DISTRIBUTION AND HABITAT USE BY JUVENILE ATLANTIC SALMON (Salmo salar) AT MULTIPLE SPATIAL SCALES, AND IMPLICATIONS FOR HABITAT MODELLING AND FISH-HABITAT MANAGEMENT

TAMMO PETER BULT

Distribution and habitat use by juvenile Atlantic salmon (*Salmo salar*) at multiple spatial scales, and implications for habitat modelling and fish-habitat management.

by

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Department of Biology
Memorial University of Newfoundland
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Abstract

Implicit assumptions of micro-habitat models are that (1) habitat limits population levels and small-scale information on habitat selection behaviours of individuals can be used to manage populations at large spatio-temporal scales (scale-up); (2) the single or few measurement scales used in habitat models are appropriate for identifying important habitats; and (3) "better" habitats are characterised by a higher density or frequency-of-use, i.e. density can be used as an indicator of habitat quality.

(1) Based on scope- and rate-diagrams from field-data and theoretical scenarios of movement and mortality, I concluded that salmonid habitat models operate in the context of processes that may not be important to the problems we would like to address. I suggested survey designs that allow problems associated with scale-up to be overcome.

(2) I evaluated distributions of juvenile Atlantic salmon (*Salmo salar*) over a range of spatial scales based on a stream-tank study (spatial scales 1 cm to 3 m) and field data (spatial scales 1 cm to 15 m), to determine whether patchiness of fish distributions or associations with depth, water velocity and substrate depended on spatial scale, to determine scales most appropriate to habitat models, and to compare multi-scale versus single-scale habitat modelling approaches. Results indicated associations with conspecifics, substrate, water velocity and depth changed with spatial scale and direction relative to water flow. Associations were most different from random at small spatial scales (ambit radius < 50 cm). Both studies indicated that single- and multi-scale habitat selection models were equally able to describe fish densities at small spatial scales (ambit radius < 4 m). The field-based study indicated that single- and multi-scale models often failed to describe fish densities at scales larger than used in the model (scale-up).

(3) I studied density-dependent habitat use by Atlantic salmon parr based on experimental riverine enclosures and field data. Results from the experimental study indicated that habitat use changed with population density. Results from the field-based study were less clear with

some of the results suggesting density-dependent distribution processes. I concluded that habitat selection by salmon parr was density-dependent and highly variable. Changes in habitat use with density were most likely due to small-scale spacing behaviour or territoriality.

I concluded that quantitative multi-scale approaches are important to habitat modelling, identified important research questions, presented some novel techniques for scaling analyses and made suggestions to improve habitat modelling and resource management.

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PREFACE

Understanding and predicting effects of man on nature depends on understanding the relations between organisms and their environment. To achieve such an understanding, distributions of organisms are studied relative to distributions of environmental features. From such study, inferences are made on the processes that underlie the observed distributions and the most important of these are expressed and linked together in a habitat model. Habitat models simplify, summarise and describe this understanding, and as such are valuable to resource management and environmental impact assessments.

In this preface I will explain why it is important to study distributions and processes at multiple scales, and will show how this relates to habitat modelling. To begin, I will use two examples: one illustrating scale dependency of associations and one illustrating scale dependency of processes. From these examples, I will introduce the main topics addressed in the thesis.

Scale dependency of associations: an example

The concepts involved in multi-scale habitat modelling are more readily conveyed by using hypothetical examples close to daily experience. Suppose we would like to understand camping behaviour of people in order to design the best possible campground. To achieve such an understanding, we could study the distribution of tents relative to the distribution of environmental features that are thought to be important, and we could then summarise this understanding in a "camping model" that describes the occurrence of tents relative to these environmental features.

We start the project by making maps of the distribution of tents and those environmental features thought to be important in camping behaviour, e.g. the availability of water, the flatness of the terrain, and the availability of firewood. The maps can be drawn at different resolutions or spatial scales.

Depending on the resolution of the maps we use, our results will vary. At a small spatial scale (1×1 m), tents are negatively associated with the availability of water and wood and positively with the flatness of the terrain, because campers do not put their tents in trees or in lakes but do put them on level ground. At larger spatial scales (1000×1000 m), however, tents are positively associated with the availability of water and wood, as water is used for activities such as fishing, swimming or sailing, and wood is used for cooking and campfires. Because small-scale flat places may often be found within larger areas that are generally steeply sloping, such as mountains, the flatness of the terrain may not be a good predictor at larger spatial scales. Negative associations with flatness may even be found at these large spatial scales when mountainous areas are the ones preferred for recreational activities such as climbing or hiking.

These relations may be summarised quantitatively in a camping model. Using this model, we then may try to evaluate different areas with respect to suitability for camping. However, depending on the scale of this model, our conclusions with respect to suitability will differ: a small-scale model may predict that desert plains are suitable for camping as wood and water are hardly present and the terrain is quite level; a large-scale model may predict that mangrove swamps are suitable for camping as trees and water are abundant. Obviously, neither one of these conclusions is right, despite the fact that both models do give a valid, although incomplete, description of how someone chooses where to place a campsite. The problem is that camping behaviour operates at multiple scales, whereas the models operate only at the scale appropriate to the original resolution.

This example shows that associations modelled at small scales may give opposite results from those modelled at large scales. This implies that a comparison of results from studies that differ in measurement scale cannot be done without some understanding of how scale affects results, and that results from studies done using inconsistent measurement scales cannot be interpreted.

Scale dependency of processes: an example

Distributions of organisms are the result of four processes: mortality, movement, reproduction and growth. If one aims to describe the distribution of organisms it is helpful to have some idea of which of these processes are important and which are not. Research could then be directed at the more important processes, unimportant processes could be ignored and, from this, a simpler model could be made without sacrificing model efficiency. However, the relative importance of different processes varies with scale. This may be best explained using another example.

Suppose that we are interested in the distribution of mice. To begin, we visualise the continent as a huge checkerboard with mice scattered randomly across it. When the cells that compose the checkerboard are small (say 1×1 m), changes in the number of mice over short periods of time (say 1 hour) in each cell are mainly influenced by the way in which mice run about, i.e. the distribution of mice at small space/time scales (1 m, 1 hour) is dominated by movement. By contrast, when cells are large (say 100×100 km) and times are long (say 1 year), this very same distribution is dominated by mortality, instead of movement, as the chance an individual mouse will live and die within a single cell is larger than the chance it will move to a different cell.

This example shows that small-scale processes may not be that relevant to describing distributions at larger scales: A model describing movement of mice at small space/time scales may not adequately describe this very same distribution at larger space/time scales, because the distribution of mice at these larger scales is driven by reproduction and mortality rather than movement. In addition, different variables may be differentially important in their contribution to movement and reproduction/mortality. In other words, what is seen at larger scales may not be simply the summation of small-scale processes.

Scaling analyses

These two examples illustrate that, depending on the scale we use to study a system, our results and understanding of the system in terms of distributions, associations and processes may differ: The associations between tents and environmental features, the models that summarised these associations, and the recommendations made based on these models were all scale-dependent (example 1); different processes were perceived as being important in determining the distribution of mice, depending on the scales used to study them (example 2).

Because observational results vary with scale, it is important to consider explicitly the measurement scales one chooses in a study. Multi-scale analyses that explicitly evaluate distributions, associations and processes over a range of scales can aid in determining which scales are most relevant in a particular problem. Consider the camping model: by studying the associations between tents and the availability of water and wood over a range of scales one could identify the several scales at which camping behaviour operates and then, with that knowledge, make the best model to answer the question "How far is one willing to travel from a tent site to gather wood or water? " Without multi-scale analyses, the choice of a particular measurement scale for making the model could easily become purely personal and subjective.

Multi-scale analyses could also help to understand how the structure and orientation of landscape elements - the landscape mosaic - affects the suitability of an area for camping, i.e. is it better for a campground to have a few large lakes or a lot of smaller ponds, and how does the distribution of smaller and larger lakes affect the suitability of a terrain for camping? In addition, multi-scale approaches may act as a framework to incorporate results obtained at different scales and to evaluate the validity of extrapolating small-scale models in order to address problems operating at much larger scales, i.e. is it possible to make inferences on the suitability for camping of very large areas, based on observations on the distribution of tents and environmental features within such areas (scale-up)?

Multi-scale approaches in salmonid habitat modelling and thesis questions

Salmonids are probably among the best studied fish species in the world. Habitat models that describe relations between the occurrence of salmonids and riverine habitats are widely used in impact analyses and instream improvement projects. Despite the considerable research effort that has gone into these models, associations of salmonids and their habitats and the processes that govern salmonid distributions have hardly been studied using explicit quantitative multi-scale approaches.

The choice of measurement scale is often based on the biological intuition of the researcher constrained by logistics. For example, previous work has shown that salmonids select positions in streams based on their competitive abilities and the profitability of positions in terms of potential net energy intake rate and predation risk, with profitability of positions being largely determined by the physical habitat in terms of cover, bottom topography and current flow patterns. As such, the area within a stream is often regarded as a hierarchy of potential positions, ranging from inaccessible to ideal, with each fish choosing the most profitable position that its rank in the social hierarchy will allow. Territoriality, small-scale spacing behaviour or pre-emptive exclusion are thus assumed to regulate use of preferred positions and space which, if in short supply, are assumed to regulate population density. Thus, the physical habitat is regarded as a template determining distribution patterns of fish. Based on this, use of available habitat by salmonids is often described at small spatial scales using so-called micro-habitat modelling approaches (habitats described at scales $<1\text{m}^2$). But the intuitive wish to work at this fine scale may have to be changed depending on the resolution of available maps on riverine habitats or other logistical constraints, such as the time and funding available for the study. The result is that measurement scales vary both among and within habitat modelling studies.

The fact that measurement scales vary constitutes a problem when interpreting, comparing and applying results from various studies. In particular, the scale-up from habitat model to management problem has hardly been evaluated quantitatively: What is the relevance of a model that describes the distribution of fish over small-scale habitats to the density of fish in a much larger area, i.e. how relevant are small-scale models to large-scale problems?

Multi-scale analyses are needed that evaluate salmonid distributions, associations between salmonids and their habitats, and the processes that govern salmonid distributions. Critical questions are: At what scales are salmonids associated with their habitats? Do multi-scale analyses confirm the importance of scales as determined by other studies? What processes predominate at what spatio-temporal scales? Such studies could act as a framework to incorporate ideas from studies operating at different scales.

This thesis makes a start at multi-scale analysis of salmonid distributions. Processes important to salmon distributions were studied over a range of spatio-temporal scales to determine which processes predominate at which space-time scales, as in the mouse distribution example, and to explore the problems associated with scale-up (Chapter 2). Atlantic salmon distributions and associations between salmon and their habitats were studied over a range of scales, as in the camping example, to determine the scales most important to habitat modelling (Chapter 3). Because use of habitats by salmonids is generally considered a result of competition for preferred habitats, special attention was given to effects of this process on the distribution of salmon (Chapters 3, 4).

Chapter 1: Habitat selection behaviours in habitat modelling and fish-habitat management

1.1. Habitat models in resource management

An understanding of how organisms are distributing among available habitats is crucial to managing natural populations of animals. To achieve such an understanding, distributions of organisms are studied relative to distributions of resources and conditions thought to be of importance. Habitat models aim at quantifying relations between distributions of organisms and habitats, and as such are an important part of resource management: Habitat models are widely used for a variety of aquatic as well as terrestrial species and habitats (cf. Duel et al. 1996).

Implicit assumptions of such habitat modelling approaches are that (1) habitat limits population levels; (2) "better" habitats are characterised by a higher density or frequency-of-use, i.e. density can be used as an indicator of habitat quality; (3) habitat selection is important to distributions of organisms, i.e. these distributions are largely driven by habitat selection behaviours; and (4) habitat selection models based on observations of individuals or small groups of organisms can be used to address problems at the population level, i.e. processes that operate at small space-time scales are important to dynamics at space-time scales much larger than those of the initial observations and small-scale habitat selection models can be used to predict or describe distributions at large space-time scales.

It is well known that associations between organisms and their habitats vary with scale (cf. Wiens 1973, Morris 1987A-C, Piatt 1990, Syms 1995, Poizat and Pont 1996) and that the relative importance of processes varies with scale (Horne and Schneider 1994). Because of this, a scale-explicit approach is needed to identify important processes, variables, and scales.

Nevertheless, most habitat modelling studies use a single or few measurement scales and an implicit use of scaling, despite an awareness of the importance of scale (cf. Frissell et al. 1986, Minshall 1988, Imhof et al. 1996, Lewis et al. 1996, Allan et al. 1997). The measurement scale chosen is often not the result of a quantitative multi scale approach, but is based on the biological intuition of the researcher combined with logistical constraints; the scale-up from observation to problem is intuitive, seldomly made explicit, and rarely quantified.

In this thesis I show the importance of scale to habitat models and resource management: I develop several new scaling techniques that can be used in habitat selection and habitat modelling studies. These techniques allow for a quantitative and scale-explicit assessment of fish-habitat associations and an evaluation of the importance of habitat selection to habitat models and resource management. Based on these techniques, I investigate whether possibilities exist for improving habitat models by using scale-explicit approaches. The thesis focuses on Atlantic salmon (*Salmo salar*). The ideas I present, however, are not restricted to management of salmon populations alone.

1.2. Habitat models in fisheries and fish-habitat management

Habitat models are widely applied to riverine fish populations where they find use in stream habitat investigations and in the resolution of conflicts arising from water allocation and hydropower development (Fausch et al. 1988, Reiser et al. 1989, Armour and Taylor 1991). Habitat models are basically dose-response relations, with "habitat" as dose and "habitat use" as response. The mathematical form of these models may be multivariate models, frequency-of-use curves, preference curves, or weighted-useable-areas, with explanatory variables mostly referring to abiotic habitat components (Orth and Maughan 1982, Fausch et al. 1988). Variables most commonly included in fish habitat models are (1) drainage descriptors, such as total stream length, stream order and stream gradient, or chemical parameters such as conductivity (macro-scale variables), (2) channel morphometry and flow descriptors, such as discharge, stream width, mean water velocity and stream depth, or broad-scale features such as pools, riffles and runs (meso-scale variables), and (3) fish micro-habitat descriptors, such as water depth, water velocity, cover and substrate (micro-scale variables) (Fausch et al. 1988). Variables referring to biological habitat components, such as invertebrate drift or food availability, are seldom included, despite the fact that food availability and drift concentrations affect fish distributions (Jenkins et al. 1970, Griffith 1974, Gibson and Galbraith 1975, Wankowski 1981, Fausch 1984, Hughes and Dill 1990, Hughes 1992A, 1992B). This focus on physical habitat variables originates from the fact that other variables are more difficult to measure and require an often unrealistic time demand for data-gathering (Gore and Nestler 1988). Habitat models must refer to variables that can be affected by management actions (Fausch et al. 1988). Decision-support systems that rely on habitat models, such as the instream flow incremental methodology (IFIM/PHABSIM, Bovee 1982, 1986, Milhous et al. 1989) often aim at relating biotic values in equivalent terms to those used to estimate other uses of available water (Gore and Nestler 1988).

Fish habitat models can be classified as micro-, meso- or macro-habitat models, depending on the spatial resolution or "scale" of the explanatory variables. Micro-habitat models describe the distribution of individual fish over small-scale habitat features. Meso- and macro-habitat models describe fish densities as a function of medium to large-scale habitat features. The distinction between micro-, meso- and macro-habitat models is not well defined. In this paper I will refer to micro-habitat models as models based on habitat features smaller than 1 m^2, to meso-habitat models as models based on habitat features ranging from 1 m^2 to 1000 m^2, i.e. one to several times the width of the river, and to macro-habitat models as models based on habitat features larger than 1000 m^2 (large reach, tributary, or river scales).

Examples of salmonid micro-habitat models can be found in Shirvell and Morantz (1983), DeGraaf and Bain (1986), Raleigh et al. (1986), Morantz et al. (1987), Lambert and Hanson (1989), Heggenes (1990), Heggenes and Saltveit (1990), Heggenes (1991), Harris et al. (1992) and Nehring and Anderson (1993). These models are generally derived from direct observations of individual fish, often obtained by snorkelling or electroshocking (Bovee 1986). The spatial scales of these observations are in the range 10^{-4} to 1 m^2, depending on the precision of position determination and resolution of habitat observations. The temporal scales of these observations range from seconds to several minutes, depending on the time spent observing individual fish. At these spatial and temporal resolutions, habitat use will vary primarily due to habitat selection behaviours and individual movements.

Examples of salmonid meso- and macro-habitat models can be found in Binns and Eiserman (1979), Raleigh (1982), Bowlby and Roff (1986), Lanka et al. (1987), Kozel and Hubert (1989A), Bozek and Hubert (1992), Amiro (1993), Gibson et al. (1993) and Scruton and Gibson (1993). These models are generally based upon information on fish density and habitat in river sections. This information is obtained by removal- or mark-recapture estimates, using electrofishing equipment, barrier-nets or seines. The spatial scales of observations that underlie these models are usually in the range of 10^2 to 10^4 m^2. The temporal scales range from 1 sec to more than several weeks, depending on whether observational units were blocked off and hence densities reflect an instantaneous picture of fish density at the observational unit, or whether densities were monitored over a period of time, e.g. as in mark-recapture estimates from unclosed areas. At these spatial and temporal resolutions, habitat use will vary due to a complex mixture of movement and mortality. Some studies use a combination of micro- and meso-macro-habitat approaches (cf. Bozek and Rahel 1991).

The current state-of-the-art of habitat models was developed largely within the last two decades, and habitat modelling techniques are fast changing. Habitat models have been developed since the 1970's (Fausch et al. 1988), although biologists have studied relations between fish and their habitats for a lot longer. In particular, the PHABSIM component of the Instream Flow Incremental Methodology (Bovee 1982), a micro-meso-habitat modelling approach, is frequently used in water allocation conflicts and hydropower development (Orth 1987). Current research efforts focus on the development of local models for different river systems or regions (e.g. DeGraaf and Bain 1986, Scruton and Gibson 1993), or on an evaluation of the spatio-temporal generality of models (e.g. Kozel and Hubert 1989B, Heggenes and Saltveit 1990, Bozek and Rahel 1992). In addition, efforts are made to increase the descriptive and predictive power of models by adding more and more detail and realism. Examples are a change in focus towards two and three dimensional flow models, the development of dynamic habitat models that address changes in habitats and habitat requirements over time, the development of models of fish metabolism and drift feeding, and the determination of micro-habitat requirements of stream insects, an important source of food for fish (cf. Leclerc et al. 1996).

Habitat modelling approaches have been widely criticised (cf. Orth and Maughan 1982, Van Horne 1983, Mathur et al. 1985, Bleed 1987, Orth 1987, Fausch et al. 1988, Gore and Nestler 1988, Barinaga 1996). In short, few efforts have been made to test the predictive capacity of models with independent data. There is little evidence that fishes respond to changes in model parameters. Models are often based on few data. Observational data on fish densities, individual fish and habitat variables may be biased. Sound statistical procedures are often overlooked. Methods for choosing the best model are poor. Fish density may not be limited by habitat, but by other factors such as exploitation. Variables that are more realistic with respect to the biology of the fish, such as food availability and biotic interactions, are often overlooked. Effects of flow alterations may take many years before the full impact on habitats and fish may be recognised, which limits the possibility to assess these changes. Habitat models mostly refer to game animals or other species that are of interest to the general public, but ignore other species. Temporal variations in habitat and habitat requirements are seldom included. Habitat models are often derived from specific locations at specific moments in time. Most habitat models are based on observations on habitat use in summer. Models rarely include habitat use in winter, at night, during high flow or flood conditions, or at places where sampling is difficult. From this, important habitats or critical life stages may be overlooked. Fish density may not be a good indicator of habitat quality. Synergistic effects among resources and/or conditions are often ignored.

In spite of many shortcomings, habitat modelling approaches are still widely used due to their argued efficiency, their apparent simplicity and corresponding ease-of-use, and for lack of better alternatives (Gore and Nestler 1988).

1.3. Development of effective habitat models

Three aspects of models are of importance: realism, precision and generalism (Levins 1966). From this, the ultimate habitat model would be based on functional relations between fish and habitat (realism), explain a large portion of the observed variance and give repeatable results (precision), and be applicable to different aquatic systems at different moments in time (generalism). Levins (1966) proposed that at most two of these three assets can be attained. This is supported by findings of Fausch et al. (1988) who concluded from a review of a large number of habitat models that precise habitat models often stem from relatively short periods (one season) or from small geographic areas (single stream or watershed) and that precise models often lack generality. In addition, it is important to note that a model is a simplification of reality, i.e. simplicity is a model's virtue and not necessarily its weakness. Complex models are often implicitly favoured over simpler ones, as more complex models seemingly take into account more of the processes that are thought to be of importance and from this, are assumed to mimic reality better than simpler models do. However, model complexity may not necessarily be positively associated with model realism or precision. When adding complexity to models, e.g. to increase model realism or precision, we have to balance possible benefits with the associated increase in research costs. In addition, we have to carefully assess if the complexity of the model corresponds to a real understanding of the system rather than merely supporting some speculation. In general, an increase in model complexity will put a disproportionate demand on the ability of the researcher to understand and describe model components and interrelations and on model validation efforts. Simple models may be less effective in describing observed fish distributions (explained variance lower) than more complex models, but may better predict distributions when extrapolated over space or time, i.e. simple models may be more robust (cf. Fausch et al. 1988).

Therefore, it is important to identify clearly the objectives of habitat models before undertaking field work by prioritising generalism, realism and precision: models aimed at studying fundamental mechanisms governing fish distributions in a particular watershed may have to sacrifice generalism for realism and precision; models for fisheries management that are to be used over wide geographic ranges may have to sacrifice precision and/or realism to attain generality. The most successful approach for fisheries management may be to develop models that are realistic in the first place. Habitat models of different complexity should be compared to assess effects of model complexity on model generalism and precision. Habitat models should aim at describing the most important processes first before including others. Variables that most increase model precision and/or model generality, with the least effects on model complexity, should be included first. A theoretical framework is necessary that clearly links theories of distribution with habitat modelling practices. Because of this, tools are needed that allow for (1) a prioritisation of distribution processes and (2) a prioritisation of variables to be included in habitat models. These two aspects will be discussed in the next two sections (1.4 and 1.5).

1.4. Prioritisation of distribution processes

The problem is to develop an understanding of the possibilities and limitations associated with the use of small-scale observations of individual behaviours or density information on small groups of fish, to dynamics at scales relevant to management problems (scale-up), which generally arise at time scales of years to decades and space scales of rivers or watersheds (cf. Imhof et al. 1996, Richards et al. 1996). This scale-up can be quantified as the range of the problem relative to the resolution of the observations and can be graphically depicted in a so called "scope-diagram" as proposed by Schneider et al. (1997). This approach is illustrated in Figure 1.1 for a generic micro- and meso-habitat modelling study, assuming a river of 50 km length with an average width of 10 m. The lengths of the arrows connecting data resolution and problem range indicate the degree of scale-up or "scope".

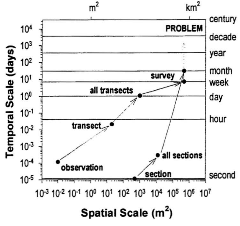

Figure 1.1. Scope-diagram illustrating scale-up in habitat modelling. The arrows connecting observation to problem relate to scale-up from direct observations of fish behaviours by snorkelling in micro-habitat modelling; the arrows connecting section to problem relate to a meso-habitat modelling approach where river sections were blocked off and sampled by electrofishing (see text). Dotted arrows indicate assumed or intuitive scale-up. Solid arrows indicate scale-up verifiable by statistical inference.

When surveying this hypothetical river by snorkelling along transects (typical micro-habitat modelling approach), the arrow connecting "observation" and "transect" indicates the degree of scale-up from individual fish observations (10 sec, 0.01 m^{-2}) to individual transects (30 min; 20 m^2). The arrow connecting "transect" and "all transects" indicates the degree of scale-up from individual transects to a total survey consisting of 50 transects (50*30 min, 50*20 m^2). Transects are generally not surveyed concurrently, nor are they positioned adjacently. Rather, transects are positioned over the length of the river, and transects are visited over a period of several days to weeks. All transects combined, therefore, represent a larger space-scale (river) and an "average" habitat use of a longer time-scale (one week; assuming this is the time needed to visit all 50 transects). This scale-up is represented by the arrow connecting "all transects" and "survey". Many habitat models are derived from a single survey done in early summer, since flow conditions in fall, winter and spring often preclude sampling. Therefore, an assumed or intuitive temporal scale-up is done by using information from a single survey as a basis on which to manage fish populations at time scales relevant to most management problems: summer habitats are assumed to be limiting This is represented by the arrow connecting "survey" and "problem". "Intuitive" in this context contrasts with the other scale-up routines (core → visit → survey) which are verifiable using statistical inference.

A similar scale-up is done for meso-habitat models. In the example of Figure 1.1, fish densities are assessed by electrofishing in 25 sections of 50 m length that are blocked-off with barrier nets prior to removal of the fish. Assuming that sections were sampled consecutively over a period of one month, the arrow connecting "section" and "survey" indicates the degree of scale-up from observations at individual river sections to the total survey (500 m^2 per section; 25*500=12500 m^2 total; one month period). The arrow connecting "survey" and "problem", indicates the intuitive scale up from this single survey to scales relevant to most management problems.

From Figure 1.1 it is obvious that for habitat modelling surveys, the degree of scale-up is often considerable, as the total area surveyed and the total amount of time spent surveying is only a fraction of the spatio-temporal range associated with typical management problems (river, watershed; years to decades). In addition, the variables of habitat models are measured at spatio-temporal scales that are much smaller than are those of most management problems, especially in the context of micro-habitat modelling.

The relative importance of processes is known to vary with spatio-temporal scales (Horne and Schneider 1994). Because of this, small-scale behavioural processes that are important to habitat selection may not necessarily be relevant at the larger scales of our problems and small-scale fish-habitat associations as described in micro-meso-habitat models may not necessarily be important to larger-scale distributions. E.g., small-scale habitat selection models will not be effective at describing differences in fish densities among tributaries when these differences are driven by demographic processes instead of habitat selection behaviours. Therefore, the scale-up from observation to problem will have to be validated. This validation process is largely ignored in fish habitat modelling, in spite of the fact that problems associated with scale-up have been recognised (cf. Imhof et al. 1996). The reason for this is that the collection of data needed for a quantitative evaluation of scale-up is labour intensive, as large geographical areas will have to be sampled over long periods of time. Another reason may be a lack of knowledge of mathematical techniques that can be used for quantitative evaluations of scale-up. These problems will be further discussed in Chapter 2.

1.5. Prioritisation of variables in habitat models

Fish are associated with their environment over a range of spatial and temporal scales. This is because they react to their environment at a range of scales, because processes that affect fish distributions operate over a range of scales and because of the propagation of effects from one scale to another. An example of behaviour operating at more than a single spatial scale is the selection by salmonids for specific holding positions (small-scale) with relatively low snout velocities in areas of high current conditions (larger scale) where drift is concentrated (Chapman and Bjornn 1969, Everest and Chapman 1972, Wankowski and Thorpe 1979, Fausch and White 1981). An example of the propagation of effects across scales are the effects of flood events and ice scour (small temporal / large spatial scale events) on riverine fish populations (large spatio-temporal scale effect) (cf. Erman et al. 1988, Fausch and Bramblett 1991, Pearsons et al. 1992). Although flash floods may have detrimental influences on riverine salmonid populations at the time they occur, the long-term effect of flash floods may be that suitable substrates are maintained, that fish species are favoured that are adapted at re-colonising and minimising exposure of vulnerable life history stages (Pearsons et al. 1992), or that organic matter from the terrestrial environment is added to the riverine ecosystem, and thus actually sustains the standing stock of salmonids. Another example of the propagation of effects across scales is the process of expansion and contraction, where large-scale distributions are influenced by small-scale habitat selection processes (MacCall 1990, Swain 1993, Marshall and Frank 1995).

Because organisms are associated with their environment at a range of spatial and temporal scales, a comprehensive understanding of factors affecting the distribution and abundance of fish can only be achieved by studying factors affecting fish distributions at a range of scales, rather than one or even a few selected scales. From this, multi scale habitat models may be more effective in describing associations of fish with their habitats than single scale approaches. "Effective" in this context refers to models with good descriptive or predictive capacities, based on a selected and small number of variables and scales.

An example of this in the spatial domain is selection by salmonids for specific holding positions with relatively low snout-water-velocities in areas of high current conditions. A habitat model of this behaviour will indicate a negative association with high water velocities at small spatial scales, but a positive association at larger spatial scales. As there is no single "right" scale to describe this behaviour, a multi scale approach may be more appropriate for describing such behaviours.

Another example in the spatial domain is selection by salmon of spawning substrates. If salmon need spawning substrates in patches of a certain minimum size, rivers that harbour spawning substrates in smaller patches only may not be suitable for spawning. Further, the relationship between spawning substrate patch size and suitability for spawning may not be linear for patches exceeding the scales of redds either. Current spawning surveys generally operate at scales of river sections (several times the river width), largely because surveys are done either by helicopter or by a quick walk along the river bank, i.e. measurement scales are very much determined by logistics. However, the scale-mismatch between the scale of the survey and the scale of redd-selection-behaviour may lead to wrongful predictions on spawning habitat quality and availability, which may affect subsequent instream improvement decisions.

An example in the temporal domain is the influence of high temperatures on mortality of salmonids. If high temperature peaks occur at the scale of hours, mortality may not be affected. However, if high temperatures occur at the scale of days, no fish may survive.

Currently, the majority of habitat modelling approaches tends to operate at a single or few selected scales. Because of this, other important scales may have been overlooked. In addition, by studying fish distributions and associations of fish with their habitats over a range of scales, rather than a single or few selected scales, one may avoid a situation where measurement scales are chosen primarily from an anthropocentric interpretation of fish behaviours and life-history (cf. Kotliar and Wiens 1990).

Habitat modelling may greatly benefit from a more explicit use of scale within the context of quantitative multi scale approaches. This would involve an assessment of how patchiness of fish distributions and habitats varies with scale and of how associations of fish with their habitats vary with scale. This would help identify important processes that affect fish distributions and the scales at which they operate. The identification of scales at which fish distributions are most extreme, i.e., scales at which patchiness is most different from random and variability is largest, and the identification of scales of maximum association between fish and their habitats, may help to identify measurement scales that are most efficient to habitat models.

Multi scale approaches allow for an assessment of how the spatial and temporal heterogeneity of habitats within a landscape or landscape mosaic influences species occurrence and habitat use (cf. Turner 1989). Fish habitat models tend to focus on the effects of habitat availability on habitat use but tend to ignore the effects of the orientation and structure of landscape elements, especially those used within IFIM/PHABSIM. Systems that consist of similar habitats but where habitats occur at different patch sizes or where habitats are positioned differently within the landscape may harbour different species and densities of organisms (cf. Rieman and McIntyre 1995). Examples include effects of habitat fragmentation (cf. Oehler and Litvaitis 1996), patchiness of resource distributions and dispersion of organisms on species occurrence, community structure and abundance, such as work by Charnov (1976) and Parker and Stuart (1976) (Marginal Value Theorem), the Habitat Templet, proposed by Southwood (1977), Grime's (1974, 1979) classification of plant life histories, the distinction between r and K selecting habitats (Pianka 1970), and theories relating to island biogeography (MacArthur and Wilson 1967).

Because spatio-temporal habitat heterogeneity is of such importance to habitat quality (cf. Wiens 1976), measures of habitat quality that include heterogeneity may perform better than those which do not. Several authors have tried to address this problem by classifying stream habitats at multiple (hierarchical) scales (e.g. Frissell et al. 1986, Hawkins et al. 1993, Imhof et al. 1996) that can be used as a framework for evaluating fish-habitat relations in river restoration projects. However, the scales in these classifications are often based on an anthropocentric interpretation of processes and, because of this, may lead to a situation where scales and processes important to fish are overlooked. Multi scale analyses based on empirical studies will be needed to further identify important processes and scales, and to evaluate the relative importance of processes with scale. These various aspects will be further discussed in Chapter 2 and Chapter 3.

1.6. Density as indicator of habitat quality

So far, I have discussed the study of distribution patterns as a means to identify underlying processes. However, the relation between pattern and process is not unidirectional and distribution processes may vary with distribution pattern and density; processes induce patterns and patterns determine processes:

Previous work has shown that salmonids select positions in streams based on their competitive abilities and the profitability of positions in terms of potential net energy intake rate and predation risk, with profitability of positions being much determined by the physical habitat in terms of cover, bottom topography and current flow patterns (Fausch 1984, Hughes and Dill 1990, Hughes 1992A, 1992B, Grand 1997, Grand and Dill 1997). As such, the area within a stream may be regarded as a hierarchy of potential positions, ranging from inaccessible to ideal, with each fish choosing the most profitable position that its rank in the social hierarchy will allow (Fausch 1984, Hughes 1992A). Territoriality, small-scale spacing behaviour or pre-emptive exclusion will thus regulate use of preferred positions and space, if in short supply, will regulate population density (Bohlin 1977, Grant and Kramer 1990). From this, the physical habitat may be regarded as a template determining distribution patterns of fish (Hughes 1992B).

These processes suggest that salmonid distributions may be best described using the ideal-despotic distribution theory of Fretwell (1972). This theory describes how animals select their habitats assuming that they are "ideal" in knowing where profitability is highest but where access to resources are governed by territorial behaviours. When organisms distribute ideal despotic, the most desirable positions will be occupied first, followed by positions in progressively less desirable habitats. Because of this, the average gain per individual may differ and habitat use may change with density. From this, habitat models may vary with population density.

The ideal-free distribution theory (Fretwell and Lucas 1970) contrasts with this ideal-despotic theory in that access to resources is not restricted by competitive behaviours but all individuals are equal and "free" to move among patches without constraints or restrictions. When organisms distribute ideal free, fitness of individuals declines with density as individuals occupy the best habitats, the average gain per individual will stabilise to be equal in all habitats, and the fraction of a population in each habitat should equal the fraction of resources occurring there (cf. input matching; Parker 1974). When organisms distribute ideal free among habitats and the rate of resource renewal in these habitats is not affected by organisms density or distribution and all habitats are occupied at low population densities, then relative densities in habitats do not vary with population density.

When distributions change with density, habitat models are expected to change with density as well. As a consequence, managerial actions may vary with population level. However, a quantitative evaluation of how important density-dependent effects are relative to density-independent effects in shaping fish distributions has not been done. Because of this, it is not known if or how much habitat models change with density. This will be further addressed in Chapter 4.

1.7. Conclusions, research questions and thesis outline

Fish distributions are the result of multiple processes operating at multiple scales. From this, fish are associated with their environment at multiple scales. Because fish are associated with their environment over a range of spatio-temporal scales, a comprehensive understanding of processes affecting fish distributions can only be achieved by studying associations of fish with habitats over a range of scales. Scaling analyses and theory can act as a framework that allows for connecting results from studies operating at different space-time scales.

Tools for fish-habitat management may be most successfully developed within the framework of realistic habitat models, i.e. models that are derived primarily from biological knowledge rather than from correlation alone. As fish distributions are ultimately the result of individual decisions, an understanding of habitat selection behaviour of individuals will be important to fish habitat-management. Important research questions in this context are: (1) how do fish perceive and react to their environment; (2) is habitat use or density indicative of habitat quality; (3) to what extent are fish distributions driven by habitat selection and to what extent by other processes; and (4) how can we extrapolate individual fish behaviours to scales relevant to management problems?

The thesis focuses on questions 1, 3 and 4 in the context of habitat use by juvenile Atlantic salmon in rivers. Habitat selection was defined as a process of individuals choosing among options (different habitats) based on some preference. A habitat in this context is a space where an organism lives, with "space" referring not only to area or volume but also to the resources that may be obtained and the conditions within this area or volume.

I mostly aimed at achieving an understanding of "how" salmon parr select their habitat rather than "what" they are selecting for, and of the implications of habitat selection behaviours to habitat models. Habitat is described largely in terms of substrate, water depth and water velocity, as these are the variables most often included in habitat models of riverine fish species (Orth and Maughan 1982, Fausch et al. 1988, Heggenes 1990). My fieldwork (Chapters 3-4) concentrated on spatial analyses operating at small to intermediary scales (<100 m^2), because these are important to habitat selection and habitat modelling and because of logistics.

In this thesis, I first evaluated the scale-up in habitat modelling from behavioural observation to fish-habitat problem (Chapter 2). Next, I presented a new scaling method that can be used in habitat selection and habitat modelling (Chapter 3.1), extended this technique using data from an experiment done in a stream tank (Chapter 3.2), and applied the techniques developed in Chapter 3.1 and Chapter 3.2 to a field-based study (Chapter 3.3). Chapter 3 is largely focused on effects of habitat selection on distribution patterns. By contrast, in chapter 3.2 and chapter

4 I showed how distribution patterns may affect habitat selection processes. This was done by studying density-dependent habitat use, using a combination of an experimental (Chapter 3.2, 4.1) and observational (Chapter 4.2) approach. In the last chapter (Chapter 5) I summarised the various studies and discussed implications to habitat modelling and fish-habitat management. To facilitate readability, I organised the thesis such that chapters and study projects can be read separately. Because of this, the different chapters may show some overlap.

The objectives of this thesis were (1) to illustrate how a variety of newly developed scaling-techniques can be used in habitat modelling and behavioural studies; (2) to evaluate limitations of using information on small-scale observations and experiments to address problems at scales relevant to fish-habitat management; (3) to identify scales important to habitat models for juvenile Atlantic salmon; (4) to formalise observed habitat selection behaviours that operate at multiple scales into explicit multi scale habitat selection models; (5) to study density-dependent habitat selection; and (6) to compare explicit multi scale approaches with single scale approaches in regard to their ability to identify how fish select their habitats and in their ability to describe and predict fish distributions.

I hypothesised that (1) multi scale approaches are better for understanding and describing fish distributions because habitat selection behaviours themselves operate at multiple scales; (2) habitat use changes with density due to small-scale spacing behaviour or territoriality of individual fish; (3) multi scale habitat models perform better than single scale habitat models, especially when extrapolating small-scale habitat selection behaviours to density-predictions at larger spatial scales, i.e. observed and predicted distributions will be more similar when using multi-scale habitat models; (4) small-scale behavioural processes or small-scale fish-habitat associations will be limited for explaining larger scale distributions or addressing large-scale habitat management problems.

Chapter 2: Mortality versus spatial dynamics at multiple scales: scaled-rate plots for salmonids and implications for habitat modelling

2.1. Scale-up in ecological studies

Understanding how organisms interact with their natural environment is crucial to the management of natural populations. To obtain this understanding, man uses surveys, field and laboratory experiments to study the distributions of organisms relative to environmental factors. The relative importance of processes is known to vary with spatio-temporal scales (Horne and Schneider 1994). Consequently, processes that are important at the smaller scales of experiments or most field observations may not necessarily be important at the larger scales of ecological problems. Developing the ability to determine which processes predominate at any space and time scale would greatly improve the efficiency of research and confidence in its generality. In turn, this should ideally lead to more effective environmental management.

Horne and Schneider (1994) recently proposed a technique to evaluate the relative importance of processes in a scale-explicit manner. This method can also be an aid in scaling-up from experiments (i.e. extrapolating) to address environmental problems at regional or global scales (Schneider et al. 1997). This technique compares demographic, growth and kinematic rates via dimensionless ratios, which are subsequently used to indicate which processes predominate at a given scale. This procedure consists of five steps: (1) state the quantity of interest; (2) write a conservation equation incorporating the sources of variability in the quantity[*]; (3) form dimensionless ratios from the terms of the equation; (4) obtain values from the literature and calculate these dimensionless ratios for "benchmark" spatio-temporal scales; (5) create a graph with "temporal scale" and

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[*] E.g.: number of individuals = births - deaths + immigration - emigration

"spatial-scale" as Y and X axes, respectively, and draw contour lines separating spatio-temporal scales where denominator and nominator of rates prevail. As this technique uses information from a limited number of spatio-temporal scales (benchmark scales) with interpolation, I will further refer to this technique as the "benchmark" approach.

