HABITAT SELECTION IN BROOK TROUT,
Salvelinus fontinalis

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HABITAT SELECTION IN BROOK TROUT, *Salvelinus fontinalis*

by

Thomas W. Knight, B.Sc., M.Sc.

A thesis submitted to the School of Graduate Studies in partial fulfilment of the

requirements for the degree of

Doctor of Philosophy

Department of Biology

Memorial University of Newfoundland

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ABSTRACT

I combined field and laboratory experiments to test theories of density-dependent habitat selection and habitat preference in brook trout (*Salvelinus fontinalis*) from Cape Race, Newfoundland, Canada. My primary objective was to test whether theory allows us to correctly infer the behaviour of individuals in a population based only on field census data. Secondarily, I tested whether patterns of habitat use are influenced by the habitat composition of a river as indicated by models of evolution in heterogeneous landscapes.

Theories of density-dependent habitat selection predict that competitive interference for preferred sites should produce curvilinear or non-linear relationships in population density. I tested the theory by manipulating population densities of brook trout in four separate stream enclosures containing flat and riffle habitats. Regressions of density in the paired habitats (isodars) were curvilinear, suggesting that brook trout are site-dependent habitat selectors. Body-size distributions between flat and riffle habitats were consistent with the hypothesis of site pre-emption by larger, presumably dominant individuals. The isodar analysis, based only on density data, revealed the competitive behaviours that are believed to underlie brook trout distributions.

To test whether individual behaviour is consistent with the hypothesis of site dependence, I used observations of brook trout in an experimental stream tank. Brook trout were introduced into the stream tank over a range of population densities, at two flow treatments, and their precise location was mapped at consistent intervals over 2 to 3 days. My observations support the site-dependent model of habitat selection, confirming 3 *a priori* predictions: 1) brook trout recognise and respond to differences in site quality; 2) individuals select the highest quality site available; 3) larger, presumably dominant, individuals occupy the sites of highest quality. Observed habitat-selecting behaviour is consistent with behaviour inferred from population census data, further supporting ideas of density-dependent habitat selection and strengthening the theoretical basis of isodar analysis.

Finally, I tested whether habitat use differs between populations as predicted by theoretical models of evolution among heterogeneous landscapes. Habitat preferences of brook trout captured from two isolated rivers were observed in an experimental stream tank. Individuals from a river composed primarily of flat habitat used the flat portion of the stream tank significantly more than brook trout from a river composed primarily of riffle habitat. I conclude that habitat preference in salmonid fish may evolve partially in response to the landscape composition of a given watershed.

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Chapter 1

INTRODUCTION

1.1 OVERVIEW OF CURRENT THEORY

1.1.1 Density-Dependent Habitat Selection: Isodar Theory

Density-dependent habitat selection provides a mechanistic link between the optimal behaviour of individuals and their distribution across heterogeneous environments (Morris and Brown 1992, Morris 1994). It should be possible, therefore, to infer underlying optimal behaviours from the various density patterns they create (Rosenzweig and Abramsky 1985, Morris 1994, Rodríguez 1995). Interference by dominant or established individuals that prevents later-arriving individuals from occupying preferred sites, for example, should lead to a pre-emptive distribution across habitats (Pulliam 1988, 1996, Pulliam and Danielson 1991, Rodenhouse et al. 1997). But how do we distinguish among the various mechanisms of habitat selection based on field census data? One theory, using only graphs of density in different habitats and assuming ideal habitat selection (isodars; Morris 1987a, 1987b, 1988, 1989, 1990, 1992, 1994, 1995, 1997), links behaviour to patterns of abundance according to the shape of the resultant curve. An isodar is a line of equal fitness plotted in density space. It identifies the distribution of individuals among habitats for which no individual can profit by moving. Whereas scramble competition for resources produces straight-line isodars, pre-emptive interference should frequently produce curved isodars (Morris 1994).

