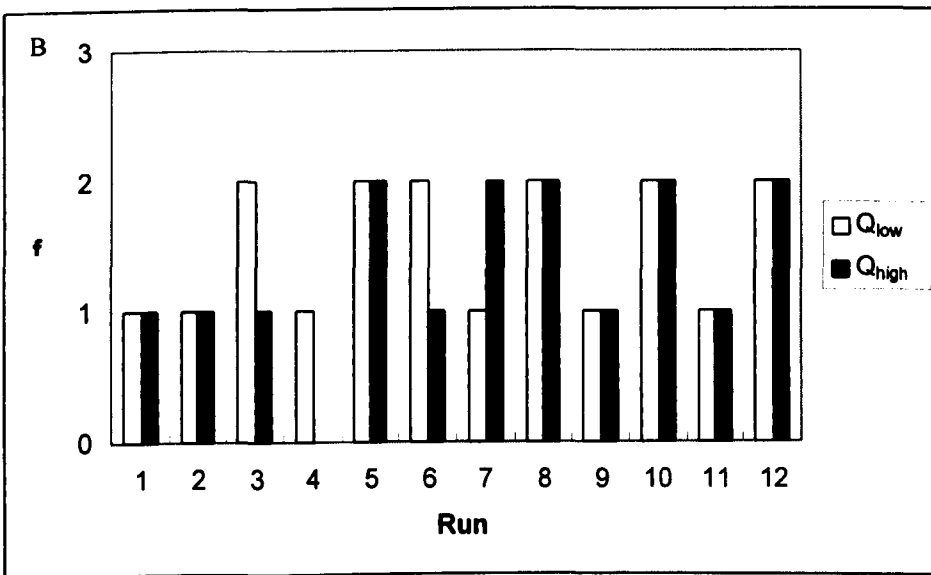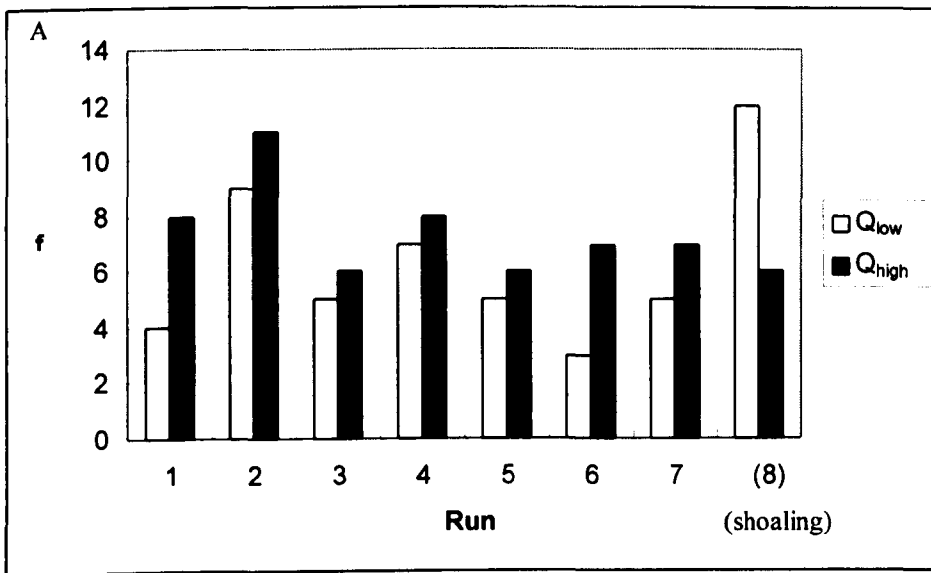
Fig. 5.2.: Number of fish in pool during Q_{low} and Q_{high} at density 4.4 fish m^{-2} (A) and density 0.55 fish m^{-2} (B)

5.3. Microhabitat use at low and high density during three different stream discharges

To begin with, the mean column velocities experienced by the two groups of fish with the same fish density were compared between the three different discharges. Mean column velocities at the fish positions were significantly different between all discharges with one exception. On a whole, velocities used

varied with discharge at density 0.55 fish m^{-2} (K-W Test, Chi-Square= 11.58, P= 0.003) and density 4.4 fish m^{-2} (K-W Test, Chi-Square= 124.58, P< 0.001) (see Table 5.2.). The velocities that fish used were highly different between Q_{high} and the two lower discharges (see Fig. 5.3.) for both fish densities. Between Q_{low} and Q_{medium}, velocities differed only at density 4.4 fish m^{-2} (Mann-Whitney U= 5575.5, P= 0.04) but not density 0.55 fish m^{-2} (Mann-Whitney U= 205.5, p= 0.391). Therefore, fish experienced higher velocities at their holding positions with every increment of stream discharge with the exception of one case, that of Q_{low} to Q_{medium} at density 0.55 fish m^{-2}, where velocities did not differ between the discharges.

Table 5.2.: Mean column velocities (cm s^{-1}) at fish positions at three discharges and two population densities, (cells with different letters are significantly different at p≤ 0.05)

Density (fish m^{-2})	Q_{low} Median (Lower, Upper Quartile)		Q_{medium} Median (Lower, Upper Quartile)		Q_{high} Median (Lower, Upper Quartile)	
0.55	13 (9, 19)	a	18 (5, 26)	a	24.5 (18, 34)	b
4.44	7 (4, 12)	c	10 (3, 17)	d	24 (18, 30)	b

In a second analysis, mean column velocities experienced by the fish at low and high population density were compared at each discharge. Physical microhabitat availability was precisely the same at density 0.55 and 4.4 fish m^{-2}, because runs at both fish densities were conducted in alternating order throughout the summer. Fish used higher velocities at population density 0.55 fish m^{-2} during the low and medium discharges, but the same during high discharge (Table 5.2., Fig. 5.3.). During Q_{low}, fish on average used higher velocities at the density of 0.55 fish m^{-2}

(median = 13 cm s^{-1}) than at the density of 4.4 fish m^{-2} (median = 7 cm s^{-1}) (Mann-Whitney U= 777.5, p= 0.004). The same was found at Q_{medium}, with a median of 18 cm s^{-1} at a density of 0.55 fish m^{-2} but a median of 10 cm s^{-1} at a density of 4.4 fish m^{-2} (Mann-Whitney U= 909.5, p= 0.037). However, at Q_{high} a median of 24.5 cm s^{-1} and 24 cm s^{-1} was not different between both population densities (Mann-Whitney U= 1145.5, p= 0.647).
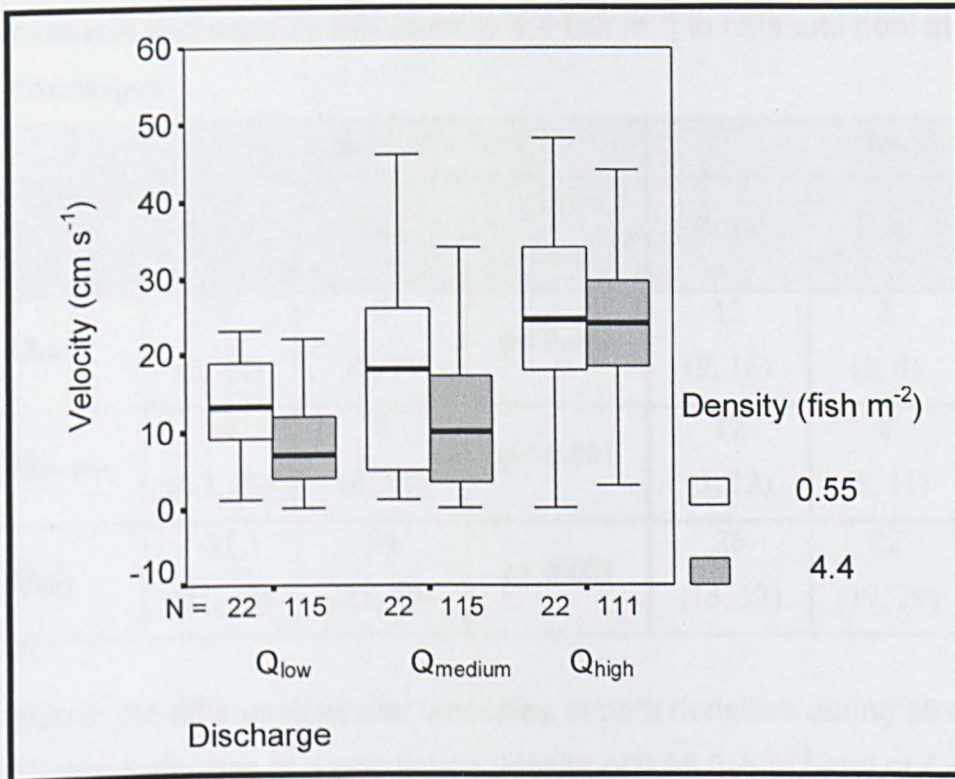
Fig. 5.3.: Velocity used by all fish at two population densities during three discharges. Median (line), interquartile range (box) and range (whiskers)