Step 1 requires that the problem be defined using quantities such as biomass or count data. The conservation equation (step 2) ensures closure of the first moment (average) of the quantity of interest. Forming all possible ratios (step 3) re-normalises the terms in the equation, i.e. the rate of change in the numerator is measured relative to the rate of change of the denominator.

The advantages of this approach are that all important processes are included and that ratios are readily obtained for literature values of component rates. A disadvantage is that interpolation between benchmarks is difficult because benchmarks are few in number. Because of this, rate-diagrams may be rough, approximate, and dependent on intuition.

In this chapter I extended the technique by using intensive computation rather than hand-drawn lines between benchmarks, in an individual-based Lagrangian approach with randomisation (Chapter 2.2). I illustrated this technique using several theoretical examples first (Chapter 2.3). Next I developed rate-diagrams of movement versus mortality for cutthroat-trout (*Oncorhynchus clarki*) and Atlantic salmon parr (*Salmo salar*) from published data (Saunders and Gee 1964, Heggenes et al. 1991) (Chapter 2.4). This combination of examples and real data was necessary because I found that detailed rate-diagrams are difficult to obtain from benchmark scales alone, partly due to scarcity of movement information and partly due to difficulties associated with interpolation from benchmark values. By first calculating rate-diagrams from relatively simple computer-generated movement and mortality scenarios and next combining these with rate-diagrams from observed data, I was able to evaluate where information was lacking and how this affects conclusions. An additional objective was to provide reference rate-diagrams for future studies.

2.2. Scaled-rate plots: method and calculations

The model simulates movement and mortality of individual organisms. Based on these FORTRAN-based simulations, critical scales are identified, i.e. space-time scales at which movement (M, year^{-1}) equals mortality (D, year^{-1}; M/D = R = 1). Random numbers, needed for several of the analyses, are generated using the FORTRAN system-supplied random number generator, upgraded by the shuffle-routine as outlined by Press et al. (1986).

Movement can be modelled along a transect (1D), in a plane (2D), or in a volume (3D). For all three approaches, the main computational flow is similar. In this chapter the computational flow for the one dimensional transect application is presented.

Determination of critical scales involved a series of calculations:

(1) 10^4 random locations were chosen along a transect (length = 1000 km) as initial positions of fish.

(2) The transect was subdivided into consecutive bins of equal length (L). For this, a random location along the transect was chosen as a starting point. Next, I determined the section or bin in which each individual fish was positioned.

To avoid the problem of having sections cut-off by either the start or the end of the transect, I connected these, leading to a circular or infinite transect. This greatly facilitated computations and judged not to affect conclusions, given the length of the transect. This was verified in additional analyses using longer and shorter transects.

(3) Movements and deaths of individuals were modelled for a period of time T (days), using a random point in the annual cycle as a starting point. After this period of time (T), I determined the number of organisms that had died (N_D), the number that were alive and stayed within the original section (N_S), and the number that were alive and moved from the original section (N_M) within period T. From this, I determined whether N_M exceeded N_D.

(4) These calculations were performed for a range (i) of section lengths (L_X, x=1,i).

(5) Calculations 1-4 were repeated for a range (j) of time periods (T_Y, y=1,j), each time using a different random transect starting location and a different random starting time in the annual cycle.

(6) Calculations 1-5 were repeated NRR times (Number Repeat Randomisations; see Table 2.1). From these repetitions, I recorded the total number of cases where N_M exceeded N_D (=NC_M) and the total number of cases where N_D exceeded N_M (=NC_D) for all space-time scales (L, T) involved. If NC_M exceeded NC_D, I concluded that movement dominated mortality ($R>1$), i.e. the distribution was driven by movement rather than mortality. If NC_D exceeded NC_M, I concluded that mortality dominated movement ($R<1$). I determined critical scales ($R=1$) using a subroutine that compared NC_D and NC_M over all spatial scales (L_X, x=1,i) for time scales (T_Y, y=1,j) separate. Critical scales were identified from a shift of $NC_M>NC_D$ at L_x,T_y to $NC_M<NC_D$ at L_{x+1},T_y.

Transect length, number of organisms and repetitions, and space- (L) and time- (T) scales may vary with scenario. I decided on the transect length, number of organisms and repetitions as outlined in the text above and in Table 2.1, as results did not change in additional analyses that used longer transects, higher numbers of organisms and more repetitions.

In general, I recommend calculating three movement/mortality scenarios: (1) one describing movement and mortality in the best possible manner, given available information, (2) one describing a low-movement/high-mortality scenario, and (3) one describing a high-movement/low-mortality scenario. Rate-diagrams of these three scenarios can then be compared to indicate the range of plausible outcomes.

2.3. Scaled-rate plots: examples

I calculated critical scales for 5 movement scenarios of fish distributed along the length of a river. These scenarios were chosen to represent a range of plausible outcomes, with movement and mortality ranging from very low to very high, as described in the previous section.

(1) *Territory* (TER): Fish were modelled to occupy individual territories. Fish never left their territories, but were free to reposition themselves within individual territories. This was modelled by randomly repositioning fish within 1 meter of positions marking the centre of individual territories at each time step of the calculation. "Territory" in this context does not refer to an area that is defended and territories may overlap.

(2) *Diurnal movement* (DM): To mimic diurnal movements within a home range, individual fish were modelled to move along the length of the river according to a sine function with an amplitude of 100 m and a wavelength of 24 hours.

(3) *Seasonal movement* (SM): Individual fish were modelled to move along the length of the river, according to a sine function with an amplitude of 1000 m and a wavelength of one year.

(4) *Total-1* (TSIN): Fish were modelled to display territorial-, diurnal-, and seasonal movements combined: territories were occupied (1) and positions marking the centre of individual territories were relocated based on the sine functions of 2-3.

(5) *Total-2* (TSQ): Fish were modelled as for TSIN. However, instead of sine waves for diurnal and seasonal movements, square waves were used.

Critical scales were calculated for each of these 5 behaviours*, with the relative rate of mortality modelled at 0.5 year^{-1} (TER-M50; DM-M50; SM-M50; TSIN-M50 and TSQ-M50 respectively) and 0.75 year^{-1} (TER-M75; DM-M75; SM-M75; TSIN-M75 and TSQ-M75 respectively; see Table 2.1). In addition, I calculated critical scales for TER-M50; DM-M50; SM-M50; TSIN-M50 and TSQ-M50, with 5% of the fish being randomly relocated within 100 m of their positions as determined by TER, DM and SM, for every 24 hours (TER-M50/R; DM-M50/R; SM-M50/R; TSIN-M50/R and TSQ-M50/R respectively). I will explain later in Chapter 2.3 why I chose this dispersion level. Estimates of critical scales were done for spatio-temporal scales ranging from 3 hours to 2 years and 1 cm to 100 km.

Table 2.1 summarises the scenarios. Figures 2.1-2.5 display the results. The lines in these figures consist of all critical values of R (i.e., R=1), separating space-time scales where movement dominates (R>1) from space-time scales where mortality dominates (R<1).

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* These movement scenarios were based on a combination of field experience of the author and information from the literature (most notably Saunders and Gee 1964 and Heggenes et al. 1991). In addition, J. Hutchings (pers. comm.) confirmed that the movement scenarios were generally supported by results from a study on brook trout movements in the Cape Race area of Newfoundland with the exception of the diurnal movements, which were probably overestimated.

Table 2.1. Scenarios used for calculating critical scales of movement versus mortality. Scenarios comprised a combination of movement and mortality (RMR, year^{-1}). Movement behaviours included: Territoriality (TER-), diurnal movement (DM-), seasonal movement (SM-) and random behaviours (/R), as explained in the text. For TSQ-*, diurnal and seasonal movement were modelled using square waves. For all other scenarios, diurnal and seasonal movements were modelled using sine waves. NRR refers to the number of repeat randomisations used to estimate critical scales.

#	TER	DM	SM	R	Scenario	RMR	NRR
1	yes	no	no	no	TER-M50	0.50	100
2	yes	no	no	no	TER-M75	0.75	100
3	yes	no	no	yes	TER-M50/R	0.50	100
4	no	yes	no	no	DM-M50	0.50	500
5	no	yes	no	no	DM-M75	0.75	500
6	no	yes	no	yes	DM-M50/R	0.50	500
7	no	no	yes	no	SM-M50	0.50	100
8	no	no	yes	no	SM-M75	0.75	100
9	no	no	yes	yes	SM-M50/R	0.50	100
10	yes	yes	yes	no	TSIN-M50	0.50	500
11	yes	yes	yes	no	TSIN-M75	0.75	500
12	yes	yes	yes	yes	TSIN-M50/R	0.50	500
13	yes	yes	yes	no	TSQ-M50	0.50	2000
14	yes	yes	yes	no	TSQ-M75	0.75	2000
15	yes	yes	yes	yes	TSQ-M50/R	0.50	2000

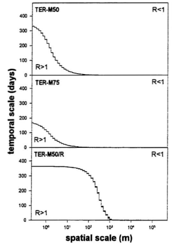

Figure 2.1. Critical scales of territorial fish. Scenarios include TER-M50 (top, 50% mortality per year), TER-M75 (middle, 75% mortality per year) and TER-M50/R (bottom, 50% mortality per year + random movements). Territorial behaviours are modelled as explained in the text. (R = movement (year^{-1}) versus mortality (year^{-1}).)

Figure 2.1 shows the rate-diagrams for fish displaying territorial behaviour (TER). The "jagged" outline of the lines are the result of the approximation routine used to determine critical scales. In general, movement dominated at small space-time scales and mortality dominated at large space-time scales. Mortality always dominated over movement at time scales larger than one year for TER-M50 and TER-M50/R and at time-scales larger than 183 days for TER-M75. The reason for this is that 50% of the fish died during intervals of one year for TER-M50 and TER-M50/R (mortality=0.5 year^{-1}) and 50% during intervals of 183 days for TER-M75 (mortality=0.75 year^{-1}). During longer intervals, more than 50% of the fish died and, because of this, mortality always dominated at these time-scales. During shorter intervals, domination of movement over mortality depended on space-time scale. The difference in mortality of 0.5 year $^{-1}$ (TER-M50) and 0.75 year $^{-1}$ (TER-M75) resulted in a minor shift to the left and a major shift down of the line of critical values from TER-M50 to TER-M75. Note that movement may dominate over mortality at space scales much larger than that of the size of individual territories, especially when time-scales are small. TER-M50/R is largely determined by random behaviours, with little influence of territoriality.

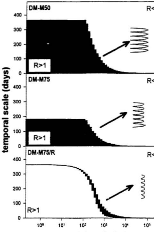

Figure 2.2. Critical scales of fish displaying diurnal movements. Scenarios include DM-M50 (top, 50% mortality per year), DM-M75 (middle, 75% mortality per year) and DM-M50/R (bottom, 50% mortality per year + random movements). Diurnal movements are modelled using sine waves, as explained in the text. (R = movement (year^{-1}) versus mortality (year^{-1}).)

Figure 2.2 shows the rate-diagrams for fish displaying diurnal movements (DM). The "jagged" outline of the lines are primarily due to diurnal movements and only to a small degree due to the approximation routine used: no fish moved at time-scales of 1,2,3,... day, and movement is maximal at time-scales of 0.5, 1.5, 2.5,... day. From this, diurnal movements induced a characteristic regular pattern with a wavelength of 1 day-scale. The small wavelength of this regular pattern, in combination with the resolution of the Y-axis (temporal scale), makes the lines of critical values (R=1) appear as a broad black band. This is further illustrated in Figure 2.2 by expanding portions of the graphs for temporal scales of 95 to 100 days. As in the previous figure, dominance of movement over mortality is restricted to smaller space-time scales. Again, we see a dominance of mortality over movement at time scales longer than one year for DM-M50, DM-M50/R and at time scales longer than 183 days for DM-M75. The difference in mortality of 0.5 year^{-1} (DM-M50) and 0.75 year^{-1} (DM-M75), resulted in a minor shift to the left and a major shift down of the line of critical values from DM-M50 to DM-M75. The rate diagram of DM-M50/R is largely determined by random behaviours at space-time scales left of the band of critical values. At larger space-time scales, diurnal movements determine the rate-diagram. An impression of this can also be obtained by overlaying the rate-diagrams of DM-M50 and TER-M50/R: movement dominated mortality in DM-M50/R at scales where either one or both of the rate diagrams of TER-M50/R and DM-M50/R indicated that R>1. The level of dispersion was chosen such that this overlay-procedure could be illustrated.

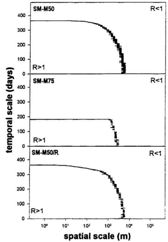

Figure 2.3. Critical scales of fish displaying seasonal movements. Scenarios include SM-M50 (top, 50% mortality per year), SM-M75 (middle, 75% mortality per year) and SM-M50/R (bottom, 50% mortality per year + random movements). Seasonal movements are modelled using sine waves, as explained in the text. (R = movement (year^{-1}) versus mortality (year^{-1}).)

Figure 2.3 shows the rate-diagrams for fish displaying seasonal movements (SM). The "jagged" outline of the lines are the result of the approximation routine used. Similar to the previous figures, movement dominated at smaller scales and mortality at larger ones. The lines of critical values are all shifted to the right compared to Figure 2.2. This is because the seasonality lead to larger-scale movements over the range of temporal scales studied. Again, mortality dominated movement at time scales longer than one year for SM-M50, SM-M50/R and at time scales longer than 183 days for SM-M75. SM-M50/R resembled SM-M50, as movement of SM-M50/R is dominated by seasonal movements, with little effect of random behaviours.

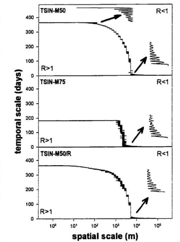

Figure 2.4. Critical scales of territorial fish displaying diurnal and seasonal movements. Scenarios include TSIN-M50 (top, 50% mortality per year), TSIN-M75 (middle, 75% mortality per year) and TSIN-M50/R (bottom, 50% mortality per year + random movements). Diurnal and seasonal movements are modelled using sine waves, as explained in the text. (R = movement (year^{-1}) versus mortality (year^{-1}).)

Figure 2.4 shows the rate diagrams for fish displaying territorial behaviours, diurnal- and seasonal movements combined. As in the rate-diagram of DM-M50/R, an impression of these figures can be obtained by the overlay-procedure mentioned above: TSIN-M50 can be obtained by overlaying TER-M50, DM-M50 and SM-M50; TSIN-M75 can be obtained by overlaying TER-M75, DM-M75 and SM-M75; TSIN-M50/R can be obtained by overlaying TER-M50/R, DM-M50/R and SM-M50/R. The rate-diagrams of Figure 2.4 are determined by either diurnal movements or seasonal movements, depending on space-time scale. E.g. TSIN-M50 resembles SM-M50 at time scales ranging from 10 days to 355 days as seasonal movements predominate. For other space-time scales the rate-diagram is determined by a combination of diurnal and seasonal movements, with little effect of territorial movements. This is further illustrated in Figure 2.4 by expanding portions of the graphs for temporal scales shorter than 10 days and longer than 355 days.

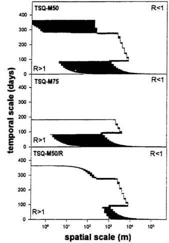

Figure 2.5. Critical scales of territorial fish displaying diurnal and seasonal movements using square waves. Scenarios include TSQ-M50 (top, 50% mortality per year), TSQ-M75 (middle, 75% mortality per year) and TSQ-M50/R (bottom, 50% mortality per year + random movements). (R = movement (year^{-1}) versus mortality (year^{-1}).)

Figure 2.5 shows the rate diagrams for fish displaying the behaviours as in Figure 2.4, but with seasonal and diurnal movements based on square waves, rather than sine waves. This mimics a situation in which seasonal and diurnal shifts are more abrupt than in Figure 2.4. Shifts occur during short periods of activity, followed by relative inactivity. From this, the bands of critical values are much wider than those of Figure 2.4. For time scales ranging from 100-250 days, the rate diagrams are determined by seasonal movements. For other time-scales, the rate-diagrams are largely determined by either territoriality, diurnal movements or random behaviours, depending on space-time scale. This can be seen by overlaying Figures 2.5 and 2.1. At space-time scales left of the lines of critical values of Figure 2.1, rate-diagrams of Figure 2.5 are determined by territoriality (TSQ-M50, TSQ-M75) and/or random behaviours (TSQ-M50/R). At larger space-time scales, diurnal movements prevail.

As expected, movement dominated mortality at small space-time scales, and mortality dominated movement at large space-time scales (Figures 2.1 - 2.5). Movement often dominated mortality at spatial scales that are several orders of magnitude larger than of movements of individuals, especially at smaller time scales. The line of critical values separating dominance of movement from dominance of mortality were complex (Figure 2.5), or simple (Figure 2.1), depending on the processes involved. Complex lines occurred especially when distributions were the result of periodic processes with small wavelengths. Simple lines in rate-diagrams allowed for an easy separation of dominance scales ($R>1$ vs. $R<1$). Complex lines allowed for this as well, but in addition to scales where movement clearly dominated over mortality and scales where mortality clearly dominated over movement, scales existed where dominance rapidly changed with small changes in scale. These scales appear in the figures as broad bands. In these situations, three dominance regions can be identified: $R>1$, $R<1$, $R\approx1$). The figures show that a combination of processes may lead to characteristic rate diagrams, that rate diagrams cannot be drawn from few benchmark scales with any accuracy, that computational boundaries do not always match intuited boundaries, and that computational methods are required to identify the boundary between scales where movement prevails, and scales where mortality prevails.

2.4. Scaled rate plots: juvenile Atlantic salmon

Mortality of salmonids from egg to hatching has been reported to generally fall within the range of 10 to 25%; mortality from emergence to the end of the first growing season from 70 to 90%, and in subsequent growing seasons from 25-50% per year (cf. Mills 1989). Few quantitative information is available on how mortality varies with season or time-of-day, although we do know that mortality is related to temperature, season, stream discharge, water chemistry, etc., which are all subject to diurnal and seasonal cycles (Gibson 1993).

In spite of the fact that a considerable number of papers on salmonid movement have been published (cf. Northcote 1984, 1992), little quantitative information is available on the consequences of this process on production and standing stock. We do have a general impression of the timing and direction of movement processes over the season (cf. Youngson et al. 1983, Hutchings 1986), but little quantitative information is available on how this affects the distribution or production of salmonid biomass in the river. Most studies on salmonid movement seem to indicate that the extent of the movement is rather limited even over longer periods of time, except in spawning season. The general consensus among researchers is that the majority of juvenile salmonids move very little: home ranges of various salmonid species are reported to vary from 5-200 meter along the river length, with most home-ranges covering a few tens of meters (Saunders and Gee 1964, Heggenes 1988, Heggenes et al. 1991, Northcote 1992). Even when salmonids are introduced and competition is low, dispersion into un-colonised areas seems to be a slow process (Heggenes and Borgstrøm 1991).

It is difficult to derive explicit rate-diagrams for juvenile salmonids from available information. This is in part due to the fact that information is collected or presented at one time-scale only (movement over one year, season etc.) or for groups of fish, rather than individuals. Such information cannot be interpreted at multiple scales. Because of scarcity of movement information, Figures 2.1 to 2.5 were used to obtain an impression of possible salmonid parr rate-diagrams. Assuming that mortality ranges from 0.5 to 0.75 $year^{-1}$ for 0+/1+ salmon parr (cf. Gibson 1993) and assuming that movement will most likely be larger than that of scenario TER-M50, but smaller than that of TSQ-M50/R, salmon parr rate-diagrams may be obtained by overlaying the rate-diagrams of TER-M50, TER-M75, TSQ-M75, and TSQ-M50/R in Figure 2.6. From this, a first guess was that the line of critical values resided somewhere within the band $R \approx 1$ of Figure 2.6 (left figure). This figure also includes the scope-diagram of Figure 1.1 (re-scaled for 1D).

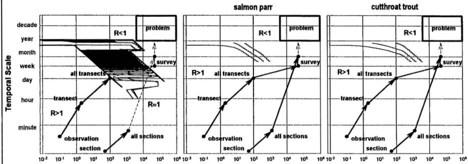

Figure 2.6. Critical scales of movement versus mortality of simulated fish behaviours including territoriality, diurnal and seasonal movements (left; overlay of TER-M50, TER-M75, TSQ-M50/R and TSQ-M75), and observed salmon parr (middle, based on Saunders and Gee (1964)) and cutthroat trout movements (right, based on data of Heggenes et al. (1991)) assuming a mortality of 0.25, 0.5 and 0.75 $year^{-1}$. Arrows connecting observation to problem relate to the scale-up in micro-habitat modelling; the arrows connecting section to problem relate to the scale-up in macro-habitat modelling (cf. scope-diagram Figure 1.1). (R = movement ($year^{-1}$) versus mortality ($year^{-1}$).)

One of the few studies that allows for a multi-scale interpretation is a study by Heggenes et al. (1991) on cutthroat trout. For this study, trout were sampled fortnightly over a period of eight months (January - August) in a small river (about 2.6 m width average). All trout were marked individually and individual trout positions determined relative to benchmarks positioned along the length of the river. Trout movement was limited. Over an average fortnightly period, 68.3% of the fish were recaptured within 10 m off their original position; only 17.9% had moved more than 50 m. This pattern of movement did not seem to vary much over the season or with period in between mark and recapture. A similar study on salmon parr movement during summer to early winter from Saunders and Gee (1964) indicated movements similar to those of Heggenes et al. (1991) (see below).

Based on the information from these two papers, I derived the rate diagrams of Figure 2.6. For this, I used the procedure as outlined in Chapter 2.2. Mortality was modelled as 25%, 50% and 75% per year. Movement for cutthroat-trout (Heggenes et al. 1991) was modelled by randomly repositioning 32.4% of the fish within one meter of original position along the length of the river; 15.6% within 1-3 m; 15.2% within 3-10 m; 6.8% within 10-20 m; 12.1% within 20-50 m; and 17.9% within 50-400 m. Movement of salmon parr (Saunders and Gee 1964) was modelled by randomly repositioning 13.3% of the fish within one meter of original position along the length of the river; 24.0% within 1-3 m; 37.3% within 3-10 m; 21.3% within 10-20 m; 1.3% within 20-50 m; and 2.7% within 50-400 m. Movement direction (upstream/downstream) of individual fish was determined by randomisation. This distribution scenario was used independent of time-period. From this, I estimated critical scales within the sampling interval and study range of Heggenes et al (1991) (14 days to 8 months). Note that the implicit assumption of this procedure is that fish that were not recaptured displayed the same movements as those recaptured.

The critical scales calculated from Heggenes et al. (1991) and Saunders and Gee (1964) are within the expected range of the left figure of Figure 2.6. Figure 2.6 shows that the fish observations and the scales of variables in habitat models refer to scales where movement predominates. This information is subsequently used for management problems at scales where mortality predominates. This change in dominance with scale-up underlines the fact that research is needed that explicitly examines if large-scale distributions may be inferred from small-scale observations: movement and habitat selection behaviours may explain small-scale observations quite well, as these processes predominate at these scales, but may be of limited importance to large-scale distributions where mortality predominates. However, Figure 2.6 also underlines the fact that movement may be important to dynamics at scales larger than individual fish movements. This underlines the importance of movement and habitat selection studies for an understanding of distribution processes.

It could be argued that the individual-based approach produces rate-diagrams that are more detailed than our understanding of population processes involved. My experience with this method so far, however, is that even a combination of rather cartoon-like descriptions of the various processes involved allows for reliable inferences at scales most important to research problems. Figure 2.6 shows that critical scales differed among the movement scenarios, but these differences occur at space-time scales that are much larger than those of most field observations, and much smaller than those of many environmental problems we would like to address. From this, uncertainty with respect to movement did not lead to uncertainty with respect to dominance of processes at the scales most relevant to research: none of the dots in the scope-diagrams of Figure 2.6 are within the range of scales where dominance varied with movement scenario.

2.5. Rate-diagrams in habitat modelling

Rate diagrams can be used to identify important research problems and appropriate sampling scales and make explicit the scales and scope of observations, surveys, experiments and problems (Horne and Schneider 1994). I will illustrate this based on the information presented in Figure 2.6:

Information on habitat use by salmonids is mostly obtained from field observations or experiments done at scales where movement predominates, whereas management problems are at scales where mortality dominates. Because of this, available information may not necessarily apply to processes occurring at the scales of the problems we would like to address (cf. Minns et al. 1996), and the scale-up from information to problem will have to be validated. Rate diagrams can aid in this validation process.

For example, sampling could be done using many repetitions but over a small area, or using few repetitions but with more sampling units distributed over a wider area. The first approach will permit a greater confidence in observations at the study area, as the number of repeat-observations is larger, but the scope of the survey is relatively small. By contrast, the second will permit less confidence in observations at individual sampling units, but the scope of the study will be considerably larger (cf. Schneider 1994). Preferably, surveys or experiments should be designed such that extrapolation of results is possible to scales where the same processes predominate that are relevant to the ecological problems we would like to address. Rate-diagrams that include the scale and scope of observations and surveys will make explicit important information needed for such experiment and survey designs. This is illustrated in the Scope-diagrams of Figure 2.6.

Extrapolation from "observation" and "section" (movement predominates) to scales where mortality predominates ("survey") is possible, provided that sampling is done over a long-enough time period and with sections located throughout a large enough area. If sections are located closer together or when sampling is done during a shorter period, the dots in Figure 2.6 that indicate the survey-scales will be positioned within the band of critical scales ($R \approx 1$) or at scales where movement predominates ($R > 1$). That is, processes different from the ones operating at the scales of our problems determine the observed distributions.

From Figure 2.6 and the dots that indicate survey-scales it may seem that most habitat-use surveys will allow for an extrapolation to scales where mortality predominates. However, since sections are often visited consecutively and by a single visit, it will be difficult to separate effects of time, time-scale, space and space-scale. That is, it will be difficult to ascertain whether fish-habitat associations observed at large spatial scales are due to changes in distribution processes with time or due to processes operating at large spatial scales. By contrast, a survey where sections are located within a representative part of the river and where sections are visited repeatedly over a long enough period would allow for a scale-up to scales where mortality predominates (e.g. length of representative river section = 5 km; period = 3 months; see Figure 2.6, middle, right). This scale-up would involve an explicit evaluation of how well larger-scale distributions of fish could be described from small-scale associations. I am not aware of studies that explicitly address this question and that operate over a range of scales. However, results from several papers indicate larger scale distributions are subject to processes different form the ones that underlie small-scale associations (e.g. Jackson and Harvey 1989, Rabeni and Sowa 1996). In addition, several studies have indicated that there is no significant relationship between weighted usable area, an index of habitat quality based on small-scale fish, and habitat observations, and standing stock (large-scale distributions) (cf. Orth and Maughan 1982, Conder and Annear 1987, Shirvell 1989, Bourgeois et al. 1996), although some studies did find such a relationship (Stalnaker 1979, Orth and Maughan 1982). This may suggest that possibilities for using small-scale observations or habitat models to infer larger scale fish distributions (scale-up) are limited. A careful examination of scale-up in habitat modelling is important, to identify processes and research questions important to fish-habitat management.

2.6. Rate-diagrams in ecological studies

The individual-based technique differs from the benchmark technique proposed by Horne and Schneider (1994). The benchmark approach uses information on processes at several specific spatio-temporal scales. However, information at one benchmark may be available at a different moment in the season or location than information at other benchmarks, and combining information at a certain benchmark scale from information derived from various moments in season or locations becomes difficult. Because of this, interpretation of dominance of processes may change not only due to differences in scale, but also due to differences in time and location. Consequently, benchmark rate-diagrams may be rough and approximate. This problem does not apply to the individual-based approach.

The individual-based approach as outlined leads to rate-diagrams that are independent of the initial distribution or density of the organisms, provided the processes involved are density-independent (cf. results do not change when increasing transect length, number of organisms, or clumpedness of initial distribution: see Chapter 2.2). The individual-based approach can be adjusted to incorporate density-dependent processes. However, results may then vary with distribution and density of organisms.

The individual-based approach leads to rate-diagrams that are also independent of location or time of observation, i.e. "time" and "time-scale" as well as "location" and "space-scale" are effectively de-coupled by randomising transect-start and starting-time in the dynamic simulations. Often, however, we may be interested in developing rate-diagrams for specific locations or specific moments-in-time, as when interested in dominance of processes at a specific location or a specific point in the season. The individual-based approach can be adjusted to develop such rate-diagrams. This would require that in the calculations either location is fixed, i.e. we do not use a randomised transect-start, and starting-time of the simulations is determined by randomisation, or that time is fixed and transect-start is determined by randomisation. This would re-establish the coupling between space and space-scale and time and time-scale. An example of where such time-specific or location-specific rate-diagrams are of use is selection for appropriate measurement scales for quantifying mortality in a particular moment in the season. Another example is the determination of the area of a nature-reserve needed to protect a variety of organisms. The area of this reserve could be determined such that movement out of the reserve is small compared to the mortality as experienced within the reserve (ratio: movement/mortality). Another possibility may be to use the ratio Fnat/Fman, which would scale the natural mortality of organisms within the reserve (Fnat, day^{-1}) to the human-induced mortality (Fman, day^{-1}) as experienced by organisms that were originally within the reserve, but happened to cross the reserve boundary. Assuming that Fman should be small (e.g. one tenth) compared to Fnat, critical scales could be calculated (scales where Fman = 10* Fnat) thus determining the reserve area needed to protect these organisms over a range of time periods (time-scales). Such rate-diagrams could be developed for all organisms to be protected with this reserve. By overlaying these, one could assess which species would be protected and which ones not at a given reserve area.

Ecological research can be made more efficient by carefully considering at what moments in time or at what locations observations should be done, e.g. by sampling at locations and moments that are important to life history or by sampling at locations and moments where variance is greater or density higher. Parallel to this, ecological research can be made more efficient by carefully considering at what spatio-temporal scales observations should be done, e.g. by sampling at scales where variance is greater or at scales where processes predominate that are important to the problems we would like to address. Rate- and scope-diagrams make this decision process explicit. In this context, I consider rate- and scope-diagrams as complementary to Stommel-diagrams (Stommel 1963, Haury et al. 1978): rate-diagrams depict the importance of processes over spatio-temporal scales; Stommel-diagrams depict variability over spatio-temporal scales; scope-diagrams allow for weighting pros and cons of various survey designs, given information made explicit by rate- and Stommel-diagrams. By using information from Stommel-, rate-, and scope-diagrams in combination, I expect efficiency of research to improve.

2.7. Conclusions

Scaled rate-diagrams are useful in judging the relevance of spatially and temporally limited data to larger scale questions. Intensive computation based on theoretical but plausible scenarios uncovered features that are difficult to detect with benchmark methods. Information on individual movement is important to development of rate-diagrams.

Chapter 3: Multi-scale analyses of habitat use by juvenile Atlantic salmon

3.1. New technique describing spatial scaling and habitat selection in riverine habitats

3.1.1. Introduction

3.1.1.1. Scale in ecological studies

Ecological studies aim at achieving an understanding of the processes that affect the distribution and abundance of organisms. To achieve such an understanding, distributions of organisms are studied relative to distributions of environmental features. This generally involves an evaluation of the level of heterogeneity or patchiness of organism distributions (uniform, random, clumped), and an evaluation of associations of organisms with their habitats (positive, negative). However, distributions of organisms are the result of multiple processes operating over a range of spatio-temporal scales, and patchiness and associations will vary with measurement scale. Because of this, an understanding of distribution processes can be best achieved by studying distributions of organisms and habitats over a range of scales rather than at a single scale.

The influence of scale on ecological studies has long been recognised. Recent publications re-iterate the importance of scale (Addicott et al. 1987, Wiens 1989, Menge and Olson 1990, Holling 1992, Levin 1992, Horne and Schneider 1995). Nevertheless, most ecological studies use a single or few measurement scales and a rather implicit use of scaling: The measurement scale chosen is often not the result of a quantitative multi-scale approach, but is based on biological intuition of the researcher combined with logistical constraints.

Single-scale approaches to multi-scale problems arise for a combination of reasons. The first reason is that "scale" has numerous meanings in the ecological literature. In this thesis, I define "scale" as "the resolution within the range of a measured quantity" (Schneider 1994). A second reason could be an unfamiliarity among ecologists with the mathematical tools available to deal with scaling, in spite of several publications on the subject (Platt and Denman 1975, Ripley 1981, Greig-Smith 1983, Upton and Fingleton 1985, Legendre and Fortin 1989, Schneider 1994, Horne and Schneider 1995). A third reason is that multi-scale analyses often require large data sets collected over a range of scales. This has confined most empirical multi-scale analyses to studies based on techniques such as echo sounding or remote sensing, which generate large amounts of data (e.g. Weber et al. 1986, Horne 1994).

A number of mathematical tools are available to assess patchiness of fish distributions and associations of fish with habitats at a range of scales. Some of these tools can be used to cover a fixed number of scales; others can be used to examine a wide range of scales simultaneously. To assess patchiness at a fixed scale, a variety of indices were developed based on variance to mean ratios, such as Morisita's index (Morisita 1959), Lloyd's index of mean crowding (Lloyd 1967), or the exponent of Taylor's Power law (Taylor 1961). Correlation, regression, and frequency analyses can be used to assess associations of fish with habitats at a fixed scale. These techniques are generally not applied over a range of scales, although all can be. Methods that examine patchiness over a range of scales are pattern analysis (Greig-Smith 1983), correlograms and variograms (Sokal and Oden 1978, Rossi et al. 1992), variance analysis on hierarchical models (e.g. Downes et al. 1993), second-order neighbourhood analysis (Getis and Franklin 1987, Muotka and Penttinen 1994), Moran's-I (Sokal and Oden 1978), and spectral analysis (Platt and Denman 1975). Coherence analysis explicitly examines associations over a range of scales (Chatfield 1980).

3.1.1.2. Scale in habitat models and fish habitat management

Habitat models aim at describing relations between fish and their habitats. These models are widely used, especially for management of riverine fish populations (Fausch et al. 1988). Scale is known to be important to fish habitat management and fish habitat models (c.f. Frissell et al. 1986, Minshall 1988, Fausch et al. 1994, Lewis et al. 1996, Minns et al. 1996, Allan et al. 1997). Recently, several studies have used explicit multi-scale approaches to study fish populations (e.g. Syms 1995, Poizat and Pont 1996, Richards et al. 1996). However, these studies operated at a few selected scales only and other important scales may have been overlooked. In general, papers on fish habitat and scale tend to be theoretical, rather than empirical; habitat models are characterised by a rather informal treatment of scale, with variables measured at a single or a few selected scales.

This informal treatment may be due to a lack of mathematical techniques that are suitable for studying fish in rivers in addition to the reasons outlined in the previous section. Multi-scale analyses at a fixed set of scales only provide information at these scales and no information is obtained on intermediary scales. Pattern analysis, correlograms and variograms, spectral analysis and coherence analysis could theoretically be used to cover a wide range of scales. However, use of these methods is limited in empirical studies because methods based on variance analysis are sensitive to low densities where zeros are common (Fasham 1978, Upton and Fingleton 1985), and because of the irregular system boundaries of riverine habitats: two-dimensional spectral analysis or two dimensional coherence analysis can only be used for rectangular distribution maps; irregularity of system boundaries limits the use of pattern analysis because of the difficulty of positioning random or nested quadrates.

3.1.1.3. Transect versus grid-system approaches

Habitat selection studies generally operate from spatial scales far smaller than the river width (micro-habitat modelling) to several times the river width (meso- or macro-habitat modelling). To cover this range of spatial scales in multi-scale analyses, the measurement resolution will have to be high. However, at high resolutions, many of the bins or cells that compose the transect or grid-system will be empty, i.e. in many of the bins no fish will be observed. This may prevent interpretation of data at small spatial scales.

This sensitivity to zero-observations varies among transect and grid system approaches. Transect and grid systems are characterised by their length, width, resolution and range. When using a transect approach, it makes sense to use a transect width that is similar to the length of the bins within the transect at the highest transect resolution, unless this bin length is larger than the river width. In this case transect width equals river width and bin length may be larger than transect width. Because of this, when decreasing the spatial resolution of data from grid systems, the occurrence of zeros declines more rapidly than in a transect approach. For example, halving the transect resolution will double the average number of observations per bin, but doubling the width of square cells in a grid system approach will quadruple the number of observations per cell. Because of this, multi-scale analyses at high spatial resolutions in environments of low densities may be more effective when using grid-based rather than transect systems.

3.1.1.4. Objectives

I present a new quantitative multi-scale approach, based on a grid-system approach, for analysing patchiness of fish distributions and associations of fish with habitats over a wide range of spatial scales, from far smaller than the river width to several times the river width. This method is based on frequency analysis with randomisation. The method will be illustrated using simulated fish distributions as well as field data collected in North

Harbour River, Newfoundland, in 1994.

3.1.2. Methods

3.1.2.1. Study site

North Harbour River is located on the Avalon Peninsula of Newfoundland, Canada (47°12'0" N, 53°37'30" W). The river drains a watershed of 73 km^2, consisting of boreal forest and open bog underlain by Precambrian sedimentary rock. The fish community in North Harbour River is composed of Atlantic salmon, *Salmo salar*, brook trout, *Salvelinus fontinalis*, brown trout, *Salmo trutta*, threespine stickleback, *Gasterosteus aculeatus*, and American eel, *Anguilla rostrata*. The river is further described by DeGraaf and Bain (1986). The study reach was approximately 5 km upstream from the river mouth and consisted of a combination of riffle, run and pool habitats. The length of the study reach was 120 m and the average width 9 m. The fish community at the study site is predominantly juvenile Atlantic salmon. Brook and brown trout were relatively rare (<10% by number).

3.1.2.2. Habitat mapping

The study reach was mapped for substrate, water depth (cm), water velocity (cm sec^{-1}) and cover, although in this chapter only the depth data are used. These habitat observations were evenly distributed over the study reach. For this, I established an XY-grid covering the study section using measuring tapes and T-posts as reference points.

To facilitate the taking of evenly distributed habitat observations, I used a 1 m^2 PVC frame, divided into 4 (50*50 cm) and 9 (33*33 cm) cells with coloured twine. The frame was positioned in the XY-grid, using measuring tapes and the reference T-posts. Next, the habitat observations were done at the centre of the cells within the frame: substrate and cover were mapped with a resolution of 9 observations per square meter; depths were mapped with a resolution of 4 observations per square meter. Water velocities (at 60% of depth and bottom) were mapped with a resolution of 1 observation per square meter, without the use of a frame.

3.1.2.3. Fish distribution and habitat

Fish distribution surveys were made on 17 August and 25 August, 1994. One survey took approximately 6 hours (10.00 h - 16.00 h). The weather conditions, flow conditions and water temperatures during the surveys were similar. The water temperatures during the course of both surveys varied from 16 (10.00 h) to 21 °C (16.00 h), which is normal at this time of year.

Fish were observed by snorkelling in an upstream direction in a zigzag pattern to minimise disturbance of fish. Observed fish positions were identified by using numbered weights. Data recorded during snorkelling included: species, age class (0+, 1+, 2+, >2+, estimated from size), height above bottom (cm), and activity (moving, holding position). All fish observed were recorded. The numbered markers were mapped relative to the XY-grid, to the nearest 5 cm. Water velocities, snout velocities (cm sec^{-1}), depth (cm), cover and substrate were mapped at locations of markers.

Both the habitat mapping and the fish distribution surveys were done at a discharge estimated at 0.25 $m^3 s^{-1}$, as this was the most prevalent discharge in the summer of 1994.

3.1.2.4. Computational procedures

A FORTRAN program was written to address a series of questions.