Habitat selection models generally characterise a habitat in terms of its basic suitability (fitness) for an individual in the absence of competition and then assume that suitability decreases with increasing densities of conspecifics or heterospecifics competing for resources (Morris 1988, Rodríguez 1995). The negative effects of density on a given habitat selector, however, will differ depending on the competitive behaviour of individuals. An ideal distribution (e.g., Fretwell and Lucas 1970) will occur when habitat selectors distribute themselves between habitats such that an individual's expectation of fitness would be the same in all occupied habitats; no individual can profit from moving to another habitat. Exploitation (scramble) competition leads to an ideal-free distribution in which mean fitness among habitats is equalised and fitness declines for all individuals with each new entrant into the habitat (Fretwell and Lucas 1970, Fretwell 1972, Parker and Sutherland 1986, Łomnicki 1988, Rodenhouse et al. 1997). With interference competition (Fretwell and Lucas 1970, Fretwell 1972, Pulliam 1988, 1996, Pulliam and Danielson 1991, Rodenhouse et al. 1997), dominant or established individuals will reduce the fitness of new arrivals (ideal despotic or ideal pre-emptive distribution) such that "perceived" habitat suitability (i.e., habitat suitability discounted by the interference experienced by an individual) is equalised. Pre-emption is a special form of interference in which individuals compete for sites within habitats (e.g., territory, feeding station, refuge, etc.; Pulliam 1988, Danielson 1991, 1992, Pulliam and Danielson

1991), a mechanism known as site-dependent regulation (Rodenhouse et al. 1997). Dominant or early-colonising individuals occupy the best available sites and pre-empt their use by subordinates or late colonisers. Mean fitness will typically be unequal among habitats while the fitness of the lowest-ranking individual, or of the last arrival, is equal among habitats (Milinski and Parker 1991, Morris 1991, 1994, 1995, Pulliam and Danielson 1991, Rodríguez 1995, Rodenhouse et al. 1997).

There are at least three different distributions described for site-dependent habitat selection. Each of the three is characterised by the common principle that population distribution patterns are based on the relative availabilities of suitable sites among habitats, where sites represent relatively fine-grained (*sensu* Levins 1968) environmental variation within habitats. The ideal pre-emptive distribution (Pulliam 1988, 1996, Pulliam and Danielson 1991) incorporates the assumption that site occupation is determined only by the order in which sites are colonised. Habitats of high quality contain predominantly high-quality sites whereas habitats of lower quality contain predominantly low-quality sites. Site-dependent regulation (Rodenhouse et al. 1997) incorporates the argument that dominant individuals can also pre-empt sites from subordinates but that site qualities are not clearly linked to a particular habitat type. Site selection in a third, unnamed, distribution for *Pemphigus* aphids (Whitham 1980) is also based on dominance with strongly structured site-quality distributions within and among habitats.

In this thesis, I use the term "site dependence" to refer to the common principle in all three distributions; sites are occupied in the order of their suitability such that the quality of an occupied site, and the corresponding fitness of its current occupant, remains unchanged as population density increases and less suitable sites begin to fill. I use "pre-emption" and "pre-emptive interference" to describe the mechanism in which dominant or early colonising individuals occupy the most suitable site possible and exclude others from it.

All forms of habitat selection tend to produce isodars with distinct signatures (Morris 1994). Ideal-free and ideal-despotic habitat selectors are assumed to assess mean fitness at the habitat scale. Habitat suitability declines by a constant amount or proportion as new individuals enter the population. To illustrate, consider an ideal-free distribution in which habitat-selecting behaviour results from exploitation only. If we assume that each individual reduces habitat suitability in an equal and additive manner, and that fitness is determined by the consumption of limited resources, then

$$W_i = R_i - N_i\alpha_i \qquad (1)$$

where W_i is the expected fitness in habitat i, R is the availability of resources corrected by renewal rate, N is population density, and α is the *per capita* demand on resources. For a pair of habitats (1 and 2) with an ideal-free distribution, the mean fitness is the same in both habitats and

$$N_1 = \frac{R_1 - R_2}{\alpha_1} + \frac{\alpha_2}{\alpha_1}N_2 \qquad (2)$$

where equation (2) describes a straight-line isodar (e.g., Morris 1987a, 1988, 1989). Alternatively, when habitat suitability declines as a function of the resource-density to consumer-density ratio (Parker and Sutherland 1986, Milinski and Parker 1991, Kacelnik et al. 1992),

$$W_i = \frac{R_i}{(N_i \alpha_i)^{m_i}} \quad , \tag{3}$$

where *m* is an interference coefficient that specifies the reduction in an individual's intake rate with increased intraspecific density (Hassell and Varley 1969, Sutherland 1983, Milinski and Parker 1991, Morris 1992, 1994), the isodar is logarithmic

$$\log N_1 = \frac{\log R_1}{m_1} - \frac{\log R_2}{m_1} + \frac{m_2}{m_1}\log \alpha_2 - \log \alpha_1 + \frac{m_2}{m_1}\log N_2 \tag{4}$$