5.4. Microhabitat use within and between mesohabitats

Meso- and microhabitat use have been shown to be density-dependent in all scenarios but one (microhabitat use during high discharge). Because water velocities were significantly higher in the riffle than in the pool at all discharges (Table 5.3.) and a much larger proportion of the population used the pool during a density of 4.4 fish m^{-2} (see chapter 5.2.), the differences in velocity use

between a density of 0.55 and a density of 4.4 fish m^{-2} could be due to the shift of mesohabitat use only. Higher velocity use at low population density could thus be an indirect effect of mesohabitat choice. An test was therefore conducted to see if velocity use would vary with density within the riffle habitat. The sample size for the pool habitat was too low for this analysis.

Table 5.3. : Mean column velocity, (median, lower and upper quartile, in cm s^{-1}) available and used by fish (density 4.4 fish m^{-2}) in riffle and pool at three discharges

Discharge	*Available*			*Used*		
	Riffle	Pool	*Different?* *Mann-W.U*	Riffle	Pool	*Different?* *Mann-W.U*
Q_{low}	7 (2, 14)	5 (2, 7)	p< 0.001	12 (9, 16)	5 (3, 8)	p< 0.001
Q_{medium}	14 (4.3, 23)	8 (6, 11)	p< 0.001	17 (3, 22)	8 (5, 11)	p= 0.001
Q_{high}	31 (21, 43)	24 (21, 29)	p< 0.001	26 (15, 32)	22 (19, 29)	p= 0.847

Fish in the riffle used similar velocities at both densities during all discharges. Median velocities at a population density of 0.55 fish m^{-2} and of 4.4 fish m^{-2} respectively were 15 cm s^{-1} and 12 cm s^{-1} at Q_{low}, 18 cm s^{-1} and 17 cm s^{-1} at Q_{medium} and 28 cm s^{-1} and 26 cm s^{-1} at Q_{high}. Although the median at a density of 0.55 fish m^{-2} was slightly lower than the median at a density of 4.4 fish m^{-2} (Fig. 5.4) in all three cases, the differences were not significant (Q_{low}: Mann-Whitney U= 344.5, p= 0.356; Q_{medium}: Mann-Whitney U= 283, p= 0.502; Q_{high}: Mann-Whitney U= 266.5, p= 0.477).

The suggestion, that the density-dependent differences in mean column velocity use are mostly caused by the large number of fish in the slower pool at high population density is further confirmed by the fact that these fish used lower

velocities in the pool than in the riffle at Q_{low} and Q_{medium} (Table 5.3.). At Q_{high}, no differences in velocity use between the two densities was found (chapter 5.4.).
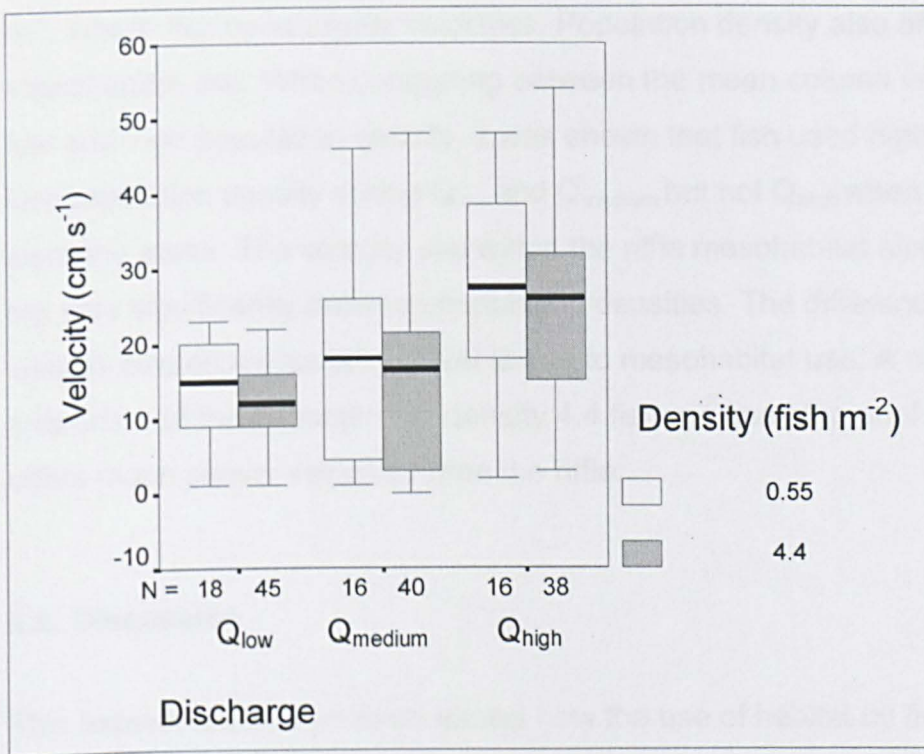
Fig. 5.4.: Velocity used by fish in the riffle at two population densities during three discharges. Median (line), interquartile range (box) and range (whiskers)

5.5. Summary of results

The findings of the experiment described above illuminate several effects of density and discharge on habitat use of salmon parr on meso- and microscales. The use of mesohabitat was most strongly dependent on population density. Only 18-27% of the population used the pool at low population density, but during high density it were 47-57% of the population. Discharge also affected the use of mesohabitat. With the exclusion of the last run of the season, when fish were shoaling instead of holding feeding positions, more fish were found in the pool during Q_{high} than during Q_{low} at high population density. No effect of discharge could be detected for the low population data.

Microhabitat use, regarding mean column velocity, varied with discharge in most cases. Velocities experienced between discharges were always higher at the higher discharge except between Q_{low} and Q_{medium} at population density 0.55 fish m^{-2}, where fish used similar velocities. Population density also affected microhabitat use. When comparing between the mean column velocities used by low and high population density, it was shown that fish used higher velocities at low population density during Q_{low} and Q_{medium} but not Q_{high} when velocities used were the same. The velocity use within the riffle mesohabitat alone however did not vary significantly between population densities. The difference found for velocity use on a population level is due to mesohabitat use. A much higher proportion of the population at density 4.4 fish m^{-2} used the pool habitat which offers much slower velocities than the riffle.

5.6. Discussion

This experiment and analysis shows how the use of habitat by fish is controlled by factors other than actual physical habitat quality alone and how density effects vary across spatial scales. The use of meso- and microhabitat was highly affected by changes in stream discharge and fish population density. The findings regarding density-dependent use of mesohabitats was consistent with those by Greenberg (1994) for brown trout and Bult et al. (1999) for older parr, who found that pool use increased with population density. Importantly, here this pattern was shown to be consistent over the wide range of hydraulic conditions of a 15-fold discharge variation. The distribution of fish apparently changed so much between low and high population density, that preference switched from riffle to pool. In relation to the areal extent of the habitats, a strong avoidance was observed for the pool at low population density, but the trend was reversed at high population density when the fish concentration in the pool exceeded that of the riffle. This further confirms the sensitivity of preference in its usual sense (identified as proportional overuse of area) to availability that has already been demonstrated for microhabitat in chapter 4. It also raises issues of scale:

whereas the preference of the population seemingly changes from riffle to pool, the preference of each individual fish can not automatically be deduced from the population census. However, both Greenberg (1994) and Bult et al. (1999) concluded from their results, that preferred habitats were saturated first and secondary habitats only used consequently with increasing population density. Hughes (1992b) demonstrated this impressively with removal experiments with Arctic grayling (*Thymallus arcticus*), which occupied positions in a pool in rank order parallel to their dominance status and readily moved into the more favourable position once the competitor was removed. Whereas this pattern, based on the Ideal Despotic Distribution Theory (Fretwell, 1972), can be the correct explanation for the fish distribution observed, the possibility remains that other density-dependent biotic processes interact with the habitat choice of the fish. For example, overall invertebrate food abundance could be reduced by a high fish population density (e.g., Flecker, 1984) to a degree that the food available to the individual fish might not suffice to cover the higher metabolic holding costs in the faster flows of the riffle habitat.