1. How are fish positioned relative to each other? This was addressed by computing spatial autocorrelations of fish positions. *(fish to fish)*
2. How are fish of group 1 positioned relative to fish of group 2? This was addressed by computing spatial associations between positions of two groups of fish (cohorts, species). *(group 1 to group 2)*
3. How are fish distributed relative to a previously recorded distribution? This was addressed by computing spatial associations between fish positions recorded on separate surveys. *(temporal)*
4. How are fish distributed relative to the distribution of a habitat feature? This was addressed by computing spatial associations of fish positions with habitat features. *(fish to habitat)*
5. How are habitat features positioned relative to each other? This was addressed by computing spatial autocorrelations of habitat features. *(habitat to habitat)*

In the following text, these questions will be referred to as components 1-5. The computational flow was similar for each component, as demonstrated below by an example based on component 4 (fish to habitat). Figure 3.1.1 shows the steps involved in the multi-scale program.

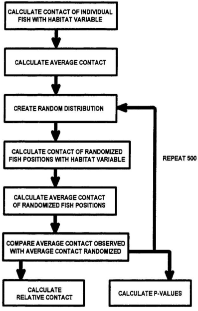

Figure 3.1.1. Flow of calculations used to investigate associations of fish with habitats over a range of spatial scales.

Component 4 (fish to habitat) compares differences in the habitat surrounding observed fish positions with the habitat surrounding computer-generated random fish positions. This comparison is made over a range of ambit radii (Figure 3.1.2).

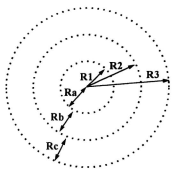

Figure 3.1.2. Illustration of the ambit concept. Multi-scale analyses can be done at increasingly larger ambit radii (R1-R2-R3) or at increasingly larger distance slots (Ra-Rb-Rc).

First, the Contact of each observed individual fish with the habitat feature of interest is calculated as the percentage occurrence of a specified class of a habitat variable (e.g. depth class, substrate class) from a map of evenly positioned habitat observations, i.e. based on a uniform grid. Next, the average Contact is calculated by averaging the Contact across all individual fish observations:

$$C_{obs,i} = \frac{1}{n} * \sum_{f=1}^{n} \frac{Nh_{if}}{Nt_{if}}$$

Equation 3.1.1

$C_{obs,i}$: average Contact of fish with specified habitat at ambit radius i

n: total number of fish observed

Nh_{if}: number of observations of specified habitat within distance i from fish position f

Nt_{if}: total number of habitat observations within distance i from fish position f

To evaluate the observed Contact relative to a random outcome, a randomised fish distribution is created by randomly repositioning all fish within the grid for each survey separately. The random distributions were created using the FORTRAN system-supplied random number generator, upgraded using the shuffle procedure (Press et al. 1986) to break up possible sequential correlations. From the randomised distributions, the average Contact (C_{ran}) is calculated for each survey and as an average of all surveys. This procedure is repeated 500 times, i.e. 500 randomised distributions are created each leading to different estimates of C_{ran}. For each of these 500 randomised distributions, C_{obs} is compared to C_{ran}. From this, p-values are derived that can be used as selection criteria to test if the Relative Contact is significantly different from 0, i.e. if the observed distribution is significantly different from the randomised distribution. Finally, an average C_{ran} is calculated based on all 500 observations of C_{ran}. From this, the Relative Contact at radius i is calculated (RC_i):

$$RC_i = \log_{10}(C_{obs,i}) - \log_{10}(C_{ran,i})$$

Equation 3.1.2

The Relative Contact presented over a range of ambit radii describes how fish are associated with habitat features over a range of spatial scales.

The procedure for components 1, 2, 3 and 5 differs slightly from component 4 (fish to habitat). For analyses aimed at investigating spatial autocorrelations of fish positions (component 1, fish to fish), or analyses aimed at investigating spatial associations of different fish populations (component 2, group 1 to group 2; component 3, temporal), Contact is quantified by using fish densities. To obtain density estimates, the program creates a uniform distribution of dummy positions within the study site. The ratio of fish observations versus dummy positions is subsequently used as an estimate of fish densities. E.g. if 400 dummy positions are created per square meter, one fish observation to 200 dummy positions indicates a density of 0.5 fish m^{-2}.

To facilitate a comparison of separate surveys for component 1 (fish to fish), which may differ in the number of fish observations, all density estimates are re-scaled as a percentage of the number of fish observed per survey minus one (1 was subtracted because this percentage refers to the number of conspecifics). For component 2 (group 1 to group 2) and 3 (temporal), all densities are re-scaled as a percentage of the total number of fish observed per survey. C_{obs} will therefore provide an estimate of the Contact of an average fish in a particular group with the other fish of the same group (component 1, fish to fish) or with fish of another group (components 2 (group 1 to group 2) and 3 (temporal)). The randomised fish distributions in components 2 (group 1 to group 2) and 3 (temporal) are created by randomly repositioning only one of the two fish groups. For component 5, the randomised distribution is created by randomly allocating the habitat observations to the positions where these habitat observations were made, using sampling without replacement. Note that in a situation of 2 surveys, 3 estimates for RC are obtained per ambit radius in components 1 (fish to fish), 2 (group 1 to group 2) and 4 (fish to habitat) (one for each survey separate and one based on both surveys). One estimate per ambit radius is obtained for components 3 (temporal) and 5 (habitat to habitat).

Analyses are done both over a range of ambit radii at increasingly larger ambit radii and at increasingly larger distance slots, as illustrated in Figure 3.1.2. The smallest ambit radius will differ among analyses, due to differences in resolution of the mapping of the habitat and fish distributions. For associations of fish positions, the smallest ambit radius should exceed 5 cm to ensure that at least one other possible fish position is within the ambit of each possible fish position. For associations of fish with depth, the smallest ambit radius should exceed 36 cm ($=\sqrt{25^2 + 25^2}$) to ensure that at least one depth observation is within the ambit of each possible fish position. For analyses aimed at spatial autocorrelation of depth observations, the smallest ambit radius should exceed 50 cm to ensure that at least one other habitat observation is within the ambit of each habitat observation.

The value of Relative Contact allows positive associations ($RC>0$) to be distinguished from negative associations ($RC<0$). A Relative Contact of 1 indicates that the average fish observed has 10 times more contact with a particular habitat feature compared to an average fish of the randomised distribution. A Relative Contact of -1 indicates that the average fish observed has 10 times less contact with a particular habitat feature compared to an average fish from the randomised distribution. The RC is therefore more readily interpretable than the Habitat Preference Indices used in many habitat selection studies.

3.1.2.5. Analyses

Components 1 (fish to fish) and 5 (habitat to habitat) were tested, using the program on a total of 290 fish that was evenly distributed within 6 randomly positioned clusters or "schools" in a 100*100 m area (=group 1 fish). The minimum distance between group 1 fish in a school was 1.5 m and schools were arbitrarily assumed to approximate circles with a radius of 6 m. Relative Contact was quantified at increasingly larger ambit radii. The Relative Contact was expected to show a minimum at small spatial scales (ambit radius <1.5 m, $RC<0$) due to the minimum fish distance, and a maximum at intermediate spatial scales (ambit radius = 2-6 m, $RC>0$) due to schooling. The Relative Contact was expected to decline to 0 at spatial scales larger than 6 m because of the random positioning of schools.

Components 2 (group 1 to group 2) and 3 (temporal) were tested by using the program to an additional 292 fish that were evenly distributed within the same grid within 6 randomly positioned schools. There was no overlap between schools. Minimum distance between fish and school radius was similar to the test of components 1 (fish to fish) and 5 (habitat to habitat). Relative Contact between fish of group 1 with fish of group 2 was quantified at increasingly larger ambit radii. The Relative Contact was expected to show a minimum at small spatial scales (ambit radii <10 m, RC<0) due to the spatial separation of schools. The Relative Contact was expected to approach 0 at ambit radii larger than 10 m, as schools were randomly positioned.

To test component 1 (fish to fish) against an observed situation, the spatial autocorrelation of the 0+ salmon distribution of both surveys in the North Harbour river study reach was investigated. It was expected that the RC would be negative at small ambit radii (<15 cm) due to spacing behaviour and competitive interactions. At larger ambit radii (15 cm - 2 m) a positive and gradually declining RC was expected due to selection by the 0+ salmon for primarily small-scale (<1 m^2) environmental features.

To test component 4 (fish to habitat) against an observed situation, the depth preference of the 0+ salmon was investigated over a range of spatial scales (maximum ambit radius=10 m) using the distribution data of both surveys. Depth observations were re-scaled into 6 depth classes: class 1: depth [0-4] cm; class 2: <4-8] cm; class 3: <8-16] cm; class 4: <16-32] cm; class 5: <32-64] cm; class 6: >64 cm. It was expected that the 0+ salmon would be positively associated with the intermediate depth classes (16-32 cm) and negatively associated with the shallow depth classes (0-8 cm) at small spatial scales, as observed in other studies (DeGraaf and Bain 1986, Heggenes 1990). At larger spatial scales, however (>4-7 m), the reverse was expected due to avoidance of pool areas and selection for riffle/run areas by the fish.

To test component 4 (fish to habitat) against a known situation, the 0+ salmon were randomly re-positioned within the North Harbour river study section for both surveys. Associations of these distributions with depths were investigated over a range of spatial scales (maximum ambit radius=10 m). It was expected that the RC would not be significantly different from 0 across all spatial scales investigated.

3.1.3. Results

I observed a total of 977 juvenile salmon, 47 brook trout, and 8 brown trout during both surveys. Fish distributions were similar on both surveys. Figure 3.1.3 illustrates the distributions of the 0+ juvenile salmon on 17 August and 25 August, 1994. The percent occurrence of the depth classes 1-6 was 7%, 12%, 26%, 39%, 15%, and 1% respectively.

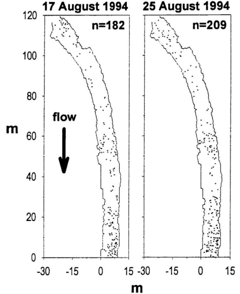

Figure 3.1.3. Distribution of 0+ Atlantic salmon, as observed by snorkelling on 17 August and 25 August, 1994, in North Harbour River, Newfoundland, Canada.

I detected scale-dependent patterns in the simulated distributions of the schooling fish (Figure 3.1.4): The Relative Contact for the spatial autocorrelations of group 1 fish showed a minimum at small spatial scales (ambit radius < 1.5 m, RC<0) and a maximum at intermediate spatial scales (ambit radius = 2-6 m, RC>0). The Relative Contact declined to 0 at larger spatial scales. The Relative Contact for the spatial associations between the first and the second group of schooling fish showed a minimum at small spatial scales (ambit radius < 10 m, RC<0). At larger spatial scales (ambit radius >10 m) the RC approached 0.

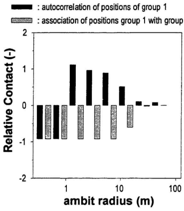

Figure 3.1.4. Spatial autocorrelation of group one fish positions (1) and spatial association of group one with group two fish positions (2) at increasingly larger ambit radii, quantified in terms of Relative Contact*.

When applied to field data, the multi-scale approach showed that the 0+ salmon distribution was not significantly different from random at small spatial scales (ambit radii < 0.2 m) (Figure 3.1.5). At larger spatial scales the distribution of 0+ salmon was clumped (RC>0). The RC reached a maximum at an ambit radius of 0.7 m (RC=0.43). The 0+ salmon were negatively associated with shallow depths (0-8 cm) and positively with intermediate depths (8-32 cm) at small spatial scales (RC=-0.66 and 0.19 for depth class 1 and 4 respectively, at an ambit radius of 40 cm, Figure 3.1.6). However, at large spatial scales (ambit radii > 4-6 m) the 0+ salmon were positively associated with shallow depths (RC=0.10 and 0.08 for depth class 1 and 2 respectively, at an ambit radius of 10 m). The associations were most different from random at small spatial scales. The randomised 0+ salmon distributions were not significantly associated with any of the depth classes (Figure 3.1.7).

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[*] Note that low numbers of conspecifics at small ambit radii can often be found by chance alone, i.e. in the absence of spacing behaviour. From this, the large and negative RC measures at small ambit radii were not-significant.

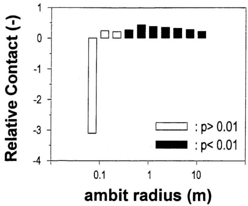

Figure 3.1.5. Spatial autocorrelation of 0+ Atlantic salmon distributions on 17 and 25 August, 1994, in North Harbour River, at increasingly larger ambit radii, quantified in terms of Relative Contact.

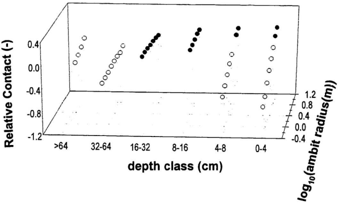

Figure 3.1.6. Spatial association of the 0+ juvenile salmon with depth as observed on 17 August and 25 August, 1994, in North Harbour River, Newfoundland, Canada. Spatial associations were quantified in terms of Relative Contact for a range of depth classes at increasingly larger ambit radii. Closed dots represent "significant" positive associations, open dots represent "significant" negative associations. A screening criterion of α=0.01 was used to separate "significant" from "non-significant" relations.

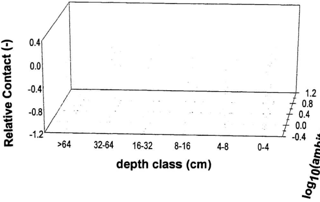

Figure 3.1.7. Spatial association of the randomised 0+ juvenile salmon with depth, from observations on 17 August and 25 August, 1994, in North Harbour River, Newfoundland, Canada. Spatial associations were quantified as the Relative Contact with a range of depth classes at increasingly larger ambit radii. None of the Relative Contact estimates was "significantly" different from zero. A screening criterion of α=0.01 was used to separate "significant" from "non-significant" relations.

3.1.4 Discussion

Fish are associated with their environment over a range of spatial scales. This is because fish distributions are the result of multiple processes that operate over a range of scales, because fish react to their environment at a range of spatial and temporal scales, and because of the propagation of effects from one scale to another. An example of selection behaviour operating at more than a single spatial scale is the selection by salmonids for specific holding positions (small-scale) with relatively low snout velocities in areas of high current conditions (larger scale) where drift is concentrated (Chapman and Bjornn 1969, Everest and Chapman 1972, Fausch and White 1981). Examples of the propagation of effects across scales are the effect of small-scale refuge locations (small spatial scale event) for rare flood events or ice scour (small temporal / large spatial scale events) for fish occupying a much larger area (large spatio-temporal scale effect) (Erman et al. 1988, Fausch and Bramblett 1991, Pearsons et al. 1992), and the process of expansion and contraction, where large-scale distributions are influenced by small-scale habitat selection processes (MacCall 1990, Swain 1993, Marshall and Frank 1995).

Because organisms are associated with their environment at a range of spatial and temporal scales, a comprehensive understanding of factors affecting the distribution and abundance of fish can only be achieved by studying factors affecting fish distributions at a range of scales, rather than one or even a few selected scales. In addition, multi-scale approaches can potentially serve to integrate knowledge obtained from studies operating at a wide variety of spatial and temporal scales, such as micro-habitat studies, macro-habitat studies, stock-recruitment studies and movement studies.

The proposed multi-scale technique offers several advantages over existing techniques. Relative Contact measures are readily interpretable. The program concept is simple. The technique can be used over any range of spatial scales in an environment with irregular boundaries. The distribution of the statistic needed for significance testing is generated within the program. The technique can be used to analyse associations of fish with habitats as well as to test for patchiness. Results based on various distribution surveys can be assimilated into the analysis. The model is easy to apply to transect data.

Disadvantages of the method are that the analyses require much computing time for analyses where density estimates are obtained by high resolution dummy positions. The habitat mapping has to be done at evenly-spaced positions and is labour intensive. A grid system approach generally assumes that the distributional heterogeneity is isodiametric. In riverine habitats, however, the distributional heterogeneity is likely to be elongated in the flow direction. A transect approach would be amenable to test if patterns differ among transect orientations. However, the fish distribution in riverine habitats is inherently 2 dimensional rather than linear. In addition, it is important to note that the study reach has two types of boundaries: a real boundary by way of the shorelines and an imposed boundary by way of the start and end of the study reach. In the analyses, it is assumed that the region outside the imposed boundaries has a spatial pattern similar to that of nearby areas within the boundaries. If this assumption cannot be met, the results should be limited to the areas that are located at a distance of the ambit radius of interest from the imposed boundaries. The problem of imposed system boundaries applies to any multi-scale approach, such as spectral analysis, pattern analysis and second-order neighbourhood analysis.

The Relative Contact method has similarities with the Potential Contact method, as proposed by Schneider et al. (1987, Schneider 1994) and with Lloyd's (1967) measure of per capita contact rate. Potential Contact is calculated based on local abundances of organisms and an environmental factor ($\sum {}^{i}N_x$ and $\sum {}^{i}Z_x$ respectively) over a series of n consecutive bins or quadrates of size i (m or m^2 respectively; range = n*i):

$$PC_i = \sum n * \frac{\sum {}^i N_x * \sum {}^i Z_x}{\sum {}^i N_x} \qquad \textit{Equation 3.1.3}$$

with:

PC_i = Potential Contact at bin or quadrate size i

If the environmental factor refers to the number of conspecifics (Z = N-1), then Potential Contact is identical to Lloyd's measure of per capita contact rate with conspecifics.

In the Relative Contact method, associations are calculated using ambits centred around positions of individual organisms. By contrast, Potential Contact measures and Lloyd's index are calculated using geographic units such as transects or quadrates that are not centred on individuals. Therefore, the Relative Contact method is more focused on individuals and how they perceive and react to their environment, which may be appealing to individual-based studies. A further advantage of the Relative Contact method over Potential Contact methods and Lloyd's index is that the Relative Contact method allows for an easy creation of organism distributions by computer according to specified habitat selection rules. Merits of this application, as well as detailed calculation procedures, will be outlined in Chapter 3.2 and 3.3.

The Relative Contact method has similarities with second-order neighbourhood analyses (c.f. Ripley 1981, Getis and Franklin 1987, Muotka and Penttinen 1994). However, second-order neighbourhood analyses are generally confined to analyses within the context of components 1 (fish to fish) and 2 (group 1 to group 2). In addition, advantages of the proposed method are that because of the randomisation scheme used, boundary corrections are not necessary and the method is easily applied in systems having irregular boundaries. The mathematical equations underlying second-order neighbourhood analyses are less easy to interpret, especially for non-statisticians, whereas the method based on

Relative Contact with randomisation makes sense intuitively and would probably appeal to behavioural ecologists. The symmetry of Relative Contact measures (avoidance versus preference), when compared to the K-function of second-order neighbourhood analyses (Ripley 1981) is appealing for a graphic display of results (cf. RC=1 versus RC= –1).

I have shown that the proposed multi-scale approach detects differences in patchiness of fish distributions and associations of fish with habitats at various spatial scales in simulated as well as in field data. Conclusions with respect to fish-habitat associations, as well as spatial (auto)correlations of fish distributions varied from positive at one scale to negative at another (Figures 3.1.4-6), indicating either preference or avoidance behaviour, respectively.

The changes in patchiness of the 0+ salmon distributions across spatial scales were probably due to a combination of habitat selection for small-scale environmental features, to small-scale spacing behaviour, and possibly to competitive interactions at small spatial scales (Figure 3.1.5). At small spatial scales, the 0+ salmon preferred intermediate depths and avoided shallower and deeper areas, but preferred shallow depths at larger spatial scales (Figure 3.1.6). This pattern is probably due to a combination of avoidance of shallow depths at small spatial scales, preference for riffle areas that have a high number of shallow depth observations, and avoidance of pool habitats.

These results show that conclusions with respect to the distribution of juvenile salmon depend on scale. A micro-habitat approach would lead to the conclusion that 0+ salmon avoid shallow depths (RC<0, Figure 3.1.6) and that 0+ salmon distributions are repulsed (RC<0, Figure 3.1.5). A meso-habitat approach would lead to the conclusion that juvenile salmon prefer shallow depths (RC>0, Figure 3.1.6) and are clumped (RC>0, Figure 3.1.5). In addition, they show that multi-scale techniques may allow for an identification of scales that are most effective in explaining observed fish distributions: In the North Harbour River study, the habitat selection seemed primarily aimed at small-scale habitat features

(<1 m^2) as the patchiness of the fish distributions and associations of fish with depths were most extreme at small spatial scales. Therefore, a micro-habitat approach (<1 m^2) is likely to be more effective compared to a meso-habitat approach (>100 m^2).

These results imply that the scale of measurement will determine the perceived relative importance of a habitat variable in habitat selection behaviour. Therefore, Habitat Suitability Indices and Habitat Use indices, commonly used in habitat modelling approaches, must also depend on scale. From this, it follows that managerial actions may differ based on the scale of measurement of the study used to support managerial decisions. The results also emphasise the fact that interpretation of results should be limited to the spatial scales over which the study was conducted.

A single-scale approach in habitat modelling, be it either a "macro" or "micro" approach, fails to appreciate that organisms may be associated with their environment over a range of spatio-temporal scales. Current habitat models may be improved by a more explicit use of scale. This may improve possibilities for assessing and prescribing habitat requirements of fish. Future habitat selection studies should focus on the identification of spatial scales that are most effective (see Chapter 1.3-5) in explaining observed fish distributions.

3.2. Habitat selection by juvenile Atlantic salmon: a test for density-dependent habitat use at multiple scales from stream tank observations

3.2.1. Introduction

Habitat models aim at quantifying relations between organisms and their environment and as such are important to the management of renewable resources. These models are widely applied to riverine fish populations where they find use in stream habitat investigations and in the resolution of conflicts arising from water allocation and hydropower development (Fausch et al. 1988, Reiser et al. 1989, Armour and Taylor 1991).

As distributions of organisms result to a large extent from individual decisions (Krebs and Kacelnik 1991), an understanding of habitat selection behaviours of fish will be important to fish habitat models and fish habitat-management. Important research questions in this context are: (1) how do fish perceive and react to their environment; (2) how are limited resources distributed among competitors; (3) is habitat use or fish density truly indicative of habitat quality; (4) to what extent are fish distributions driven by habitat selection behaviours and to what extent by other processes; and (5) how can individual fish behaviours be extrapolated to scales relevant to management problems? In this study I address the first two of these questions by studying density-dependent habitat selection by juvenile Atlantic salmon (*Salmo salar*) in an artificial stream tank. The habitat there was described in terms of substrate, water depth and water velocity, the variables most often included in habitat models of riverine fish species (Orth and Maughan 1982, Fausch et al. 1988, Heggenes 1990).

This study differs from previous studies on density-dependent habitat selection by salmonids (e.g. Elliott 1986, Rodríguez 1995) or from Atlantic salmon habitat modelling studies in general (e.g. DeGraaf and Bain 1986, Heggenes 1990), in that associations of fish with habitats were studied within the context of an explicit multi-scale approach:

Associations of fish with habitats were studied over a range of spatial scales, rather than at a single or a few selected scales. I believe that a multi-scale approach is more appropriate for describing how fish perceive and react to their environment because habitat selection behaviours themselves operate at multiple scales. An example is selection by salmonids for specific holding positions (small-scale) with relatively low snout velocities in areas of high current conditions (larger scale) where drift is concentrated (Chapman and Bjornn 1969, Everest and Chapman 1972, Wankowski and Thorpe 1979, Fausch and White 1981). Subsequently, this behaviour may be best identified and made explicit within the context of quantitative multi-scale techniques, i.e. a multi-scale problem is best studied using a multi-scale approach.

The objectives of this study were: (1) to illustrate how a variety of newly developed scaling-techniques can be used in habitat modelling and behavioural studies; (2) to identify scales important to habitat models for juvenile Atlantic salmon; (3) to formalise observed habitat selection behaviours that operate at multiple scales into an explicit multi-scale habitat selection model; (4) to study changes in habitat use with changing density; and (5) to compare multi-scale approaches with single-scale approaches in regard to their ability to identify how fish select their habitats and in their ability to describe and predict fish distributions.

3.2.2. Material and methods

3.2.2.1. Stream tank

The stream tank I used for the experiment is located at the Department of Fisheries and Oceans in St. John's, Newfoundland, Canada (see Figure 3.2.1). This tank has an oval shape and consists of two sections that are separated by plastic wire-mesh screens. One section is used for observing fish, the other contains a paddle-wheel, connected to an electric motor, that can be used to create a clockwise current. The observational section (14.4 m^2) further consists of a wide and shallow part (riffle hereafter; 6.9 m^2), a wide and deep part (pool hereafter; 5.0 m^2), and a narrow and shallow part (run hereafter; 2.5 m^2; see Figure 3.2.1).

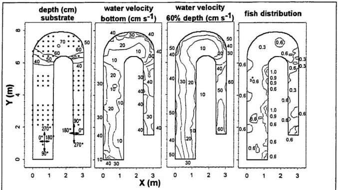

Figure 3.2.1. Tank habitat and fish distributions. Black dots in the left figure refer to positions of cobble-stones. Contour lines on habitat use by fish in the stream tank were based on all 3888 fish observations: I averaged fish densities within 30 cm circles surrounding all 15492 possible positions in the tank, which were subsequently re-scaled using a uniform transformation. XY-grid-systems oriented relative to water flow, used for calculations as explained in the text, are depicted in the left figure for two positions.

The bottom of the tank was covered with gravel (8-16 mm), on top of which I positioned small cobble-stones (64-128 mm) grouped in patches of different size. In addition, I positioned light-coloured gravel in a 30 cm * 30 cm grid pattern to facilitate determination of fish positions. Water flow and depths were kept constant. Light conditions were controlled by artificial lights and an electronic timing device (16 h. of light and 8 h. of darkness). The tank was enclosed by black plastic to block external light. Temperatures were maintained at 15-16°C. Substrate, water depth (cm), and water velocities (at 60% depth and at 5 cm off the bottom, cm s^{-1}) were measured at evenly distributed locations in the tank using a resolution of 100, 25 and 4 observations per square foot respectively.

Water velocities were measured using an electronic flow-meter (FLO-MATE, Model 2000, Marsh-McBirney Inc.). Figure 3.2.1 shows the tank habitat in terms of substrate (gravel/cobble), water depth (range: 26-72 cm) and water velocity at bottom (range 0-48 cm s^{-1}) and at 60% depth (range: 0-63 cm s^{-1}).

Fish were observed through windows from within the centre of the tank. To minimise effects of the observer on fish behaviours, this centre was kept dark and windows were covered with black mesh. To further obscure the observer from the fish's view, I fixed black plastic on top of this mesh, leaving a narrow slit for observations.

3.2.2.2. Experimental procedures

The experiment took place from 18/08/95 to 05/10/95. Wild Atlantic salmon (fork-length 10.5-11.5 cm) were collected by electrofishing in North Harbour River, Newfoundland (47°12'N, 53°37'W), and kept in a holding tank (up to two weeks) prior to introduction into the stream tank. Fish were introduced into the tank at three different densities: 0.21, 0.63, and 1.0 m^{-2} (i.e. 3, 9 and 15 fish respectively). Each density was repeated once (six introductions in total). These densities were chosen to represent a range of densities found in Newfoundland rivers (Gibson et al. 1993). Individual fish were used only once.

After an acclimation period of five days, fish were observed for three days during two 2.5-hour periods in the morning and in the afternoon (10.00 - 12.30 h. / 14.00 - 16.30 h.), and a one-hour period in the evening during darkness (19.00 - 20.00 h.; tank was dark by 18.00 h.). Night-time observations were made using a small flashlight. Fish were fed with chopped squid, which was taken eagerly, at 12.00 h, 16.00 h and 19.30 h. Observations were made by surveying the tank every 10 minutes in an upstream direction. For the lowest two densities, similar downstream surveys were done as well to assess possible effects of the survey direction on results. These were done every 10 minutes and in between upstream surveys.

I recorded the snout-positions of fish at first encounter on maps of the tank. These were later digitised using a 3 cm resolution (nearest 0.1 foot). In addition, I noted the distance of the fish from the bottom (cm), the orientation of the fish relative to the current, as well as various behaviours during a 10 second period after first encounter. These behaviours included aggressive behaviours (attack/defence), feeding behaviours (yes/no), and movement (yes/no). At the lowest two densities, I was able to distinguish individual fish from differences in natural coloration patterns.

3.2.2.3. Analytical procedures

I analyzed the data to address a series of questions:

1. (*Habitat selection*) How are fish associated with their habitats: What variables were selected for and at what spatial scale(s)?

2. (*Habitat model*) What is the best way to incorporate associations of fish with habitats into a formal habitat model describing and predicting fish distributions?

3. (*Expansion and contraction*) Does habitat use change with density and if so, how strong is this effect?

4. (*Fish behaviour*) Are fish behaviours (aggression, feeding, movement) different among preferred and avoided habitats, and do fish behaviours change with density?

5. (*Scaling approach*) To what extent does an explicit multi-scale approach improve our understanding of habitat selection behaviours of fish, relative to a single-scale approach?

The analytical procedures related to these five questions are outlined below. Analyses were done using FORTRAN and SAS (SAS 1988). Random numbers, needed for several of the analyses, were generated using the FORTRAN system-supplied random number generator, upgraded by the shuffle-routine as outline by Press et al. (1986).

To facilitate computations, I interpolated depth and water velocities to the resolution of fish and substrate distribution maps (100 per square foot). This was done based on the inverse distance of measurements located within a distance of 1/2 foot (water velocity) or 1/5 foot (depth). Next, water depths were re-scaled into two classes (≤ 40 cm; > 40 cm) and water velocities into 7 classes ([0,5], <5,10], <10,20], <20,30], <30,40], <40,50], >50 cm s^{-1}).

For the analyses I only used the upstream observations collected in the two-hour time periods 10.00 - 12.00 and 14.00 - 16.00. This was done as I was uncertain about the effect of the observer on fish distributions during night-time observations and because accurate determination of individual fish behaviours and positions was difficult to quantify immediately after feeding.

1a. Habitat selection, omnidirectional

I quantified associations of fish with substrate, water velocities, depth and conspecifics over a range of spatial scales using measures of Relative Contact (RC). This statistic compares observed densities of conspecifics or habitat features surrounding individual fish positions (DO; # m^{-2}) with similar densities obtained from computer-generated random fish distributions (DR; # m^{-2}). These comparisons can be made for a range of ambit radii (S) which define circles surrounding individual fish positions (see Chapter 3.1). From this, a scale-dependent description of habitat use is obtained:

$$RC_S = LOG_{10}(DO_S) - LOG_{10}(DR_S) \qquad \textit{Equation 3.2.1}$$

For example, $RC_S=2$ indicates that at ambit radius S, an average fish has 10^2 times more contact with conspecifics or a specific habitat feature (depth, water velocity or substrate class), than in a case where fish are randomly distributed. This statistic allows positive associations ($RC>0$ to be distinguished from negative associations ($RC<0$) and random ($RC=0$) from even ($RC<0$, repulsion) or clumped ($RC>0$) distributions. DR_S can be obtained by averaging results of a large number of randomised fish distributions or by averaging results for all 15492 possible positions in the tank. In this study, I used this last approach. Density estimates were obtained by assuming a 3.048*3.048 cm area (0.1*0.1 foot) around all 15492 possible fish positions. P-values, used to assess if associations differed significantly from random, were obtained from 500 randomised fish distributions. Because of the oval shape of the tank, I had to use a set of subroutines that allowed for calculating shortest distances "around the bend of the tank", e.g. when calculating the distance between a location in the run and a location in the riffle habitat. A more complete description of the Relative Contact method is provided in Chapter 3.1. I analyzed associations of fish with conspecifics, water velocities, depth and substrate at ambit radii ranging from 0 to 350 cm (0, 1, 5, 10, 15, 20, 25,...,350 cm). Analyses were done for all six introductions separately, as well as based on all introductions combined.

1b. Habitat selection, directional

To assess possible anisotropy in associations of fish with habitats or conspecifics, I devised a statistic inspired by RC measures and exhaustive non-ergodic cross-correlograms (Rossi et al. 1992). I called this statistic RCEX (exhaustive measure of Relative Contact):

$$RCEX_{LAG-X,LAG-Y} = LOG_{10}(DO_{LAG-X,LAG-Y}) - LOG_{10}(DR_{LAG-X,LAG-Y})$$

Equation 3.2.2

RCEX compares observed densities of conspecifics or habitat features at various spatial lags surrounding observed fish positions with similar densities obtained from computer-generated random fish distributions, and allows for a scale-explicit two-dimensional appraisal of the data's spatial dependence. For example, $\text{RCEX}_{-1, +3} = -1$ indicates that an average fish has 10 times less contact with conspecifics or a particular habitat feature at lag -1 in the X-direction and lag +3 in the Y-direction. Note that RC is calculated at increasingly larger ambit radii, whereas RCEX is calculated at consecutive lags, and that RCEX measures are directional, whereas RC measures are not. Also note that RC and RCEX measures are similar at spatial scales approaching 0 cm.

RCEX measures are most easily obtained from rectangular distribution maps. This is obviously not the situation in the stream-tank. However, in the analyses the X- and Y-directions did not refer to the X-Y grid system of the tank (c.f. Figure 3.2.1), but to a grid system relative to water flow and fish-position: The 90° and 270° directions referred to directions directly into and with the current respectively; The 0° and 180° directions referred to directions perpendicular (left and right) to the current. This grid system is different among fish positions in the tank (see Figure 3.2.1). Reliable estimates of RCEX require a large number of fish observations. Therefore, I only performed these analyses on observations of all six introductions combined.

2. Habitat model

Based on the results of the previous section, I developed a formal model to describe habitat use by fish in the tank. Preferably, such a model would combine realism (model parallels habitats as experienced by the fish) and simplicity (few variables included, few classes per variable) with strong descriptive capabilities (observed and predicted distributions or habitat use similar). To develop such a model, I devised a method based on the RC statistic that paralleled stepwise multiple regression. First I decided on an initial model that combined the variable thought to be most important, measured at a scale where associations were most extreme (i.e., RC measures of the different classes most different from 0). Next, I created fish distributions based on this model. Fish were distributed by randomisation with all positions in the tank having a different probability of being selected (15492 positions in total). This probability ($P_{POS=i}$; i=1-15492) was determined by a weight given to each position ($W_{POS=i}$) and the total of all weights of all possible positions (W_{TOT}), with $W_{POS=i}$ determined by the Relative Contact associated with the habitat at this position as of the initial model:

$$P_{POS=i} = \frac{W_{POS=i}}{W_{TOT}} = \frac{10^{RC_{HAB(POS=i)}}}{\sum_{j=1}^{15492} 10^{RC_{HAB(POS=j)}}} = \frac{10^{RC_{HAB(POS=i)}}}{15492} \qquad \textit{Equation 3.2.3}$$

With this done, I then compared densities of habitat features surrounding observed fish positions (DO) with similar densities surrounding these computer-generated distributions (DD), in a manner similar to equation 3.2.1. This was done over a range of ambit radii (S):

$$RCD_S = LOG_{10}(DO_S) - LOG_{10}(DD_S) \qquad \textit{Equation 3.2.4}$$

From this, RCD values that differ from 0 indicate that additional habitat selection behaviours may have to be included into the initial habitat model: additional variables may have to be included, or the same variable defined at multiple scales rather than a single one, or a combination of both. For example, fish distributions could be generated according to observed habitat use related to water velocity, and evaluated by means of the RCD statistic as a function of depth. Positive values of RCD for a particular depth class may then indicate that this depth is selected, even after correcting for selection for water velocities, i.e. habitat selection behaviours are directed towards both depth and water velocity. This method is of use in a environment where habitat variables are correlated (cf. Richards 1982), when habitats are perceived in a non-independent manner by fish (cf. Orth and Maughan 1982), or when habitat selection behaviours operate at more than a single scale.

3. Expansion and contraction

I hypothesised that when population densities increase, primary (high density) habitats are occupied first and secondary (low density) habitats mostly after primary habitats are filled. The implication is that densities at secondary habitats will increase more with population level than will densities in primary habitats. To address this hypothesis, I first estimated the slopes of the equations relating the number of fish (N) in the different habitats (H) as identified in the previous section (N_H) to the total number of fish in the tank (N_{POP})[*]:

$$log_{10}(N_H + 0.1) = \gamma + \delta\ log_{10}(N_{POP} + 0.1) \qquad \textit{Equation 3.2.5}$$

If $\delta_i=1$ for all habitats, habitat use responded proportionally with introduction density, i.e.

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[*] Throughout this thesis a varies constants were used to prevent taking a log of 0. This was the result of the following procedure: Constants were chosen as one tenth of the smallest observed value, excluding 0, and rounded to the nearest 10^I (I=integer) . Next, additional analyses were done using a constant that was one order of magnitude larger and one order of magnitude smaller to see whether results varied with this constant. These additional analyses were not reported in this thesis, but indicated that results did not vary with this constant.

habitat use was independent of introduction density (cf. Myers and Stokes 1989). Each estimate of δ_i is based on six observations. The constant of 0.1 fish prevented taking $\log_{10}(0)$. This value represents a subjective assessment of habitat use for unoccupied habitats.

Next, I analyzed whether δ_i, a series of slopes, was negatively correlated with the Relative Contact of the fish with the habitats as identified in section 2 (RC_H), with RC_H calculated based on the average percentage of fish observations in these habitats for all six introductions separate ($PO_{H,P}$) and the percentage of fish in these habitats assuming a random distribution over the surface area of the tank (PR_H):

$$RC_H = LOG_{10}\left(\left(\frac{\sum_{p=1}^{6} PO_{H,p}}{6}\right) + 10^{-4} \right) - LOG_{10}(PR_H + 10^{-4}) \qquad \textit{Equation 3.2.6}$$

δ negatively correlated with RC_H would support my hypothesis, i.e. use of habitats that are preferred at low densities ($RC_H > 0$) does not change much with density, whereas use of habitats that are avoided at low densities ($RC_H < 0$) increases with density. In these analyses, δ_i were weighted by the inverse of the associated $MS_{ERROR,\,i}$. Note that Equation 3.2.6 and Equation 3.2.1 are similar, only that Equation 3.2.6 gives an equal weight to the six introductions in determining RC, whereas Equation 3.2.1 gives more weight to the higher density introductions.

To quantify the relative importance of density dependent changes in habitat use to habitat models, I related the percent of fish observations in the habitats identified as described under section 2 for introductions separately ($PO_{H,P}$), to the variables "Habitat" (class variable), "Introduction Density" (ratio variable) and the interaction of these two variables, using the GLM procedure in SAS and type I SS (SAS 1988). Next, the percent variance explained by the different levels in this model was used to assess possible improvement of the descriptive power of habitat models by incorporating density dependent behaviours: When habitat use changes strongly with introduction density, the interaction term will be large compared to the variable "Habitat". I stress that this approach was not meant for significance testing, but was solely intended to obtain an impression of the relative importance of changes in habitat use with density.

In addition, I studied the possible extent of changes in habitat use with density in the stream tank, in a situation where habitat selection behaviours do not change with density but where habitat use and distributions change with density due to competitive exclusion and territorial behaviours. For this computer-based study, I generated distributions based on a single habitat selection model and different territories, and compared differences in habitat use with territory size. First, I calculated the Relative Contact of fish with the habitats identified in section 2, using the low-introduction-level-observations only (3 fish). Next, I distributed 54000 fish over the tank habitat for the high density situation (15 fish), with the chance of an individual position being selected, determined by the Relative Contact associated with the habitat at this position (see section 2) and the distribution of conspecifics. The first fish of each computer generated introduction (54000/15=3600 introductions) was distributed based on habitat and RC only, as described above. The second fish was distributed in this manner as well, but after choosing a position, I evaluated if territories overlapped. If so, I re-sampled the second fish position until a position was selected without overlap of territories. This procedure was repeated up to and including the 15th fish position, with none of the territories surrounding individual fish positions overlapping. Next, I compared the habitat use of the observed and computer-generated distributions: If observed and computer-generated distributions were similar, even when using larger territories, the tank habitat may not be suitable to study density-dependent habitat use as preferred habitats are too far separated and readily available, so fish seldom have to compete to occupy primary locations. From this, one might conclude that competitive exclusion may not lead to expansion and contraction. (The number of 54000 was chosen rather arbitrarily. Unpublished data indicate that increasing this number would not have altered the results significantly.)