(Morris 1992, 1994, Rodríguez 1995). At low density, however, per capita resource use becomes unrealistically large in equation (3). Interference likely occurs over relatively small spatial scales. A more appropriate model incorporates interference into isodars using Beddington's (1975) equation with a Type II functional response (Holling 1959), where per capita resource consumption in habitat *j* is given by

$$\frac{R_{ej}}{N_j T} = \frac{a_j R_j}{1 + a_j h_j R_j + \theta_j t_j (N_j - 1)} \quad , \tag{5}$$

and R_e is the amount of resource consumed by *N* foragers, *T* is the total time allocated to foraging, *a* is the 'attack rate', *h* is the handling time per unit resource, θ is the encounter rate with other individuals, and *t* is the time lost from foraging by each encounter (Morris et al., in press). The resulting isodar is linear

$$N_1 = \frac{\omega_1(1+\omega_2 h_2) - \omega_2(1+\omega_1 h_1) + \omega_2 I_1 - \omega_1 I_2}{\omega_2 I_1} + \frac{\omega_1 I_2}{\omega_2 I_1} N_2 \qquad (6)$$

where ω_j = the maximum harvest rate ($a_j R_j$) and I_j = interference ($\theta_j t_j$) (from Morris et al. in press). The key point for my analysis of brook trout habitat selection is that straight-line and possibly logarithmic isodar solutions usually indicate habitat selection based on exploitation or interference competition at the habitat scale.

Site-dependent distributions represent a special case of interference that produces curved isodars. Imagine two habitats, A and B, each with a different distribution of site qualities (Figure 1.1, top left). Assuming that dominant (Whitham 1980, Rodenhouse et al. 1997) or early colonising (Pulliam and Danielson 1991) individuals attain exclusive access to the best sites, the quality of the poorest occupied site will be similar in both habitats (Pulliam and Danielson 1991). We can present the site-dependent solution graphically. For a given number of individuals, we draw a vertical line that represents sites of equivalent quality (the poorest occupied site in each habitat, Morris 1994; Figure 1.1, top left). All sites of equal or better quality (i.e., to the right of the vertical line) will be occupied. Solving the integral for each habitat to the right of the vertical line gives the number of sites occupied, equivalent to the density of individuals in each habitat. The site-dependent isodar is the plot of those densities across a range of population sizes (Figure 1.1, bottom).

An equivalent solution is to plot the quality of the poorest occupied site (vertical lines in Figure 1.1, top left) against population density in each habitat to create fitness-density curves (*sensu* Fretwell and Lucas 1970; Figure 1.1, middle). Horizontal lines identify sites of equivalent quality. The site-dependent isodar (Figure 1.1, bottom) emerges by plotting the paired density estimates where site quality is the same in both habitats (the intersection of horizontal lines with the fitness-density curves, Morris 1994). The site-dependent isodar (for this example) is markedly curved (Figure 1.1, bottom). Site occupancy based on either relative dominance or colonisation history would translate into the same curved isodars. One can imagine situations where site-dependent isodars are not curved, e.g., when there is no overlap in site qualities among habitats. The point is that when isodars are curved they imply site dependence.

1.1.2 Habitat Selection by Brook Trout

Habitat use by riverine salmonids depends on a number of factors, including the age and size of individuals, the time of day, and the season in which observations are taken. Fry, for example, often prefer lateral habitats that are shallow and have low water velocities (Chapman and Bjornn 1969, Cunjak and Green 1983, Cunjak and Power 1986, Moore and Gregory 1988, Baltz et al. 1991) while juveniles and adults tend to position themselves in deeper and faster water (Heggenes and Traaen 1988, Moore and Gregory 1988). In this thesis, I consider only daytime habitat selection by juvenile and adult brook trout during the summer growth season.