Both Greenberg (1994) and Bult et al. (1999) only looked at the effects of density on mesohabitat use but not microhabitat use. The observed difference in mesohabitat use with population density could be due to differences in microhabitat quality between the mesohabitats. However, microhabitat quality changes with discharge in the mesohabitats so that the observed pattern of density-dependent mesohabitat use should vary with discharge. At high population density, more fish used the pool during Q_{high} than during Q_{low}. During low population density, no effect of discharge was detectable. In part this may be due to the smaller sample size at this density with its limited range of possible combinations (i.e., at two fish per arena, only nil, one or two fish were possible in the pool). The effect of discharge on mesohabitat use at high population density was only slight in comparison to the overall difference in mesohabitat use between the two population densities. The increase in discharge causes water velocities to increase in both pool and riffle, and a move of more fish to the pool can be the result of either a contraction of suitable habitat in the riffle or expansion of suitable habitat in the pool or even both. There is no way of

determining if "push" or "pull" factors are operating for the fish. It seems reasonable to assume the riffle to be a preferred habitat, based on the preferential choice behaviour at low population density. Consequently it can be concluded that the discharge-related increase in fish numbers in the pool and decrease in the riffle is caused by a contraction of suitable habitat in the latter. If water velocity microhabitat choice on an individual level is the reason for the mesohabitat use of the population, density-specific differences on the microscale must exist. These were observed in the experiments at both Q_{low} and Q_{medium}. Fish used higher velocities at low population density, which is not surprising, because the majority of fish at this density used the riffle with it's higher mean water velocity. Consequently, when testing for differences in velocity used only by those fish in the riffle, no differences were found between the densities. Therefore, fish occupied positions with similar velocities in the riffle during both densities, but more fish were using the slower pool at high population density which brought down the overall average. The velocity use of the fish in pool and riffle at high population density mirrored the availability in these mesohabitats in that fish used higher velocities in the riffle than in the pool during Q_{low} and Q_{medium}. In contrast, during Q_{high} the available velocities in the riffle exceed those in the pool too, but fish used the same velocities in both mesohabitats. The reason for this is the avoidance of the highest available velocities in the riffle by the fish on the one hand and a good availability of intermediate velocities (10- 25 cm s^{-1}) in the pool on the other.

In conclusion, the majority of a population was found in the riffle during low population density, but in the pool during high population density which suggest that more suitable microhabitats are found in the riffle and that these are saturated first. This is confirmed by the fact that no differences existed in microhabitat use in the riffle between low and high population density and that mesohabitat use at high population density responded to the differences in changes of microhabitat conditions with discharge. These interactions between density-dependent and physical variables demonstrate how the interpretation of fish frequency data for building habitat suitability criteria could be unrealistic with regards to the true density- and discharge-dependent habitat suitability.

6. Site fidelity at different discharges: how different are microhabitats of maintained and vacated positions?

6.1. Introduction

Salmon parr in streams are thought to occupy stationary feeding positions. These positions are typically maintained over long periods of time and defended against intruders. Such territorial behaviour is termed "sit-and-wait" strategy and optimises the exploitation of limited food resources for individuals in spatially confined systems like that of a stream (Gibson, 1988). Although some fish resort to benthic feeding and parts of a population can adapt a strategy of roaming (Armstrong et al., 1999), the "sit-and-wait" strategy while drift feeding is considered the dominant form of foraging for stream-dwelling salmon parr (Gibson, 1993). Fish move from their waiting position to intercept drifting macroinvertebrates and return to the initial position. Fish optimise the net energy gain with this behaviour by waiting in low velocity areas (e.g., on the substrate) while harvesting from areas of higher drift rates which are related to higher water velocity (e.g., zones of converging flow)(Hughes 1992b). This behaviour should be most prevalent in shallow and fast flowing mesohabitats like riffle, runs and shallow pools, as are typically found in large parts of Scottish spawning streams. Such behavioural patterns have been investigated by biologists for decades (Gibson, 1988). As a result of territoriality, the carrying capacity of a stream is traditionally seen as a function of the number of territories it can provide. This in turn depends on factors like physical habitat features (e.g., stream bed slope, substrate composition, overhead cover; Boussu, 1954), food productivity (e.g., invertebrate abundance; Ensign & Strange, 1990), interspecific competition (e.g., Atlantic salmon and brown trout, Kennedy & Strange, 1986), and predation (e.g.,

brown trout and pike *Esox lucius*; Greenberg, 1994). More recently, preference for discrete microhabitat conditions has been found to affect spatial habitat use of stream salmonids strongly as well. Although the before-mentioned preferences change over time (e.g., food can change diurnally and seasonally) and space (e.g., substrate varies between reaches and mesohabitats), they are not as variable as hydraulic microhabitat conditions which change with flow fluctuations. In theory, this raises a conceptual conflict between the behaviour of territoriality on the one side and microhabitat selection on the other. The question must be asked as to whether fish adjust their positions to the preferred microhabitat, which could mean leaving their territory, or whether they tolerate suboptimal microhabitat conditions to remain at an established position? Both scenarios by themselves seem equally unlikely and the behavioural response of fish movement may be a balancing act between territoriality and microhabitat suitability, subject to threshold conditions. In reality, the decision of the fish to shift positions can be expected to be the result of a combination of factors, of which the before-mentioned are only two. However, small movements of a few centimetres might suffice to adjust microhabitat conditions but not result in the loss of territory. To address this question, the spatial resolution of the fish position data needs to be very high, probably beyond the accuracy achievable in normal field observations, but such data have been obtained in the flume experiments conducted as part of this research. The technical details of these experiments are summarised in chapter 3.10.4.

The use of spatial data permits a new approach to the questions of velocity preference by comparing the hydraulic conditions at the positions fish used after a change in discharge to those at the positions they had used at the other discharges. The actual choice is compared to the conditions that would have occurred at the other positions. The advantage of this comparison over commonly applied approaches to the problem is that it avoids comparisons *across* different discharges, which suffer from the problem of habitat availability. Microhabitat changes greatly with discharge so that the different range and

frequency of conditions available to the fish make the comparison of the habitats used at different discharges very difficult to interpret (see chapter 4). The use of electivity indices can compensate for the abundance of each habitat type to a degree but not for differences in the range of habitat types and has proven to be statistically flawed (Strauss, 1979; Lechowicz; 1982; see chapter 3.8. for discussion). Instead, by comparing the true locations with those vacated separately at each discharge, the comparison operates at the scale relevant to the decision process of the fish which according to the theory of territoriality should prefer to stay near the previous location but must accommodate its needs within the conditions present.

In this analysis, the site-fidelity of the fish in the flume is examined at two different temporal scales, using permanent five-minute observations of individual fish in the one case and single positions between days with different discharges in the other case. Firstly, the movements of individual fish over five minute observation periods are analysed to see if fish maintained positions and if this varied with discharge or between mesohabitats. It was decided to conduct these analysis with the data at hand although the experiments were not designed specifically to assess site fidelity and the data can not cover all aspects of site fidelity in effect. In particular some temporal aspects of site fidelity are unresolved (e.g., how long did fish use particular positions) and a control would have been very desirable (i.e., how did fish maintain positions during constant discharge). Armstrong et al. (1999) has recently challenged the classic view for juvenile salmon of simple territories with clear boundaries, so that it appeared advisable and worthwhile to examine the spatial behaviour of the fish in the flume before conducting further analysis based on the assumption that fish maintain positions. In the second and main part, fish positions are examined between different discharges to find out if the same positions were occupied despite the discharge-related changes in microhabitat. The positions taken at each discharge are then analysed at *all* discharges to see if microhabitats at chosen positions were different from those at the vacated positions. Finally, water velocity at the chosen

positions are compared to velocities at random positions to see if preference occurred in relation to general availability.

The following site fidelity and microhabitat questions are therefore addressed:
1. Do fish change their positions with changes in discharge?
2. Does site fidelity vary with discharge and between mesohabitats?
3. What are the differences in microhabitat conditions at each discharge between the positions fish actually used and those positions they had used at the other discharges?
4. How do microhabitat conditions at the chosen positions differ from random?