4. Fish behaviours

I studied whether the number of aggressive (attack/defence), movement, and feeding behaviours per fish observation (attack/defence) changed with introduction density. In addition, I studied whether the number of aggressive (attack/defence), movement, and feeding behaviours per fish observation (attack/defence) differed among preferred and avoided habitats.

5. Scaling approach

Multi-scale approaches to habitat modelling may give a different impression of how fish perceive and react to their environment than single-scale approaches do. These differences may result in different variables being identified as important and the scales at which variables are measured, but may also result in differences with respect to the ability of habitat models to describe fish distributions from habitat associations. If a habitat model accurately describes the rules according to which fish perceive and react to their environment and if fish distributions are primarily driven by these behaviours, computer-generated distributions according to these rules would be very similar to observed distributions, regardless of the scale at which these distributions are measured. If a habitat model does not accurately describe these rules, computer-generated distributions would be different from observed distributions, especially if distributions are measured at scales different from the scale(s) of the model.

To evaluate how well larger scale distributions can be predicted from either a single-scale micro-habitat modelling approach or a multi-scale approach, I generated distributions for each of these two approaches, as described in the previous sections (54000 fish positions). Next, I compared the observed and computer-generated fish distributions at the scale of pool, riffle, and run. If the multi-scale approach had superior descriptive capacities, the differences between the observed and predicted habitat use at the scale of pool, riffle and run would be small compared to a similar comparison from a single-scale approach. These analyses were done with RC measures obtained from introductions separately as well as from all fish observations combined

3.2.3. Results

3.2.3.1. Habitat selection

Surveys generally took 45 seconds (lowest fish density) to 4-5 minutes (highest fish density). Fish seemed to select for a set of fairly specific small-scale locations within the tank, which were rather similar for all six introductions. These locations are illustrated in Figure 3.2.1: fish in the riffle were mostly positioned at specific locations along the inner side of the tank; fish in the pool section were mostly positioned in a fairly distinct area around (X=2 m, Y=7.2 m) and just upstream of the transition pool/run; fish in the run section were mostly positioned in areas surrounding (X=2.5, Y=5.5), (X=2.8, Y=2.8), and (X=2.5, Y=1.8).

Fish were negatively associated with each other at small spatial scales (ambit radius < 50 cm; RC<0; see Figure 3.2.2, omnidirectional approach), but distributions were similar to random distributions at larger spatial scales (ambit radius > 50 cm; RC≈0). Avoidance was strongest at ambit radii smaller than 15-20 cm, and was anisotropic (see Figure 3.2.2, exhaustive directional approach), with an elongation of interfish distances in the 220° and 40° directions. Patchiness of fish distributions were most extreme at small spatial scales (RC most different from 0, i.e. RC>0 or RC<0).

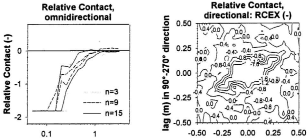

Figure 3.2.2. Associations of fish positions in the stream tank, quantified by means of Relative Contact (RC) and Relative Contact Exhaustive (RCEX) over a range of spatial scales. For an explanation of RC/RCEX: see text. RCEX/RC estimates were significant ($p<0.05$) at ambit radii < 40 cm; Much of the patterns at larger spatial scales were significant as well. I did not further illustrate this, as I considered general trends in patterns more interesting than the significance of individual points composing patterns.

The omnidirectional approach as of Figure 3.2.3 suggests that fish strongly avoided cobble at small spatial scales (ambit radii < 15 cm; $RC<<0$), but reacted indifferently to cobble at larger spatial scales (ambit radius > 15 cm; $RC=0$) (see Figure 3.2.3: RC). However, the directional approach of Figure 3.2.3 suggests that associations with cobble were strongly anisotropic, with negative associations at small spatial scales (ambit radii <.5-10 cm), positive associations at lags of 15-30 cm in the 30° and 150° directions, and positive associations at lags of 30-40 cm in the 225° and 315° directions. Associations of fish with cobble were most extreme at small spatial scales.

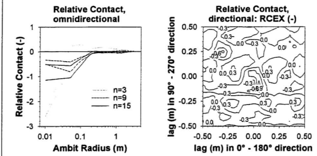

Figure 3.2.3. Associations of fish with cobble in the stream tank, quantified by means of Relative Contact (RC) and Relative Contact Exhaustive (RCEX) over a range of spatial scales. (For an explanation of RC/RCEX: see text.). All patterns were significant ($p<0.05$) at ambit radii < 25 cm (left figure)r < 50 cm (right figure) Much of the patterns at larger spatial scales was significant as well. I did not further illustrate this, as I considered general trends in patterns more interesting than the significance of individual points composing patterns.

Associations with depth were most extreme at small spatial scales, with deeper locations (>40 cm) being avoided and shallow locations (≤40 cm) preferred for all of the six introductions (see Table 3.2.1, Figure 3.2.4). I did not calculate associations using a directional approach (RCEX) for lack of small-scale depth-variations in the tank. I assigned the depths of the transition zones between the riffle/pool and pool/run sections to a separate class (<40,60] cm) in Figure 3.2.4 and Table 3.2.1. This was done for illustration purposes. For all other analyses in this study I used the classes "≤40 cm" and ">40 cm" because of the similarity in the patterns of the classes "<40,60] cm" and ">60 cm" at small spatial scales.

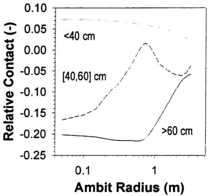

Figure 3.2.4 Associations of fish with depths in the stream tank, quantified by means of Relative Contact (RC) over a range of spatial scales. For an explanation of RC: see text. All patterns were significant ($p<0.05$) at ambit radii < 30 cm; Much of the patterns at larger spatial scales was significant as well. I did not further illustrate this, as I considered general trends in patterns more interesting than the significance of individual points composing patterns.

Table 3.2.1. Associations of fish with water depths quantified by means of Relative Contact (RC) at 5 cm ambit radii (see text) for each of the 6 introductions separate. Positive associations (RC>0) are printed in bold.

Density	$RC_{\leq 40}$	$RC_{<40,60]}$	$RC_{>60}$
low	**0.05**	-0.15	-0.12
low	**0.13**	-1.23	-0.38
medium	**0.11**	-1.06	-0.31
medium	**0.10**	-0.25	-0.31
high	**0.04**	**0.04**	-0.14
high	**0.05**	-0.09	-0.14
total	**0.07**	-0.17	-0.20

Based on an omnidirectional approach (RC), associations with water velocities were most extreme at small spatial scales (see Figure 3.2.5), except for associations with water velocities of 0 to 5 cm s^{-1}, which were most extreme at ambit radii of 20-30 cm (water velocity at bottom) and 40-60 cm (water velocity at 60% depth). This "dip" was observed for all medium and high density introductions, but not for the low density observations. Analyses on all fish observations combined indicated that water velocities of 5 to 10 cm s^{-1} and 40 to 50 cm s^{-1} were preferred, and water velocities of 0 to 5 cm s^{-1}, 10 to 20 cm s^{-1} and larger than 50 cm s^{-1} were avoided (see Figure 3.2.5). However, considerable variation in associations existed among introductions, especially for water velocities of 20 to 40 cm s^{-1} (see Table 3.2.2). An exhaustive directional approach (RCEX) indicated that these associations were anisotropic. The main results of these analyses were: Associations with water velocities of 0-5 cm s^{-1} (both at bottom and at 60% depth) tended to become more negative in the 315°-45° directions (towards outer edge tank) (see Figure 3.2.6); Associations with water velocities of 5 to 10 cm s^{-1} and 10 to 20 cm s^{-1} (both at bottom and at 60% depth) were most positive at lags of 0 to 15 cm, i.e. directly at the position of the fish (see Figure 3.2.6). Associations with water velocities of 20 to 30 cm s^{-1} and 30 to 40 cm s^{-1} were anisotropic, but patterns were rather irregular and difficult to describe. This may be due to differences among introductions and because most RCEX values were fairly close to 0, as also illustrated in Figure 3.2.5 and Table 3.2.2 for small spatial scales. Associations with water velocities of 40 to 50 cm s^{-1} (both at bottom and at 60% depth) tended to become more positive in the 20°-40° and 190°-240° directions (towards edges of tank, see Figure 3.2.6). Associations with water velocities larger than 50 cm s^{-1} (at 60% depth) were most negative at lags of 20 to 40 cm in the 135°-225° directions (towards inner edge tank; see Figure 3.2.6);

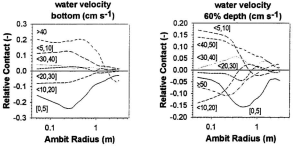

Figure 3.2.5 Associations of fish with water velocities at 5 cm from the bottom (Figure 5a) and at 60% of depth (Figure 5b) in the stream tank, quantified by means of Relative Contact (RC) over a range of spatial scales. For an explanation of RC: see text. Most of the patterns were significant ($p<0.05$). I did not further illustrate this, as I considered general trends in patterns more interesting than the significance of individual points composing patterns

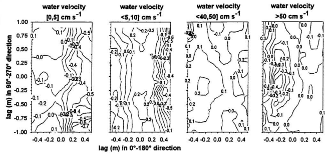

Figure 3.2.6 Associations of fish with water velocity classes [0,5], <5,10], <40,50] and >50 cm s^{-1} measured at 60% depth (Figure 3.2.6a-d respectively), quantified by means of Relative Contact Exhaustive (RCEX) over a range of spatial scales. Most of the patterns of Figure 3.2.6 were significant ($p<0.05$). I did not further illustrate this, as I considered general trends in patterns more interesting than the significance of individual points composing patterns.

Table 3.2.2. Associations of fish with water velocities (cm s^{-1}) close to the bottom (WB) and at 60% depth (W6), quantified by means of Relative Contact (RC) at 5 cm ambit radii. Positive associations (RC>0) are printed in bold.

Density	var.	$RC_{[0,5]}$	$RC_{<5,10]}$	$RC_{<10,20]}$	$RC_{<20,30]}$	$RC_{<30,40]}$	$RC_{<40,50]}$	$RC_{>50}$
low	WB	-0.53	-0.13	**0.22**	-0.10	-0.11	-4.2	-
low	WB	-0.19	**0.37**	-0.07	-0.48	-0.35	-4.2	-
medium	WB	-0.17	**0.20**	-0.10	-0.07	**0.03**	**0.03**	-
medium	WB	-0.76	**0.04**	-0.24	**0.09**	**0.40**	**0.49**	-
high	WB	-0.01	**0.08**	-0.12	**0.05**	-0.06	**0.37**	-
high	WB	-0.07	**0.10**	-0.04	**0.04**	-0.16	**0.002**	-
total	WB	-0.15	**0.11**	-0.08	**0.01**	**0.04**	**0.20**	-
low	W6	-0.31	**0.08**	**0.05**	**0.01**	-0.02	**0.22**	-1.30
low	W6	-0.24	**0.53**	-0.05	-0.12	-0.14	-0.41	-4.96
medium	W6	**0.17**	**0.09**	-0.08	-0.06	-0.16	**0.23**	-0.27
medium	W6	**0.03**	-0.02	-0.42	-0.37	**0.22**	**0.32**	**0.29**
high	W6	-0.19	**0.25**	-0.13	**0.07**	-0.03	**0.08**	-0.23
high	W6	-0.06	**0.12**	-0.14	**0.09**	-0.01	**0.04**	-0.01
total	W6	-0.03	**0.17**	-0.14	-0.01	**0.01**	**0.14**	-0.07

3.2.3.2. Habitat model

An initial model identified habitats based on a combination of substrate and water velocity at the bottom. For substrate I used 3 different classes: Class 1 referred to situations where cobble was present directly at positions; Classes 2 and 3 referred to situations where cobble was not present directly at positions, with Class 2 referring to positions where cobble was present in four 10 cm * 10 cm areas surrounding positions, and Class 3 referring to positions where cobble was not present in any one of these areas, with centres of these areas located at a distance of 20.6 cm in the 14° and 166° directions (relative to water flow) and a distance of 32.0 cm in the 231° and 309° directions. These classes were so defined to describe the avoidance of cobble at small spatial scales (Figure 3.2.3 left), and preference for cobble at larger spatial scales (Figure 3.2.3 right).

In addition, I identified 7 water velocity classes. Class 1 referred to positions where water velocities were ≤ 5 cm s^{-1} and average water velocities within an ambit radius of 25 cm were ≤ 5 cm s^{-1} as well; Class 2 referred to positions where water velocities were ≤ 5 cm s^{-1} and average water velocities within an ambit radius of 25 cm were >5 cm s^{-1}. Classes 3-7 were identical to the classes used for water velocities larger than 5 cm s^{-1}, and measured directly at fish positions. Classes 1 and 2 were used to describe the differences in associations of fish with low-water-velocity positions in areas of low water velocity and low-water-velocity positions in areas of higher water velocities, as indicated by the previously mentioned "dip" of Figure 3.2.5:

From this, the initial model identified (3*7=) 21 possible habitat classes. All of these were present in the tank. I created fish distributions from RC measures and these 21 habitats for the six introductions separately to test whether additional variables or measurement scales may need to be included in the model. These computer-generated distributions indicated that, for all six introductions, shallow areas (≤ 40 cm) were preferred over deeper areas, in addition to the habitat selection behaviours as defined by the initial model ($RCD_{SHALLOW}>0$). These associations were most extreme at small spatial scales and are summarised in Table 3.2.3 for ambit radii of 5 cm. These computer-generated distributions also indicated additional habitat selection behaviours directed to water velocities at 60% depth, as RCD values were often different from 0 especially at small spatial scales. However, these associations differed considerably among introductions (see Table 3.2.4). No additional associations were found with depth or water velocity at bottom at any scale ($RCD \approx 0$ for ambit radii of 0-350 cm).

Table 3.2.3. Associations of fish with water depths (cm) quantified by means of Relative Contact (RCD) at 5 cm ambit radii (see text). Positive associations (RCD>0) are printed in bold.

Density	$\mathrm{RCD}_{\leq 40\ \mathrm{cm}}$	$\mathrm{RCD}_{>40\ \mathrm{cm}}$
low	**0.07**	-0.16
low	**0.12**	-0.47
medium	**0.08**	-0.33
medium	**0.04**	-0.15
high	**0.03**	-0.06
high	**0.06**	-0.14

Table 3.2.4. Associations of fish with water velocities (cm s^{-1}) at 60% of depth, quantified by means of Relative Contact (RCD) at 5 cm ambit radii (see text). Positive associations (RCD>0) are printed in bold.

Density	$\mathrm{RCD}_{[0,5]}$	$\mathrm{RCD}_{<5,10]}$	$\mathrm{RCD}_{<10,20]}$	$\mathrm{RCD}_{<20,30]}$	$\mathrm{RCD}_{<30,40]}$	$\mathrm{RCD}_{<40,50]}$	$\mathrm{RCD}_{>50}$
low	-0.11	**0.13**	0.00	-0.10	**0.04**	**0.35**	-1.27
low	-0.32	**0.32**	-0.19	-0.04	**0.22**	-0.05	-4.63
medium	**0.21**	0.00	-0.11	**0.02**	-0.03	**0.23**	-0.32
medium	**0.41**	0.00	-0.30	-0.21	**0.19**	**0.06**	0.00
high	-0.19	**0.18**	-0.09	**0.12**	-0.03	**0.01**	-0.27
high	-0.03	**0.05**	-0.16	**0.11**	**0.02**	**0.06**	**0.03**

Based on these results, I decided on a formal habitat model that included the variables substrate (3 classes), water velocity at bottom (7 classes) and depth (2 classes), with substrate and water velocity at bottom defined at multiple scales. 35 of all 42 (=3*7*2) possible habitats were present in the tank. I did not include (scale-dependent) associations of fish with water velocities at 60% depth in a formal model, because of the differences among introductions as described in Table 3.2.4 and because inclusion would greatly increase the number of habitat classes.

Habitat use at upstream surveys was very similar to habitat use at downstream surveys. The percent fish observations in the 35 habitats identified above were similar to percentages in the downstream surveys (n=35; p=0.0001; r^2= 0.967, 0.994, 0.981 and 0.961) for the two low-densities and the two medium-densities respectively).

3.2.3.3. Expansion and contraction

The percent fish observations in pool, riffle, and run did not change with density in the tank (pool: r=0.673, p=0.143; riffle: r=-0.545, p=0.264; run: r=0.246, p=0.639; n=18).

Prior to calculating δ_i, I removed observations on habitats that were never occupied (7 habitats) as δ_i could not be estimated for these. Based on the remaining information, δ was not significantly associated with RC_H (n=28, r=-0.159, p=0.412).

Incorporating density dependent changes in habitat use into a density-independent distribution model led to a minor improvement of predictions: $PO_{H,P}$ was significantly associated with the variables Habitat, Introduction Density and (Habitat)*(Introduction Density) (n=210, r^2=0.761, p=0.0001), with 70% of the variance in $PO_{H,P}$ explained by the variable "Habitat" (df=34, p=0.0001), 0% by the variable "Introduction Density" (df=1, p=1.00), and 6% by the interaction term (df=34, p=0.474).

Table 3.2.5 shows that habitat use was unlikely to change with density, even when territories were large: $RC_{H,\ \text{territory}=0\ \text{cm}}$ was strongly correlated with $RC_{H,\ \text{territory}=5\ \text{to}\ 40\ \text{cm}}$ (n=35, p<0.001, r^2>0.98 for all territory sizes). I did have some indication that distributions changed for territories larger than 20-25 cm, as the percent of the variance in $RC_{H,\ \text{territory}=X\ \text{cm}}$ explained by the line $RC_{H,\ \text{territory}=X\ \text{cm}} = RC_{H,\ \text{territory}=0\ \text{cm}}$ (Y=X) decreased for territories larger than 20 cm, but these changes were minor.

Table 3.2.5. Similarity of distributions generated assuming the low-density rules of habitat selection and different territories. Territories were simulated using ambit radii of 5 to 40 cm. Summary statistics include intercept (Int.), slope, and associated standard errors (s.e.) of the relationship between $RC_{H,\ territory = 0\ cm}$ and $RC_{H,\ territory = 5\ to\ 50\ cm}$ ($n=18$; $p<0.001$ for all analyses), as well as the percent variance ($PE_{Y=X}$) explained by the line Y=X (model: percent observed = percent predicted).

Ambit Radius	r^2	Int.	Slope	s.e. Int.	s.e. Slope	$PE_{Y=X}$
5	0.973	0.016	0.968	0.0755	0.0279	99.9
10	1.000	0.011	1.003	0.0037	0.0014	99.9
15	0.986	0.034	0.994	0.0552	0.0204	99.6
20	1.000	0.034	1.008	0.0097	0.0036	98.6
25	0.999	0.043	1.010	0.0127	0.0047	96.9
30	0.999	0.056	1.014	0.0164	0.0061	93.5
35	0.984	0.014	1.010	0.0600	0.0224	89.1
40	0.997	0.070	1.016	0.0258	0.0096	82.1

3.2.3.4. Fish behaviour

Table 3.2.6 summarises the observed fish behaviours. In general, fish were stationary and periods of inactivity were interrupted with sudden short bursts of activity, with fish moving and displaying aggressive interactions. Feedings led to a temporary disruption of fish distributions, with many of the fish moving into the riffle area. After movement, individual fish often moved back to their original positions. This is also evident from Figure 3.2.7, which indicates that even after a period of 3 days, 8% of the fish were observed within 5 cm of their original positions.

Three regions can be identified from Figure 3.2.7: For spatial scales of 0-5 cm, the chance of observing a fish within the particular distance off the original position increases with spatial scale; For spatial scales of 5 to 20 cm this chance is relatively invariable; For spatial scales larger than 20 cm, this chance increases with spatial scale. Analyses as in

Figure 3.2.7 for introductions separately, indicated that low-density distributions were more stable than medium density distributions for temporal scales of 10 - 60 min (within feedings), as the lines of low-density distributions were all located above the lines of medium-density distributions. Stability of low and medium density distributions was comparable for temporal scales exceeding 60 min.

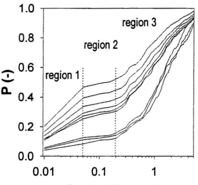

Figure 3.2.7. Movement of individual fish as a function of spatio-temporal scale. Lines refer to the chance (P) of observing an individual fish within a certain distance (Spatial Scale) of it's original position after a certain period of time (temporal scale), for periods of 10, 20, 30, 40, 50, 60 min, 4h, 1 day and 2 days (top to bottom lines respectively). Figure based on all low and medium density introductions (n=1728).

Table 3.2.6. Summary of stream tank observations. Variables include: number of fish in tank (Ntank); total number of observations (Ntot); number of attack (Natt) and defense behaviours (Ndef); number of observations of fish moving (Nmov) and feeding (Nfeed).

Density	Ntank	Ntot	Natt	Ndef	Nmov	Nfeed
low	3	216	1	1	6	51
low	3	216	2	2	5	20
medium	9	648	33	33	85	144
medium	9	648	25	23	39	105
high	15	1080	6	6	13	32
high	15	1080	34	34	48	159
total	-	3888	101	99	196	511

Fish were mostly positioned on top of, or within a few cm off the bottom. Introductions varied considerably with respect to the display of aggressive, movement and feeding behaviours (Table 3.2.6). I did not observe significant changes in the number of aggressive, movement or feeding behaviours per fish with introduction density (Table 3.2.7), or differences with respect to the relative incidence of these behaviours among preferred and avoided habitats (Table 3.2.8).

Table 3.2.7. Changes in fish behaviours with introduction density. Variables include: Relative incidence of aggressive behaviours (RIagr), which included attacks (RIatt) and defence (RIdef) behaviours, and movement (RImov) and feeding behaviours (RIfeed). Relative Incidence is calculated as the total number of observed behaviours divided by the total number of fish in the tank. Results from linear regression (n=6).

Response Variable	r	p
RIagr	0.267	0.609
RIatt	0.264	0.613
RIdef	0.270	0.605
RImov	0.029	0.957
RIfeed	0.434	0.389

Table 3.2.8. Differences in fish behaviours among preferred (RC>0) and avoided (RC<0) habitats. Variables include: Relative incidence of aggressive behaviours (RIagr), which included attacks (RIatt) and defence (RIdef) behaviours, and movement (RImov) and feeding behaviours (RIfeed). Relative Incidence is calculated as the total number of observed behaviours divided by the total number of fish observations per habitat type (preferred/avoided habitat). Results from analysis of variance (n=12).

Response Variable	r^2	p
RIagr	0.122	0.266
RIatt	0.158	0.201
RIdef	0.080	0.372
RImov	0.148	0.217
RIfeed	0.000	0.949

3.2.3.5. Scaling approach

Multi- and single-scale approaches (21 and 35 habitat classes, respectively) were equally able to describe habitat use at the scale of pool, riffle, and run (see Table 3.2.9). Habitat models from separate introductions were similar to observed distributions ($PE_{Y=X}$=96%, both for single- and multi-scale approach). Habitat models from all observations combined were less able to describe the observed distributions ($PE_{Y=X}$=76% for both single- and multi-scale approach). Habitat models derived from low-density observations that included territoriality (ambit radius 20 cm, c.f. Figure 3.2.2) and similar habitat models that did not include territoriality were equally able to describe habitat use at the scale of the pool, riffle and run ($PE_{Y=X}$=77% for multi-scale approaches; $PE_{Y=X}$=70-72% for single-scale approaches). A model where fish were randomly distributed over the surface of the tank described observed distributions at the scale of the pool/riffle/run least well ($PE_{Y=X}$=54%).

Table 3.2.9. Similarity of observed and modelled distributions in the stream tank at the scale of pool/riffle/run. Distribution models were derived from observed habitat use (DATA) in terms of substrate, water velocity and depth, of introductions separate (SEP), and of the two low-density introductions (LOW) or all observations (TOT) combined; using either a Single-Scale (SS) or Multi-Scale (MS) approach; and with or without incorporating territorial behaviours (ambit radius 20 cm; NOTERR/TERR), as explained in the text. Distribution model "Random" refers to a model where fish were distributed randomly over the surface of the stream tank. Summary statistics include intercept (Int.), slope, and associated standard errors (s.e.), of the relationship between the observed and predicted percentage of fish in the pool, riffle and run, as well as the percent variance explained by the line Y=X ($PE_{Y=X}$; model: percent observed = percent predicted).

Model	DATA	r^2	Int.	Slope	s.e. Int.	s.e. Slope	$PE_{Y=X}$
RANDOM	-	0.575	-0.109	1.326	0.1014	0.2847	54.1
SS-NOTERR	SEP	0.964	-0.012	1.037	0.0196	0.0499	96.3
MS-NOTERR	SEP	0.963	-0.021	1.064	0.0204	0.0524	96.0
SS-NOTERR	TOT	0.775	-0.042	1.127	0.0569	0.1519	76.5
MS-NOTERR	TOT	0.773	-0.053	1.158	0.0585	0.1570	75.9
SS-NOTERR	LOW	0.770	0.078	0.766	0.0437	0.1045	69.8
SS-TERR	LOW	0.778	0.071	0.788	0.0436	0.1053	72.2
MS-NOTERR	LOW	0.786	0.043	0.871	0.0456	0.1135	76.9
MS-TERR	LOW	0.791	0.043	0.870	0.0450	0.1118	77.3

3.2.4. Discussion

3.2.4.1. General findings

This study showed that juvenile salmon were associated with habitats over a range of scales, rather than a single characteristic scale. Associations with conspecifics, substrate, water velocity, and depth were scale-dependent, were generally most extreme at small spatial scales (ambit radius < 50 cm), and were often anisotropic. Fish were sensitive to contrasts in habitat features within an area of 40-50 cm surrounding positions: Positions were often selected for or avoided not solely because of characteristics of the habitat directly at positions, but because of the habitat at these positions in concert with surrounding habitats.

These results underline the importance of spatial heterogeneity of the landscape mosaic to habitat quality, with spatial heterogeneity having two components: (1) the complexity in composition, which is non-spatial, and (2) configuration, which is spatial (Li and Reynolds 1994). Current habitat models account for the first component, as habitat preference is known to be a function of habitat availability (cf. DeGraaf and Bain 1986, Heggenes 1990), but generally ignore the latter.

Ignoring habitat configuration and effects of scale on heterogeneity in habitat modelling may limit effectiveness of managerial decisions based on these models (see Chapter 1.5). To incorporate both complexity as well as configuration in the spatial domain, spatially-explicit analyses of fish and habitat distributions are necessary. The current shift in research focus from one-dimensional towards two-dimensional flow-models may aid in this as well (cf. Leclerc et al. 1996). As heterogeneity occurs over a range of spatio-temporal scales, multi-scale approaches may serve to identify important scales and processes and allow for incorporating both complexity as well as configuration in habitat models. From this, habitat models and management decisions may be improved.

I did not observe significant changes in habitat use with introduction density. Relative incidences of aggressive, movement and feeding behaviours did not differ significantly among densities or among preferred and avoided habitats. Additional analyses suggested that observed spacing behaviour or territoriality was unlikely to cause changes in habitat use in the tank, as preferred locations were distributed such that occupation of these locations was possible without interference competition or pre-emptive exclusion, even at high densities (cf. Figure 3.2.2, Table 3.2.5). To observe changes in habitat use with density, higher densities of fish should have been used, using larger fish having larger territories or larger scale spacing behaviour, or by creating an environment having less preferred locations, positioned in closer proximity (cf. Grant and Kramer 1990).

Several other studies have addressed density-dependent habitat selection by salmonids. Elliott (1986) observed density dependent habitat selection by trout (*Salmon trutta*). Rodríguez (1995) studied density dependent interactions between sympatric salmon and brook charr (*Salvelinus fontinalis*) based on 12 pool/riffle pairs, and concluded that interspecific interactions changed habitat preference among pools and riffles with density, but intraspecific interactions did not. Bult (Chapter 4.1) observed a shift in habitat preference of salmon parr from run to pool habitats with density. This study (Chapter 3.2) contrasts with these other studies in that no density-dependent habitat selection was observed, which may be due to the distribution of preferred habitats within the tank as outlined previously. It is interesting to note that all of these previous studies used a single large-scale approach (habitat in terms of pool, riffle, run). However, the results of this study suggest that fish behaviours are primarily directed towards habitat features at much smaller spatial scales. From this, habitat classifications based on broad scale features may not necessarily reflect the habitat as experienced by fish, which may limit effectiveness of habitat models based on these classifications.

3.2.4.2. Specific findings

Fish reacted indifferently to conspecifics at larger spatial scales (ambit radius > 50 cm), but seemed to avoid each other at smaller spatial scales (ambit radius < 50 cm). Avoidance was most extreme for ambit radii < 15-20 cm, which is most likely due to spacing-behaviour or territoriality.

Fish reacted indifferently to cobble at larger spatial scales (ambit radii>40 cm), i.e. areas with and without cobble were equally favoured. When cobble was present within an ambit radius of 40 cm, fish were positioned in a characteristic manner relative to surrounding cobble-stones. Fish were seldom positioned directly above cobble-stones (see Figure 3.2.3). Similar behaviours may have been observed by Rimmer et al. (1984) who reported salmon parr being associated with specific "home stones". However, in this study (Chapter 3.2), fish were not positioned on top, but adjacent to preferred stones.

Fish were associated with water velocities over a range of spatial scales. Fish differentiated low-water-velocity positions in areas of low water velocities from low-water-velocity positions in areas of higher water velocities (see Figure 3.2.5). Fish preferred water velocities of <40,50] cm s^{-1}, but maximised contact with these water velocities not at small spatial scales, but at larger spatial scales (30-50 cm; see Figure 3.2.6c). Fish avoided high water velocity positions (>50 cm s^{-1}) located to the right (relative to water flow) of high water velocity areas (>50 cm s^{-1}; see Figure 3.2.6d). Associations with water velocities of <5,10] cm s^{-1} were most extreme and positive (i.e. RC(EX) maximal) at the position of the fish (small scale). These may indicate a selection for specific holding positions with specific low snout velocities close to high current conditions (larger scale) where drift is concentrated (cf. Chapman and Bjornn 1969, Everest and Chapman 1972, Fausch and White 1981), and an avoidance of excessive water currents because position holding is too difficult or energetically unfavourable: Contact with velocities of <5,10] cm s-1 were maximised at small-scale "snout-" positions; Contact with water velocities of <40,50] cm s^{-1} was maximised at larger spatial scales, as fish may veer into these preferred water velocities to capture food from positions of lower water velocities. Due to the shape of the stream tank, water velocities at the outer edge of the tank were larger than at the inner edge, and so positions located to the right of avoided high flow locations are likely to be of even larger flows and avoided even more, leading to the pattern of Figure 3.2.6d. The slight oval shape of the area in Figure 3.2.2 that indicates spacing or territorial behaviours may be caused by this as well, as defence of holding positions may be easiest in a downstream direction towards the inner edge of the tank or an upstream direction towards the outer edge of the tank. These results suggest behaviours aimed at maximising energy intake (cf. Bachman 1984, Fausch 1984) and are in line with findings of Heggenes (1990) who reported from an extensive literature review that salmon parr generally avoided slow-flowing areas (<5 cm s^{-1}), preferred water velocities in the range of 5-25 cm s^{-1} (nose velocity; fish of 7-10 cm), and avoided fast-flow habitats.

Distributions of individual fish were more similar (stable) when the period in between distribution surveys was small (small temporal scales) and when mapped using larger spatial scales (Figure 3.2.7). This was expected, but an explicit description of how stability of fish distributions changes with spatio-temporal scale, as of Figure 3.2.7, may provide cues to habitat selection behaviours: The sudden change in the slope of the lines at the transition between regions 1/2 (Spatial Scale = 5 cm), the relative flatness of the lines in region 2 and the sudden change in the slope of the lines at the transition between regions 2/3 (Spatial Scale = 20 cm) may be due to fish being positioned at a particular location within a larger area, e.g. at the centre of territories, with the transition between regions 2/3 indicating the size of these larger areas and the transition between regions 1/2 indicating the accuracy with which fish were positioned within these larger areas. Note, however, that the patterns of Figure 3.2.7 at spatial scales smaller than 5 cm may also be partly due to sampling errors associated with the accuracy of fish position measurements of the observer. The difference in stability of low (more stable) and medium density distributions (less stable) for temporal scales of 10 to 60 min, and the similarity in stability at larger temporal scales, may be due to the effect of feeding on redistribution of fish at the larger temporal scales and a less changeable distribution of low density distributions at smaller temporal scales in between feedings. In addition, information from analyses as summarised in Figure 3.2.7 may assist in determining limitations associated with the extrapolation of small-scale habitat selection observations to address problems at the larger spatio-temporal scales that are relevant to fish management (see Chapter 2).

3.2.4.3. Selection of measurement scales

As measurement scale can have a profound influence on results and interpretations (Wiens 1989, Menge and Olson 1990, Levin 1992, Horne and Schneider 1995), a careful consideration of scale is important to habitat models. Habitat models effective for resource management problems should focus on a description of the more important processes first before including others. Multi-scale descriptions of distribution patterns of organisms and their habitats may serve to identify important processes and the scales at which they operate. Rate-diagrams, which rank processes by importance as a function of spatio-temporal scale (Horne and Schneider 1994), may further aid in identifying important processes. Important processes should be described at scales most efficient to habitat models. This may be best achieved by concentrating on scales where distributions and associations are most extreme, i.e. different from random (Schneider 1994). When measurement scales are different from scales relevant to management problems, a careful consideration of the validity of extrapolating information across scales is important (cf. Dayton and Tegner 1984, Carpenter et al. 1995, Schneider et al. 1997, see Chapter 2).

In this study, associations were generally most extreme at small spatial scales. This suggest that small-scale approaches may be more efficient than larger-scale approaches to describe distributions of fish relative to habitats. Because associations of fish with habitats changed rapidly with spatial scale, especially for ambit radii of 0-50 cm, a clearly defined measurement scale may be crucial to habitat selection studies: small variations in measurement scales may have strong effects on habitat models. The use of ill-defined or variable measurement scales in habitat modelling is unfortunately rather prevalent. The scales of substrate and cover measurements are most often ill-defined and these measurements may often be autocorrelated over much smaller spatial scales than e.g. water velocity or depth. Because of this, slight variations in measurement scale may result in large differences among fish-substrate or fish-cover associations. Subsequently, substrate and cover are less likely to be consistently identified as important, compared to water velocity and depth, even if habitat selection behaviours were similar among studies.

3.2.4.4. Scale-up in habitat models

Most ecological studies operate at relatively small scales, especially those involving experimental manipulations (seconds to years; cm^2 to regional scales). However, most ecological problems operate at much larger scales (years to decades; national to global). From this, a discrepancy exists between the scales of our information and problems (cf. Lima and Zollner 1996, Schneider et al. 1997). An ability to translate fine-scale information across scales could facilitate the development of a mechanistic explanation of distribution patterns and processes, which in turn would greatly facilitate the resolution of questions relating to resource management. An inability to predict larger scale distributions from small-scale information may indicate that different processes are involved and that important information may be missing (Horne and Schneider 1994, cf. With and Christ 1996, see Chapter 2). In this context it is interesting to note that several studies have shown that weighted usable area, a measure of habitat quality based on small-scale (space/time) observations on fish distributions, may not be a good predictor of standing stock in river sections (cf. Orth and Maughan 1982, Bowlby and Roff 1986, Conder and Annear 1987, Pajak and Neves 1987, Hubert and Rahel 1989, Shirvell 1989, Bozek and Rahel 1991, Bourgeois et al. 1996), although some studies did find such a relationship (Stalnaker 1979, Orth and Maughan 1982). This may suggest that small-scale habitat selection processes cannot simply be extrapolated to larger spatio-temporal scales: large-scale fish distributions are not the result of a simple composite of small-scale habitat selection processes; habitat models may be able to indicate where fish will be, but not how many will be present (cf. Orth 1987).

Results from this study suggested several habitat selection behaviours operating at multiple spatial scales rather than a single one. Because of this, multi-scale models were initially expected to perform better than single-scale models, especially at the larger scales of pool, riffle and run. However, further analyses revealed that a multi-scale habitat model was not better than a single-scale model in describing distributions of fish at the these larger spatial scales. This may be due to habitat selection behaviours being aimed primarily at small-scale habitat features that were already included in the single-scale model, because of the small spatial scope of the study (limited range of scales), and because the tank consisted of only a single pool, riffle and run. For example, the variable depth in the single- and multi-scale models will effectively separate the pool from the run and riffle, regardless of the availability of other habitat features within the pool. Because of this, most of the differences between the single and multi-scale approaches are related to how fish are distributed among riffle and run.

3.2.4.5. Stream tank versus natural river

Stream tank observations are relatively easy to obtain and study conditions are largely under the control of the researcher. Hence, a large number of observations can be obtained from clearly defined conditions. A stream tank is of course a caricature of a natural river and results may be an artefact of the tank habitat rather than being indicative of general and realistic "natural" habitat selection behaviours. For a general treatise on this see e.g. Diamond (1986). Because of this, results obtained from tank observations should not be extrapolated to more natural systems without validation against field data. Stream tank studies are nevertheless an important addition to field-based habitat selection studies, as they allow for detailed information under controlled conditions and development of mathematical techniques, such as the ones used here, which may aid in the design of subsequent field studies. For example, the results indicated that small-scale habitat variations within an area of 40-50 cm surrounding fish positions are important and that associations of fish with habitats rapidly change with scale and direction within this area. From this, I suggest a possible field study design that compares high-resolution habitats maps of areas within 50-100 cm surrounding observed fish positions, to similar maps from random positions. This comparison can be done using the scaling-techniques as outlined in this study.

3.2.4.6. Conclusions

Multi-scale approaches lead to a more complete and better understanding of behavioural processes and habitat selection than single-scale approaches. A clearly defined use of measurement scale is crucial to habitat modelling, as associations changed rapidly with spatial scale. Multi-scale approaches were not better than single-scale approaches in describing fish distributions.

Classic micro-habitat models operate at a single or few selected scales and ignore the effects of the orientation and structure of landscape elements on habitat quality. The results indicated that habitat selection behaviours operated at multiple scales and underline the importance to fish distributions of structure and orientation of habitats within the landscape mosaic. Because of this, single-scale approaches may be limited in identifying important habitats.

Strong spatio-temporal heterogeneity is characteristic of rivers, especially when compared to lakes and other aquatic habitats, with wide variations in temperature, depth and water flow over short spatio-temporal scales. Species inhabiting these environments are adapted to this heterogeneity and management actions resulting in a more predictable and less heterogeneous environment may diminish the very uniqueness of the habitats and species they intend to protect (cf. Barinaga 1996). Multi-scale approaches as described in this study may aid in incorporating habitat heterogeneity in habitat models by identifying important scales and processes. From this, multi-scale habitat models may be better at evaluating how organisms are associated with their habitats and be more efficient for resource management than single-scale habitat models. Future habitat modelling studies should focus on the identification of spatio-temporal scales that are most effective in explaining observed fish distributions.

3.3. A multi-scale analysis of habitat use by juvenile Atlantic salmon and brown trout in two Newfoundland rivers

3.3.1. Introduction

Models that quantify the importance of habitats to organisms are widely used in resource management. Often, these models are based on behavioural observations of individual organisms obtained at small spatio-temporal scales, with relations between organism and habitat defined at a single or few measurement scales. This type of information is often used to address problems that occur at a range of much larger spatio-temporal scales, i.e. at the level of populations, with time scales from years to decades and spatial scales from regional to global. The implicit assumption is that organisms are associated with their environment at specific "characteristic" space and time scales, that small-scale behavioural processes are largely responsible for the distributions we observe, and that these small-scale behavioural processes can be easily extrapolated to address resource management problems operating at much larger spatio-temporal scales (cf. Dayton and Tegner 1984, Carpenter et al. 1995, Lima and Zollner 1996, Schneider et al. 1997).