There is, in general, a dichotomy in the way researchers examine habitat selection of salmonids. One approach, at large spatial scales, helps identify limits to productivity. These "population" studies are frequently carried out at the scale of reaches or whole basins (e.g., Hankin and Reeves 1988, Baran et al. 1996, Herger et al. 1996, Inoue et al. 1997, Wiley et al. 1997) and often involve regressing salmonid population size against various habitat variables (e.g., Binns and Eiserman 1979, Bovee 1982). The second approach, and the one most relevant to this thesis, focuses on relatively small-scale distributions of fish regulated by the habitat-selecting mechanisms of individuals. Many studies conceptualise a river as a hierarchical series of microhabitats, alternatively referred to as "stations", "home stations", "positions", "holding positions", "lies", "focal points", and "territorial focal points" (Newman 1956, Kalleberg 1958, Keenleyside 1962, Jenkins 1969, Bachman 1984 and references therein), in which measures of key biophysical parameters can provide predictive models of microhabitat occupation by salmonids. Other studies consider a river more as a matrix of habitats (e.g., Rodríguez 1995). Population densities in each habitat are assumed to reflect the fishes' interpretation of the habitat's overall quality discounted by negative effects such as competition and predation.

Microhabitat studies provide insight into salmonid behaviour as it relates to proximate cues in the environment. They are useful for documenting specific habitat-selecting mechanisms but it is difficult to include all of the relevant variables influencing habitat use. Density-dependent studies at the habitat scale may better document habitat selection. They can account for a larger number of variables that control population distribution and they enable us to infer behaviours without directly observing individuals

(Rosenzweig and Abramsky 1985). Confirmation of inferred behaviours, however, may ultimately require detailed experimentation at the microhabitat scale.

At the habitat scale, brook trout are considered to be pool or flat dwellers (Gibson 1966, 1973, Griffith 1972, Cunjak and Green 1983, 1984, Peake et al. 1997), although in allopatry they generally utilise more riffle habitat than when in sympatry with other salmonids such as the Atlantic salmon (*Salmo salar*) or rainbow trout (*Oncorhynchus mykiss* formerly *Salmo gairdneri*) (Gibson 1973, Cunjak and Green 1983, 1984). Rodríguez (1995) explored the interspecific effect by constructing isodars for brook trout and Atlantic salmon cohabiting small streams in eastern Quebec. He was unable to detect habitat preference for flat or riffle in either species. He concluded that both species perceive and respond to differences between the two habitats only in the presence of heterospecifics. It appeared that interspecific competition, both exploitative and interference, was the primary factor structuring population distributions between flat and riffle habitats while intraspecific competition was relatively unimportant (Rodríguez 1995).

Intraspecific competition, however, is widely recognised as an important factor influencing salmonid distributions at the microhabitat scale (Kalleberg 1958, Jenkins 1969, Bohlin 1977, Fausch 1984, Heggenes 1988, Hughes and Dill 1990, Hughes 1992a, 1998, Hughes and Reynolds 1994, Nakano 1995a). Since riverine salmonids feed on drift, fitness is maximised when they maintain a position in slow moving water to minimise energy expenditure (Bachman 1984), but close to fast currents that transport more food per unit time (Fausch and White 1981, Fausch 1984, Hughes and Dill 1990, Hughes 1992a, 1992b). Other factors such as depth, streambed substrate, and cover are also considered important habitat parameters (e.g., Chapman 1966, Bohlin 1977, Scruton and Gibson 1993, Gibson et al. 1993, Heggenes 1996). Competition for resources within and among salmonid species is largely the result of interference between individuals for preferred microhabitats that typically manifests itself across a range of behaviours, from the defence of strict territorial mosaics (e.g., Kalleberg 1958) to loose hierarchical formations (e.g., Newman 1956). In all cases, size generally confers dominance within species (Newman 1956, Kalleberg 1958, Chapman 1962, Jenkins 1969, Bohlin 1977, Noakes 1980) and has important effects on competition between species (Newman 1956, Kalleberg 1958, Fausch and White 1986, Glova and Field-Dodgson 1995, Nakano 1995b). As a general rule, it appears that most salmonid species develop some form of size-structured distribution such that favoured microhabitats are occupied by larger, presumably dominant, fish (Fausch 1984, Heggenes 1988, Nakano 1995a, 1995b).