6.2. Short-term movements of fish

During 1997, groups of four fish were observed at Q_{low}, Q_{medium} and Q_{high}. After a acclimatisation period of at least 48 hours at Q_{medium}, fish observations took place between 9:00 and 17:00 hours and a minimum settling time of at least 6 hours was permitted after each change of discharge. Each individual fish was observed for five minutes and positions were recorded every minute. A total of 48 five-minute fish observations were made over three discharges in four runs. Fish positions were fixed with the help of two eye-sights which were checked every minute for a change in position minute (for more information see chapter 3). It was found that the fish remained stationary in 29 cases and moved positions within five minutes in 19 cases, of which some changed position only once, others several times (see Table 6.1.). Distances moved varied between 0.5 cm and 137 cm, with a median of 31.7 cm (lower quartile = 14.1 cm, upper quartile= 71.1 cm. Mean sampling error for 95% of all positions= 2.1 cm; see Table 3.1.). Only in two of the 39 individual position changes did fish change mesohabitats (as previously defined as pool and riffle). Positions were recorded five times per five-minute observation so that four changes were the highest possible number of changes to be observed. The numbers of position changes observed were tested against a theoretical distribution, based on the assumption that fish move and stay at random, so that the probability of position change for each of the observation equals p= 0.5. From this it follows that both extremes (i.e., none or four position changes) have the lowest probability (p= 0.0625) and two position changes the highest probability (p= 0.38). The observed number of moves deviated significantly from the random pattern (Chi-Square= 253.3, d.f.= 4, p< 0.001). As the residuals show (Table 6.1.), 26 cases more than expected were found to stay at their position and much less fish than expected moved one, two or three times. Therefore, fish were more likely to stay than to move over short time periods.

Table 6.1.: Number of minute-to-minute position changes of individual fish in five minutes (see text for definition of expected values)

Number of position changes	N observed	N expected	N residual	% residual
0	29	3	26	54%
1	5	12	-7	- 14%
2	10	18	-8	- 17%
3	2	12	-10	- 21%
4	2	3	-1	- 2%
Total	48	48	0	

The same data was tested further to see if site fidelity over five minutes differed between the two mesohabitats. Nine of 29 fish (31%) changed positions in the riffle and nine of 18 fish (50%) changed positions in the pool. A single fish that was found on "off" habitat and did not move and had to be excluded from the analysis for statistical reasons due to insufficient sample size for this mesohabitat. However, the apparent difference in mobility between fish in riffle and pool is statistically not significant at the 5% probability level (Fisher's Exact Test, Chi-Square= 1.691, d.f.= 1, p= 0.161), which could be due to the low sample size. The frequency of fish movements was not affected by discharge (Chi-Square= 0.73, d.f.= 2, p= 0.694). The number of movements was also not correlated to temperature (p= 0.458), the number of feeding attempts by the fish (p= 0.149), the mean water velocity at the positions (p= 0.974) or the mean water depth at the positions (p= 0.575).

Water temperature ranged between 9 and 19 degrees Celsius during the experiment, but was clustered into two groups: one at 9-11 degrees (n= 12) and the other at 16-19 degrees Celsius (n= 36). All fish movements were observed in the latter group whereas fish did not changes positions in the low temperature sample (Chi-Square= 10.483, d.f.= 1, p= 0.001). However, the finding that fish

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are more likely to hold position than to move, as reported in chapter 6.2., still holds true if the low temperature data is excluded (Chi-Square= 106.37, d.f.= 4, p= 0.000).

6.3. Site fidelity across discharge changes

Visual observation of fish movements suggested that fish did not utilise the same positions during Q_{low}, Q_{medium} and Q_{high} in most of the cases (compare Fig. 6.2. and Fig. 6.3.). During the 1998 trials with high fish densities (4.4 fish m^{-2}), observation routines of continuous five minute monitoring were not feasible because of the high number of 32 fish for which locations had to be fixed while making certain that no individual was observed more than once. Hence, no information could be gathered about short-term movements as in 1997, but the data allows analysis whether fish positions were maintained or vacated across discharges and also, with the help of GIS analyses, how far apart chosen fish positions were between the discharges. The data does not track individual fish (the reasons for not marking individual fish are stated in chapter 3.4.) but refers to positions only. However, if fish do not stay at their positions this will show, because the same position will not be occupied again, unless by chance for which the probability can be statistically determined.

Positions within 5 centimetres of the old positions, (i.e., approximately one fish length) were defined to be maintained positions, to accommodate for the mean sampling error of position fixing (i.e., 21 mm, see chapter 3.6.) and minor position changes of the fish. In total, with regard to this definition, only 27 out of 226 positions were occupied before and after a discharge change. This equates to 12% of all positions being maintained. If fish used habitat at random, the probability of any of the 16 fish occupying the pre-change position by chance would be 16 (i.e., fish per run and arena) in 880 (i.e., 5 cm cells in observation area), which equals p= 0.02, so that only 2% of pre-change positions would be

occupied again and not 12% as was observed. Thus, 10% more positions were occupied by a fish after discharge had changed than could be expected from chance (Goodness-of-fit test, Chi-Square= 131.641, d.f.= 1, p< 0.001). Although this confirms that 12% of the positions were occupied at two different discharges, it shows that 88% of positions were not used at different discharges.

6.4. Are mean column velocities different between maintained and vacated positions?

The analysis above has demonstrated that on average 12% of positions were occupied both before and after a change in discharge so that the large majority of fish had moved in response to flow variations. The mean distance for the nearest position taken up after the change was 17 cm, which means that in the most conservative case a fish moved at least this distance. In reality however, the nearest position will often be occupied by a different fish so that the true distances moved between flows should exceed this mean distance considerably. The main question in the context of instream flow modelling and the concept of microhabitat suitability in particular, is if the fish adjust their positions to optimise microhabitat conditions. If microhabitat optimisation is the case, the mean column velocity at the positions that fish chose at each flow must be different from those that fish would have experienced had they maintained their positions occupied at the other flows. Therefore, at each discharge velocities were modelled for both the true fish locations and the locations that fish had used at the two other discharges. At each discharge, the positions that fish used are called "true positions" and the positions from the other two discharges are referred to as "hypothetical positions".

Mean column velocities differed significantly between Q_{low} positions and the Q_{medium} and Q_{high} positions, but not between the latter two (see Tables 6.2. and 6.3. for all statistics). During Q_{low}, fish experienced higher velocities at the true

positions than they would have experienced had they maintained the positions occupied during the two higher flows. These positions in turn were significantly slower during their respective discharges than the hypothetical Q_{low} positions would have been. Thus, at Q_{low} fish adjusted their positions towards areas with faster velocity. In relation to the total range of velocities at this discharge, velocities were 6% higher than they would have been at the other positions. During Q_{high} and Q_{medium} however, the positions from Q_{low} were not maintained and actual positions featured mean column velocities between 10% and 13% slower than those at the Q_{low} positions. No difference in water velocities was found between Q_{medium} and Q_{high} positions.

Table 6.2.: Velocities at fish positions at three discharges (bold sets are true positions fish occupied at each discharge, the others are hypothetical)

Discharge	Positions observed at	Mean column velocity (cm s^{-1})		
		Median	Lower quartile	Upper quartile
Q_{low}	**Q_{low}**	**7.6**	**4.1**	**13.2**
	Q_{medium}	6.1	2.9	10.1
	Q_{high}	6.1	3.2	9.5
Q_{medium}	Q_{low}	16.8	8.5	22.6
	Q_{medium}	**9.5**	**4.3**	**17.7**
	Q_{high}	10	5.6	17
Q_{high}	Q_{low}	31.7	22.8	41.2
	Q_{medium}	25.8	20.9	32.3
	Q_{high}	**23.5**	**18.6**	**30.9**

Table 6.3.: Testing for differences between true (bold set) and hypothetical velocities. (p≤ 0.05 underlined)

Discharge	Comparing positions observed at	Velocity difference in % of range	Mann-Whitney U	$z =$	$p =$
Q_{low}	Q_{low}- Q_{medium}	+ 6%	3656.5	-2.467	<u>0.014</u>
	Q_{low}- Q_{high}	+ 6%	3349	-3.069	<u>0.002</u>
Q_{medium}	Q_{medium}- Q_{low}	- 13%	3160.5	-3.755	<u>0.000</u>
	Q_{medium}- Q_{high}	- 1%	4528.5	-0.459	0.654
Q_{high}	Q_{high}- Q_{low}	- 10%	3003	-3.982	<u>0.000</u>
	Q_{high}- Q_{medium}	- 1%	4216.5	-1.247	0.212