An example is the application of micro-habitat models to management of riverine fish populations in North America, such as PHABSIM/IFIM (Bovee 1982, 1986, Milhous et al. 1984, 1989). These models relate fish densities or frequency-of-use to riverine habitats, and assume that a higher density or frequency-of-use corresponds to a "better" habitat (cf. Fausch et al. 1988, Reiser et al. 1989, Armour and Taylor 1991). Information used in these models is often obtained by direct observation of individual fish and from habitats measured at small space-time scales (<1 m^2, few seconds of observation per individual fish). Subsequently, this information is used to address problems at the level of fish populations, at time scales from years to decades and spatial scales of tributaries to rivers and watersheds. This process of "scale up" can be graphically represented in a "scope-diagram", as proposed by Schneider et al. (1997) (see Figure 1.1 and 2.6).

The rationale behind this focus on small spatio-temporal scales is that distributions of organisms are to a large extent the result of decisions made by individuals (Krebs and Kacelnik 1991) which generally operate at small space-time scales. However, organisms are known to select their habitats at more than a single spatio-temporal scale. An example is selection by salmonids for specific holding positions (small scale) with relatively low snout velocities in areas of high current conditions (larger scale) where drift is concentrated (Chapman and Bjornn 1969, Everest and Chapman 1972, Wankowski and Thorpe 1979, Fausch and White 1981, see Chapter 3.2). In addition, distributions of animals are known to be the result of multiple processes operating over a range of scales (Wiens 1989, Horne and Schneider 1994, 1995), rather than being the sole result of habitat selection processes operating at a single scale. Thus, it is important to evaluate which scale or scales are most appropriate to habitat modelling and fish habitat management. Important research questions are: (1) how do fish perceive and react to their environment? (2) how are limited resources distributed among competitors? (3) is habitat use or fish density truly indicative of habitat quality? (4) to what extent are fish distributions driven by habitat selection behaviours and to what extent by other processes? and (5) how can individual fish behaviours be extrapolated to scales relevant to management problems?

In this study, I address question 1 and, to a lesser extent, question 5, by studying habitat selection by juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). The objectives were (1) to illustrate how a variety of newly developed scaling-techniques can be used in habitat modelling and behavioural studies; (2) to identify spatial scales important to habitat models for juvenile Atlantic salmon; (3) to formalise observed habitat selection behaviours in an explicit multi-scale habitat selection model; and (4) to compare explicit multi-scale approaches with single-scale approaches in regard to their ability to identify how fish select habitats and to describe and predict fish distributions, in particular when used to address problems at space-scales larger than those of individual fish-observations.

I hypothesised that a multi-scale approach is better for describing fish distributions because habitat selection behaviours themselves operate at multiple scales. Subsequently, this behaviour may be best identified and made explicit within the context of quantitative multi-scale techniques, i.e. a multi-scale problem is best studied using a multi-scale approach.

This study differs from previous studies on habitat selection and habitat modelling of salmonids in that associations of fish with habitats were studied within the context of an explicit multi-scale approach. This study differs from the few previous studies on habitat use by fish that operated at multiple scales (cf. Syms 1995, Poizat and Pont 1996, Richards et al. 1996) in that associations of fish with habitats were studied over a range of spatial scales, rather than at a few selected scales. The present study is a companion piece to a previous study on habitat use by salmon from stream tank observations (Chapter 3.2), which allowed for an evaluation of the relevance of some of the stream-tank results to field-based research.

3.3.2. Material and methods

3.3.2.1. Study sites

Selected sites were studied in North Harbour River (47°12'0" N, 53°37'30" W) and North Arm River (47° 22' 20" N, 53° 10' 0" W), both located on the Avalon Peninsula of Newfoundland, Canada. These rivers are of similar size, having axial lengths of 12.9 and 17.4 km, and drainage areas of 72.5 and 86 km^2, respectively. Watersheds consist of boreal forests and boglands, underlain by Precambrian rock. Fish communities are composed of Atlantic salmon *Salmo salar*, brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, threespine stickleback *Gasterosteus aculeatus*, and American eel *Anguilla rostrata*. The rivers are further described by DeGraaf and Bain (1986).

Study sites were visited in 1994 (North Harbour River) and 1995 (North Harbour River, North Arm river). In 1994, I studied one large section in North Harbour River (length 120 m, average river width 9 m). In 1995, I studied 3 smaller sections in North Harbour River and 3 smaller sections in North Arm river. Lengths of these sections varied from 10 to 16 m. Average river width at these sections varied from 6 to 14 m. The total surface area of the riverine habitat surveyed in North Harbour River in 1994 and 1995 was 1130 m^2 and 286 m^2 respectively. The total surface area of the riverine habitat surveyed in North Arm river in 1995 was 356 m^2. (See Table 3.3.1) Distance between sections varied from 10 to 30 m. The North Harbour River sections were all located within the larger 1994 section.

Table 3.3.1. Description of study sites in North Arm River (NAR) and North Harbour River (NHR) in 1994 and 1995, in terms of length, average width, surface area, water depth and water velocity (average, standard deviation and maximum). The 1995 surveys were done over a range of flow conditions. Sites consisted of combinations of pool, riffle and run habitats.

Yr.	River	Site	Habitat	Length (m)	Width avg. (m)	Area (m^2)	Depth avg. (cm)	Depth s.d. (cm)	Depth max. (cm)	Wvel avg. (cm s^{-1})	Wvel s.d. (cm s^{-1})	Wvel max. (cm s^{-1})
94	NHR	1	pool riffle run	120	9	1130	20.2	12.8	133	12.9	12.7	74
95	NHR	1	riffle	14	7	93	14.5	7.5	35	14.7	12.1	48
						96	15.2	7.7	36	15.3	12.2	
		2	pool	14	8	109	30.0	14.6	67	5.7	5.3	42
						110	30.6	14.9	68			
		3	run	10	9	80	16.9	10.2	44	11.0	8.4	31
95	NAR	1	pool	11	14	154	27.1	13.3	66	1.9	1.9	8
			flat			162	36.1	14.5	76	10.7	11.5	38
		2	run	13	6	77	19.7	11.6	51	7.4	9.5	41
						79	30.7	12.4	63	31.3	28.7	91
		3	pool	16	7	110	17.1	10.9	54	5.6	6.2	24
			riffle			115	31.8	11.7	70	28.8	21.6	81

Study sites were chosen on the basis of (1) representation of a range of riverine habitats in terms of water flow, depth and substrate, (2) ease of snorkelling, and (3) densities of juvenile Atlantic salmon sufficiently high to allow for the type of analyses as of this study. Study sites consisted of a combination of pool, riffle and run habitats, with substrates ranging from sand and silt to gravel, cobble and large boulders (see Table 3.3.1-2). The water was clear with visibility always more than 4 m.

Table 3.3.2. Substrate composition (%) at study sites in North Harbour River (NHR) and North Arm River (NAR) in 1994 and 1995.

River	Year	fines	4-16 mm	16-32 mm	32-64 mm	64-128 mm	128-256 mm	256-512 mm	>512 mm
NHR	1994	1	6	10	21	30	21	8	2
NHR	1994	1	2	6	19	37	25	9	2
NAR	1995	12	6	11	26	24	12	6	2

3.3.2.2. Habitat mapping

Sections were mapped for substrate, water depth (cm), and water velocity (cm s^{-1}). These are the variables most often included in habitat models of riverine fish species (Orth and Maughan 1982, Fausch et al. 1988, Heggenes 1990). Water velocities were mapped at 60% depth, using an electronic flow meter (FLO-MATE, Model 2000, Marsh-McBirney Inc.). Substrate was identified as: (1) silt: no gritty feeling when rubbed between fingers, (2) sand: gritty feeling when rubbed between fingers, (3) fine gravel: 2-8 mm, (4) gravel: 8-16 mm, (5) small pebble: 16-32 mm, (6) pebble: 32-64 mm, (7) small cobble: 64-128 mm, (8) cobble: 128-256 mm, (9) large cobble: 256-384 mm, (10) boulder: 384-512 mm, (11) large boulder: >512 mm, and (12) bedrock.

For the habitat mapping, I established XY-grids covering the study sections, using measuring tapes and T-posts as reference points. Habitat observations were evenly distributed over the study reach. To facilitate the taking of evenly distributed habitat observations, I used a 1 m^2 PVC frame, divided into 4 (50 cm * 50 cm) and 9 (33 cm * 33 cm) cells with coloured twine. The frame was positioned in the XY-grid using measuring tapes and the reference T-posts. Next, the habitat measurements were done directly at the centre of the cells within the frame. Substrate was mapped with a resolution of 9 measurements per square meter. Depth was mapped with a resolution of 4 measurements per square meter (1994) or 9 measurements per square meter (1995). Water velocities were mapped with a resolution of 1 measurement per square meter, without the use of a frame.

In 1994, substrate, depth and water velocity were measured once at a discharge estimated at 0.25 $m^3 s^{-1}$, which was the most prevalent discharge in the summer of 1994. In 1995, substrate and depth were measured twice in North Arm River to assess repeatability of habitat mapping, and once in North Harbour River. Water velocities were measured 4 times at all of the co-ordinates in the XY-grids over a range of discharge levels, ranging from just lower than the lowest discharge observed during fish distribution surveys to just higher than the highest discharge observed. Based on these, I created a 2 dimensional flow-model by relating the water level at independent fixed reference points (4 reference points per section) to water depths and water velocities at the co-ordinates in the XY-grids, using linear regression (separate regression equation per co-ordinate; n=4 per co-ordinate). An additional independent survey for water velocity was done to test this flow model. The change in survey design from 1994 to 1995 was meant to prevent a situation where much effort was spent initially to create habitat maps at a set water level, but where subsequent adverse weather conditions prevented fish distribution surveys being done at this particular water level. I concentrated on North Arm River in 1995 because visibility in North Harbour River rapidly deteriorates at elevated water levels, whereas visibility in North Arm river is always excellent (>4 m), even during flood events.

3.3.2.3. Fish distributions

In 1994, two fish distribution surveys were done in North Harbour River. These surveys were done at the same water level as that of the habitat mapping. Each survey took approximately 6 hours (10.00 - 16.00 h). The weather conditions (sunny, warm), flow conditions (discharge=0.25 $m^3 s^{-1}$), and water temperatures (16 - 21 °C) were similar during the surveys (see Table 3.3.3).

In 1995, two fish distribution surveys were done in the North Harbour River sections and 16 fish distribution surveys were done in the North Arm River sections. The two 1995 North Harbour River surveys were done at similar weather (partly cloudy, warm), flow (discharge=0.15 - 0.16 $m^3 s^{-1}$), and temperature (16 - 21°C) conditions. One survey took approximately 2 hours. Flow conditions and water temperatures during the 16 North Arm River surveys varied widely, with temperature ranging from 10 to 23 °C and discharge ranging from 0.07 $m^3 s^{-1}$ (very low water level) to 0.53 $m^3 s^{-1}$ (high water level) (see Table 3.3.3; Figure 3.3.1). Two of the 1995 North Arm River surveys were done at night (22.00 - 23.00 h) with the aid of a flashlight. All others were done in late-morning (10.00 - 13.00 h). Surveys there generally took one hour.

Table 3.3.3. Summary of fish distribution surveys in North Harbour River (NHR) and North Arm River (NAR) in 1994 and 1995. Descriptive statistics include starting-time of each survey (h), temperature (°C), discharge ($m^3 s^{-1}$), total numbers of all salmonids (Ntot), Atlantic salmon (Nsalmon), brook trout (Nbrook) and brown trout (Nbrown). Numbers of 0+ fish are shown in brackets. North Harbour River surveys are shown in italics.

Date	**Location**	**Time**	**Temp**	**Disch**	**Ntot**	**Nsalmon**	**Nbrook**	**Nbrown**
17/08/94	***NHR***	***10.00***	***16 - 21***	***0.25***	***507***	***487(182)***	***18(3)***	***1(0)***
25/08/94	***NHR***	***10.00***	***16 - 21***	***0.25***	***526***	***490(209)***	***29(5)***	***7(0)***
03/07/95	NAR	11.00	14	0.11	39	16(2)	0	23(12)
06/07/95	NAR	12.00	21	0.16	54	16(2)	0	32(10)
12/07/95	NAR	12.00	21 - 23	0.09	55	30(7)	0	23(7)
17/07/95	NAR	11.00	10- 11	0.07	25	9(2)	0	16(3)
20/07/95	NAR	11.00	12	0.24	30	14(4)	0	16(4)
23/07/95	NAR	10.30	16 - 18	0.41	46	24(6)	0	22(2)
27/07/95	NAR	11.00	18	0.44	72	35(9)	0	37(10)
28/07/95	NAR	10.30	16 - 18	0.37	63	45(13)	0	18(8)
31/07/95	NAR	10.00	17 - 18	0.26	63	36(7)	0	27(12)
04/08/95	NAR	11.00	16 - 18	0.14	57	32(12)	0	25(14)
07/08/95	***NHR***	***12.00***	***18 - 21***	***0.16***	***152***	***148(39)***	***2(1)***	***2(0)***
09/08/95	***NHR***	***11.00***	***16***	***0.15***	***137***	***124(41)***	***11(5)***	***2(0)***
08/09/95	NAR	11.00	16-17	0.26	35	14(3)	0	21(7)
16/09/95	NAR	11.00	13	0.53	22	12(5)	0	10(2)
24/09/95	NAR	10.00	14	0.37	21	9(3)	0	12(4)
27/09/95	NAR	22.00	13	0.25	43	26(0)	0	16(0)
28/09/95	NAR	22.00	10	0.22	36	21(1)	0	13(0)
01/10/95	NAR	10.30	10	0.20	15	5(3)	0	7(4)
TOTAL					1998	1594(551)	60(14)	330(109)

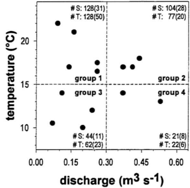

Figure 3.3.1. Temperature (°C) and discharge (m^3 s^{-1}) during the 1995 day-time surveys in North Arm River. Numbers (#) refer to the total number of Atlantic salmon (S) and brown trout (T) observed, with the number of 0+ fish shown in brackets. Group 1-4 refers to grouping of observations prior to analyses.

Fish were observed by snorkelling in an upstream direction in a zigzag pattern to minimise disturbance. Observed fish positions were marked using numbered weights. Data recorded when snorkelling included: species (Atlantic salmon, brook trout, brown trout), age class (0+, 1+, 2+, >2+; estimated from size), height above bottom (cm), and activity (moving, holding position). All fish observed were recorded. The numbered markers were mapped relative to the XY-grid, to the nearest 5 cm. Water velocities, snout velocities (cm sec^{-1}), depth (cm), cover and substrate were mapped at locations of markers that indicated positions of fish that did not move. To assess repeatability of fish-position measurements, a sample of markers was measured twice, with the first and second of these measurements done by different persons. Measuring tapes, used to establish the XY-grids, were taken down and reinstalled prior to taking second measurements.

3.3.2.4. Research questions

I analyzed the data to address a series of questions. Italicised phrases refer for convenience to sections later identified in the Results section:

1. (*Patchiness of fish distributions*) How are fish positioned relative to each other?

I hypothesised that fish were negatively associated with conspecifics at small spatial scales (<0.3 m), due to spacing behaviour or territoriality, and positively associated at larger spatial scales with associations being most positive at scales ranging from 0.5 to 2 m, due to selection for small-scale habitat features.

2. (*Associations of fish distributions*) How is one group of fish (age class, species) positioned relative to another?

I hypothesised that fish were negatively associated with other fish at small spatial scales (<0.3 m) due to spacing behaviour or territoriality. At larger spatial scales, associations were expected to be positive for groups of fish with the same attributes (age, species), and therefore negative for fish groups with different attributes.

3. (*Habitat associations*) How are fish associated with their habitats: which variables were selected for and at what spatial scale(s)?

I hypothesised that habitat features were selected at more than a single scale, but that habitat selection behaviours were primarily directed towards small-scale (<30 cm) environmental features. That is, I expected associations to be scale-dependent, with associations being most different from random (extreme) at small spatial scales.

4. (*Habitat model*) What is the best way of incorporating associations of fish with habitats into a formal habitat model to describe and predict fish distributions? Which variables should be included and at what spatial scales? To what extent does an explicit multi-scale approach improve our understanding of habitat selection behaviours of fish, relative to a more classic single-scale approach?

I expected that an explicit multi-scale approach and habitat model would lead to a better understanding of habitat selection processes. From this, explicit multi-scale habitat models were expected to perform better than single-scale habitat models, especially when extrapolating small-scale habitat selection behaviours to density-predictions at larger spatial scales, such as river sections or broad-scale environmental features such as pools, riffles and runs. I.e., observed and predicted fish distributions will be more similar for multi-scale approaches.

The analytical procedures related to these four questions are outlined below. Analyses were done using FORTRAN and SAS (SAS 1988). Random numbers, needed for several of the analyses, were generated using the FORTRAN system-supplied random number generator, upgraded by the shuffle-routine as outline by Press et al. (1986).

3.3.2.5. Scaling analyses, omnidirectional

Associations of individual fish with substrate, water velocities, depth, and other fish were studied over a range of spatial scales using measures of Relative Contact (RC), as outlined in Chapter 3.1. This statistic compares observed densities of fish or habitat features surrounding individual fish positions (DO; # m^{-2}), with similar densities obtained from computer-generated random fish distributions (DR; # m^{-2}). These comparisons can be made for a range of ambit radii (S), i.e. circles surrounding individual fish positions.

From this, RC_S serves as a scale-dependent measure of association:

$$RC_S = LOG_{10}(DO_S + 10^{-6}) - LOG_{10}(DR_S + 10^{-6}) \qquad \textit{Equation 3.3.1}$$

The statistic allows positive associations (RC>0) to be distinguished from negative associations (RC<0) and random (RC=0) from clumped (RC>0) distributions. For example, $RC_S=1$ indicates that at ambit radius S, an average fish has 10 times more contact with conspecifics or a specific habitat feature (depth, water velocity or substrate class), than if fish were randomly distributed.

The constant of 10^{-6} (Equation 3.3.1) prevented taking $\log_{10}(0)$ and was chosen such that RC measures were not affected, other than in situations where DO=0 m^{-2}. These latter situations could easily be identified from the program output, with RC ranging from -3 to -6, depending on DR. DR_S was obtained by averaging results for all possible positions. Density estimates were obtained by generating evenly-distributed dummy-positions with a resolution of 400 m^{-2} and assuming a 400^{-1} m^{-2} area around all dummy-positions. P-values, used to assess whether associations were significantly different from random, were obtained from 500 randomised fish distributions (see Chapter 3.1).

3.3.2.6. Scaling analyses, directional

Possible anisotropy in associations of fish with habitats, conspecifics, or other fish distributions was studied using the RCEX statistic (exhaustive measure of Relative Contact, see Chapter 3.2):

$$RCEX_{LAG-X,LAG-Y} = LOG_{10}(DO_{LAG-X,LAG-Y}) - LOG_{10}(DR_{LAG-X,LAG-Y})$$

Equation 3.3.2

RCEX compares observed densities of fish or habitat features at various lags surrounding observed fish positions with similar densities obtained from computer-generated random fish distributions, and allows for a comprehensive scale-explicit two-dimensional appraisal of the data's spatial dependence. For example, $RCEX_{-1,+3} = -1$ indicates that an average fish has 10 times less contact with conspecifics or a particular habitat feature at lag -1 in the X-direction and lag +3 in the Y-direction. Note that RC is calculated at increasingly larger ambit radii, whereas RCEX is calculated at consecutive lags, and that RCEX measures are directional, whereas RC measures are not. Also note that RC and RCEX measures are similar at spatial scales approaching 0 cm provided the lag-interval chosen is small.

RCEX measures are most easily obtained from rectangular distribution maps. Fish- and habitat-distribution maps from rivers are generally not rectangular. However, in the analyses the X- and Y-directions did not refer to the X-Y grid system of the river as based on the T-posts and measuring tapes, but to a grid system relative to fish position and water flow: The 90° and 270° directions referred to directions directly into and with the current, respectively; the 0° and 180° directions referred to directions perpendicular to the current. This grid system differs among fish positions in the river.

3.3.2.7. Habitat model and scaling approach

Based on results of analyses as outlined in the previous section, I developed a formal model to describe habitat use by fish in rivers. Preferably, such a model would combine realism (model parallels habitats as experienced by the fish) and simplicity (few variables included, few classes per variable) with strong descriptive and predictive capabilities (observed and predicted distributions or habitat use similar). To develop such a model, I devised a method based on the RC statistic that paralleled stepwise multiple regression. First, I decided on an initial model that incorporated the variable thought to be most important, measured at a scale where associations were most extreme (i.e. RC measures of the different classes most different from 0). Next, I created fish distributions based on this model. For this, fish were distributed by randomisation with all positions in the river having a different probability of being selected (n positions in total). This probability ($P_{POS=i}$; i=1-n) was determined by a weight given to each position ($W_{POS=i}$) and the total of all weights of all possible positions (W_{TOT}), with $W_{POS=i}$ determined by the Relative Contact associated with the habitat at this position ($HAB_{POS=i}$) as of the initial model:

$$P_{POS=i} = \frac{W_{POS=i}}{W_{TOT}} = \frac{10^{RC_{HAB(POS=i)}}}{\sum_{j=1}^{n} 10^{RC_{HAB(POS=j)}}} \approx \frac{10^{RC_{HAB(POS=i)}}}{n} \qquad \text{Equation 3.3.3}$$

Next, I compared densities of habitat features surrounding observed fish positions (DO) with similar densities surrounding these computer-generated distributions (DD), in a manner similar to Equation 3.3.1. This was done over a range of ambit radii (S):

$$RCD_S = LOG_{10}(DO_S + 10^{-6}) - LOG_{10}(DD_S + 10^{-6}) \qquad \text{Equation 3.3.4}$$

From this, RCD values (Relative Contact of fish positions Distributed by computer) that differ from 0 may indicate that additional habitat selection behaviours have to be included into the initial habitat model. This can relate to inclusion of additional variables, to inclusion of the same variable but defined at multiple scales, or to a combination of both. For example, fish distributions could be generated according to observed habitat use related to water velocity and evaluated by means of the RCD statistic as a function of depth. Positive values of RCD for a particular depth class may then indicate that this depth is preferred, even after correcting for selection for water velocities, i.e. habitat selection behaviours are directed towards both depth and water velocity. This method is clearly of use in an environment where habitat variables are correlated (cf. Richards 1982), when habitats are perceived in a non-independent manner by fish (cf. Orth and Maughan 1982), or when habitat selection behaviours operate at more than a single scale.

To evaluate how well fish distributions can be described using either a single-scale micro-habitat modelling approach or a multi-scale approach, I generated distributions (10^5 fish) for each of these two approaches, as described above. Next, I compared the densities of the observed and computer-generated fish distributions over a range of spatial scales. For this, I chose 10^5 random positions within the experimental sections, determined the densities of observed and computer-generated fish-distributions (% total population m^{-2}) for a range of ambit radii surrounding these random positions and computed the correlation coefficient between these two densities. This procedure was repeated at the scale of pool, riffle and run, after dividing the experimental reaches into these three habitat classes. If the multi-scale approach had superior descriptive capacities compared to a single-scale approach, the differences between observed and predicted densities would be smaller and correlation coefficients positive and higher for the multi-scale approach. I was especially interested in the descriptive capacities of models for describing fish densities at spatial scales larger than those used in the model.

3.3.2.8. Computational procedures

Prior to analyses, I re-scaled water depths into 7 classes ([0, 6], <6,12], <12,24], <24,36], <36,48], <48,60], >60 cm), substrate into 8 classes ((1) fines: <4 mm; (2) gravel: 4-16 mm; (3) small pebble: 16-32 mm; (4) pebble: 32-64 mm; (5) small cobble: 64-128mm; (6) cobble: 128-256mm; (7) boulder: 256-512mm; (8) large boulder/bedrock: >512 mm) and water velocities into 7 classes ([0,3], <3,6], <6,12], <12,24], <24,36], <36,48], >48 cm s^{-1}). Age classes were re-scaled into 2 classes: (1) 0+; (2) >0+. Depth and substrate were measured twice in 1995: for the analyses I used the first substrate distribution map and the average from the first and second depth distribution maps.

For analyses of associations and patchiness of fish distributions (Questions 1-2; see Chapter 3.3.2.4), observations were combined into 3 groups: (1-2) North Harbour River 1994, 1995; (3) North Arm River 1995. To facilitate computations based on surveys with different densities, density estimates were re-scaled as a percentage of the total population observed (Question 2: associations of fish distributions) or the total population minus one (Question 1: patchiness of fish distributions) (see Chapter 3.1). For analyses on habitat associations (Questions 3-4), observations were combined into 6 groups: (1) North Harbour River, 1994; (2) North Harbour River 1995; (3-6) North Arm River 1995, based on temperature and discharge (see Figure 3.3.1). I did not use the two 1995 North Arm River night-time observations as fish reacted to the observer and I could not judge the effects of this on fish distributions.

To compute RC (and RCEX) for these groups based on multiple surveys, one could either first calculate RC for surveys separately and average these (approach 1), or one could first calculate DO and DR for surveys separately, average these and then calculate RC (approach 2). The first approach is to be preferred especially when habitat availability or survey area differs among surveys, but does have the disadvantage that when few fish were observed in any of the surveys, DO may be 0 at small spatial scales for some of the habitat classes. From this, RC will be strongly negative (-3 to -6) and will highly influence the averaged RC based on all surveys combined. One could try to solve this problem by changing the constant (10^{-6}) or the weight given to individual RC estimates, but this may lead to results that are highly influenced by this constant. The second approach does not have this disadvantage, as most often at least one fish was observed in any of the habitat classes, which makes the RC estimate much less dependent on the constant of 10^{-6}. However, when habitat availability or survey area differs among surveys, the averaged DR may not correspond to the habitat as experienced by fish observed during these surveys. From this, the second approach is to be preferred when few fish were observed during surveys and when habitat availability and survey areas are similar among surveys. In this study, I used the second method because of the low densities observed in North Arm river (see Table 3.3.3). I used the fish numbers of individual surveys as weighting-factors when calculating the average DO and DR. Differences between the two calculation methods will be small for the 1994 and 1995 North Harbour River surveys, as densities were similar among surveys within groups and much higher than in North Arm River, and because survey areas and flow conditions did not differ among surveys within groups. The grouping procedure for the North Arm River surveys further ensured that percent occurrence of depth, substrate and water velocity classes and survey areas were similar among surveys. For computations where fish positions were generated according to habitat specific distribution rules, RC and RCD for survey groups were calculated using the habitat map that corresponded to the average water level within survey groups.

Analyses were completed over a range of ambit radii (up to 15 m). The smallest ambit radius differed among analyses with resolution of habitat distribution maps. For associations of fish with habitat features measured using a resolution of 1 m^{-2} (water velocity), the smallest ambit radius was 75 cm so as to ensure that at least one habitat observation was within the ambit of each possible fish position. For associations of fish with habitat features measured using a resolution of 4 m^{-2} (depth, substrate) and 9 m^{-2} (water velocity), the smallest ambit radii were 40 and 25 cm, respectively. From habitat measurements taken at snout positions of inactive fish, an additional RC was calculated for these fish assuming an ambit radius of 1 cm.

A graphic representation of results was focused on the 1994 North Harbour River surveys, as these are based on a much larger number of fish, compared to the other survey-groups. Results from survey-groups other than the 1994 North Harbour River surveys will be discussed in relation to the 1994 North Harbour River surveys. I concentrated not on individual RC(EX) values as such, but on (dis)similarities of patterns of the various survey-groups as apparent from all RC(EX) values calculated across habitat classes and spatial scales. A selection criterion of 5% was used to separate "significant" from "non-significant" effects.

3.3.3. Results

During the two 1994 North Harbour River surveys, a total of 1033 fish was observed (95% salmon, 5% brook trout, <1% brown trout, <1% unknown). During the two 1995 North Harbour River Surveys, a total of 289 fish was observed (94% salmon, 5% brook trout, 1% brown trout). Mean densities for all species were the same for all surveys (0.5 m^{-2}). A visual inspection of the fish distribution maps suggested that distributions were similar among surveys within years, with both 0+ and older fish located in or around the thalweg of the river and 0+ fish in shallower locations along the river banks as well.

During the 14 North Arm River day-time surveys in 1995, a total of 597 fish was observed (50% salmon, 48% brown trout, 0% brook trout, 2% unknown). I observed more fish when temperatures were higher and discharge was lower (Tables 3.3.3-4, Figure 3.3.1). A visual inspection of the fish distribution maps suggested that distributions were similar among surveys, with both 0+ and older fish located in or around the thalweg of the river and 0+ fish in shallower locations along the river banks as well. This pattern did not seem to change with discharge or temperature.

Table 3.3.4. Total number of fish observed during the 1995 North Arm River day-time surveys as a function of temperature (°C) and discharge ($m^3 s^{-1}$) (r^2=0.807, n=14, p<0.001). Residuals were normally distributed.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Temperature	1	27.048384	27.048384	0.32	0.5845
Discharge	1	713.851496	713.851496	8.43	0.0157
Temperature*Discharge	1	778.941552	778.941552	9.20	0.0126
Corrected Total	13	4391.21429			

Repeated fish position measurements indicated that 70% of these were identical; 27% of second measurements differed by 5 cm from first measurements (either in X or Y directions); and 3% differed by 10 cm from first measurements (n=74 co-ordinates, measured twice). Repeated substrate measurements indicated that 84% of second measurements were identical to first measurements (n=3096). Depth (cm) as predicted by the flow model was significantly correlated with independent repeated depth measurements (n=2885, p<0.001, r=0.864). 59% of these independent depth measurements were identical in terms of depth class to predictions from the flow model. Water velocity (cm s^{-1}) as predicted by the flow model was significantly correlated with independent repeated water velocity measurements (n=246, p<0.001, r=0.901). 59% of these independent water velocity measurements were identical in terms of water velocity class to predictions from the flow model. For several of the analyses below I compared results from first and second depth and substrate maps. A visual inspection of these showed that patterns were similar.

3.3.3.1. Patchiness of fish distributions

Salmon and brown trout were negatively associated with conspecifics at small spatial scales (ambit radius < 10-20 cm) but positively associated at larger spatial scales. Associations were most positive for ambit radii of 15 to 30 cm (Figure 3.3.2). This pattern was apparent for all survey groups and age classes.

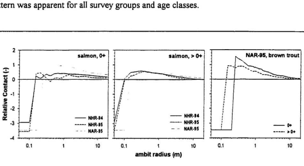

Figure 3.3.2. Spatial autocorrelation of Atlantic salmon parr and brown trout distributions (0+, >0+), as observed in North Harbour River in 1994 and 1995 (NHR-94; NHR-95) and North Arm River in 1995 (NAR-95), quantified in terms of Relative Contact for ambit radii ranging from 5 cm to 15 m.

The RC values of -3 to -4 of Figure 3.3.2 indicated no conspecifics were observed within the corresponding ambit radii. These negative values may be obtained by chance alone, especially for ambit radii approaching 0 cm. For example, assuming a random position choice, it is unlikely that 2 fish will occupy the same position because of the large number of possible positions involved. Because of this, I aimed at evaluating whether the drop in RC to RC=-3 to -4 for ambit radii less than 30 cm was indicative of small-scale avoidance behaviour or due to chance alone. To do this, I generated random fish positions within in a square area (AREA, m^2), such that the total number of fish distributed (Ndis) corresponded to those observed at individual surveys and the densities in this area (Ddis) corresponded to the fish densities associated with the "peaks" in RC from Figure 3.3.2 ($Ddis = 10^{RCpeak}$; $AREA = Ndis / Ddis$). Next, I calculated RCs for these distributions, in a manner similar to the calculations as of Figure 3.3.2, and evaluated whether no conspecifics were observed for ambit radii ranging from 5 to 30 cm. This was repeated 10^5 times. From this, p-values were obtained that indicated the chance of having no conspecifics within a particular ambit radius due to chance alone within patches as indicated in Figure 3.3.2. These analyses showed that the chance of having no conspecifics due to chance alone at a 10 cm ambit radius was smaller than 0.05 for all of the lines of Figure 3.3.2, with the exception of the 1995 0+ salmon distributions in North Harbour River.

Figure 3.3.3 shows that spatial autocorrelations of the 1994 North Harbour River salmon (0+, >0+) positions were anisotropic. Salmon were concentrated in patches that were elongated in directions parallel to water flow: RCEX values more rapidly declined towards RCEX=0 in directions perpendicular to water flow than in other directions, especially for >0+ salmon. Fish numbers of surveys other than 1994 North Harbour River were so low that results as in Figure 3.3.3 were difficult to interpret. Nevertheless they did not seem to indicate that patterns differed from the patterns as described above, both for salmon as well as for brown trout. Note that the discrepancy between RCEX and RC for spatial scales approaching 0 cm, as apparent from Figures 3.3.2 and 3.3.3 (RCEX>0, RC<0), is due to the rather large lag-interval (1 m) used. This lag-interval was necessary because of the low fish numbers involved. Also note that analyses in Figure 3.3.3 (RCEX) generally require many more fish observations to allow for interpretation, compared to analyses in Figure 3.3.2 (RC).

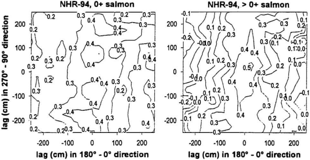

Figure 3.3.3. Autocorrelation of 0+ and older Atlantic salmon parr distributions as a function of spatial-scale and direction relative to water flow from observations in North Harbour River in 1994 (NHR-94), quantified in terms of Relative Contact Exhaustive (RCEX).

3.3.3.2. Associations of fish distributions

Salmon aged 0+ year were negatively associated with 1+ salmon at ambit radii smaller than 10 to 30 cm but positively associated with one another at larger spatial scales for all three survey groups (North Harbour River 1994, 1995; North Arm River 1995; see Figure 3.3.4). Associations were most positive for ambit radii of 15 to 30 cm. RC was not significantly different ($p<0.05$) from 0 for ambit radii smaller than 15 (North Harbour River 1994), 25 (North Harbour River 1995) and 40 cm (North Arm River 1995), but significantly different from 0 for larger ambit radii. Trout aged 0+ year were negatively associated with 1+ trout at all ambit radii (North Arm River 1995; see Figure 3.3.4), with RC significant ($p<0.05$) for ambit radii of 1.5 to 7.5 m. Salmon aged 0+ year were negatively associated with 0+ brown trout in North Arm River in 1995 for ambit radii < 25 cm and positively associated for ambit radii of 25 cm to 1 m. At larger spatial scales, RC approached 0. Few of these RC measures differed significantly from 0 ($p<0.05$; significant: ambit radii 30-35 cm). >0+ Salmon were negatively associated with >0+ brown trout in North Arm River in 1995 for ambit radii < 2 m. At larger spatial scales, RC approached 0. Few of these RC measures differed significantly from 0 ($p<0.05$; significant: ambit radii 40-45 cm, 100-170 cm). In short: 0+ Salmon and >0+ salmon, and 0+ salmon and 0+ trout were found at the same locations. 0+ Trout and >0+ trout, and >0+ salmon and >0+ trout were found in different areas. Fish always avoided each other at very small spatial scales (ambit radii <10 cm).

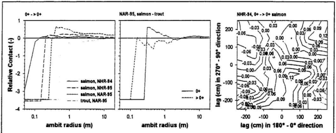

Figure 3.3.4. Associations of 0+ and >0+ salmon and trout distributions in North Arm River (NAR) and North Harbour River (NHR) from distribution surveys in 1994 and 1995 (left 2 figures: omnidirectional approach (RC); right figure: directional approach (RCEX)).

I only applied the directional approach (RCEX) to 0+ - >0+ salmon distributions from the 1994 North Harbour River surveys because of low fish numbers in other surveys. Results indicated that associations between 0+ and >0+ salmon were anisotropic, with more >0+ salmon at positions in 270° to 90° directions from 0+ salmon positions, than in other directions (Figure 3.3.4).

3.3.3.3. Habitat associations

Associations of 0+ salmon with substrate, water velocity, and depth were calculated in terms of RC for the 1994 and 1995 North Harbour River surveys. 0+ Salmon distributions from North Arm River were not analyzed because of low fish-numbers (see Figure 3.3.1). Results are summarised in Table 3.3.5. In general, associations were scale-dependent and most extreme at small spatial scales. Shallow depths (<12 cm) were avoided for ambit radii <5-7 m but were preferred at larger spatial scales. Intermediate depths (12-36 cm) were preferred and larger depths avoided (Figure 3.3.5). Low water velocities were avoided (<12 cm s^{-1}). Higher water velocities were preferred, but with a shift from preference to avoidance for the highest water velocities at ambit radii of 2-3 m (Figure 3.3.6) and a local maximum in associations with water velocity class 4 (1995, 12-24 cm s^{-1}) and 5 (1994, 24-36 cm s^{-1}) at ambit radii of 1-4 m. Fines (class 1) were avoided at ambit radii > 30 cm for 1994 North Harbour River 0+ salmon and at all ambit radii for 1995 North Harbour River 0+ salmon. (Large) boulders (class 7-8) were also avoided. Fish reacted indifferently towards intermediate substrates (Figure 3.3.7). For 0+ fish that were stationary, an additional RC could be calculated from habitat measurements taken at the position of these fish (ambit radius approaching 0 cm). Results from these analyses indicated that patterns were similar to those described above, but with associations being more extreme for ambit radii approaching 0 cm (Figure 3.3.5).

Table 3.3.5. Summary of associations of 0+ salmon with the variables (V) depth (D), water velocity (W) and substrate (S) as a function of scale, quantified in terms of Relative Contact at increasingly larger ambit radii, from surveys in North Harbour River in 1994 and 1995 (NHR94, NHR95). Loc: location; Yr: year; Nt: total # fish observed; Nst: # stationary fish; Np: # fish positions from stationary fish where additional small-scale habitat observations were done.

Loc/Yr	Nt	Nst	Np	V	Results
NHR94	391	331	197	D	* associations most extreme at small spatial scales with exception of associations class 6, which were most negative ambit radii around 60 cm (see Figure 3.3.5) * class 1-2 avoided at ambit radii < 5-7 m but preferred at larger spatial scales; class 3-4 preferred; class 5-7 avoided * stationary fish: patterns similar to above, but with associations being more extreme for ambit radii approaching 0 cm
NHR95	80	47	44	D	* associations most extreme at small spatial scales * class 1-2 avoided at ambit radii < 5-7 m but preferred at larger spatial scales; class 3-4 preferred; class 5-7 avoided * stationary fish: patterns similar to above, but with associations being more extreme for ambit radii approaching 0 cm
NHR94	391	331	237	W	* associations most extreme at small spatial scales, with exception of associations class 5, which were most extreme at ambit radii of 1-4 m (see Figure 3.3.6) * class 1-3 avoided; class 4-6 preferred; class 7 preferred at ambit radii < 3 m but avoided at larger spatial scales * stationary fish: patterns similar to above, but with associations being more extreme for ambit radii approaching 0 cm
NHR95	80	47	44	W	* associations most extreme at small spatial scales, with exception of associations class 4, which were most extreme at ambit radii of 1 m * class 1-3 avoided; class 4-5 preferred; class 6 preferred at ambit radii < 2 m but avoided at larger spatial scales; no class 7 watervelocities present * stationary fish: patterns similar to above, but with associations being more extreme for ambit radii approaching 0 cm
NHR94	391	331	297	S	* associations most extreme at small spatial scales * class 1 avoided at ambit radii >30 cm, but indifference towards class 1at smaller spatial scales; indifference towards class 3-6; class 7-8 avoided (see Figure 3.3.7) * stationary fish: patterns were similar to above, but with associations being more extreme for ambit radii approaching 0 cm
NHR95	80	47	44	S	* associations most extreme at small spatial scales * class 1 avoided; indifference towards class 3-6; class 7-8 avoided at ambit radii < 30 cm but preferred at larger ambita radii; RC most positive at ambit radii of 0.4 to 1.5 m * stationary fish: patterns similar to above, but with associations being more extreme for ambit radii approaching 0 cm

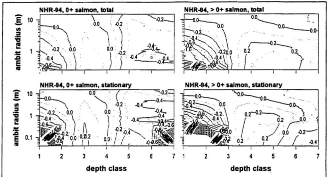

Figure 3.3.5. Associations of 1994 North Harbour River salmon with depth at increasingly larger ambit radii, quantified in terms of Relative Contact.