1.2 OVERVIEW OF STUDY

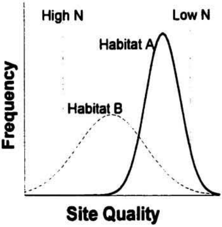
1.2.1 Outline of Experiments and Thesis

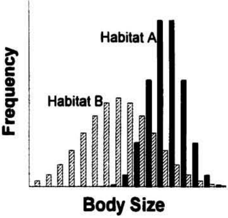
Review of the abundant literature on salmonids suggests that these fishes provide an ideal opportunity to test theories of habitat selection. This thesis develops that opportunity by examining whether isodars can correctly elucidate the habitat-selecting mechanisms of brook trout, based only on estimates of population density data in paired habitats. Chapter 2 outlines the creation of 4 brook trout isodars from experimental stream sections at Cape Race. This field study generates curved isodars, suggesting that brook trout are site-dependent habitat selectors. In Chapter 3, I test the hypothesis of site dependence with observations of individual behaviour in a laboratory stream tank. My results are consistent with site-dependent regulation by brook trout. I complete my experiments in Chapter 4 by examining whether interpopulation differences in habitat use exist and whether such differences could be related to the habitat composition of rivers. I conclude that brook trout populations may evolve adaptive habitat preferences that reflect the relative proportions of flat and riffle habitat available in their respective rivers. This latter component elevates the study of individual behaviour to the evolutionary scale. Finally, Chapter 5 offers a brief synthesis of the conclusions reached by this work.

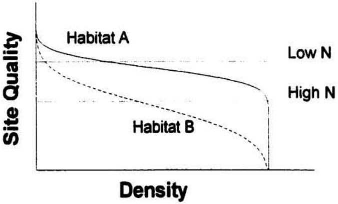
1.2.2 Study Area

Brook trout were collected and experiments were conducted in streams at Cape Race (an area of 120 km^2 bounded by 53°04' W, 53°16' W, 46°38' N, 46°45' N) located in southeastern Newfoundland, Canada (Figure 1.2). Cape Race is a region of coastal barren land with patches of stunted boreal forest traversed by a parallel series of short low-order streams. The streams are separated by very small (1-3 km) distances and share almost identical climatic conditions. Winters are relatively mild and summers are cool with frequent ocean fog (Banfield 1983). Mean annual air temperature at Cape Race is 4.3°C and mean annual precipitation 1379 mm (Environment Canada 1982). Brook trout are the only fish species present in many of the streams but several of the streams also have populations of Atlantic salmon, American eels (*Anguilla rostrata*), and / or small populations of threespine stickleback (*Gasterosteus aculeatus*). Brook trout densities range from 0.1 to 4.8 m^{-2} in different habitats of Cape Race rivers (Hutchings 1990, J.A. Hutchings and D.W. Morris unpublished data). Terrestrial predators are virtually absent from the area (Hutchings 1990) although some mink (*Mustela vison*) have been observed (R.J. Gibson personal communication). Detailed descriptions of rivers used in each experiment are included in the appropriate chapters.

Figure 1.1: A hypothetical example illustrating a site-dependent isodar. Top left: Distributions of habitat quality for habitats A and B. Vertical lines represent the poorest occupied sites for a given population size (high and low N in this example); all sites to the right should be occupied. If competition is resolved by a size-dependent hierarchy, as in brook trout, the same distributions of habitat quality will be reflected in the distributions of body size (top right). We can determine the site-dependent distribution of individuals between the two habitats from the corresponding relationships between site quality and fitness, plotted as cumulative frequency distributions (middle, after Morris 1994). When the population size is high (lower horizontal line), for example, the density in habitat A has stabilised at its maximum value (all sites occupied) whereas the density in habitat B is increasing (many sites of lower quality still to be occupied). Plotting the population density in habitat A against density in habitat B for a range of population sizes yields a curvilinear isodar (bottom) indicative of site-dependent habitat selection. If the isodar (bottom) is created from empirical data, we can infer the corresponding relationships between site quality and density (middle) and distributions of habitat quality (top left) to predict the distribution of body sizes (top right).


High N
Low N
Habitat A
Habitat B
Frequency
Site Quality


Habitat A
Habitat B
Frequency
Body Size


Habitat A
Low N
High N
Habitat B
Site Quality
Density

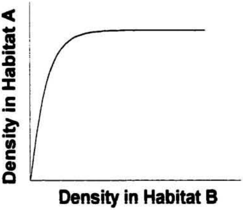
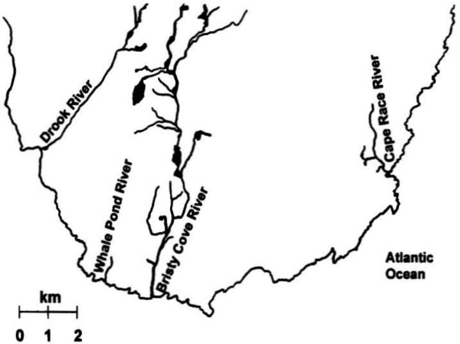

Density in Habitat A
Density in Habitat B

Figure 1.2: Rivers containing study populations of brook trout at Cape Race, Newfoundland, Canada.