6.5. Water velocity at true fish positions in comparison to random positions

Sets of random positions were generated for all discharges and mesohabitats in both observation arenas. The number of random positions equals that of observed fish positions for each of these groups. Mean column velocities were determined for each random position and compared to the velocities fish experienced at their positions. Fish experienced velocities significantly different from random at their positions during high and low discharge, but not during medium discharge (Fig. 6.1.). During Q_{low}, mean column velocities at fish positions were higher on average (Mann-Whitney U= 3532.0, p= 0.018). Mean column velocities were the same as random during Q_{medium} but lower than random (Mann-Whitney U= 3574.5, p= 0.007) at Q_{high}. In relative terms fish used velocities 7% faster at Q_{low} and 5% slower at Q_{high} on average than randomly available.
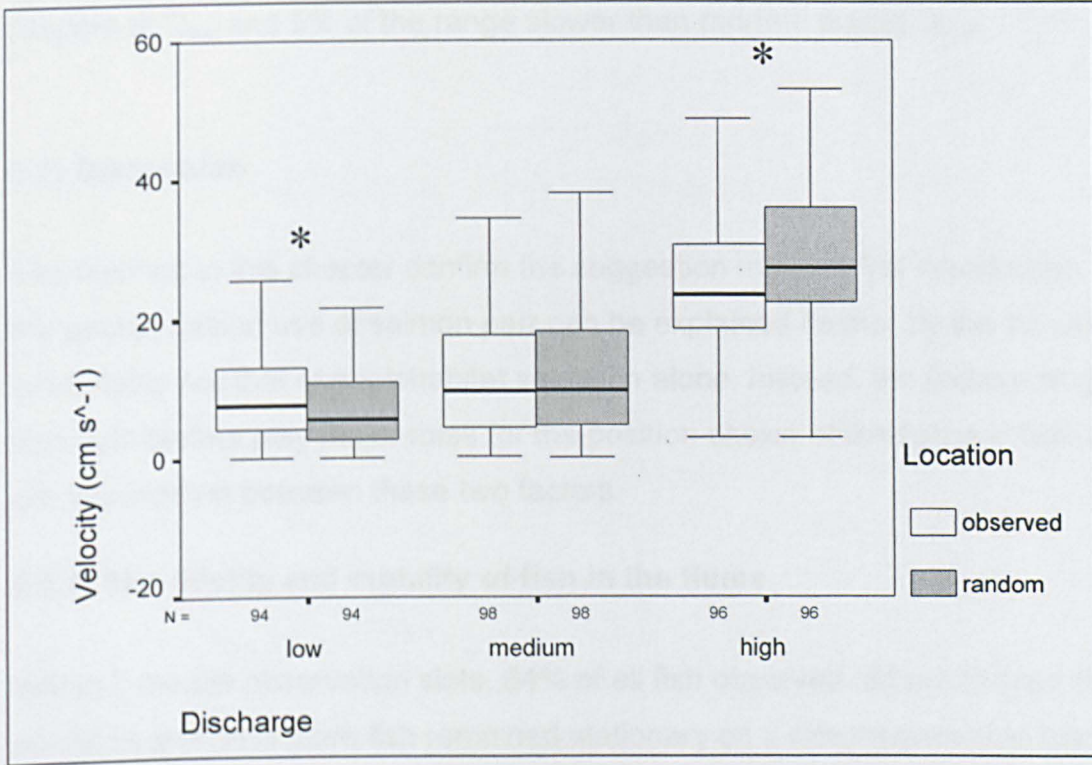
Fig. 6.1.: Mean column velocities at true fish locations and random locations
(* are different at p≤ 0.05)

6.6. Summary of results

At a density of 1.1 fish m^{-2}, 64% of all fish did not change position within a five
minute time slot. The other fish moved approximately six fish length on average
(30 cm), which equates to nearly a third of the width and length of both the pool
and riffle habitat. This illustrates that fish displayed site fidelity to a degree but
were certainly not all permanently fixed to one position. Fish did not change
positions at day-time during a run with temperatures of 9-11 degrees Celsius.
Fish adjusted their positions for velocity between Q_{low} and the other flows. As a
result they occupied positions 6% faster during Q_{low} compared to the positions
from the other discharges and vacated the low flow positions in favour of 10% to
13% slower positions at the higher discharges. Fish chose positions at random

with regard to velocity at medium discharge, but 7% of the range faster than random at Q_{low} and 5% of the range slower than random during Q_{high}.

6.7: Discussion

The findings in this chapter confirm the suggestion made in the introduction, that the spatial habitat use of salmon parr can be explained neither by the concepts of territoriality nor that of microhabitat selection alone. Instead, the findings suggest that both factors play major roles for the position choice of the fish and that there are interactions between these two factors.

6.7.1. Site fidelity and mobility of fish in the flume

Within 5 minute observation slots, 64% of all fish observed did not change their positions and 54% more fish remained stationary on a minute-to-minute basis than could be expected by chance. Although this illustrates that many fish were keeping positions on these time scales, mobility found here seems higher than what the stereotype of sessile "sit-and-wait" predators would suggest. These observations for YOY salmon are consistent with those made for 1^+ salmon parr by Armstrong et al. (1999). One possible explanation for the higher than expected mobility might be the fact that densities were low so that fish had the possibility of moving without encountering other antagonists. Secondly, the fairly homogeneous and mostly level gravel substrate of the flume did not provide many physical features which could serve as visual isolation features or as landmarks for territory boundaries, which both are major factors for territory size (Kalleberg, 1958, cited in Gibson, 1993; Keeley & Grant, 1995).

The frequency of fish movements was not affected by discharge changes. Apparent differences in mobility between riffle and pool (i.e., 50% of the fish in the pool but only 31% of the fish in the riffle moved) were only bordering on significance, but this observation seems reasonable in the light of the energetic

differences of these two environments: due to higher water velocities in the riffle, energy expenditure for positions changes are higher in the riffle. At the same time, the volume of water (and with it the suspended drift food particles) passing per unit area is smaller due to the slower water velocities, so that a larger area needs to be covered by the fish in the pool to have access to the same amount of food. Finally, Kalleberg (1958) and Gibson (1978) showed that Atlantic salmon parr were less aggressive in pools than in riffles, which would permit fish to move more freely in the pool habitat.

Of all the other variables that were assessed, only water temperature was shown to have a major effect on mobility rates. Fish were not seen changing positions at temperatures around 9-11 degrees Celsius, which occurred at the last run of the trials, in September. This temperature-related shift in behaviour has often been documented (e.g., Cunjak, 1988; Heggenes& Saltveit, 1990). It is not possible to separate the temperature effect from season, because temperatures were constantly high during the earlier runs and low during the late run. In another study, Faser et al (1995) did show however that salmon parr reduced feeding levels and increased sheltering behaviour at low water temperatures even during summer.

6.7.2. Does mean column velocity affect position choice?

"Why did the chicken cross the road?" The fact that fish used different positions during the different discharges suggests that the reasons for the position shifts could be related to the change in stream flow. It was decided to investigate this question by comparing microhabitat conditions fish experienced at a given discharge with those they would have experienced had they stayed at the positions they used at the other discharges. Any non-random patterns would indicate a significant reason for the fish to have changed the positions.

It was found that mean column velocity differed significantly between positions that fish had used at Q_{low} from those at the other flows. Positions had been adjusted at Q_{low} to locations with higher velocities than found at the positions

occupied at Q_{medium} and Q_{high}. On the other hand, the true positions fish used at Q_{medium} and Q_{high} featured slower velocities than they would have by staying on the Q_{low} positions. No differences were found between medium and high discharge, so that fish seemed to select very similar locations with regard to velocity at these discharges.

Velocities experienced at fish positions also differed from random at low and high discharge but not a medium flow. This means that fish adjusted their microhabitat both in relation to past positions and general availability. The comparison to random positions offers an absolute measure of the direction of this adjustment, because it would be possible that fish had displayed the differences between positions reported above while being much higher or lower in all cases. The finding that in fact velocities used were 7% faster than the velocity range available at Q_{low}, equal to random at Q_{medium} and 5% slower at Q_{high} confirms that fish displayed preferential choice behaviour within the constrains of habitat availability for the total population. It follows from this, that average velocities available in the flume were slower than preferred during low flow, preferred during medium discharge and faster than preferred during high flow.