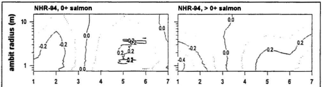

Figure 3.3.6. Associations of 1994 North Harbour River salmon with water velocity (at 60% depth) at increasingly larger ambit radii, quantified in terms of Relative Contact (-).

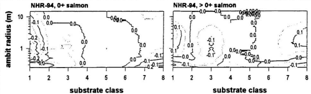

Figure 3.3.7. Associations of 1994 North Harbour River salmon with substrate at increasingly larger ambit radii, quantified in terms of Relative Contact.

Associations of >0+ salmon with substrate, water velocity and depth were calculated in terms of RC for the 1994 and 1995 North Harbour River surveys and group 1 and group 2 of the 1995 North Arm River surveys. Group 3-4 of the 1995 North Arm River surveys were not analyzed because of low fish-numbers (see Figure 3.3.1). Results are summarised in Tables 3.3.6-7. In general, associations were scale-dependent and most extreme at small spatial scales. Shallow depths (<24 cm) were avoided at ambit radii <7-10 m but were often preferred at larger spatial scales. Intermediate depths (24-36 cm) were preferred. Larger depths were preferred at ambit radii < 2-7 m, but often avoided at larger spatial scales (Figure 3.3.5). Low water velocities were avoided (<12 cm s^{-1}); higher water velocities were mostly preferred (Figure 3.3.6). Associations with fines and boulders were most extreme, with relative indifference towards other substrates (Figure 3.3.7). Fines were generally avoided. Large boulders were often avoided at small spatial scales (ambit radius <50 cm) but preferred at larger spatial scales. For >0+ salmon that were stationary, an additional RC could be calculated from habitat measurements taken at the position of these fish (ambit radius approaching 0 cm). Results from these analyses indicated that patterns were similar to those described above, but with associations being more extreme for ambit radii approaching 0 cm and an avoidance of larger depths (>48 cm) and coarser substrates (cobble, (large) boulders).

Table 3.3.6. Summary of associations of >0+ salmon with the variables (V) depth (D) and water velocity (W) with scale, quantified in terms of Relative Contact at increasingly larger ambits, from surveys in North Harbour River in 1994 and 1995 (NHR94, NHR95) and North Arm River in 1995 (NAR95). Loc: location; Yr: year; group: see Figure 3.3.1; Nt: total # fish observed; Nst: # stationary fish; Np: # fish positions from stationary fish where additional small-scale habitat observations were done.

Loc/Yr	Nt	Nst	Np	V	Results
NHR94	586	461	274	D	* associations most extreme at small spatial scales * class 1-3 avoided at ambit radii < 7-10 m but preferred at larger spatial scales; class 4 preferred; class 5-7 preferred at ambit radii < 5-7 m but avoided at larger spatial scales; see Figure 3.3.5 * stationary fish: patterns were similar to above, but with associations being more extreme for ambit radii approaching 0 cm; class 6-7 avoided
NHR95	192	110	103	D	* see: NHR94
NAR95 group 1	97	65	44	D	* associations most extreme at small spatial scales * class 1-3 avoided at ambit radii < 5 m but preferred at larger spatial scales; class 4 preferred; class 5-6 preferred at ambit radii < 2-4 m but avoided at larger spatial scales; class 7 avoided * stationary fish: patterns were similar to above, but with associations being more extreme for ambit radii approaching 0 cm and avoidance of class 6-7
NAR95 group 2	76	56	56	D	* associations most extreme at small spatial scales * class 1-2 avoided; class 3 avoided at ambit radii < 5-6 m but preferred at larger spatial scales; class 4 preferred; class 5-6 preferred at ambit radii < 2-4 m but avoided at larger spatial scales; class 7 avoided * stationary fish: patterns were similar to above, but with associations being more extreme for ambit radii approaching 0 cm and avoidance of classes 6-7
NHR94	586	461	289	W	* associations most extreme at small spatial scales * class 1-3 avoided; class 4-7 preferred; see Figure 3.3.6 * stationary fish: patterns were similar to above, but with associations being more extreme for ambit radii approaching 0 cm
NHR95	192	110	103	W	* see NHR94
NAR95 group 1	97	65	44	W	* associations most extreme at small spatial scales * class 1-2 avoided; class 3-6 preferred; class 7 preferred for ambit radii < 3-4 m but avoided at larger spatial scales * stationary fish: patterns were similar to above, but with associations being more extreme for ambit radii approaching 0 cm and avoidance of classes 6-7
NAR95 group 2	76	56	56	W	* associations most extreme at small spatial scales * class 1-3 avoided; idifference towards class 4; class 5-7 preferred * stationary fish: patterns were similar to above, but with associations being more extreme for ambit radii approaching 0 cm

Table 3.3.7. Summary of associations of >0+ salmon with the variable (V) substrate (S) as a function of scale, quantified in terms of Relative Contact at increasingly larger ambit radii, from surveys in North Harbour River in 1994 and 1995 (NHR94, NHR95) and North Arm River in 1995 (NAR95). Loc: location; Yr: year; group: see Figure 3.3.1; Nt: total # fish observed; Nst: # stationary fish; Np: # fish positions from stationary fish where additional small-scale habitat observations were done.

Loc/Yr	Nt	Nst	Np	V	Results
NHR94	586	461	371	S	* associations most extreme at small spatial scales, with exception of associations class 1, which reach maximum at ambit radii of 2-3 m * class 1 preferred at ambit radii >50-60 cm, but avoided at smaller spatial scales; indifference towards class 2-7; class 8 avoided at ambit radii <50-60 cm but preferred at larger spatial scales; associations with class 8 and 1 reach maximum at 1-2 m ambit radii * stationary fish: patterns were similar to above, but with associations being more extreme for ambit radii approaching 0 cm; class 6-8 avoided at ambit radii < 30-40 cm * see Figure 3.3.7
NHR95	192	110	103	S	* associations most extreme at small spatial scales * class 1 avoided; indifference towards class 2-7; class 8 avoided at ambit radii <40 cm but preferred at larger spatial scales * stationary fish: patterns were similar to above, but with associations being more extreme for ambit radii approaching 0 cm; class 6-8 avoided at ambit radii < 30-40 cm
NAR95 group 1	97	65	44	S	* associations most extreme at small spatial scales * class 1-2 avoided; class 3 avoided at ambit radii <3 m but preferred at larger spatial scales; class 4-5 preferred; class 6 preferred for ambit radii < 4-5 m, but avoided at larger spatial scales; class 7-8 avoided at ambit radii <40 cm and ambit radii > 3-5 m, but preferred at intermediate spatial scales; associations class 1-2 most extreme * stationary fish: patterns were similar to above, but with associations being more extreme for ambit radii approaching 0 cm; class 6-8 avoided at ambit radii < 30-40 cm
NAR95 group 2	76	56	56	S	* associations most extreme at small spatial scales * class 1-2 avoided; class 3 avoided at ambit radii <2 m but preferred at larger spatial scales; class 4-5 preferred; class 6 preferred for ambit radii < 3-4 m, but avoided at larger spatial scales; class 7-8 avoided with exception of preference for class 8 at ambit radii <50 cm; associations class 1-2 most extreme * stationary fish: patterns were similar to above, but with associations being more extreme for ambit radii approaching 0 cm

Associations of >0+ brown trout with substrate, water velocity and depth were calculated in terms of RC for group 1 and group 2 of the 1995 North Arm River surveys. >0+ brown trout from other surveys and 0+ brown trout distributions were not analyzed because of low fish numbers (see Figure 3.3.1, Table 3.3.3). For the same reason, analyses were not repeated for stationary fish. Results are summarised in Table 3.3.8. In general, associations were scale-dependent and most extreme at small spatial scales. Patterns were similar to those of >0+ salmon. Shallow depths (<24 cm) were avoided for ambit radii <7-10 m but were often preferred at larger spatial scales. Intermediate depths (24-36 cm) were preferred. Larger depths were preferred at ambit radii < 2-7 m, but avoided at larger spatial scales. Low water velocities were avoided (<12 cm s^{-1}). Higher water velocities were mostly preferred. Fines were avoided and large boulders were preferred.

Table 3.3.8. Summary of associations of >0+ brown trout with the variables (V) depth (D) and water velocity (W) as a function of scale, quantified in terms of Relative Contact at increasingly larger ambit radii, from surveys in North Arm River in 1995 (NAR95). Loc: location; Yr: year; group: see Figure 3.3.1; Nt: total # fish observed.

Loc/Yr	Nt	V	Results
NAR95 group 1	78	D	* associations most extreme at small spatial scales * class 1-3 avoided at ambit radii < 7-10 m but preferred at larger spatial scales; indifference towards class 4; class 5-7 preferred at ambit radii < 5-7 m but avoided at larger spatial scales
NAR95 group 2	57	D	* associations most extreme at small spatial scales * class 1 avoided; class 2-3 avoided at ambit radii < 7-10 m but preferred at larger spatial scales; indifference towards class 4; class 5-7 preferred at ambit radii < 5-7 m but avoided at larger spatial scales
NAR95 group 1	78	W	* associations most extreme at small spatial scales * class 1-2 avoided; class 3-7 preferred
NAR95 group 2	57	W	* associations most extreme at small spatial scales * class 1-2 avoided; class 3-7 preferred
NAR95 group 1	78	S	* associations most extreme at small spatial scales * class 1-2 avoided; indifference towards class 3-7; class 8 preferred
NAR95 group 2	57	S	* associations most extreme at small spatial scales * class 1-2 avoided; indifference towards class 3-7; class 8 preferred

A directional approach based on RCEX indicated that associations of 1994 North Harbour River salmon (0+, >0+) with depth, water velocity and substrate were generally most extreme at small spatial scales (lag <1 m). Patterns in associations of fish with these variables were elongated in directions with and against the flow directions, as illustrated in Figure 3.3.8 for associations of the 1994 North Harbour River salmon (>0+) with depth. Fish numbers in surveys other than 1994 North Harbour River were so low that results as in Figure 3.3.8 were often difficult to interpret. Nevertheless they did not seem to indicate that patterns differed from the patterns as described above, for salmon as well as for brown trout.

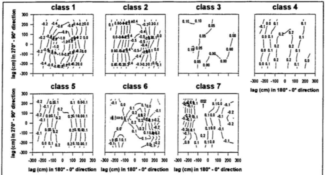

Figure 3.3.8. Associations of 1994 North Harbour River salmon (>0+) with depth as a function of spatial scale and direction relative to water flow, quantified in terms of Relative Contact Exhaustive (RCEX) (-).

3.3.3.4. Habitat model: multi- or single scale?

I first aimed at understanding the extent to which the scale-dependent associations, as outlined in the previous section, were the result of small-scale habitat selection behaviours only, rather than being the result of habitat selection behaviours operating over a range of scales. For this, I first calculated RC for all possible depth-water velocity combinations (7*7=49 possible classes), using the depth and water velocity observations closest to individual fish positions. Based on these RC measures I generated fish distributions as outlined in the Material and Methods section. Next, I calculated RCD for associations with substrate, water velocity and depth for the survey groups separate. Note that RCD should be close to 0 for associations with depth and water velocity at ambit radii approaching 0 cm (cf. Chapter 3.2.2.3). (See "Material and Method" section for how a RCD different from 0 may indicate multi-scale behaviours.)

Results from these analyses suggested that many of the associations at larger spatial scales are the result of small-scale habitat selection behaviours, rather than being the result of habitat selection behaviours operating at a range of spatial scales: RCD estimates were closer to 0 across spatial scales compared to RC estimates (illustrated in Figure 3.3.9 for 1994 North Harbour River salmon). Some results, however, suggested habitat selection behaviours operating at multiple scales:

For salmon (0+/>0+) and brown trout (>0+), I found that associations with low water velocities (<12 cm s^{-1}) were negative and generally most extreme at ambit radii <2 m. Positive associations were found with water velocity classes 5-7 (> 24 cm s^{-1}) at ambit radii of 1-10 m (see Figure 3.3.9). These results, in combination with results in terms of RC as outlined above, suggest that fish may differentiate between low-flow locations within low-flow areas and low-flow locations within high-flow areas. They may also differentiate between high-flow locations within high-flow areas and high-flow locations within low-flow areas. This behaviour cannot be described by a model based on depth and water velocity operating at a single small-scale only.

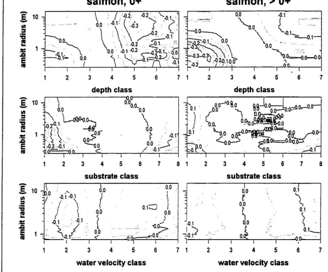

Figure 3.3.9. Associations of 1994 North Harbour River salmon (0+, >0+) distributions, generated by computer and single small-scale habitat selection rules related to water velocity and depth, with depth, water velocity and substrate across a range of ambit radii or spatial scales, quantified in terms of Relative Contact (RCD).

For salmon (0+/>0+) and brown trout (>0+), I found that associations with shallow depths (<6 cm) were negative for ambit radii <3 m (most extreme at 50 cm to 1 m) but close to 0 at other spatial scales. In North Arm River (1994, 1995), associations with larger depths (>36 cm for 0+ salmon, > 48 cm for >0+ salmon) were negative and most extreme for ambit radii > 3 m (see Figure 3.3.9). These results, in combination with results in terms of

RC as outlined above, suggest that fish may differentiate between shallow locations in shallow areas and shallow locations and deeper areas, and between deep locations in deep areas and deep locations within shallower areas. This behaviour cannot be described by a model based on depth and water velocity operating at a single small-scale only.

For salmon (0+/>0+), I found that associations with fines (class 1) were similar to as described above in terms of RC. Associations with larger substrates being generally close to 0 (see Figure 3.3.9). For brown trout (>0+) I found results similar to those in terms of RC. These results, in combination with results in terms of RC as outlined above, suggest that associations of salmon and trout with fines may not be explained by a model based on water velocity and depth alone, but that associations of salmon with (large) boulders may have been partly due to selection for water velocity and depth, and that associations of salmon and trout with other substrates may be negligible.

3.3.3.5. Habitat model, single- versus multi-scale approaches

Based on the previous results, I chose a single small-scale model and a multi-scale model. The single-scale model distinguished all possible depth-water velocity combinations (7*7=49 possible classes). The multi-scale model consisted of 5 depth classes from shallow to deep, distinguishing shallow locations in shallow areas from shallow locations in deeper areas and deep locations in deep areas from deep locations within shallower areas, and 5 water velocity classes from slow to faster, distinguishing low-flow locations in low-flow-areas from low-flow locations in higher-flow areas and distinguishing high-flow locations in high-flow-areas from high-flow locations in low-flow areas (5*5=25 possible classes): Depth 1: $\leq$ 12 cm at location and $\leq$ 12 cm average depth within 1 m ambit radius; Depth 2: depth <12 cm at location and > 12 cm average depth within 1 m ambit radius; Depth 3; 12-36 cm at position; Depth 4: >36 cm at location and > 36 cm average depth within 3 m ambit radius; Depth 5: >36 cm at location and $\leq$ 36 cm average depth within 3 m ambit radius; Water velocity 1: ≤ 6 cm s^{-1} at location and ≤ 6 cm s^{-1}

average water velocity within 1 m ambit radius; Water velocity 2: ≤ 6 cm s^{-1} at location and > 6 cm s^{-1} average water velocity within 1 m ambit radius; Water velocity 3: 6-24 cm s^{-1} at location; Water velocity 4: >24 cm s^{-1} at location and ≤ 24 cm s^{-1} average water velocity within 1 m ambit radius; Water velocity 5: >24 cm s^{-1} at location and > 24 cm s^{-1} average water velocity within 1 m ambit radius. To determine habitat at fish positions, I used the depth and water velocity observations closest to individual fish positions. Substrate was not included to limit the number of habitat classes in the model and because substrate-selection behaviours were mostly restricted to fines. I purposely chose a multi-scale model consisting of fewer habitat classes compared to the single-scale model to prevent a situation where descriptive capacities of the multi-scale approach would be superior to the single-scale approach solely because of the number of habitat classes involved, rather than being the result of using the multiple scales.

Based on these models and associated RC measures, I generated fish distributions as outlined in the Material and Methods section. A visual inspection of computer-generated and observed fish distribution maps suggested that all were similar in that fish were concentrated in the same small-scale locations within the river (1-2 m^2). The multi-scale model generally performed better than the single-scale approach, especially at larger spatial scales (ambit radius > 4 m, Figure 3.3.10; Table 3.3.9). Nevertheless, correlations (r) between the single- and multi-scale computer-generated distributions and observed distributions were often small and sometimes even negative at spatial scales larger than those of the model (see Figure 3.3.10, Table 3.3.9), in spite of a much higher and positive correlation between computer-generated and observed distributions at small spatial scales ($r=0.5$ to 0.8 at ambit radii < 4 m). I tried several additional models with various depth/water velocity classes defined at various spatial scales, but was unable to develop a model that performed well at small as well as at larger spatial scales for all survey groups.

Table 3.3.9. Correlation (r) between observed fish densities (% total population m^{-2}) and fish densities generated by single- (SS) and multi-scale (MS) habitat selection models, at the spatial scales of pool, riffle and run, for distributions of brown trout (>0+) and salmon (0+, >0+) in North Harbour River (NHR: 1994, 1995) and North Arm River (NAR: 1995). (n: # fish observed; group: see Figure 3.3.1)

Species	Age	n	Location	Year	r - SS	r - MS
salmon	0+	391	NHR	1994	0.60	0.91
salmon	0+	80	NHR	1995	0.78	0.71
salmon	>0+	586	NHR	1994	-0.20	0.91
salmon	>0+	192	NHR	1995	-0.57	-0.27
salmon	>0+	97	NAR-group 1	1995	0.19	0.34
salmon	>0+	76	NAR-group 2	1995	0.57	0.63
trout	>0+	78	NAR-group 1	1995	0.94	0.92
trout	>0+	57	NAR-group 2	1995	0.68	-0.47

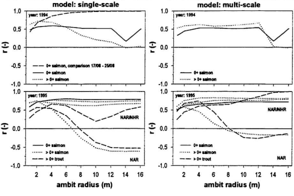

Figure 3.3.10. Correlation (r (-)) between observed fish densities (% total population m^{-2}) and fish densities generated by single- and multi-scale habitat selection models as a function of spatial scale (ambit radius, m) for distributions of trout (>0+) and salmon (0+, >0+) in North Harbour River (1994, 1995) and North Arm River (1995). For comparison I added results of a similar analysis, relating the densities of 0+ salmon of the first visit in North Harbour River in 1994 to those of the second visit.

3.3.4. Discussion

Associations of individual salmon and trout with other fish, substrate, water velocity, and depth were highly scale-dependent, and most extreme at small spatial scales (ambit radii < 50 cm). In addition, scale-dependency of associations changed with direction relative to water flow. Associations with depth, water velocity, and substrate at larger spatial scales were to a large extent the result of small-scale habitat selection behaviours, but with some selection behaviours operating at multiple-scales rather than at a single one: fish seemed to differentiate between shallow positions in shallow areas and shallow positions in deeper areas, deep locations in deep areas and deep locations within shallower areas, low-flow positions in low-flow-areas and low-flow positions in high-flow areas, and high-flow positions in high-flow-areas and high-flow positions in low-flow areas (cf. riffle-run versus pool habitats); 0+ salmon of the 1994 North Harbour River survey avoided fines at larger spatial scales (ambit radii > 30 cm), but were indifferent to fines at smaller spatial scales; >0+ salmon often avoided larger substrates (cobble to large boulder) at small spatial scales (ambit radii <40 cm), but often preferred larger substrates at larger spatial scales. Single- and multi-scale habitat selection models were equally well able to describe small-scale fish distributions (ambit radii < 4 m). Multi-scale models were often better at explaining these distributions at larger scales (Figure 3.3.10; Table 3.3.9). However, both single- and multi-scale approaches often failed to describe distributions at spatial scales much larger than those used in the models, even when larger scale distributions were described in terms of relatively homogenous broad-scale features such as pools, riffles, and runs.

These results indicate behaviours primarily directed towards small-scale habitat features (< 1 m^2), probably aimed at maximising energy intake (cf. Bachman 1984, Fausch 1984) by selection for specific holding positions with low snout-velocities close to higher current conditions (larger scale) where drift is concentrated (cf. Chapman and Bjornn 1969, Everest and Chapman 1972, Fausch and White 1981), and an avoidance of excessive water currents probably because position holding is too difficult or energetically unfavourable. Due to these behaviours, fish were concentrated in patches. These patches were elongated parallel to water-flow. This elongation was apparent more so for >0+ salmon and >0+ trout than for 0+ salmon. This difference is likely due to older fish being concentrated in the centre of the river where flow is higher and depths larger (run type habitat), whereas 0+ fish are primarily found in shallower riffle-type river sections, using more of the cross-section of the river. Spacing-behaviour or territoriality further reduced the clumpedness of fish within these patches at small spatial scales (ambit radius 10-30 cm).

Results at small spatial scales were in line with findings of a micro-habitat study on trout and salmon done earlier in these rivers (DeGraaf and Bain 1986). They support findings of Heggenes (1990), who reported from a literature review that salmon parr generally avoided slow flowing areas (<5 cm s^{-1}), smaller substrates, deep low-flow areas and fast-flow habitats, and preferred water velocities in the range of 5-25 cm s^{-1}. A differentiation by fish between low-water-velocity-positions in areas of low water velocities and low-water-velocity-positions in areas of higher water velocities as well as an avoidance of larger substrates at small spatial scales (stream tank: ambit radius < 15 cm; this study: <30-40 cm) shifting to indifference or preference at larger spatial scales were also found in the stream-tank study reported earlier (Chapter 3.2). However, the low-resolution of the water velocity maps used in this field-based study (1 m^{-2}) did not allow me to clearly identify the scales at which this behaviour operated, in contrast to the the stream-tank study (area: 30-50 cm ambit radius; resolution water velocity measurements: 43 m^{-2}).

The low-resolution of the flow-map also limits analyses along the lines of Figure 3.3.9 (RCD), because water velocities at co-ordinates (XY-grid) closest to fish positions, used for generating the distributions of Figure 3.3.9, may not accurately reflect water velocities as experienced by fish. From this, I interpret the results of Figure 3.3.9 as suggesting that habitat selection behaviours operate at multiple scales, but still do not provide solid proof for this type of behaviour. More convincing in this respect are results from analyses along the lines of Figure 3.3.5-8 (RC), which, for example, suggest for 0+ salmon that contact with water velocity class 5 (24-36 cm s^{-1}) is maximised at ambit radii of 1-4 m. However, without analyses as in Figure 3.3.9 it is impossible to ascertain whether associations as in Figures 3.3.5-7 are indeed due to habitat selection behaviours that operate at multiple scales or due to single-scale habitat selection behaviours, the effect of which is to generate characteristic patterns at larger spatial scales. Further study based on a high-resolution flow-model may be needed to address this problem. Because of similarities in results from the stream-tank study and this field-based study, I concluded that habitat selection behaviours most likely did operate at multiple scales in this field-based study as well.

Concerns with respect to the use of low-resolution flow measurements also apply to the analyses of Figure 3.3.10. However, a low-resolution flow-map was expected to lead to a reduction in the correlation between observed and computer-generated distributions at small spatial scales in particular, whereas effects will be minimal at larger spatial scales. From this, the reduction in correlation (r) from ambit radii of 2 to 1 m in Figure 3.3.10 may be due to the low-resolution flow measurements, whereas the reduction in r at ambit radii larger than 4 m is most likely due to a mismatch between the habitat selection behaviours of the fish and the model used to describe these behaviours.

3.3.4.1. Implications of results

Associations varied with spatial scale. From this, conclusions with respect to the distribution and habitat use by juvenile salmon and trout will depend on scale as well. From this, micro-habitat (<1 m^2) and macro-habitat (> 100 m^2) modelling approaches may lead to different management actions. This is especially a problem when variables are considered separately, as is current practise when using the univariate functions within IFIM (cf. Bovee 1986, Gore and Nestler 1988). For example, at small spatial scales, salmon avoided shallower areas, but preferred shallow depths at larger spatial scales (Figure 3.3.5). This is probably due to a combination of avoidance of shallow depths at small spatial scales, preference for riffle areas that have a high number of shallow depth observations and where flow is high, and avoidance of pool habitats where flow is low. From this, a habitat model based on a combination of water velocity and depth may be able to explain much of this pattern using a single and small spatial scale only, but when considering depth separately, a multi-scale approach is needed.

Because associations of fish with habitats change rapidly with spatial scale, especially for ambit radii < 1 m, measurement scales need to be clearly defined for observations on habitat selection in habitat modelling studies. The use of ill-defined and inconsistent measurement scales in habitat modelling, however, is unfortunately rather prevalent. This is the case especially for substrate, which is often measured based on dominance within ill-defined areas surrounding fish positions. Inconsistent and ill-defined measurement scales limit the efficiency of variables for describing habitat use in habitat models of individual studies, and a comparison of findings among studies.

I found micro-position models often lost their predictive capacity at scales larger than the resolution of the model, despite the limited spatial scope of this study. This may indicate that selection for important larger-scale habitat features was overlooked, or that small-scale habitat features were overlooked, the effect of which is most apparent at larger spatial scales. This has important implications for the use of micro-habitat models for resource management, as these models are often used to address problems occurring at scales much larger than those of individual fish observations (see Figure 3.3.1). An example is an impact analysis for a hydro-dam, using micro-habitat modelling techniques. Such an analysis is primarily aimed at long-term effects on fish populations in the entire river, instead of being aimed at small-scale distributions of fish within the river. However, results from this study indicate that a micro-habitat model may predict quite well where fish will be positioned within a river after installation of the dam, but this information may not be that easy to translate to effects at larger spatial scales (cf. Orth 1987).

A discrepancy between observed and computer-generated distributions was also apparent when larger-scale distributions were described in terms of pools, riffles, and runs. The reason for this may be that the classification of riverine habitats in terms of (assumed homogeneous) pool, riffle, and run habitats, does not adequately reflect the habitat as experienced by fish, as fish primarily select for small-scale features within these habitats and because average depth and average water velocity, used to separate pools from riffles and runs, does not reflect the small-scale habitat heterogeneity within these gross features.

By studying habitat selection behaviours at the scale of pool, riffle, and run, only an indirect impression of fish behaviours will be obtained.

The problem of scale-up should become a central focus of habitat modelling (see Chapter 2). I should point out that current habitat modelling studies focus on how to extrapolate models derived from one river to another, or from one moment in time to another, but that these analyses are different from the scaling analyses I propose in that the former relate to "time" and "location" whereas the latter relate to "time-scale" and "space-scale", which, although related, are different issues altogether (cf. Schneider 1994). That is, the former relate to how associations differ among river systems or moments in time, the latter relate to how large spatio-temporal scale distributions can be described using small spatio-temporal scale observations and associations.

3.3.4.2. Scaling approaches in habitat modelling

Scale is increasingly recognised as being important to habitat models and management of riverine fish species (e.g. Frissell et al. 1986, Minshall 1988, Lewis et al. 1996, Allan et al. 1997), but few empirical and quantitative multi-scale studies on habitat use by fish have been done. Recently, several studies have used multi-scale approaches to study fish distributions and habitat use (e.g. Syms 1995, Poizat and Pont 1996, Richards et al. 1996). The difference between the approach in this study and these other multi-scale approaches is that the proposed approach is based on an individual-based concept operating over a range of spatial scales, instead of using fish densities analyzed at a few selected scales. By analyzing distributions over a range of scales, one reduces the chances that important scales were overlooked or that analyses were confined to scales determined from an anthropomorphic interpretation of fish behaviours and life-history. Although the analyses can be used for organisms that may not select their habitat, such as plants, the approach, when used for fish, tends to focus the researcher on how individuals perceive and react to their environment and effects of these small-scale behavioural processes on larger scale distributions. Individual behaviours are central to the approach, larger scale distributions are explained in terms of small-scale behavioural processes, and the line-of-thought is very much from small-scale to large-scale processes.

The focus on individuals and small-scale behavioural processes of the Relative Contact method may make the approach more suitable for describing distributions that are primarily driven by behavioural processes, as these are ultimately the result of small-scale individual decisions rather than of groups of fish. In addition, the Relative Contact method allows for an interpretation at scales smaller than possible when using approaches based on density-information and variance-analysis (see Chapter 3.1). However, habitat selection behaviour is not the only process that underlies fish distributions: distributions are the result of multiple processes that operate over a range of scales (Wiens 1989, Menge and Olson 1990, Levin 1992, Horne and Schneider 1994, 1995); processes that operate at one scale can have effects at other scales as well; the relative importance of processes varies with spatio-temporal scale (Horne and Schneider 1994); the relative importance of habitat selection behaviour diminishes at larger spatio-temporal scales (cf. Chapter 2). In addition, small-scale observations may often be more difficult to obtain than larger-scale information, especially when the scope of these observations is large (cf. description of a river in terms of pool, riffle, and run habitat versus small-scale water velocity gradients). From this, the approach based on Relative Contact may not always be most efficient, especially at large space-time scales.

A careful consideration of a combination of mathematical techniques is probably most suitable to study fish in rivers, with the approach based on Relative Contact covering the small to intermediate spatial scales ($<10^3$ m) and others covering the larger spatial scales. In this context are important research questions: How does the relative importance of behavioural processes change with spatio-temporal scale? How do small-scale processes affect large-scale distributions and vice versa?

3.3.4.3. Conclusions

Classic micro-habitat models generally operate at a single or few selected scales, using small-scale observations on individual fish (<m^2, seconds) to address problems occurring at much larger spatio-temporal scales (rivers, years). The results of Chapter 3.3 indicated that habitat selection behaviours operate at multiple scales rather than a single one. Single- and multi-scale micro-position models were equally able to identify the small-scale locations within rivers that are preferred by fish, but both modelling approaches were limited when used to make density predictions at larger spatial scales (>50-100 m^2). This implies that important processes and associations may have been overlooked and that the scale-up from individual fish observation to management problem may be more difficult than is realised by most fish-habitat managers using micro-habitat modelling techniques. Large-scale fish distributions may not be the result of a simple composite of small-scale behavioural processes. More research should be directed towards this problem of scale-up. Multi-scale approaches will be crucial to this.

Strong spatio-temporal heterogeneity is characteristic of rivers with wide variations in temperature, depth, and water flow over short spatio-temporal scales, especially when compared to lakes and other aquatic habitats. Species inhabiting these environments are adapted to this heterogeneity and habitat modelling approaches that result in a more predictable and less heterogeneous environment, such as PHABSIM/IFIM (Bovee 1982, 1986, Milhous et al. 1989), may diminish the very uniqueness of the habitats and species they intend to protect (cf. Barinaga 1996) as they concentrate on habitat availability and do not take into account the importance of spatio-temporal habitat heterogeneity to fish. Multi-scale approaches such as those described in this study may aid in incorporating habitat heterogeneity in habitat models by identifying important scales and processes. From this, multi-scale habitat models may be better than single-scale habitat models at evaluating how organisms are associated with their habitats and be more efficient for resource management.

The scale of measurement will determine the perceived relative importance of a habitat variable in habitat selection behaviour. Therefore, Habitat Suitability Indices and Habitat Use indices, commonly used in habitat modelling approaches, must also depend on scale. From this, it is clear that managerial actions will differ based on the scale of measurement of the study used to support managerial decisions. Future habitat modelling studies should focus on the identification of spatio-temporal scales that are most effective in explaining observed fish distributions. A clearly defined use of measurement scale is crucial to habitat modelling. Interpretation of results should be limited to the spatial scales over which the study was conducted.

Chapter 4: Density-dependent habitat selection by juvenile Atlantic salmon

4.1. Density-dependent habitat selection by juvenile Atlantic salmon in experimental riverine habitats

4.1.1. Introduction

Organism density is often used to identify important habitats and as an indicator of habitat quality (for a discussion: Van Horne 1983). In fisheries management, relationships between fish density and habitat are often mathematically described in habitat models. Microhabitat models describe the distribution of individual fish over small-scale (< 1 m^2) habitat features; macrohabitat models describe fish densities as a function of intermediate to large-scale habitat features (>10 m^2).

In spite of the widespread use of habitat modelling techniques to predict fish distributions, some underlying assumptions are seldom explicitly stated, tested or discussed, with most research effort seemingly focused on the development of local models for different river systems or regions (e.g. DeGraaf and Bain 1986), or on the spatio-temporal generality of models (e.g. Bozek and Rahel 1992). Two implicit assumptions in habitat modelling are that (1) organism density and habitat quality are positively correlated and that (2) habitat selection does not change with density. The objective of this study was to investigate if use of pool, riffle and run habitats by juvenile Atlantic salmon (*Salmo salar* L.) is affected by population density.

Previous work has shown that salmonids select positions in streams based on their competitive abilities and the profitability of positions in terms of potential net energy intake rate and predation risk, with profitability of positions being much determined by the physical habitat in terms of cover, bottom topography and current flow patterns (Fausch 1984, Hughes and Dill 1990, Hughes 1992A, 1992B, Grand 1997, Grand and Dill 1997). As such, the area within a stream may be regarded as a hierarchy of potential positions, ranging from inaccessible to ideal, with each fish choosing the most profitable position that its rank in the social hierarchy will allow (Fausch 1984, Hughes 1992A). Territoriality, small-scale spacing behaviour or pre-emptive exclusion will thus regulate use of preferred positions and space, if in short supply, will regulate population density (Bohlin 1977, Grant and Kramer 1990). From this, the physical habitat may be regarded as a template determining distribution patterns of fish (Hughes 1992B).

These processes suggest that salmonid distributions may be best described using the ideal-despotic distribution theory of Fretwell (1972). This theory describes how animals select their habitats assuming that they are "ideal" in knowing where profitability is highest but where access to resources are governed by territorial behaviours. When organisms distribute ideal despotic, the most desirable positions will be occupied first, followed by positions in progressively less desirable habitats. Because of this, the average gain per individual may differ and habitat use may change with density. From this, habitat models may vary with population density.

The ideal-free distribution theory (Fretwell and Lucas 1970) contrasts with this ideal-despotic theory in that access to resources is not restricted by territorial behaviours but all individuals are equal and "free" to move among patches without constraints or restrictions. When organisms distribute ideal free, fitness of individuals declines with density as individuals occupy the best habitats, the average gain per individual will stabilise to be equal in all habitats, and the fraction of a population in each habitat should equal the fraction of resources occurring there (cf. input matching; Parker 1974). When organisms distribute ideal free among habitats and the rate of resource renewal in these habitats is not affected by organisms density or distribution and all habitats are occupied at low population densities, then relative densities in habitats do not vary with population density.

We hypothesised that riffles and runs would offer the best feeding positions for parr as drift is concentrated in these habitats, even though there are areas in these habitats that are relatively inhospitable due to high water velocities. By contrast, parr can occupy most of the total area of pool habitat with low energy expenditure, but the "quality" of individual positions in these areas may not be as high due to the lack of large water velocity gradients (Fausch 1984, Hughes and Dill 1990). Because of this, we expected parr to be most dense in riffle or run habitat at low overall densities, but pools would support more parr at higher densities. This process may be best described using ideal-despotic, rather than ideal-free theory.

4.1.2. Material and methods

4.1.2.1. Study site

The study was conducted in an abandoned spawning channel in the North Harbour River on the Avalon Peninsula of Newfoundland, Canada (47°12'N, 53°37'W), in late August to early October of 1993 and 1994. This channel was used as part of an experimental transplant of pink salmon (*Oncorhynchus gorbuscha*) in the late fifties and sixties (Lear 1975). The channel parallels the main stem of North Harbour River for a distance of about 550 m. The width of the channel ranges between 1.5-5 m and a sluice at the intake allowed for control of water flow. North Harbour River is further described by DeGraaf and Bain (1986).

Three sections of the channel were blocked off by metal posts and wire mesh (1/4 inch, zinc coated). Sections were approximately 25 meters long and had a surface area of approximately 100 m^2. Within each section, a riffle/run/pool sequence was created. The sequence of the habitats (riffle/run/pool) within the main sections was varied: travelling along the channel in an upstream direction, the first section (section 1 hereafter) consisted of a run / riffle / pool sequence, the second section (section 2) of a riffle / pool / run sequence, and the third section (section 3) of a pool / riffle / run sequence.

To determine the surface area of subsections (= habitat within section), the length of each subsection was measured at three equally spaced transects parallel to the flow and the width was measured at every meter perpendicular to the flow, all to the nearest 0.05 m. Substrate (according to the American Geophysical Union as in Platts et al. (1983)), water depths (m) and water velocities (m s^{-1}; at 60% of depth) were measured in all subsections at seven equidistant points in four equally-spaced transects, established perpendicular to the flow.

The average surface area of pool, riffle and run sections was 46.7 m^2 (range: 41.5-51.3 m^2), 37.4 m^2 (range: 33.1-41.9 m^2) and 19.2 m^2 (range: 15.3-24.6 m^2) respectively. The average depth of pool, riffle and run sections was 28.4, 10.6 and 22.8 cm respectively. The average water velocity of pool, riffle and run sections was 7.1, 25.5 and 26.5 cm.s^{-1} respectively. The substrate in the channel consisted primarily of coarse to very coarse gravel (16-64 mm). I randomly placed 10 particles of large cobble (128-256 mm) into each subsection to increase small scale habitat variation.

4.1.2.2. Experimental procedures

Atlantic salmon parr were introduced into the three experimental sections at densities of 0.1, 0.25, 0.5, 0.75, and 1.0 fish m^{-2} in 1993 and at densities of 0.1, 0.25, 0.5, 0.6, 0.75, 1.0 and 1.25 m^{-2} in 1994. This range of densities is similar to the range of densities of 1+ and older parr observed in various stations in two nearby rivers (Northeast Trepassey Brook and Freshwater River; Gibson et al. 1993). Prior to introducing fish, all fish present in the experimental sections were removed. In 1993, each density was repeated within each section. In 1994 each density was established once within each section. The sequence of input densities was varied randomly within each section.

The lengths of the parr used in the experiment varied from 7.0 to 11.5 cm in fork-length (mostly 1+ fish). Fish were caught by electrofishing a variety of pool, riffle and run habitats.

These were located downstream of the entrance to the spawning channel to minimise possible homing behavior after introduction (cf. Saunders and Gee 1964). In 1993 all fish were anaesthetised (MS222), measured, weighed and marked with an adipose fin-clip before introduction into the sections. In 1994 the fish were introduced into the sections immediately after capture, without further handling. The difference in procedures was necessary because of the higher afternoon water temperatures in 1994, which made the fish more sensitive to handling, and because of logistics. The marking in 1993 allowed us to check for holes in the fencing material and to determine if fish caught for introduction had been used previously. No fish were introduced that were known to have been used previously. At introduction, fish were evenly distributed over the surface of the experimental sections.

After a three-day period, the habitats within each experimental section were blocked with barrier nets. These nets had heavy chains attached to the footropes which allowed us to block the habitats completely within two seconds and minimised parr redistribution. All fish were then removed by electroshocking until no more fish were captured even after repeated passes. The downstream section 1 was always emptied first, followed by sections 2 and 3. I did not vary this sequence because my activities in the channel caused suspension of silt and debris. Fish were removed from the sections in the morning. In the afternoon, new fish were caught for introduction and were released into the sections.

At the time of removal, water temperature and water level were recorded at a fixed location in the pool subsections. The discharge ($l\ s^{-1}$) in the spawning channel was measured at different water levels to establish a relationship between discharge and water level.

On several occasions the enclosures did not work properly, with fish escaping or entering the experimental sections. I tried to repeat observations where the enclosures had obviously malfunctioned. 46 observations, out of a total of 60, were eventually used in the analyses, after removal of observations where the enclosure was not considered to have worked.