Drook River
Whale Pond River
Bristy Cove River
Cape Race River
Atlantic Ocean
km
0
1
2

Chapter 2

DOCUMENTING DENSITY-DEPENDENT HABITAT SELECTION

2.1 INTRODUCTION

2.1.1 Overview

It is first necessary to determine whether brook trout are indeed density-dependent habitat selectors and whether isodar analysis is an appropriate vehicle for studying their habitat use. In this chapter I construct isodars from experiments in which I manipulated brook trout density in paired-habitat enclosures. All isodars are significant and curvilinear, suggesting that brook trout are density-dependent habitat selectors with pre-emptive selection behaviour. To test this conclusion, I use the curvilinear isodars to infer the distribution of site qualities between habitats and then compare it with the size distribution of brook trout between habitats. Results are consistent with the hypothesis of site dependence and suggest that the isodars have identified correctly the size-related dominance believed to occur in this species.

2.1.2 Empirical Isodars

Creating an empirical isodar requires simultaneous density estimates in paired habitats replicated over a range of population densities. Replication can be achieved by sampling geographically separate pairs of habitats (Morris 1987a, 1988, 1989, Rodríguez 1995, Knight and Morris 1996, Hansson 1996), or by experimentally manipulating densities in a single pair of habitats (Ovadia and Abramsky 1995, Abramsky et al. 1997). In this study, I manipulated population densities in enclosed habitat pairs. In total I created 4 separate stream enclosures, each containing a section of flat habitat adjacent to a section of riffle habitat.

Empirical isodars should allow me to infer behaviours from population density data. My goal was to determine whether brook trout isodars are straight or logarithmic, suggesting an ideal-free or ideal-despotic distribution respectively, or otherwise curved, suggesting site dependence. As such, the creation of isodars in this chapter represents a largely exploratory approach in which I use statistical analyses to determine best-fit lines to my experimental data.

2.1.3 Testing Isodar Theory with Field Census Data

Fitting census data to different isodars, while consistent with the theory, does not test its assumptions. To do so, we need to identify the nature of competition between individuals and we could do this by actually examining the predicted distribution of dominant individuals in the population. But how does one infer that distribution?

Consider the isodar example from Chapter 1 (Figure 1.1). Imagine that we have constructed the isodar from empirical data (as in Figure 1.1, bottom). We could then infer the associated fitness-density curves (Figure 1.1, middle) and, assuming that individuals are selecting habitat in an optimal manner, the underlying distributions of habitat quality (Figure 1.1, top left). The distribution of dominant individuals in the population should correspond to the distribution of site qualities in the two habitats, particularly in an experimental setting where all individuals are introduced to the habitats simultaneously. In this example, habitat A contains most of the highest quality sites so we would predict that the most dominant individuals would occupy habitat A. Habitat B, especially when density is high, should contain individuals with an overall lower mean but a greater variance in dominance.

Body size is one easily obtained measure commonly used as an index of relative dominance and one that is especially recognised as important in salmonid species (Newman 1956, Jenkins 1969, Chapman 1962, Noakes 1980, Bachman 1984, Heggenes 1988, Hughes 1992b, Keeley and Grant 1995, Nakano 1995a, 1995b), including brook trout. If brook trout obey an ideal-free distribution, mean fitness should be equal in both habitats; there would be no difference in mean body size between habitats. There should, however, be differences in body size when competition is resolved by interference. For an ideal despotic distribution, dominant individuals select the best quality habitat and exclude others from it. Habitat choice is based on mean site quality such that all individuals in the habitat with lower mean quality are subordinate. The largest mean body size should be found in the best habitat with virtually no overlap in the body-size distributions between habitats. Site dependence is based on a range of site qualities and, therefore, the distribution of dominant individuals among habitats. Inferred distributions of habitat quality (Figure 1.1, top left) predict that mean body size should be greater in the habitat with the highest mean site quality. Overlap in body size should frequently be extensive at all population sizes and the range of overlapping body sizes will tend to vary depending on the overlap in distributions of site quality (Figure 1.1, top right).