In the context of habitat preference indices these velocity differences of 6%-10% of the velocity range seem rather slight, but this is due to the fact that the fish are selecting their microhabitat within the socio-spatial limitations of territorial behaviour. In reality, only by shoaling could all fish utlise the most suitable spot. The data demonstrates that the fish positions are affected by territorial behaviour, microhabitat selection and general habitat availability alike. If fish had not moved between discharges, the number of maintained positions would be much higher. More importantly, had the movements they made been irrespective of microhabitat considerations, there would have been no difference in microhabitat conditions between true and hypothetical positions.

Run 1

Run 2

Run 3

Run 4

Q low

Q medium

Q high

direction of flow
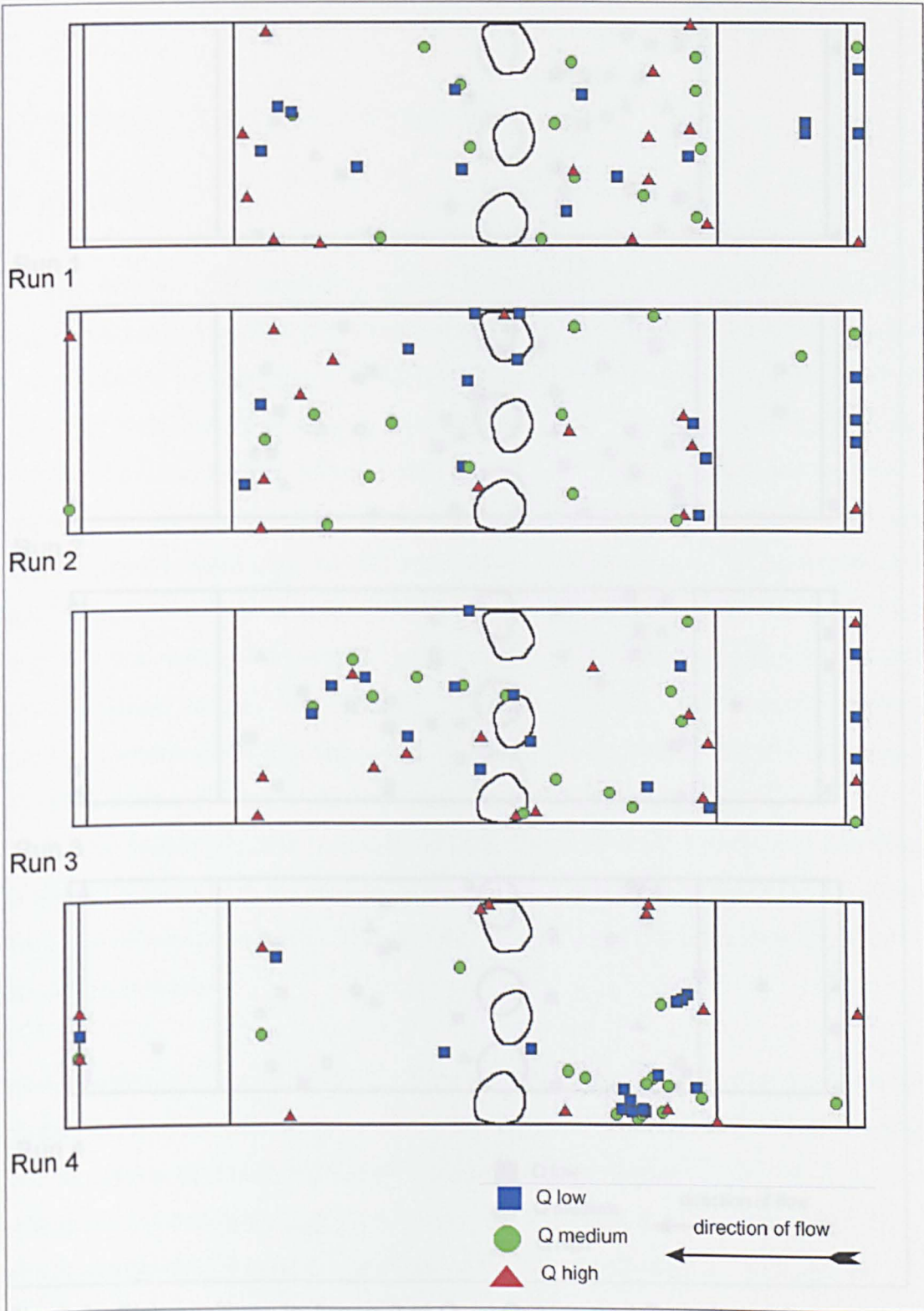
Fig. 6.2.: Fish positions in Arena 1 at Q_{low}, Q_{medium} and Q_{high} during four runs

Run 1

Run 2

Run 3

Run 4

■ Q low
● Q medium
▲ Q high

direction of flow
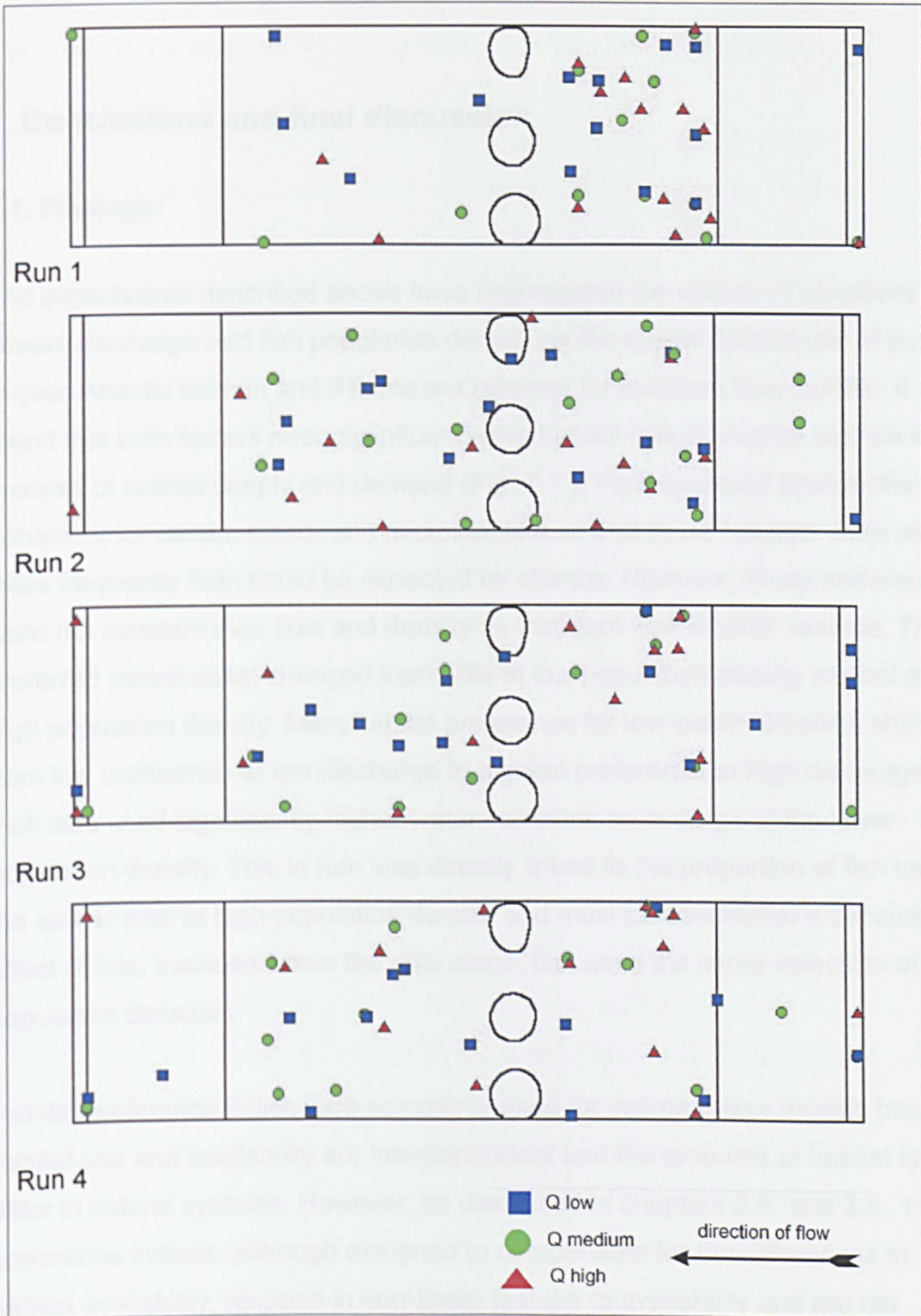
Fig. 6.3.: Fish positions in Arena 2 at Q_{low}, Q_{medium} and Q_{high} during four runs