4.1.2.3. Acclimation period

I conducted two experiments to assess if a 3 day acclimation period was sufficient to establish a stable fish distribution and to determine if the location where fish were introduced influenced the final distribution. In the first experiment fish were introduced by even distribution over the surface of the sections and the acclimation period was varied from 3 to 13 days. In the second experiment fish were introduced in different locations within the experimental sections (upstream, downstream, even) and removed after 3 days.

A general effect of acclimation period or introduction method on the distribution of the fish was not detectable (Bult, unpublished data). However, the acclimation period might have affected the fish distributions in section 2, with fish moving from the run to the pool habitat at longer acclimation periods. The introduction method might have affected the distributions in section 3, with more fish in the upstream subsection at upstream introductions, but upstream introductions coincided with higher temperatures and temperature effects could not be clearly separated from introduction effects.

4.1.2.4. Calculation procedures

I did not analyse my data by explaining the density in one habitat as a function of the density in a contrasting habitat, an approach often used when studying density dependent habitat selection (cf. Rodríguez 1995). I did this because habitat densities of individual removals were not independent in my experiment. I quantified selection of parr for pool, riffle and run habitat by using selection indices (SI):

$$SI_{h1\text{-}h2} = \log_{10}(D_{h1} + 0.01) - \log_{10}(D_{h2} + 0.01) \quad \textit{Equation 4.1.1}$$

$SI_{h1\text{-}h2}$: Selection Index (-), quantifying selection for habitat 1 over habitat 2

D_{h1}: fish density in habitat 1 (# m^{-2})

If the distribution over habitats is proportional, i.e. an x-fold increase in density in the run habitat due to an increase in population density shows an x-fold increase in the pool habitat as well, selection indices do not change with population density. If habitat selection is density dependent, selection indices vary with population density.

The explanatory variables discharge and section density were re-scaled using a logarithmic transformation. Transformations were done assuming a multiplicative effect on selection indices. To avoid spurious correlations, selection indices were analysed as a function of the section density at introduction rather than at removal. This was valid because the overall density at introduction did not vary considerably from the density at removal, as I removed observations where the enclosure did not work properly and fish were able to enter or escape the experimental sections.

To facilitate a comparison of changes in the distribution of the fish among sections and years due to temperature, discharge or fish densities, selection indices were re-scaled relative to the average selection index observed per section per year:

$$RSI_{h1\text{-}h2_{s,y,i}} = SI_{h1\text{-}h2_{s,y,i}} - \frac{\sum_{j=1}^{n_{s,y}} SI_{h1\text{-}h2_{s,y,j}}}{n_{s,y}} \qquad \textit{Equation 4.1.2}$$

$RSI_{h1\text{-}h2,s,y,i}$: Relative Selection Index (-), quantifying $SI_{h1\text{-}h2}$ of observation i in section s in year y, relative to the average observed $SI_{h1\text{-}h2}$ of section s in year y ($SI_{h1\text{-}h2,s,y,i}$).

$n_{s,y}$: number of observations on section s in year y

For analyses based on relative selection indices, the explanatory variables temperature (TMP), discharge (DIS), and section density (DE) were re-scaled relative to the average temperature, discharge and density per section per year:

$$(TMP_{ad,i} = TMP_i - \frac{\sum_{j=1}^{n_{s,y}} TMP_j}{n_{s,y}} \qquad \textit{Equation 4.1.3}$$

$$DIS_{ad,i} = \log_{10}(DIS_i) - \frac{\sum_{j=1}^{n_{s,y}} \log_{10}(DIS_j)}{n_{s,y}} \qquad \textit{Equation 4.1.4}$$

$$DE_{ad,i} = \log_{10}(DE_i) - \frac{\sum_{j=1}^{n_{s,y}} \log_{10}(DE_j)}{n_{s,y}} \qquad \textit{Equation 4.1.5}$$

The use of relative selection indices and the re-scaling of equations 4.1.3-5 focused the analyses on changes in habitat use relative to deviancies from the average conditions within each section and year, and was done because I was primarily interested in changes in selection indices due to changes in water temperature, discharge and density, rather than differences in selection indices among sections and years, and because a clear separation of section and year effects from temperature, discharge and density effects was not possible. This is because temperatures in section 3 were always higher than in sections 1 and 2, and temperatures in section 2 were always higher than in section 1, due to the sequence in which sections were sampled in the course of the day. The average discharge, temperature and section density varied among years. In addition, the unbalanced design of the experiment, especially after removal of several of the observations because of malfunctioning of the enclosures, precluded a clear separation of effects. The use of relative selection indices, rather than selection indices, and the re-scaled temperature, section density and discharge data, facilitated analysis aimed at general changes in habitat selection behaviour due to temperature, discharge and density, but was less suitable for analyses aimed at revealing differences between sections and years.

Condition Factors (CF) of individual fish were calculated as the residuals of a $\log_{10}$(length (cm)) versus $\log_{10}$(weight (g)) regression analysis, using data from 1993. I tested for differences between the condition of fish at introduction and at removal by means of a t-test on the differences in average CF of fish at introduction and removal. In addition, I tested if fish in the pool, riffle and run habitats differed in length or CF and if these differences were subject to changes in overall densities. For these analyses I used data from both 1993 and 1994 and subtracted the average CF and lengths of fish in the pool, riffle and run habitats from the average observed CF and length of all fish within each removal event (=RCF and RL respectively).

Analyses were done using SAS statistical software (SAS 1988). Residual analyses involved a visual check for patterns in plots of residual versus predicted values, as well as tests for normality. Tests for normality involved both a visual check and the Shapiro-Wilks statistic (α=0.05). If residuals deviated from normality, p-values were obtained by randomisation to test the significance of effects of habitat variables on fish densities: Observations on response variables were randomised 5000 times, using sampling without replacement, with observations of explanatory variables held constant. A p-value was obtained by calculating the proportion of randomisations with F-ratios larger than the observed F-ratio. A 5% level was used as a screening criterion to separate "significant" effects from "non-significant" effects.

4.1.3. Results

In 1993, the temperature at removal varied from 13.0 to 19.0°C, (mean=15.9, sd=1.6) and the discharge varied from 69 to 165 l.s^{-1} (mean=121, sd=29). In 1994, the temperature at removal varied from 11.0 to 19.5°C, (mean=13.9, sd=2.3), and the discharge varied from 79 to 131 l.s^{-1} (mean=93, sd=12).

The run habitat was preferred over the pool habitat, and the pool habitat was preferred over the riffle habitat in all sections. Few fish were observed in riffle habitats and most fish were observed in the run and pool habitats. The average density in the run habitat was 2.6 times the density in the pool habitat (average $SI_{pool\text{-}run}$=-0.42), and 24.5 times the density in the riffle habitat (average $SI_{riffle\text{-}run}$=-1.39).

Density significantly affected $SI_{pool\text{-}run}$, with more fish moving from the run to the pool habitat at higher section densities (Figure 4.1.1; Table 4.1.1: analysis 1, p=0.011, n=46). This effect was similar among all sections (interaction density*$SI_{pool\text{-}run}$ non-significant). Figure 4.1.1 shows that in sections 1 and 3 a selection for runs ($SI_{pool\text{-}run}$ negative) at low section densities shifted towards a selection for pools ($SI_{pool\text{-}run}$ positive) at higher section densities. Section densities did not significantly affect $SI_{riffle\text{-}run}$ and $SI_{riffle\text{-}pool}$. Discharge did not significantly affect $SI_{pool\text{-}run}$, $SI_{riffle\text{-}run}$ or $Si_{riffle\text{-}pool}$ (p>0.082, n=46). Water temperatures significantly affected $SI_{pool\text{-}run}$ and $SI_{riffle\text{-}run}$, with fish moving from the riffle to the run and from the pool to the run habitat at higher temperatures (Table 4.1.1: analysis 2). Effects of temperature on $SI_{pool\text{-}run}$ differed significantly among sections and years, while effects of temperature on $SI_{riffle\text{-}run}$ were similar among sections and years. A model including the variables section, year, temperature, density and all possible interaction terms, showed none of the variables to be significant for $SI_{riffle\text{-}pool}$ and $SI_{riffle\text{-}run}$ ($p>0.07$, $n=46$). $SI_{pool\text{-}run}$ was affected by temperature and density, but these effects were significant only as part of an interaction term with section and/or year.

Table 4.1.1. Selection of pool versus run habitat ($SI_{pool\text{-}run}$), riffle versus run habitat ($SI_{riffle\text{-}run}$) and riffle versus pool habitat ($SI_{riffle\text{-}pool}$) by parr as a function of parr density (DE, $\log_{10}(\# \ m^{-2})$) and the temperature at removal (TMP, °C) in three experimental sections (SE) in 1993 and 1994 (Y). p-Values that are displayed were based on type III sums of squares and 46 observations. Significant effects are printed in bold ($\alpha=0.05$).

Analysis	**Variable**	**df**	**$SI_{pool\text{-}run}$**	**$SI_{riffle\text{-}run}$**	**$SI_{riffle\text{-}pool}$**
density	SE	2	**0.000**	**0.000**	**0.000**
	Y	1	0.351	0.216	0.064
	DE	1	**0.011**	0.859	0.108
	SE*Y	2	0.054	0.295	**0.017**
	DE*SE	2	0.230	0.165	0.146
	DE*Y	1	0.803	0.343	0.270
	DE*SE*Y	2	0.131	0.572	0.540
temperature	SE	2	**0.014**	0.865	0.475
	Y	1	**0.002**	0.636	**0.031**
	TMP	1	**0.010**	**0.009**	0.250
	SE*Y	2	**0.030**	0.665	0.212
	TMP*SE	2	**0.001**	0.802	0.128
	TMP*Y	1	**0.002**	0.895	0.057
	TMP*SE*Y	2	0.062	0.686	0.493

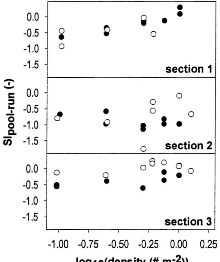

Figure 4.1.1. Selection of pool habitat versus run habitat ($SI_{pool-run}$ (-), see text for details) at varying densities within the experimental sections in 1993 (closed) and 1994 (open) (n=46).

Section densities significantly affected $RSI_{pool-run}$ in sections 1 and 3 and $RSI_{riffle-pool}$ in section 3, with more fish moving from the run to the pool habitat (sections 1, 3) and from the riffle to the pool habitat (section 3) at higher densities (Table 4.1.2). Density did not affect relative selection indices in section 2. Discharge affected $RSI_{pool-run}$ and $RSI_{riffle-pool}$ in section 3, with fish moving from the pool to the run and riffle habitats at higher discharges. Water temperature significantly affected $RSI_{pool\text{-}run}$ in section 2, with fish moving from the pool to the run habitat at higher temperatures.

Table 4.1.2. Selection of pool versus run habitat ($\mathrm{RSI}_{\mathrm{pool\text{-}run}}$), riffle versus run habitat ($\mathrm{RSI}_{\mathrm{riffle\text{-}run}}$) and riffle versus pool habitat ($\mathrm{RSI}_{\mathrm{riffle\text{-}pool}}$) by parr as a function of temperature, discharge and section density: correlation coefficients and p-values (r/p). Temperature, discharge and density observations were rescaled prior to analyses, as explained in the text. Significant correlations are printed in bold (α=0.05, n: number of observations).

Variable	**Section**	**n**	**temperature**	**discharge**	**density**
$\mathrm{RSI}_{\mathrm{pool\text{-}run}}$	1	15	-0.504/0.055	+0.319/0.246	**+0.743/0.002**
$\mathrm{RSI}_{\mathrm{pool\text{-}run}}$	2	15	**-0.723/0.002**	+0.075/0.789	+0.060/0.832
$\mathrm{RSI}_{\mathrm{pool\text{-}run}}$	3	16	+0.216/0.421	**-0.710/0.002**	**+0.632/0.009**
$RSI_{pool\text{-}run}$	*total*	*46*	***-0.339/0.021***	*-0.018/0.907*	***+0.405/0.005***
$\mathrm{RSI}_{\mathrm{riffle\text{-}run}}$	1	15	-0.358/0.191	+0.209/0.455	+0.420/0.119
$\mathrm{RSI}_{\mathrm{riffle\text{-}run}}$	2	15	-0.476/0.073	+0.109/0.699	+0.097/0.731
$\mathrm{RSI}_{\mathrm{riffle\text{-}run}}$	3	16	-0.495/0.051	+0.397/0.128	-0.402/0.124
$RSI_{riffle\text{-}run}$	*total*	*46*	***-0.434/0.003***	*+0.211/0.159*	*+0.014/0.928*
$\mathrm{RSI}_{\mathrm{riffle\text{-}pool}}$	1	15	+0.115/0.683	-0.092/0.744	-0.287/0.299
$\mathrm{RSI}_{\mathrm{riffle\text{-}pool}}$	2	15	+0.095/0.737	+0.054/0.849	+0.054/0.849
$\mathrm{RSI}_{\mathrm{riffle\text{-}pool}}$	3	16	-0.461/0.073	**+0.614/0.011**	**-0.581/0.018**
$RSI_{riffle\text{-}pool}$	*total*	*46*	*-0.162/0.283*	*+0.213/0.155*	*-0.285/0.055*

When combining data from all sections, $RSI_{pool\text{-}run}$ was significantly affected by section density (Figure 4.1.2, Table 4.1.2) and water temperature (Figure 4.1.3, Table 4.1.2). A stepwise regression approach showed that $RSI_{pool\text{-}run}$ was significantly related to both temperature ($n=46$, partial $r^2=0.129$, $p=0.008$) and section density ($n=46$, partial $r^2=0.164$, $p=0.005$):

$$RSI_{pool-run} = (0.3482 * DE) - (0.0553 * TMP) \qquad \textit{Equation 4.1.6}$$

$$(n=46, r^2=0.293, p=0.001)$$

$RSI_{riffle\text{-}run}$ was significantly affected by water temperature (Figure 4.1.3; Table 4.1.2; $n=46$, $r^2=0.188$, $p=0.003$):

$$RSI_{riffle-run} = -0.0862 * TMP \qquad \textit{Equation 4.1.7}$$

$RSI_{riffle\text{-}pool}$ was not significantly affected by water temperature, section density or discharge.

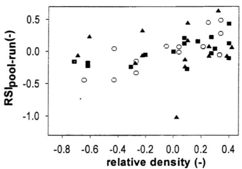

Figure 4.1.2. Selection of pool habitat versus run habitat ($RSI_{pool\text{-}run}$ (-), see text for details) at varying densities within the experimental sections in 1993 and 1994 (n=46; section 1: circle; section 2: triangle: section 3: square). Densities ($\log_{10}$(# m^{-2})) were re-scaled relative to the average density per section per year, as explained in the text.

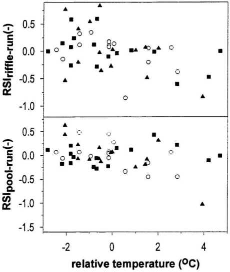

Figure 4.1.3. Selection of pool habitat versus run habitat ($RSI_{pool-run}$ (-), see text for details) and selection of riffle habitat versus run habitat ($RSI_{riffle-run}$ (-)) at varying temperatures (°C) within the experimental sections in 1993 and 1994 (n=46; section 1: circle; section 2: triangle: section 3: square). Temperatures were re-scaled relative to the average temperature per section per year, as explained in the text

To obtain an impression of the relative importance of habitat, temperature and section density for the selection behaviour of the fish, $SI_{pool\text{-}run}$ and $SI_{riffle\text{-}run}$ were compared to $\Delta RSI_{pool\text{-}run}$ and $\Delta RSI_{riffle\text{-}run}$, with $\Delta RSI_{pool\text{-}run}$ and $\Delta RSI_{riffle\text{-}run}$ calculated based on equations 4.1.6 and 4.1.7 and by varying the temperatures from 12 to 19°C ($\Delta RSIt_{pool\text{-}run}$, $\Delta RSIt_{riffle\text{-}run}$) and section densities from 0.1 to 1.0 m^{-2} ($\Delta RSId_{pool\text{-}run}$). Similarities in the absolute values of SI and ΔRSI would indicate that effects were comparable. $SI_{pool\text{-}run}$, $\Delta RSId_{pool\text{-}run}$ and $\Delta RSIt_{pool\text{-}run}$ were -0.42, 0.35 and -0.39 respectively. $SI_{riffle\text{-}run}$, $\Delta RSIt_{riffle\text{-}run}$ were -1.39 and -0.60 respectively.

The condition factor of parr at removal was 0.013 less than at introduction (n=25, T=0.8286, $p<0.001$). This parallels a 1.6% reduction in weight (significant). Fish from the pool, riffle and run habitats did not differ in RCF (n=119, $F_{2,116}=1.88$, p=0.157), but did differ in RL (n=121, $F_{2,118}=23.38$, $p<0.001$). Parr in pool habitats were 0.35 cm larger than parr in run habitats (significant, GT2, $\alpha=0.05$). Parr in riffle habitats were 0.2 cm smaller than parr in run habitats (not significant, GT2, $\alpha=0.05$) and 0.55 cm smaller than parr in pool habitats (significant, GT2, $\alpha=0.05$). RL and RCF were not significantly correlated with section densities ($\log_{10}$(section density)) for the pool (RL: n=46, r=-0.129, p=0.398; RCF: n=45, r=-0.127, p=0.418), riffle (RL: n=29, r=-0.044, p=0.819; RCF: n=29, r=-0.232, p=0.226) or run habitats (RL: n=46, r=-0.093, p=0.537; RCF: n=45, r=0.152, p=0.319).

4.1.4. Discussion

Results indicated that section density and temperature affected habitat use, with parr distributions shifting towards pools from runs at higher densities, and towards runs from pools and riffles at higher temperatures. Riffles were strongly avoided, possibly due to a lack of overhanging cover in combination with shallow depths (cf. Gibson 1978). The effects of population density and temperature on fish distributions were often comparable to the effect of hydromorphological differences between pool/riffle/run habitats over the range of densities observed. As neither temperature nor population density information are included in current habitat modelling approaches, a reconsideration of these models is warranted, as temperatures at one place often vary over more than 7°C within a few hours in summertime (when most habitat models are developed), and juvenile salmonid populations can vary in excess of 1 order of magnitude among years (cf. Kennedy and Crozier 1993).

Effects of density and temperature on habitat use were found regardless of the upstream-downstream sequence of the habitats within the enclosures. This indicates that habitat selection was primarily aimed at differences between pool/riffle/run habitats, rather than the upstream or downstream location of habitats within sections. Habitat use may have been affected by preconditioning and availability of habitats in the main river. However, it is unlikely that observed density-dependent effects are the result of this as all fish were pooled before introduction and randomly allocated to the experimental sections.

Lengths of parr in pools were largest, lengths of parr in riffles smallest. Parr lost 1.6% of their weight during the experiment. I suspect that handling is largely the reason for this weight reduction, rather than food scarcity, because the condition of the fish did not vary with section density.

These results suggest that ideal despotic theory may be more appropriate for describing parr distributions than ideal free theory, as both runs and pools were used at low section densities and relative densities in pools and runs changed with section density. However, lacking information on the resource distribution as experienced by the fish and also small-scale habitat selection observations, I could not infer with certainty which one of these theoretical models, or combination of models, was most appropriate. If fish select "ideal free" for habitats at a spatial scale much smaller than that of pools, riffles and runs, a disproportionate distribution at increasing population densities at the larger scales of pool, riffle and run habitats could result when small-scale secondary habitats within the larger scale pool/riffle/run habitats are occupied only after primary small-scale habitats are filled. If fish select "ideal despotic", a disproportionate distribution could result regardless of the spatial scale at which selection occurs. This also underlines the need for quantitative information on the scales at which fish are associated with their environment.

I suspect that the observed shift in habitat use is best described by a combination of ideal free and ideal despotic behaviour occurring at small spatial scales. Runs offered relatively more primary positions than pools, and pools offered more intermediate quality positions than runs. Primary positions were defended first and because of this, habitat use shifted from runs to pools with increasing density. Parr have been observed to be territorial in riffles and less aggressive in pools (Kalleberg 1958, Gibson 1978, Gibson and Cunjak 1986). If parr densities are limited by territoriality, as suggested by Grant and Kramer (1990), or by small-scale spacing behaviour, parr in the run habitats may have occupied primary spots by ideal despotic behaviour, whereas parr in the pool habitats might have displayed more of an ideal free behaviour (cf. Gotceitas and Godin 1992). From this, one may expect the larger and more competitive individuals in the run habitat, which is contrary to my findings that showed that individuals in the pool habitat were larger than those in the run habitat. Possibly, the larger individuals occupied the deeper habitats because of competitive segregation or differences in habitat selection between smaller and larger individuals (Bohlin 1977, Bohlin 1978, Kennedy and Strange 1986), which may be an adaptation to avoid predation.

The observed shift in selection from pool and riffle habitat to run habitat at higher temperatures may be explained in terms of energy maximisation. At higher temperatures, routine metabolic rates increase and thus oxygen demands do as well (Brett 1962). Fish that hold positions on the bottom of run and riffle habitats, using their pectoral fins and water currents, may be more efficient in taking up oxygen than fish that are positioned in pool areas, as oxygen uptake for fish in pool habitats will be more of an active process of opercular ventilation and swimming. Riffle habitats were avoided in particular at higher temperatures, possibly because of an increased risk of predation at low water levels in combination with high temperatures in these habitats.

Results differed with respect to the generality of the observed effects. Analyses based on selection indices suggest that density affected fish distributions only under certain conditions (temperatures, sections, years) as no general temperature or density effect was found based on a model including section, year, density, temperature and all possible interaction terms. However, when temperature and density were treated within separate models, a general effect of temperature and density was observed (Table 4.1.1: analyses 1 and 2). Analyses based on relative selection indices also suggest a general effect of temperature and density on habitat use (Table 4.1.2). These differences may be partly due to the effects of section, year, density and temperature being confounded in combination with the unbalanced design of the experiment. However, they may also suggest a limited generality of results. In addition, selection indices varied widely, even within sections and years, and in spite of my efforts to make habitats in the different sections as similar as possible, large differences were found in habitat use among sections (Figure 4.1.1, Table 4.1.1).

The observed variation in habitat use among sections and years may be due to variable habitat selection behaviours or a mismatch between the scale of observations at pools, riffles and runs and the much smaller spatial scale at which fish select habitats (< 1 m^2; see Chapter 3). The habitats as experienced by fish may therefore be seen as far more diverse than suggested by variables that are based on environmental conditions averaged over larger scales. From this, a macro-habitat approach will only give an indirect impression on habitat use. This suggests that a macro-habitat modelling approach is likely to explain only a limited portion of the observed variation of fish density observations, that models are not likely to perform well when extrapolated over space or time, and that managerial decisions from habitat models may be improved when habitat models take into account variability or flexibility in habitat use.

Bohlin (1977, 1978) previously studied density dependent habitat use by trout (*Salmo trutta*). From small-scale experiments (riverine enclosure of 217 m length; stream-aquarium 3.6 m length) he showed that habitat use of 1+ trout varied with population density. Also Elliott (1986) concluded that habitat use of trout was density dependent. However, these studies did not provide information on how the effect of population level on fish distributions compared to the effect of the physical habitat. Bohlin (1977) further showed that distributions of 1+ trout may be explained by intracohort competition for territories of different quality and that distributions of 0+ trout may be affected by older fish by intercohort competition or predation, resulting in deeper areas being occupied by larger fish. Bohlin (1977, 1978) also showed that these processes of intercohort competition or predation may affect 0+ trout abundance at the population level as well, i.e. small space-time scale behavioural processes had large space-time scale effects. Effects of density on distribution by social interactions were also studied by Hughes (1992A, 1992B) who showed that when numbers of Artic grayling (*Thymallus arcticus*) increase, positions are occupied in an order that reflects the desirability of positions and the dominance rank of individuals. Social interactions thus regulate fish distribution and habitat use may vary with population size. These findings were in line with results from my study that showed that habitat use varied with section density and that larger parr were found in pools and smaller ones in riffles.

My results contrast with findings of Rodriguez (1995), who studied density dependent interactions between sympatric salmon and brook charr (*Salvelinus fontinalis*) based on 12 pool/riffle pairs, and concluded that interspecific interactions changed habitat selection among pools and riffles with density, as charr were displaced from riffles to pools at increasing salmon densities, but intraspecific interactions did not. This contrast with my study may be due to a limited generality of the observed patterns, which in turn may be partly due to a mismatch between the scale of observations at pools, riffles and runs and the much smaller spatial scale at which fish select habitats (see Chapter 3). The occurrence of brook charr may be more indicative of the quality of small-scale habitat features within pools and riffles as experienced by salmon than the definition of pools and riffles itself, i.e. relations between salmon and brook charr densities may not necessarily be due to interspecific interactions alone. In addition, intraspecific effects may be more easily detectable in the absence of interspecific effects, i.e. in sympatry, intraspecific effects are simply hidden by stronger interspecific interactions. My experimental set up with repeated use of standardised habitats should be more able to pick up the effect of intraspecific interactions on habitat use and contrast this effect with the effect of the physical habitat itself, which may account for the fact that I did observe density dependent habitat selection due to intraspecific interactions and Rodríguez (1995) did not.

I concluded that habitat selection by juvenile Atlantic salmon parr is temperature- and density-dependent. Parr densities in pool/riffle/run habitats became more similar at increasing population densities. From this, fluctuations in population abundance mainly induce fluctuations in abundance in habitats that harbour low densities at low overall population density (secondary habitats): at higher population densities, the occupied habitat will expand to increasingly include secondary habitats; at lower population densities, the occupied habitat will contract into the primary habitats. The implications are that habitat models may be expected to vary with temperature and population density. Therefore, habitat quality assessments based on density information and conclusions with respect to preferred and avoided habitat probably also vary with temperature and population density, and can thereby influence subsequent managerial actions such as the creation of preferred habitats and discharge regulations. In addition, results illustrate that the quality of habitats can only be evaluated within the context of all available habitat, as habitat quality is a relative rather than absolute measure (Heggenes 1991), and points to a fundamental problem of extrapolating habitat suitability criteria from one region or river to another, or from one flow level to another, because under different conditions habitat availability will certainly differ. Results varied among years and experimental enclosures, despite controlled experimental conditions. This may be due to variable selection behaviours or a discrepancy in spatial scales of observations (pool/riffle/run) and habitat selection behaviours (<1 m^2). How fish select their habitats and how variable or flexible this behaviour is, may be best addressed using an experimental set-up, because conditions are much in control of the researcher. Additional field observations are needed to assess if results of such experiments can be extrapolated to scales relevant to fisheries management. In short, my results underline the need for information on habitat selection behaviour for fish-habitat management.

4.2. Density-dependent habitat use by juvenile Atlantic salmon and brook trout in two Newfoundland rivers

4.2.1. Introduction

Macro-habitat models are widely used for the management of fish populations (e.g. Binns and Eiserman 1979, Bowlby and Roff 1986, Fausch et al. 1988), despite several problems that have been identified with such models (Shirvell 1989). These models describe fish densities as a function of intermediate- to large-scale (>10 m^2) habitat features, mostly referring to abiotic factors, such as depth, water velocity, and substrate (cf. Fausch et al. 1988). Habitat models are used to predict fish densities under present, proposed or future conditions (Fausch et al. 1988). From these models, habitat quality is often quantified in terms of habitat suitability indices, habitat use curves, or weighted usable area (e.g. Scruton and Gibson 1993, Stanley and Trial 1995). Such measures are used as a basis for determining management practices such as instream improvements.

In spite of the widespread use of habitat modelling techniques to predict fish distributions, some underlying assumptions are seldom explicitly stated, tested, or discussed, with most research effort seemingly focused on the development of local models for different river systems or regions (e.g. DeGraaf and Bain 1986, Scruton and Gibson 1993), or on the spatio-temporal generality of models (e.g. Kozel and Hubert 1989B, Heggenes and Saltveit 1990, Bozek and Rahel 1992). One assumption is that organism density and habitat quality are positively correlated and that models do not change as population levels vary. However, as habitat suitability declines with increasing densities, distributions may change as organisms move from one habitat to another to optimise benefits (Fretwell and Lucas 1970, Fretwell 1972, Sutherland 1983, MacCall 1990, Milinski and Parker 1991). Therefore, conclusions with respect to limiting habitats may vary with population level. The objective of this study was to investigate whether habitat use by sympatric Atlantic salmon parr (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) changes with population size, and to evaluate the extent to which density-dependent processes are important to habitat modelling.

I hypothesised that primary habitats that accommodate high salmonid densities will always be filled near to some optimum carrying capacity, but that secondary habitats that accommodate low salmonid densities will be filled only after primary habitats are occupied. Therefore, fluctuations in population abundance should primarily induce fluctuations in secondary habitats, whereas density variability in primary habitats should be minimal. From this, habitat models may vary with overall population density.

4.2.2. Material and Methods

4.2.2.1. Study sites

Densities of Atlantic salmon parr and brook trout were estimated at sampling stations in two rivers in south-eastern Newfoundland: Freshwater River at Cape Race (46°38'50" N; 53°05'40" W) and Northeast Trepassey Brook (46°46'00" N; 53°21'10" W). These are third-order rivers with basin areas of 16.8 and 21.2 km^2, respectively. The rivers are located in the eastern hyper-oceanic barrens eco-region (Damman 1983) characterised by boglands and patches of stunted boreal forest. No development has taken place in the catchments with exception of roads near the mouths of each river. Angling is prohibited.

Northeast Trepassey Brook has a natural run of anadromous salmon, with egg deposition rates of over 5 m^{-2} (Gibson et al. 1993); Freshwater River does not have a natural run of anadromous salmon, as the river flows over a cliff before plunging into the ocean. However, adult salmon were introduced into Freshwater River annually from 1985 to 1990, providing egg depositions in the fluvial habitat from 2.0 - 6.0 m^{-2} (Gibson et al. 1993). Both rivers have a natural population of brook trout. The growth of parr and trout in both rivers is relatively slow, and median smolt ages for Freshwater River and

Northeast Trepassey Brook are three and four years, respectively. Eels (*Anguilla rostrata*) are present only in Northeast Trepassey Brook, and three-spined stickleback (*Gasterosteus aculeatus*) are present only in Freshwater River. Gibson et al. (1993) present a more detailed description of the rivers.

4.2.2.2. Sampling procedures

Twenty-four fixed stations were established in Northeast Trepassey Brook and 36 in Freshwater River. A variable number of these were sampled annually from 1984 to 1993 in late July or early August; 7-21 stations were sampled annually in Northeast Trepassey Brook and 13-27 stations in Freshwater River. Each sampling station was a short reach of relatively uniform habitat characteristics, i.e. each station was an entire run, riffle, pool or pond, chosen to represent the range of habitat types present (Gibson et al. 1993) and were located throughout the catchments. Most stations were sampled by electrofishing (see Table 4.2.1). A few stations were sampled with a seine as this technique was considered more effective in areas that were deep and wide. In general, the majority of fish present at stations were caught (see Table 4.2.2).

Table 4.2.1. Sampling procedures used at stations in Northeast Trepassey Brook and Freshwater River in 1984-1993. E: electrofishing, S: seine. Information depicted in Bold-Italics indicate stations where mark-recapture techniques were used for density estimates. Density-estimates at other stations were done using removal estimates.

	River	84	85	86	87	88	89	90	91	92	93
1	NET	E	E	E	E	E	E	E	***E***	E	E
2	NET	E	E	E	E	E	E	E	E	E	E
3	NET	***S***	***S+E***	***S***	***S***	***S***	***S***	***S***	***S***	***S***	***S***
4	NET	***E***	E	***S+E***	E	***E***	E	***S+E***	E	E	E
5	NET	E	E	E	E	E	E	E	***E***	E	E
1	FRW	E	E	E	E	E	E	E	E	E	E
2	FRW	E	E	E	E	E	E	E	E	E	E
3	FRW	***E***	***E***	E	E	***E***	***E***	***E***	E	***E***	E
4	FRW	***S***	***S***	***S***	***S***	***S***	***S***	***S***	***S***	***S***	***S***
5	FRW	***S***	***S***	***S***	***E***	***S***	***S***	***S***	***S***	***S***	***S***
6	FRW	-	E	-	E	E	E	E	E	E	E
7	FRW	-	E	-	E	E	E	E	E	E	E
8	FRW	E	E	E	E	***E***	E	E	E	E	***E***
9	FRW	***S+E***	***S+E***	***S+E***	E	***S+E***	***S***	***S+E***	***S+E***	***S+E***	***S+E***
10	FRW	***S+E***	***S***	***S***	***S***	***S***	***S***	***S***	***S***	***S***	***S+E***
11	FRW	E	-	E	E	E	E	E	E	E	***E***
12	FRW	E	-	E	E	E	E	E	E	E	E

Table 4.2.2. Description of habitat and fish densities at sampling stations in Northeast Trepassey Brook (NET; 5 stations) and Freshwater River (FRW; 12 stations). Variables include: surface area (m^2), section width (WD, m), water velocity (WV, cm s^{-1}), water depth (DEP, cm), >0+ Atlantic salmon parr (P) and trout (T) density (DEN, # fish m^{-2}), and sampling efficiency (EFF = 100 * number fish caught / estimated fish number). Averages (avg.) and standard deviations (s.d.) were calculated based on average yearly station densities from sampling periods 1984-1993 for Northeast Trepassey Brook (n=10) and 1987-1993 for Freshwater River (n=7). Depth and water velocity of the pond station in Freshwater River were recorded only once. Average and s.d. of EFF is based on trout and salmon sampling efficiencies combined.

#	River	Habitat	Area avg.	WD avg.	WV avg.	WV s.d.	DEP avg.	DEP s.d.	DEN-P avg.	DEN-P s.d.	DEN-T avg.	DEN-T s.d.	EFF avg.	EFF s.d.
1	NET	riffle	267	11.2	33.6	6.24	19.6	1.43	0.304	0.123	0.016	0.011	93	11
2	NET	riffle	105	3.5	27.6	14.49	16.1	4.28	0.354	0.147	0.129	0.061	96	6
3	NET	pool	519	12.7	7.0	2.16	59.9	11.44	0.310	0.088	0.077	0.027	86	9
4	NET	run	266	9.6	23.6	10.31	28.2	3.22	0.254	0.136	0.012	0.011	84	22
5	NET	riffle	217	7.3	34.5	11.46	14.7	4.19	0.412	0.123	0.025	0.015	92	10
1	FRW	riffle	202	9.1	23.4	8.98	13.9	4.14	0.254	0.287	0.101	0.060	96	10
2	FRW	riffle	161	7.5	32.1	13.77	14.6	4.12	0.182	0.136	0.093	0.073	97	6
3	FRW	run	293	12.2	17.0	10.21	20.7	5.94	0.111	0.095	0.176	0.107	78	19
4	FRW	pond	12432	-	0.0	-	44.0	-	0.010	0.006	0.049	0.019	62	17
5	FRW	run	493	12.7	15.0	6.68	40.4	6.32	0.086	0.051	0.138	0.084	78	12
6	FRW	riffle	105	6.0	37.9	13.89	13.1	3.24	0.418	0.130	0.059	0.033	95	8
7	FRW	riffle	64	3.3	44.4	15.08	14.3	4.68	0.534	0.206	0.067	0.065	92	12
8	FRW	riffle	133	6.7	30.7	13.39	19.6	6.45	0.242	0.081	0.328	0.123	86	14
9	FRW	run	152	8.5	11.9	7.78	23.9	2.54	0.042	0.043	0.283	0.157	78	18
10	FRW	pool	569	14.7	5.5	3.83	41.7	16.86	0.063	0.034	0.272	0.094	77	10
11	FRW	riffle	89	5.3	50.4	39.86	14.0	4.51	0.052	0.051	0.981	0.645	94	13
12	FRW	riffle	127	4.0	33.4	22.26	15.1	3.29	0.062	0.052	0.422	0.068	94	6

Before sampling, each station was isolated by 0.6 cm square mesh barrier-nets to ensure population closure. All fish captured were anaesthetised (CO_2), measured (fork length to the nearest mm), held in recovery baskets in the stream and released after electrofishing was completed. Three to six passes were made through each station with seine or electrofisher, depending on fish numbers at consecutive sweeps.

The length and width of each station was measured to the nearest 0.1 m with a measuring tape to determine surface area (Table 4.2.2). At least five depths were recorded at equidistant points along three transects, and water velocities (at 60% of depth) were measured at three equidistant points on each transect. Water temperatures were recorded immediately after isolation of the stations.

Not all stations were sampled annually and it was therefore necessary to choose subsets of the overall database for analysis. For Northeast Trepassey I used data from 5 stations that were visited yearly from 1984 through 1993 (10 years). These stations were all located within the first 700 m upstream from the mouth of the river. For Freshwater River, I used two data-sets: one based on 8 stations that were visited yearly from 1984 through 1993 (10 years, stations 1-4, 7-10; Table 4.2.2) and one based on 12 stations that were visited yearly from 1987 through 1993 (7 years). These stations were all located within the first 7 km upstream from the mouth of the river. Note that in Freshwater River parr older than 0+ were not present before 1987 due to the stocking regime.

I classified the various stations into pool, pond, riffle, and run, based on water velocity and depth. Riffles and runs had water velocities over 10 cm s^{-1}. Pools had water velocities less than 10 cm s^{-1}. Runs and pools were deeper than 20 cm and riffles less than 20 cm. This classification was in accord with a visual and subjective description of the stations.

Abundance of parr and trout (>0+) was estimated using the generalised removal estimator of Otis et al. (1978). At several stations, a mark-recapture procedure was done as this approach was considered more effective. For those, abundance was estimated using Chapman's (1951) modification of the Lincoln-Petersen estimator (Table 4.2.1). I did not estimate or use abundance of 0+ trout and 0+ parr, as these fish were small (3-6 cm) and well able to hide under cobble at many of the stations, and because I was concerned about subsequent effects on density estimates.

When primary habitats will always be filled close to some optimum carrying capacity and secondary habitats will be filled only after primary habitats are occupied, densities at primary habitats will increase less than secondary habitats with population level (*Habitat density and population level*[*]) and density-variability among stations will be less at higher population levels, i.e. at higher population levels, distributions will expand from stations that accommodate many parr at low population levels to other stations, leading to an evening out of densities (*Density variability and population level*[*]). Densities at primary habitats will vary less over time because of this, but may also vary less over time because densities at primary habitats are temporally more stable than secondary habitats, regardless of population levels (*Temporal variability*[*]). I analyzed the data to see whether such relations existed for salmonids in Freshwater River and Northeast Trepassey. In addition, I analyzed the extent to which incorporation of density-dependent habitat selection processes may improve classic habitat modelling approaches (*Habitat modelling*[*]).

4.2.2.3. Habitat density and population level

I investigated local abundance at the scale of a station ($DE_{station}$, # m^{-2}) with yearly averaged fish density at the scale of the river (DE_{river}, # m^{-2}) for all stations, for possible intraspecific processes:

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[*] The Italicized phrases above refer for convenience to sections later under Material and Methods and Results.

$$log_{10}(DE_{station} + 0.001) = \gamma + \delta\ log_{10}(DE_{river} + 0.001) \qquad \textit{Equation 4.2.1}$$

If δ_i=1 (intraspecific station-to-river response; with i = 1 to number of stations), the interpretation is that stations responded proportionally with population densities (cf. Myers and Stokes 1989). I hypothesised that δ_i, a series of slopes, should be negatively correlated with the station density in the year the population abundance in the river was lowest, as primary habitats will always be filled close to some optimum carrying capacity, whereas secondary habitats will be filled only after the primary spots within the primary habitat are occupied. In addition, I investigated whether δ_i varied significantly among habitats to test if habitats responded similarly to changes in population abundance. In these analyses, δ_i were weighted by the inverse of the associated $MS_{error,i}$.