2.2 MATERIALS AND METHODS

2.2.1 Overview of Experimental Design

To construct isodars, I required simultaneous estimates of brook-trout population density in adjacent sections of flat and riffle habitat over a range of different densities. To generate these data I constructed four stream enclosures, each containing the two habitats, and experimentally modified population densities in a series of replicates. Each enclosure was treated as a separate experimental unit; one isodar was generated from each enclosure.

2.2.2 Study Rivers and Field Methods

Experiments were conducted in Bristy Cove and Drook Rivers at Cape Race (Figure 1.2). Both are short (13 and 7 km axial length respectively), shallow, and fast-flowing. With the exception of a few American eels, brook trout are the only fish present in Drook River (Hutchings 1990). Mean densities of brook trout older than age 1 in Drook River are approximately 0.8 m^{-2} (Gibson et al. 1993). Brook trout and Atlantic salmon are the primary species in Bristy Cove River but there is also a small population of threespine stickleback and a few American eel. Typical densities of salmonids over age 1 in Bristy Cove River range from 0.1 to 1.0 m^{-2} with a mean density of approximately 0.6 fish m^{-2} (J.A. Hutchings and D.W. Morris unpublished data).

I constructed two enclosures in each river, referred to as upper and lower sections (Table 2.1), by installing wire-mesh fences across side-channels. One enclosure per river contained an upstream section of flat habitat contiguous with a downstream section of riffle habitat while the second had the reverse arrangement (Table 2.1). All fish larger than 70 mm were removed from the enclosures with a backpack electrofisher (Model 12, Smith-Root Inc., Vancouver, Washington, USA) prior to experimentation.

For each replicate, brook trout ranging in size from 70-210 mm fork length were captured from the main river channel using the electrofisher, marked with an adipose-fin clip, and held in a flow-through container for at least one hour. To minimise the likelihood of using injured or unhealthy individuals, trout that did not appear to be swimming normally within a few minutes of the capture and marking procedure were not used in the experiment. Disturbance to trout station-keeping by electrofishing and / or fin clipping is minimal (Bohlin 1977). Wild trout recover from the physiological effects of electroshocking within 3-6 h and from behavioural modifications within 24 h, although there may be some depression in their aggression rates beyond 24 h (Mesa and Schreck 1989). All individuals were introduced simultaneously into the enclosure at the boundary of the flat and riffle habitats. The trout were left for three days to allow for exploration and selection of a preferred location. On the fourth day, a weighted barrier net was dropped between the flat and riffle habitats, dividing the enclosure in two. All trout were then removed from each habitat with the electrofisher. Fork length and weight were measured for each fish and population density was calculated for each habitat. All fish were then returned to the main stem of the river; individuals were used only once. This experimental protocol was repeated in each enclosure over a wide range of trout densities to ensure that I could identify density-dependent patterns that emerged. Replicates were performed in random order for each pair of enclosures. The number of replicates varied from 10 to 14 among enclosures because of time and logistical constraints (Appendix 1).

2.2.3 Habitat Measures and Analysis

To verify the assumption that riffle and flat habitats were indeed different, I measured habitat characteristics in a series of width transects spaced at 1m intervals along the length of each habitat. Water velocity at 2/3 depth (Flo Mate Velocity Meter, Marsh-

McBirney, Frederick, Maryland, USA), depth, and substrate size were measured at five stations equally spaced along each transect.

I contrasted mean values of each measure between flat and riffle in each enclosure individually, and for all enclosures combined. F_{max} tests for homogeneity of variance (Sokal and Rohlf 1995: 399-401) identified several comparisons in which variances were not equal between flat and riffle samples. I conducted, therefore, all of my statistical tests for habitat variables using empirical distributions from 1000 Monte Carlo randomisations. For each habitat variable, I created a test statistic by subtracting its mean value in riffle from its mean value in flat. Using a randomisation routine, I reassigned each measured value to a randomly selected station (Minitab Inc. 1992; Command SAMPLE) and recalculated a new value for the statistic. Repeating this procedure 1000 times provided an empirical distribution of values for the test statistic when the null hypothesis was true. I then compared my actual test statistic with the 1000 randomised values to determine its probability value (P). For a two-tailed test, the proportion of randomised values exceeding the absolute value of the test statistic is the probability that the difference could have arisen by chance alone.