7. Conclusions and final discussion

7.1. Findings:

The experiments described above have investigated the effects of variations in stream discharge and fish population density on the spatial habitat use of young-of-year Atlantic salmon and if these are relevant for instream flow models. It was found that both factors strongly influence the habitat use of juvenile salmon by a process of habitat supply and demand (Fig. 7.1.). Fish displayed preferential behaviour for certain meso- and microhabitats so that these habitats were used more frequently than could be expected by chance. However, these preferences were not constant over flow and density as instream flow models assume. The preferred mesohabitat changed from riffle at low population density to pool at high population density. Microhabitat preference for low water velocities shifted from low preference at low discharge to highest preference at high discharge. Fish also used significantly higher water velocities on average at the lower population density. This in turn was directly linked to the proportion of fish using the slower pool at high population density and must be considered a secondary effect of this, because within the riffle alone, fish used the same velocities at both population densities.

Habitat preference indices are commonly used for instream flow models because habitat use and availability are interdependent and the amounts of habitat types differ in natural systems. However, as discussed in chapters 2.8. and 3.8., these preference indices, although designed to compensate for the differences in habitat availability, respond in non-linear fashion to availability and are not statistically comparable. Despite this, they were still used in this research to illustrate the effects of discharge-dependent habitat use on a standard instream flow model prediction. The habitat predictions varied by up to 150% between the

three preference curves derived at three different flows which illustrates that the variability in preference was highly relevant for the model application.

For the second part of the analysis, the effects of population density on habitat use, preference indices were omitted because of their statistical limitations, but also because habitat availability was the same at both densities, at least at the physical level. The observed variations in meso- and microhabitat use between low and high population density have not been tested within the framework of an instream flow model as was the case above, because the development of preference curves requires a higher sample size than was achievable for the low population density data. However, the quite detailed frequency analysis used for the preference curve development should detect even more differences than those that were traced by the more general approach of the non-parametric tests applied for this comparison. In consequence and also based on the fact that instream flow models are highly sensitive to the preference curves applied (see chapter 4 and Shirvell, 1989; Waddle, 1992), it seems logical to assume that density-dependent differences in habitat use are also significant at the modelling level. The response of the population to density changes was most pronounced at the mesohabitat level, with nearly all fish using the riffle during low density, but more fish in the pool during high density. As mentioned above, this was also the main cause for the observed difference in microhabitat use between densities, where water velocities used at low fish density were higher than at high density, because within the riffle fish used the same velocities at both densities. Similar density-dependent differences of mesohabitat use have been reported by Greenberg (1994) and Bult et al. (1999), but it remained unclear, which role microhabitat availability played for the observed shift in mesohabitat use. My research would suggest that in this flume the riffle mesohabitat provided the preferred microhabitats and fish only moved to the pool once the riffle was saturated. Territoriality appears to be the most likely reason that there was no significant difference in microhabitat use in the riffle between the densities, so that here only optimal positions were occupied at both densities. Unsuitable

habitats in the riffle should be mainly areas of velocities that are too high for the fish whereas in the pool unsuitable areas should be those of no flow, which represent suboptimal but tolerable conditions for sub-dominant fish that can not defend any preferred feeding positions. Also, Gibson (1978) found salmon in pool habitat to be less aggressive than in the riffle.

Finally, the theoretical conflict between two theorems regarding the spatial habitat use of juvenile salmon was addressed. On the one hand, salmon are considered to be highly territorial and attached to a feeding position (e.g., Gibson, 1988, 1993), but on the other hand fish are assumed to preferentially select positions with the most suitable microhabitat conditions. In particular, water velocity was identified as the single most important variable for the position choice of juvenile salmonids (DeGraaf & Bain, 1986; Morantz et al., 1987; Heggenes & Saltveit, 1990). But the microhabitat conditions at any given position, especially water velocities, will change with discharge so that one of the theories must be compromised when stream flow changes. In this experiment, only a quarter of all fish remained within 5 centimetres of their pre-change position after a change in discharge. All other fish moved further distances and microhabitat conditions at the newly occupied positions were significantly different from those at the abandoned positions between Q_{low} and both other flows but not between Q_{medium} and Q_{high}. In the cases where Q_{low} was involved, fish changed positions in favour of faster locations during low flow and slower locations when flow increased to higher discharges coming from low flow. In this experiment, it was formally confirmed that water velocity plays a major role for fish that change positions between discharges. The preference was not identified in relation to spatial availability as usual but rather with reference to the velocities fish had vacated. The distance fish moved meant certainly that immediate locations were vacated, but if fish had to establish new territories in the process as well or simply moved within their territories could not be determined. Further research into this direction would be interesting.
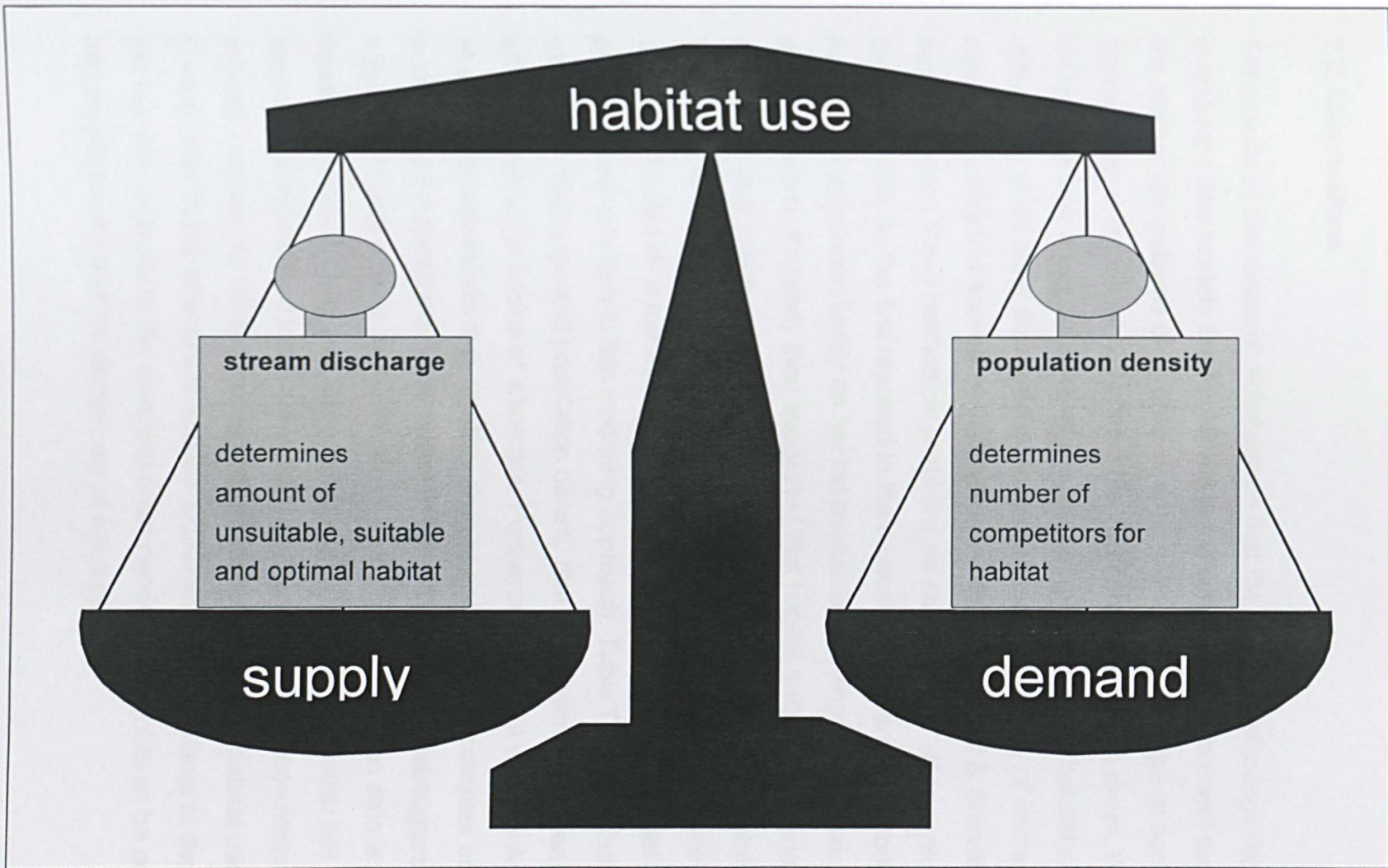
Figure 7.1.: the effects of stream discharge and population density on the microhabitat use of a population of territorial salmonids in a given stream