I investigated the selection by parr for stations ($SISA_{station}$) with yearly averaged trout density at the scale of the river ($DETR_{river}$, # m^{-2}) for all stations, for possible interspecific processes:

$$SISA_{station} = \zeta + \eta\ log_{10}(DETR_{river} + 0.001) \qquad \textit{Equation 4.2.2}$$

with:

$$SISA_{station} = log_{10}(DESA_{station} + 0.001) - log_{10}(DESA_{river} + 0.001) \qquad \textit{Equation 4.2.3}$$

If η_i=0 (interspecific station-to-river response; with i = 1 to number of stations), the interpretation is that selection by parr for stations was not associated with the population level of trout. If trout and parr select for similar habitats, η_i, a series of slopes, may be negatively correlated with the station density in the year the population abundance of trout in the river was lowest, as parr are driven from habitats that are primary to trout with an increase in trout populations. If trout and parr do not affect each others distribution as they select different habitats or because of limited interspecific competition within habitats, η_i may not be correlated with the station density in the year the population abundance of trout in the river was lowest. In addition, I investigated if η_i varied significantly among habitats to test if habitats responded similarly to changes in population abundance of trout. This calculation was repeated for trout (with $SITR_{station}$ analyzed as a function of $DESA_{river}$). In these analyses, η_i were weighted by the inverse of the associated $Ms_{error,i}$.

4.2.2.4. Density variability and population level

I studied the variation in fish densities over sampling stations for possible intraspecific processes, using Taylor's Power Law (Taylor 1986, McArdle et al. 1990), with variances and means of parr and trout densities (DE) calculated over stations per year per river:

$$log_{10}(s_{DE}^2) = \alpha + \beta_s \ log_{10}(\overline{DE}) \qquad \textit{Equation 4.2.4}$$

If β_s=2, then the variability over stations is constant from year to year. If β_s<2 then the variability is smaller in years when populations are larger, i.e. in good years low-density stations will accommodate proportionally more fish than high-density stations, leading to an evening-out of densities. If β_s>2 then the variability is greater in years where populations are larger, which means that in years when populations are larger, high density stations accommodate proportionally more fish than low density stations and that in years when populations are lower, low-density stations are less affected than high-density stations. I hypothesised that β_s<2 for both species.

I investigated the variation in fish densities over sampling stations, for possible interspecific processes, by relating the coefficient of variation (CV_s) of the one species with the yearly averaged density of the other, with CV_s and means of parr and trout calculated over stations per year per river. I hypothesised that an increase in trout and parr density would lead to a change in CV_s of parr and trout distributions respectively, as trout are driven from habitats that are primary to parr when parr populations increase, and vice versa (cf. Gibson 1993, Rodríguez 1995).

4.2.2.5. Temporal variability

I studied temporal variability in fish densities at stations for possible intraspecific processes using Taylor's Power Law (Taylor 1986, McArdle et al. 1990), with variances and means of parr and trout densities calculated over years per station:

$$log_{10}(s^2_{DE}) = \alpha + \beta_t \ log_{10}(\overline{DE}) \qquad \textit{Equation 4.2.5}$$

If $\beta_t=2$, then the variability of the populations over time is constant. If $\beta_t<2$ then the temporal variability is smaller at stations where densities are larger. If $\beta_t>2$ then the temporal variability is greater at stations where densities are larger. I hypothesised that $\beta_t<2$, i.e. low density stations fluctuate more than high density stations do.

I studied temporal variability in fish densities at stations for possible interspecific processes by relating the coefficient of variation (CV_t) of parr and trout, calculated per station over years, with the average station density of trout and parr respectively. I hypothesised that sites that are primary to parr (accommodating high parr densities) should fluctuate less over time with fluctuations in trout populations, and that sites that are primary to trout (accommodating high trout densities) should fluctuate less over time with fluctuations in parr populations. In addition, I investigated whether CV_t varied significantly among habitats.

To test for possible interspecific processes at the scale of catchments, I investigated whether the yearly averaged trout densities were correlated with the yearly averaged parr densities for Freshwater River and Northeast Trepassey Brook separately, with yearly averaged densities on a $\log_{10}$ scale.

4.2.2.6. Habitat modelling

To quantify the extent to which habitat models may change due to density-dependent habitat selection, I related observed fish densities (on a $\log_{10}$-scale) to various habitat variables using variance analysis based on the Generalised Linear Model procedure in SAS and type I Sums of Squares (SAS 1988). Habitat variables were introduced into the model using a sequence that paralleled an increasingly more complex meso-scale habitat modelling approach. Next, the percentage of the observed variance at the different levels in the model was used to assess improvement of the descriptive power of the model by the addition of complexity (see Table 4.2.8). I stress that this analysis was not meant for significance testing, but was done to obtain an impression of how habitat models may be improved by the incorporation of density-dependent processes.

1. The first variable included was the habitat type H (pool, riffle, run, and pond). This level parallels a habitat model where density estimates are provided solely based on habitat type, regardless of differences in population size, rivers, density-dependent habitat selection, or other factors.

2/3. The second and third variables were R (Freshwater River; Northeast Trepassey Brook) and R*H. These levels parallel improvement of the model by river-specific responses to habitats.

4. The fourth variable was S (station). This level represents selection of habitats at specific stations, not represented by levels 1-3. If this level (S) explains much of the variance and the first level (H) does not, the habitat classification used may be improved by a classification that better parallels the habitat as experienced by individual fish.

5. The fifth variable was the average density (on $\log_{10}$-scale) as observed per river per

year (LDESA for parr, LDETR for trout; used to explain observed parr and trout densities respectively). This level parallels proportional changes in station densities due to changes in population level (cf. δ_i=1; CV_s does not vary with population level; β_s=2; habitat selection independent of population level).

6. The sixth variable was LDESA*S or LDETR*S for explaining the parr and trout densities respectively. This level represents intraspecific density-dependent processes (cf. $\delta_i \neq 1$; CV_s varies with population level; $\beta_s \neq 2$; distribution disproportional; habitat selection is density-dependent).
7. The seventh variable was LDETR or LDESA for explaining the trout and parr densities respectively. This level represents proportional changes in station density of one species due to changes in population level of the other, and addresses the question of whether the population level of one species was affected by the population level of the other.
8. The eighth variable was LDESA*S and LDETR*S for explaining the trout and parr densities, respectively. This level represents disproportional changes in densities at stations of one species with changes in population level of the other, and addresses the question of whether the distribution over stations of one species was affected by the population level of the other species (cf. CV_s varies with population level).
9. The ninth variable was LDESA*LDETR*S, a level which represents possible higher order intra- and interspecific density-dependent processes.

One criticism of this approach may be that it explains selection for stations first (levels 1-5) before including density dependent effects (levels 6-9) which may give these variables an advantage over others in explaining the observed variance, and that variables such as station and river have no transferability to other studies or meaning to habitat models. However, I did not have data from enough stations to develop reliable (density-dependent) habitat models. In addition, the main objective of the approach was to scale the effects on fish distributions of habitat features that were stable over time (station effects) to effects of varying population levels. Some of these station effects may be reflected in habitat models by using more general descriptor variables, but not all. Some of the density-dependent effects may be reflected in density-dependent habitat models, but not all. Station effects will have to be included in the model first to allow for scaling the effects of these with density-dependent effects. In short, one should consider the above approach only as a crude and limited approach to scale density-dependent with density-independent effects. Interpretations will have to be done in light of the results from the other analyses.

4.2.2.7. Calculation procedures

Analyses aimed at describing the trout distributions in Freshwater River were done using the two Freshwater River data-sets (8 stations, 10 years; 12 stations, 7 years). Analyses aimed at describing the parr distributions in Freshwater River were done using the data-set from 12 stations and 7 years only, as no parr other than young-of-the-year were present in Freshwater River before 1987.

Taylor Power Plots were analyzed by randomisation (Manly 1991). Observations on the response variable were randomised $5*10^5$ times with the explanatory variable held constant, using sampling with replacement. A p-value was obtained by calculating the proportion of randomisations with an r^2 greater than or equal to the r^2 of the observed distribution.

To test if the slope of the Taylor Power function differed from 2, I used a randomisation approach as well. Regression analysis was done on randomly selected observed combinations of variances and means, using sampling with replacement and with the number of randomised observations being equal to the number of observations in the original analysis. Confidence limits for slopes were determined from $5*10^5$ of such randomised regression analyses. P-values were obtained by calculating the proportion of slopes, obtained by randomisation, that exceeded 2 for analysis on power functions with an observed slope smaller than 2, and the proportion of slopes that were less than 2 for analysis on power functions with an observed slope larger than 2. Analyses of Taylor Power functions were done for each river separately as well as on data from both rivers combined. To calculate slopes, and confidence limits and p-values for slopes from data from both rivers combined, I averaged the slopes for the two rivers in each randomised regression analysis.

Randomisations were done using the FORTRAN system-supplied random number generator, upgraded using the shuffle procedure (Press et al. 1986) to break up possible sequential correlations. All other analyses were done using SAS statistical software (SAS 1988). Residual analyses involved a visual check for patterns in plots of residual versus predicted values, as well as tests for normality. Tests for normality involved a visual check and the Shapiro-Wilks statistic (α=0.05). If residuals deviated from normality and any of the p-values in the analyses were less than 0.25, p-values were obtained by randomisation in SAS: Observations on response variables were randomised 1000 times with the explanatory variables held constant, using sampling without replacement. A selection criterion of 0.25 was used to decide if data were to be re-analyzed by randomisation, because randomisations in SAS were time-consuming and differences in p-values obtained by randomisation and under the assumption of normality were small. Therefore, I assumed that this procedure did not lead to an increase in the occurrence of type II errors. For all analyses I used a 5% level as a screening criterion to separate "significant" effects from "non-significant" effects.

Water depth and water velocity at stations were strongly negatively correlated, both in Freshwater River (r=-0.831, p=0.001, n=12) and Northeast Trepassey Brook (r=-0.962, p=0.009, n=5). Because of these correlations and because few pool/pond habitats were visited, I only studied the effect of the riverine habitat on δ_i, β_t, and CV_t by means of the variables water depth and water velocity separately, rather than using the classification in terms of pool/riffle/run/pond or a model including both water velocity as well as water depth.

4.2.3. Results

Stations in Northeast Trepassey Brook comprised one pool, one run, and three riffles (Table 4.2.2). No pond data were included. Average parr densities (over 5 stations) varied from 0.145 m^{-2} (1991; s.d. = 0.098) to 0.456 m^{-2} (1993; s.d. = 0.067); Average trout densities varied from 0.030 m^{-2} (1986; s.d. = 0.024) to 0.077 m^{-2} (1993; s.d. = 0.056). Stations in Freshwater River comprised one pond, one pool, three runs, and seven riffles. Average parr densities varied from 0.064 m^{-2} (1993; s.d. = 0.076) to 0.277 m^{-2} (1987; s.d. = 0.312) (period 1987-1993, 12 stations); Average trout densities varied from 0.178 m^{-2} (1989; s.d. = 0.221) to 0.469 m^{-2} (1993; s.d. = 0.648) (period 1984-1993, 7 stations). Trout densities in Freshwater River were higher than in Northeast Trepassey Brook. Parr densities in Northeast Trepassey were higher than in Freshwater River.

4.2.3.1. Habitat density and population level

Stations accommodating high parr densities at low parr population levels responded less to an increase in parr population levels than stations accommodating low parr densities at low population levels, as δ_i was negatively associated with the station density in the year the population abundance in the river was lowest (Table 4.2.3). No such relationship was found for trout. Trout densities at deeper and low flow stations responded less to an increase in population level than densities at high flow and shallow stations, as δ_i was significantly correlated with water depth (negative) and water velocity (positive) (Table 4.2.3). I did not observe any such relationship for parr. Relations between δ and density, depth or water velocity did not vary among rivers (interaction term non-significant; Table 4.2.3).

Selection by trout for stations did not vary with population levels of parr or vice-versa (Table 4.2.4). η did not vary with water depth or water velocity (Table 4.2.4).

Table 4.2.3. Summary statistics describing the δ (intraspecific station-to-river response) as a function of the station densities ($\#.m^{-2}$) of parr (δ Parr) and brook trout (δ Trout I/II) in Northeast Trepassey River and Freshwater River as observed in years when riverine densities were lowest, average station water depth (cm), and average station water velocity (cm s^{-1}). Parr/Trout I: analysis based on data from Freshwater River 1987-1993 (7 years; 12 stations) and Northeast Trepassey 1984-1993 (10 years, 5 stations) (n=17 stations total); Trout II: analysis based on data from Freshwater River 1984-1993 (10 years, 8 stations) and Northeast Trepassey 1984-1993 (10 years; 5 stations) (n=13 stations total). Significant results in bold.

	δ Parr			δ Trout I			δ Trout II		
Source	df	SS III	p	df	SS III	p	df	SS III	p
Density	1	74.7751	**0.004**	1	2.2746	0.750	1	1.2010	0.767
River	1	12.9172	0.177	1	0.2724	0.912	1	1.3433	0.754
Density*River	1	3.5776	0.466	1	1.6181	0.788	1	2.7367	0.656
Total	16	172.9023		16	299.6181		12	123.5981	
Depth	1	2.6541	0.631	1	16.3569	0.388	1	73.4481	**0.005**
River	1	17.8039	0.225	1	28.2618	0.261	1	2.4896	0.511
Depth*River	1	5.4462	0.494	1	19.4042	0.348	1	5.1982	0.349
Total	16	172.9023		16	299.6181		12	123.5981	
Water Velocity	1	2.5642	0.651	1	30.6124	0.238	1	51.1822	**0.026**
River	1	0.1304	0.918	1	6.2050	0.588	1	1.7028	0.639
Water Velocity*River	1	4.1976	0.563	1	16.5765	0.380	1	1.9622	0.615
Total	16	172.9023		16	299.6181		12	123.5981	

Table 4.2.4. Summary statistics describing η (interspecific station-to-river response) as a function of the station densities (# m^{-2}) of parr (η Parr) and brook trout (η Trout I/II) in Northeast Trepassey River and Freshwater River as observed in years when riverine densities were lowest, average recorded water depth (cm), and water velocity (cm s^{-1}). Parr/Trout I: analysis based on data from Freshwater River 1987-1993 (7 years; 12 stations) and Northeast Trepassey 1984-1993 (10 years, 5 stations) (n=17 stations total); Trout II: analysis based on data from Freshwater River 1984-1993 (10 years, 8 stations) and Northeast Trepassey 1984-1993 (10 years; 5 stations) (n=13 stations total). P-values printed in italics are obtained by randomisation.

	η Parr			η Trout I			η Trout II		
Source	df	SS III	p	df	SS III	p	df	SS III	p
Density	1	11.3256	0.297	1	0.4817	0.785	1	2.2754	*0.060*
River	1	7.0511	0.407	1	1.1689	0.671	1	1.2437	*0.196*
Density*River	1	8.1579	0.374	1	4.4693	0.411	1	0.9316	*0.154*
Total	16	138.7865		16	85.9864		12	8.2954	
Depth	1	0.0438	0.950	1	1.1521	0.671	1	0.0907	0.755
River	1	2.9359	0.605	1	0.3232	0.822	1	0.1639	0.675
Depth*River	1	1.2488	0.735	1	1.9859	0.578	1	0.3172	0.562
Total	16	138.7865		16	85.9864		12	8.2954	
Water Velocity	1	0.0284	0.958	1	1.2998	0.641	1	0.3801	0.522
River	1	4.8871	0.493	1	0.6145	0.748	1	0.0052	0.940
Water Velocity*River	1	8.8475	0.360	1	0.1457	0.875	1	0.0067	0.931
Total	16	138.7865		16	85.9864		12	8.2954	

4.2.3.2. Density variability and population level

Variability of parr densities among stations was less at higher population levels of parr in Freshwater River ($\beta_s<2$, Table 4.2.5), but not so in Northeast Trepassey River, or when data from both rivers were combined. No such relationship was found for trout. Variability of parr densities over stations did not vary with trout population levels. Variability of trout densities over stations did not vary with parr population levels. (Table 4.2.6).

Table 4.2.5. Atlantic salmon and brook trout distributions in Northeast Trepassey River (NET) and Freshwater River (FRW), described by Taylor Power Plots. The descriptive statistics for the relationship between $\log_{10}$(variance ($\#^2$ m^{-4})) and $\log_{10}$(mean abundance ($\#$ m^{-2})) include: interval, slope, 95% confidence limits of slope, r^2, p, as well as the chance of the slope being ≥ 2 for slopes < 2 and the chance of the slope being ≤ 2 for slopes > 2 (p_s)). NET: analysis based in data from 1984-1993 (10 years, 5 stations); FRW1: analysis based in data from FRW 1987-1993 (7 years, 12 stations); FRW2: analysis based in data from FRW 1984 - 1993 (10 years, 8 stations); TOT1: analysis based on NET and FRW1 combined; TOT2: analysis based on NET and FRW2 combined. Significant results in Bold.

species	river	type	n	int.	slope	95% c.l.	sl.	r^2	p	p_s
salmon	NET	β_s	10	-1.851	0.389	-0.825	4.201	0.024	0.666	0.125
salmon	FRW1	β_s	7	-0.166	1.728	0.795	2.164	0.915	**0.001**	**0.051**
salmon	TOT1	β_s	17	—	0.940	0.116	3.180	—	—	0.109
trout	NET	β_s	10	0.249	2.180	1.122	3.152	0.761	**0.001**	0.387
trout	FRW1	β_s	7	0.408	2.585	-0.456	3.017	0.911	0.072	0.337
trout	FRW2	β_s	10	-0.558	1.591	1.101	2.298	0.716	**0.003**	0.099
trout	TOT1	β_s	17	—	2.347	0.744	2.956	—	—	0.397
trout	TOT2	β_s	20	—	1.885	1.276	2.500	—	—	0.367
salmon	NET	β_t	5	-1.781	0.104	-3.950	5.374	0.002	0.932	0.109
salmon	FRW1	β_t	12	-0.714	1.669	1.056	2.180	0.842	**0.000**	0.081
salmon	TOT1	β_t	17	—	1.209	-0.019	2.593	—	—	0.071
trout	NET	β_t	5	-1.390	**1.379**	**0.736**	**1.750**	0.935	**0.008**	**0.010**
trout	FRW1	β_t	12	-0.885	1.624	0.582	2.140	0.738	**0.000**	0.104
trout	FRW2	β_t	8	-0.554	2.037	1.060	2.687	0.865	**0.001**	0.521
trout	TOT1	β_t	17	—	**1.552**	**0.778**	**1.950**	—	—	**0.013**
trout	TOT2	β_t	13	—	1.784	1.091	2.241	—	—	0.127

Table 4.2.6. Spatial variance (CV_s) of parr and trout densities in Northeast Trepassey Brook and Freshwater River as a function of the population level (LDE = $\log_{10}$(mean abundance (# m^{-2})) of trout and parr respectively. Parr/Trout I: analysis based on data from Freshwater River 1987-1993 (7 years, 12 stations) and Northeast Trepassey 1984-1993 (10 years, 5 stations) combined; Parr/Trout II: analysis based on data from Freshwater River 1984-1993 (10 years, 8 stations), and Northeast Trepassey Brook 1984-1993 (10 years, 5 stations) combined. Note that for Trout II 0.001 was added to all average parr densities for calculating LDE as no >0+ parr were present prior to 1987. P-values printed in italics are obtained by randomisation.

	Parr			Trout I			Trout II		
Source	df	SS III	p	df	SS III	p	df	SS III	p
LDE	1	0.0109	*0.544*	1	0.0306	0.402	1	0.0016	0.826
River	1	0.1181	***0.036***	1	0.0276	0.425	1	0.0587	0.200
LDE*River	1	0.0321	*0.270*	1	0.0200	0.496	1	<0.0001	0.986
Total	16	2.6060	-	16	0.5935	-	19	0.9532	-

4.2.3.3. Temporal variability

Stations accommodating low trout densities varied more over time than stations accommodating high trout densities ($\beta_t<2$, Table 4.2.5) in Northeast Trepassey Brook and for the combined data-set of Northeast Trepassey Brook and Freshwater River. No such relationship was found for Freshwater River alone. Variability of parr densities over time at stations was not affected by parr densities at these stations.

Variability of parr densities at stations over time did not change with mean station density of trout and vice-versa, or with water velocity or water depth (Table 4.2.7).

Table 4.2.7. Temporal variability (CV_t) of parr and trout densities at sampling stations in Northeast Trepassey Brook (NET) and Freshwater River (FRW) as a function of the mean density (LDE = $\log_{10}$(mean abundance (# m^{-2})) of trout and parr respectively, the mean water depth (D, cm) and water velocity (WV, cm s^{-1}) at these stations. Parr/Trout I: analysis based on data from Freshwater River 1987-1993 (7 years, 12 stations) and Northeast Trepassey 1984-1993 (10 years, 5 stations) combined; Parr/Trout II: analysis based on data from Freshwater River 1984-1993 (10 years, 8 stations) and Northeast Trepassey 1984-1993 (10 years, 5 stations) combined.

	Parr			Trout I			Trout II		
Source	df	SS III	p	df	SS III	p	df	SS III	p
Density	1	0.0171	0.597	1	0.0444	0.307			
River	1	0.1349	0.152	1	0.0831	0.169			
Density*River	1	0.0782	0.267	1	0.0784	0.181			
Total	16	1.2274		16	0.7107				
Depth	1	0.0336	0.487	1	0.0945	0.177	1	0.0969	0.092
River	1	0.1161	0.207	1	0.0024	0.824	1	<0.0001	0.977
Depth*River	1	0.0069	0.751	1	0.0011	0.880	1	0.0045	0.693
Total	16	1.2274		16	0.7107		12	0.3612	
Water Velocity	1	0.0002	0.953	1	0.0900	0.176	1	0.0640	0.184
River	1	0.0853	0.285	1	0.0004	0.927	1	0.0021	0.802
Water Velocity * River	1	0.0049	0.793	1	0.0044	0.756	1	0.0071	0.643
Total	16	1.2274		16	0.7107		12	0.3612	

Yearly averaged trout densities were not significantly correlated with yearly averaged parr densities (r=-0.088, p=0.809, n=10) for Northeast Trepassey Brook. This correlation was significant in Freshwater River (r=-0.815, p=0.025, n=7).

4.2.3.4. Habitat modelling

Density-independent effects explained more of the observed density variance of parr and trout (77.2% for parr; 77.8-79.2% for trout; levels 1-5, Table 4.2.8) than density-dependent effects (12.7% for parr; 11.8-12.0% for trout; levels 6-9, Table 4.2.8). In these models, a large portion of the variance was explained by the fourth level (station), which suggests that improvement of habitat models may be possible when using habitat criteria that are more refined than the classification I used. As this matter was not within the scope of this study, however, I did not address this question.

Table 4.2.8. Density of parr and trout ($\log_{10}(\text{density } (\#.\text{m}^{-2}) + 0.001)$ as a function of habitat (H: pool, riffle, run, pond), river (R: Freshwater River, Northeast Trepassey Brook), station (S) and population level (LDESA for parr density; LDETR for trout density). The percent variance explained at the various levels in the model illustrate how density-independent effects scale to density-dependent effects (see text). Parr/Trout I: analysis based on data from Freshwater River 1987-1993 (7 years, 12 stations) and Northeast Trepassey 1984-1993 (10 years, 5 stations) combined; Trout II: analysis based on data from Freshwater River 1984-1993 (10 years, 8 stations) and Northeast Trepassey 1984-1993 (10 years, 5 stations) combined.

Parr

Source	df	SS I	perc.	p
H	3	12.5981	26.2	<0.001
R	1	7.0131	14.6	<0.001
H*R	2	0.6509	1.4	0.002
S	10	12.3162	25.6	<0.001
LDESA	1	4.5205	9.4	<0.001
LDESA*S	16	2.0572	4.3	0.058
LDETR	1	0.1108	0.2	0.224
LDETR*S	16	3.1044	6.5	0.003
LDESA*LDETR*S	17	0.8242	1.7	0.829
Corr. Total	133	48.0431	100.0	-

Trout I					Trout II			
Source	df	SS I	perc.	p	df	SS I	perc.	p
H	3	1.2187	2.2	0.004	3	2.3457	5.5	<0.001
R	1	17.3730	31.1	<0.001	1	17.6276	41.6	<0.001
H*R	2	2.2304	4.1	<0.001	2	2.3144	5.5	<0.001
S	10	19.1843	37.4	<0.001	6	8.4156	19.8	<0.001
LDETR	1	2.3842	4.4	<0.001	1	2.3093	5.4	<0.001
LDETR*S	16	1.2937	2.4	0.482	12	0.8852	2.1	0.213
LDESA	1	0.0515	0.1	0.431	1	0.1824	0.4	0.075
LDESA*S	16	2.4713	4.6	0.038	12	0.7567	1.8	0.337
LDESA*LDETR*S	17	2.5679	4.7	0.041	13	3.2790	7.7	<0.001
Corr. Total	133	54.1867	100.0	-	129	42.4077	100.0	-

4.2.4. Discussion

Several of the results suggest that habitat selection by salmonids may be density-dependent: (1) stations accommodating high parr densities at low parr population levels responded less to an increase in parr population levels than stations accommodating low parr densities (Table 4.2.3, based on data from both rivers combined, relationship not different among rivers); (2) parr densities varied less over stations at higher population levels in Freshwater River (Table 4.2.5); (3) trout densities at deeper and low flow stations responded less to an increase in population level than at high-flow and shallow stations (Table 4.2.3, based on data from both rivers combined, relationship not different among rivers); and (4) stations that accommodated many trout fluctuated less over time than stations that accommodated fewer trout (Northeast Trepassey Brook and when based on both rivers combined; see Table 4.2.5). Trout distributions did not seem to affect parr distributions. However, observed density-dependent relations were based on 6 significant results from 45 different analyses (13% success rate; Tables 4.2.3-7) and some of these results may have been found by chance alone. In addition, Table 4.2.8 indicates that the percent variance explained by density-independent effects is 6 to 7 times larger than density-dependent effects. Therefore, I concluded that results may indicate some density-dependent relations, but they do not indicate a clear and strong effect of density-dependent processes on salmon and trout distributions.

A clear and concise interpretation from the Northeast Trepassey and Freshwater River data is difficult because (1) stations were not representative of available habitat; (2) stations were sampled using a variety of techniques (electroshocking and seining, removal and mark recapture estimates: see Table 4.2.1) with different sampling efficiencies (Table 4.2.2); (3) the range in population levels in both rivers was not large and population levels were not high; (4) the population structure in Freshwater River was unnatural due to the stocking regime; and (5) few stations were sampled.

The stations being not representative of available habitat will affect the estimates of population levels, but is not likely to be responsible for the density-dependent effects in the analyses in Tables 4.2.3-7. However, this will affect quantification of potential density-dependent effects. Inconsistencies in sampling procedures and differences in sampling efficiency will prevent a single interpretation of the analyses of Tables 4.2.3-7. Density estimates from stations that were sampled less efficiently or with a variety of sampling techniques will be subject to an added source of variance due to variable sampling efficiencies and methods. If, in addition, densities at these stations were different from stations sampled in an efficient and consistent manner, patterns may result that are seemingly density-dependent. Alternatively, real density-dependent relations may not be detected. This is mostly of concern for analyses of Tables 5 and 7 (β_t, CV_t). From this, the one significant result of Table 4.2.5 may be an artefact of sampling methods, rather than being indicative of density-dependent responses: This result was largely due to data from Northeast Trepassey. Sampling stations 1, 3 and 4 in this river were sampled inconsistently (mark-recapture and removal techniques; seining and electrofishing). Trout densities at these stations were lower. Because of this, the observation that trout densities varied more over time at stations that accommodated lower trout densities may not necessarily be due to density-dependent processes.

Density-dependent responses have previously been observed for brown trout (*Salmo trutta*) by Elliott (1986) and for Atlantic salmon parr by Talbot (1994), and in the experiment of Chapter 4.1. Findings of this study contrast with Rodríguez (1995) who observed an effect of interspecific interactions on distributions of parr and brook trout but did not observe intraspecific interactions. Findings also contrast with Gibson (1993) who suggested that distributions of salmonids are considerably affected by interspecific interactions. These variable results may be partly due to a mismatch between the scale of observations at pools, riffles and runs and the much smaller spatial scale at which individual fish actually select for habitats (cf. Fausch 1984, Hughes 1992A, 1992B, Hill and Grossman 1993, see Chapters 2, 3). Due to this scale mis-match, only an indirect impression can be obtained of the processes involved.

Habitat selection may be an important process governing fish distributions at smaller spatial scales. However, habitat selection by individuals may be of lesser importance, relative to other processes, for describing fish distributions at larger spatial scales (see Chapter 2). For example, if fish select riffles to feed in and if pools serve as cover mainly during flood events, riffles will be selected over pools at small spatio-temporal scales. However, if recurring flood events diminish fish populations in tributaries containing few pools, positive associations of fish with pools may be found at larger spatio-temporal scales as tributaries containing few pools will accommodate only a few fish. Positive associations with riffles will then be found at small spatio-temporal scales due to habitat selection; negative associations with riffles will be found at large spatio-temporal scales due to differential mortality. This example illustrates that associations depend on scale (cf. Morris 1987A, Morris 1987C, Piatt 1990, Morris 1992, Fausch et al 1994, see Chapter 3) and that the relative importance of various processes in shaping observed distributions of fish may depend on scale as well (cf. Horne and Schneider 1994, see Chapter 2). That is, habitat selection is a scale-dependent process (Morris 1987A,C). Because of this, results of small-scale experiments such as in Chapter 4.1 or field observations on adjoining or closely located habitats (cf. Elliott 1986, Rodriguez 1995), although valuable for obtaining an understanding of small-scale behavioural processes, may be difficult to extrapolate to larger spatio-temporal scales. When sampling stations are farther separated, (large-scale) processes other than (small-scale) habitat selection may become more important and, although the effects of small-scale habitat selection by individuals may propagate across scales, this propagation may be limited and not immediate.

The observed changes in habitat use can be explained in terms of the ideal free distribution (Fretwell and Lucas 1970, MacCall 1990) and/or the ideal despotic distribution (Fretwell 1972). As salmonids probably primarily (but not solely) select for habitats at scales smaller than that of pools, riffles, and runs (cf. Hughes 1992A, 1992B, Hill and Grossman

1993), I suspect that with increasing densities, first the primary small-scale habitats ("spots") within sampling stations became occupied followed the secondary spots, as the access to primary spots would have become limited with increasing densities, due to territoriality (cf. Grant and Kramer 1990), or small-scale spacing behaviour (see Chapter 3). As parr have been observed to be territorial in riffles but less aggressive and sometimes schooling in pools (Kalleberg 1958, Gibson 1978, Gibson and Cunjak 1986), a combination of ideal despotic and ideal free behaviour is most likely to be appropriate. Due to these behaviours, selection of broad-scale features such as pools, riffles, and runs may change disproportionally with population density. Unfortunately, however, this study could not address the extent to which behaviours were "ideal" or which stations or habitats were primary or secondary, for lack of an independent measure of habitat quality and because density may not necessarily reflect habitat quality (cf. Van Horne 1983).

4.2.5. Conclusions

I have shown that variability itself can be an interesting aspect of fish distributions and that analysis of spatio-temporal variability can be used to study habitat selection by fish. Some of the results did indicate possible density-dependent responses of fish. However, because of shortcomings in the available data, I recommend additional research along the lines of this paper but using survey designs based on a larger number of stations that are sampled in a more consistent manner.

Chapter 5: Summary and conclusions

5.1. Thesis context and research questions

Micro-habitat models that describe relations between organisms and their habitats are widely used to manage natural populations of animals. These models quantify habitat use based on observations of individuals taken at a single or few small spatio-temporal scales. Decisions based on these models generally aim at the management of groups of organisms at large spatio-temporal scales.

Implicit assumptions of such micro-habitat models are that (1: *scale-up*[*]) habitat is limiting population levels and small-scale observations on habitat selection behaviours can be used to identify important habitats, i.e. small-scale information on habitat use can be used to address large-scale questions; (2: *scaling-analyses*[*]) the single or few measurement scales used in habitat models are appropriate for describing distributions of organisms and identifying important habitats; and (3: *density-dependent habitat selection*[*]) habitat use does not change with density, and from this, habitat models do not vary with population level.

In this thesis, I evaluated various aspects of these three assumptions for juvenile Atlantic salmon (*Salmo salar*) in rivers. I hypothesised that (1) small-scale behavioural processes or small-scale fish-habitat associations will have limited applicability for explaining larger scale distributions or addressing large-scale habitat management problems; (2) multi-scale approaches are better for understanding and describing fish distributions because habitat selection behaviours themselves operate at multiple scales; and, because of this, (3) multi-scale habitat models perform better than single-scale habitat models, especially when extrapolating small-scale habitat selection behaviours to density predictions at larger

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[*] Words in italics refer for convenience to sections later in Chapter 5.

spatial scales; and (4) habitat selection is density-dependent due to small-scale spacing behaviour or territoriality.

5.2. Scale-up in habitat models

I evaluated possible limitations of scale-up in salmonid habitat models, using recently developed scaling-tools (scope- and rate-diagrams), field-data, and theoretical scenarios on movement and mortality. I concluded that observations underlying habitat models are done at spatio-temporal scales where movement dominates but are interpreted and used at space-time scales where mortality dominates. This discrepancy in scales and dominance of processes indicates that research is needed that explicitly evaluates the validity of scale-up: habitat models describe processes that may not be that important to the problems we seek to address with these models. However, the results of this study also underline the fact that movement may be important to dynamics at scales that are much larger than those of individual fish movements. This highlights the importance of movement and habitat selection studies for an understanding of distribution processes. I recommended that scale-up validation should become a central focus in habitat modelling. I suggested survey designs appropriate to such scale-up studies. [see Chapter 2]

5.3. Scaling analyses in habitat selection studies

I evaluated distributions of juvenile Atlantic salmon over a range of spatial scales to see whether patchiness of fish distributions or associations with depth, water velocity and substrate depended on spatial scale. This was done using direct observations of individual fish from a stream-tank study (spatial scales 1 cm to 3 m), and field data (spatial scales 1 cm to 15 m) obtained by snorkelling in two different rivers in Newfoundland, Canada. [see Chapter 3]

Results indicated associations with conspecifics, substrate, water velocity, and depth were scale-dependent and most extreme at small spatial scales (ambit radius < 50 cm). Scale-dependent associations changed with direction relative to water flow. I identified spatial scales important to habitat models and formalised observations into explicit multi-scale habitat selection models.

Most behaviours seemed directed towards substrate and combinations of water velocity and depth at small spatial scales (ambit radius < 5 cm), but some results suggested behaviours operating at multiple scales, rather than a single scale: salmon parr differentiated between shallow positions in shallow areas and shallow positions in deeper areas, deep locations in deep areas and deep locations within shallower areas (field-based study), and between low-flow positions in low-flow-areas and low-flow positions in high-flow areas (field-based and stream-tank study); >0+ salmon often avoided larger substrates (cobble to large boulder) at small spatial scales (ambit radii <40 cm), but preferred larger substrates at larger spatial scales (stream tank and field-based study).

Although associations occurred over a range of spatial scales, the results seem to indicate that three spatial scales are important: (1) small-scale (ambit radius < 5 cm), (2) medium-scale (15-50 cm), (3) large-scale (ambit radius = 1-5 m). The first scale is possibly associated with selection for small-scale environmental features at focal positions (cf. nose-velocity). Associations were generally most extreme at these spatial scales. The second scale is possibly associated with territoriality or spacing behaviour and the distance fish move from preferred focal positions into the current for feeding on passing drift and associated selection for low-flow positions closely adjacent to high-flow areas. The third scale is possibly associated with the river width. This last scale was apparent from selection for depths in the field-based study and was least well defined.

Results suggest behaviours primarily directed towards small-scale habitat features (< 1 m^2), probably aimed at maximising energy intake (cf. Bachman 1984; Fausch 1984) by selection for specific holding positions with low snout-velocities close to higher current conditions (larger scale) where drift is concentrated (cf. Chapman and Bjornn 1969, Everest and Chapman 1972, Fausch and White 1981).

Contrary to expectation, single- and multi-scale habitat selection models were equally well able to describe small-scale fish distributions (ambit radii < 4 m), despite observed multi-scale behaviours (stream-tank and field-based study). This is attributed to the predominance of selection behaviours operating at the first small-scale.

Multi-scale models seemed slightly better at explaining fish distributions at larger spatial scales (field-based study). However, both single- and multi-scale approaches often failed to describe distributions at spatial scales much larger than those used in the model, even when larger scale distributions were described in terms of assumed homogenous broad-scale features such as pools, riffles and runs, i.e., models performed well with respect to describing where fish were positioned in the river (small spatial scales), but were not well able to describe density-variability in river sections. This was surprising as the scope of underlying surveys was small. This may indicate that the scale-up from habitat model to fish-habitat problem may be much more difficult than assumed in current micro-habitat modelling. Because associations varied with measurement scale, a clearly defined measurement scale is important to habitat selection studies.

5.4. Density-dependent habitat selection

I studied density-dependent habitat use by Atlantic salmon parr, to test the implicit assumption in habitat modelling that habitat selection does not change with population density. This was done in experimental riverine enclosures in the field. The experimental enclosures were made up of pool, riffle, and run habitats. I introduced a range of densities into these enclosures (0.1 to 1.25 fish m^{-2}; 2 years, 3 enclosures) and studied changes in habitat use of pool, riffle and run habitats with density. The field-based study was done using density-estimates of juvenile Atlantic salmon and brook trout (*Salvelinus fontinalis*). These density-estimates were obtained from 13-17 fixed stations that were sampled every summer over a period of

7-10 years, in Northeast Trepassey Brook and Freshwater River, Newfoundland, Canada. Sampling was done by electrofishing and seining. [see Chapter 4]

Results from the experimental study indicated that habitat use did change with population density, with relatively more parr in pools and fewer in runs at higher population densities. Temperature influenced parr distribution, with relatively more parr in runs and fewer in riffles and pools at higher temperatures. Parr distribution was primarily affected by the pool/riffle/run habitat contrast. Effects of population density and temperature on use of pool, riffle and run habitat were often as big as effects of the pool/riffle/run habitat contrast on fish distributions over the range of temperatures and densities observed. Results varied considerably, despite controlled experimental conditions.

Results from the field-based study were less clear. Only few of the results suggested possible density-dependent distribution processes: stations accommodating high parr densities at low parr population levels responded less to an increase in parr population level than those with low parr densities in both rivers; parr densities varied less over stations at higher population levels in Freshwater River. Density-dependent effects were much smaller than density-independent effects in shaping the salmonid distributions in both rivers.

I concluded that habitat selection by salmon parr is density-dependent and highly variable. Density-dependent responses are most likely due to small-scale spacing behaviour or territoriality, the effect of which may lead to density-dependent habitat use at the larger spatial scales of pools, riffles and runs, depending on the distribution of micro-habitats within these larger-scale habitats. From this, habitat use may vary with population level, especially when preferred small-scale positions are located in close vicinity. From this, habitat models are expected to vary with population level as well.

5.5. Implications of results and suggested future research

The importance of this thesis is not that I identified new and important scales for habitat models, as most of the results are quite in line with previous findings from other studies. This thesis made explicit the relative importance of various habitat selection behaviours and the scales at which they operate and shows that interpretation of results should be limited to the spatial scales over which the study was conducted. In addition, the multi-scale techniques I outlined allow for incorporating information from studies that operate at a variety of space and time scales into a comprehensive understanding of fish distribution processes. This will be of importance for the development of effective habitat models, especially within the context of scale-up, as outlined in Chapter 2.

An important finding of this thesis is that small-scale habitat models may predict quite well where fish will be, but that this does not imply that distributions at space-scales larger than those of the model can be described using these small-scale habitat models. However, this finding was based on data from two rivers only and should be repeated elsewhere, preferably within the context of higher-resolution flow-models than were possible in this thesis. Nevertheless, I do think that this problem of scale-up is very important to habitat modelling. Inability to translate information across scales indicates that a comprehensive understanding of distribution processes is lacking. This in turn indicates that it will be difficult or inappropriate to make management decisions to address large space-time scale problems from information obtained at a variety of much smaller space and time scales. Future research should be directed towards scale-up studies, using multi-scale approaches both in the temporal as well as in the spatial domain, and survey designs as suggested in Chapter 2.

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