7.2. Conclusions

The results of this research substantiate that the habitat preference model used in instream flow models like PHABSIM is too simplified to represent realistically the habitat use patterns of juvenile Atlantic salmon over a range of conditions typically found in the highly dynamic environment of upstream rivers. What is more important, it was shown that the error introduced by the habitat suitability criteria are of an order that seriously compromises the validity of instream flow modelling using this approach. Critics (e.g., Orth, 1987; Scott & Shirvell, 1987) have predicted these methodical problems as early as 1987. Heggenes and Saltveit (1990) as the first reported in the context of instream flow models that habitat use depended highly on habitat availability varying across river sectors and seasons and already then suggested that habitat suitability criteria developed at average or low flow would perform poorly for much higher flows. The permanently increasing body of evidence that microhabitat choice behaviour of fish is affected by a multitude of variables not considered by habitat models poses a great problem to this modelling approach. Table 7.1. lists nine factors other than discharge and population density that have been confirmed to strongly affect microhabitat choice of a species. Furthermore, recent work by Armstrong et al. (1999) has shown that territory shapes and sizes are complex and that individual fish utilised the same space in different ways. All this suggests that habitat suitability criteria developed from empirical fish position data is likely to be flawed, because habitat use, especially in salmonids, is (and must be) flexible in response to spatial and temporal variations in environmental conditions. Habitat models normally do not incorporate the context in which the habitat use stands. On the other hand, attempts to accommodate all relevant factors in the model are not feasible because of the sampling effort needed or might even be near impossible because of the complexity of interactions.

Table 7.1.: Variables that can affect microhabitat choice of stream-dwelling salmonids

variable	reference
season	Heggenes & Saltveit (1990), Rincón & Lobón-Cerviá (1993)
rivers	DeGraaf & Bain (1986)
river sections	Heggenes & Saltveit (1990)
mesohabitat (i.e., pool, riffle, run)	Vondracek & Longanecker (1993)
water temperature	Cunjak (1988), Heggenes (1994)
predation	Greenberg (1994)
food	Wilzbach (1985)
interspecific competition	Kennedy & Strange (1982)
life history strategy	Huntingford, Metcalfe & Thorpe (1988)

Broader and more general habitat preference curves as recommended by Heggenes & Saltveit (1990) would be one correct way of accommodating the observed variations in habitat use, however, the degree of realism achieved by the model for any moment in time and space would be correspondingly lower so that predictions could be so general that the effort of modelling might seem unjustified. One new approach is trying to circumnavigate these problems by using individual based bioenergetic feeding models as habitat suitability criteria (e.g., Hughes, 1992a; Hill & Grossman, 1993; Rose & Cowan, 1993; Braaten et al., 1997). These models are typically built on the two main factors of energy gain (i.e., food uptake) and energy loss (i.e., energy costs of holding positions and intercepting food) and can be further refined for additional energetic costs for agonistic behaviour or predator avoidance and also for metabolic differences due to factors like water temperature.

7.3. Scope for further research

The initial reason for this research was to investigate some simple and basic assumptions that are at the heart of instream flow models but for which little research has been published so far, regarding their validity. The outcome of this study has shown how important it is to test all main aspects of a models before models are applied as management tools, in order get a realistic idea of the performance and limitations. A few critics who complain that research of this kind hinders rather than advances modelling are very wrong. If there are relevant limitations of the model it is vital to know them. Not knowing does not eliminate the problem of course, only knowledge possibly can. Hydraulic modelling is improving at a fast rate (Hardy, 1998) but there are still many uncertainties regarding habitat suitability criteria. As this study shows, errors caused by flawed habitat suitability criteria can be large and the current methods might eventually be abandoned in favour of other methods based on different data types.

Instream flow modelling is a very important tool for decision-making processes where "hard numbers" are needed to counterbalance effectively the tangible values readily provided in the debate by commercial enterprises like hydro-electric power generation. In order to improve the reliability of habitat-based instream flow models, advances of the biological models are most needed. The following aspects should provide a lot of scope for further research in this field and would be of benefit for our understanding of the spatial habitat use of fish in streams. This in turn would permit the development of more realistic instream flow models.

1. the interactions of habitat conditions and social behaviour:
The position choice of individuals of stream-dwelling salmonids also depends strongly on its social dominance status (e.g., Fausch, 1984; Hughes, 1992a). What kind of habitat do subdominant fish utilise when suitable habitat becomes

scarce? Do territory sizes and aggression levels vary with discharge and mesohabitat (and food availability, season, temperature, etc.)?

Example: In a Mid-August run of this campaign (average water temperature = 14.5 degrees Celsius), 8- 10 of the total 16 fish were suddenly observed to shoal in the pool of Arena 1 during low and medium discharge, but broke up the shoal at high discharge (e.g., see Fig.6.2., Run 4, bottom right corner of pool) . The fish repeated this behaviour over several changes of discharge. Shoaling fish were sometimes all swimming in the water column rather than sitting on the substrate.

2. *the effects of stream discharge on invertebrate food production and availability:*

Whereas the basic positive relationship between discharge and localised drift is known (e.g., Smith & Li, 1983), the effects of discharge on overall invertebrate food productivity are not incorporated into instream flow models, but would be of vital importance for instream flow models.

Example: on the day following a spate in the River Almond, which carried mostly small may-fly and case-less caddis larvae into the flume, the fish were very inactive and scarcely observed to feed on drift. It was not determined if this was a behavioural response by the fish after the spate event or if there was no drift to feed on because of the preceding spate. However, it seems highly likely that stream discharge will affect not only the drift rates but also the productivity of invertebrates.

3. *spatial aspects of habitat use and habitat modelling:*

Habitat metrics defined by approaches of landscape ecology should be tested for fish in streams. Spatial characteristics like fragmentation, edge effects, clustering and diversity to name a few (see Hardy, 1998 for more), could be of vital importance for habitat quality. Applying spatial statistics rather than traditional one-dimensional statistics should help to improve our understanding of habitat use. To demonstrate the scaling effects of data sampling and modelling is another important aspect of research into this direction.

Example: the fish position data recorded for this research project (see Fig. 6.2. and Fig. 6.3.) could provide much more information than just the pooled microhabitat conditions with regards to depth, velocity and substrate. Any position chosen by the fish stands in a spatial context as to the distance to the nearest neighbour, shelter and food source or aspects of relief which will determine the line of sight for approaching drift food items and visual isolation from neighbouring fish. Analysis of this kind becomes increasingly feasible with the help of GIS and statistics packages that can be directly linked (e.g., S-PLUS for Arc-View 3.1.).

4. Differences in habitat use between individuals and groups

Strategies of feeding (Nielsen, 1992) and space use (Armstrong et al., 1999) for example can vary between groups of fish for the same species and life-stage. Example: Huntingford et al. (1988) found that microhabitat use differed between two modal groups of juvenile Atlantic salmon adopting different life history strategies at the end of the growing season. Fish in the higher modal group (larger and smolting in the following year) occupied faster water velocities than those of the lower modal group (smaller and requiring a further year to smolt). Because fish were not individually marked in my experiments it was not possible to relate meso- and microhabitat use to fish size differences within a population, nor to relate habitat use to individuals in general. However, findings of Armstrong et al (1999) suggest distinct differences in behaviour between individuals, a phenomena that is supported by my personal observations during these experiments. The use of passive integrated transponders (PITs) (Armstrong et al., 1996) would permit to collect data sets on large numbers of individual fish.

Note: other researchers are welcome to use the data collected in the course of this study. Please inquire with David Gilvear, Department of Environmental Science, University of Stirling, Stirling, FK9 4LA, Scotland. (E-mail: djg1@stir.ac.uk)

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