2.2.4 Habitat Preference

Habitat preference can be determined from the isodar intercept of straight-line isodars (e.g., Morris 1988) but when transformations are applied to linearize curved isodars, the intercepts no longer have a direct biological interpretation. I examined habitat preference in brook trout, therefore, by documenting habitat use in all low-density replicates. My analysis included only replicates for which density in the enclosure was less than 0.5 individuals m^{-2}, a value lower than the mean density of salmonids older than age 1 for both rivers. For each replicate, I calculated the difference in population density between the two habitats by subtracting density in riffle from density in flat. I then calculated the mean difference in density between habitats and performed a t-test, for each enclosure, to determine whether flat or riffle habitat was used most frequently. Again, the number of replicates varied among enclosures. Although interference among individuals can render density a misleading indicator of habitat preference at larger population sizes (van Horne 1983), at lower population sizes interference is minimised and density likely provides a reasonable indication whether a clear preference exists at the habitat scale.

2.2.5 Isodar Analysis

I fitted a series of curves of population density in flat habitat against density in riffle for each of the enclosures to determine whether straight-line or curved isodar regressions provided the best fit to brook trout distributions. Regression models that I tested included both simple and polynomial models using both transformed and untransformed data (Appendix 2). All density pairs containing zero values were excluded from the isodar calculations. Dropping zero values is a standard procedure when calculating isodars (Knight and Morris 1996); it ensures that intercepts are not drawn to the origin by low-density replicates. This reasoning can be made clear by an example. Consider a pair of habitats in which ten trout normally occupy the flat before any move into the riffle (10, 0). A replicate with only two trout in which both occupied flat and none occupied riffle (2, 0) would artificially draw the isodar intercept toward the origin.

Using the results of least squares regression (SAS Institute 1990a; Procedures GLM, REG), I selected the best isodar model through a process of elimination by six screening criteria.

1) Reject all models with a P-value greater than 0.05.
2) Visually assess residuals plotted against predicted values, and reject all models with patterns indicative of an inappropriate model (Neter and Wasserman 1974, Draper and Smith 1981, Montgomery and Peck 1992, Sokal and Rohlf 1995).
3) Graph the relationships and reject those curvilinear and non-linear models that show erratic shifts in population distribution back and forth among habitats, even with small changes in overall population density. Note that this criterion was conservative in that it could only reject curved models.
4) Rank the remaining models by their R^2 values. When comparing models with transformed and untransformed data, calculate R^2 from backtransformed values [R_1^2 in Kvålseth (1985) and Scott and Wild (1991)].
5) Compare model likelihoods with the Akaike information criterion (AIC) (Akaike 1973, Sakamoto et al. 1986, de Leeuw 1992, Hilborn and Mangel 1997). AIC values are corrected for the number of parameters in a model so that a lower AIC

value equates directly to an improved fit for a given data set. In contrast to likelihood ratios, the AIC is suitable for non-nested models (Hilborn and Mangel 1997).

6) When all other criteria are similar, select the simplest model possible.

I calculated the isodar as the geometric mean solution for the best model (Ricker 1973, 1984, Krebs 1989: 458-464) to allow for independent variation in both the X and Y variables (e.g., Rodríguez 1995).

2.2.6 Testing the Isodar Analysis

The exploratory analysis yielded curved isodars reinforcing the *a priori* expectation that habitat selection by brook trout is based on site pre-emption by dominant or early-colonising individuals. I tested this interpretation by examining whether individuals assorted themselves between habitats based on the habitats' inferred site-quality distributions. Since all individuals were introduced into the enclosures simultaneously, I assumed that dominant brook trout would tend to occupy the best sites.

For each isodar, I inferred site-quality frequency distributions for flat and riffle habitats and then, using fork length as an index of relative dominance, I tested whether body-size distributions coincided with the predicted site-quality distributions for each habitat (Figure 1.1). For each enclosure, I used the inferred site-quality distributions to predict which of the two habitats would contain trout with largest mean body size and which habitat would have the greatest variation in body size. Analyses were conducted using fork-length data from the experimental replicate at highest density for which the most sites would be occupied. As test statistics I calculated the mean and the coefficient of variation in fork length for each habitat. Significant differences were identified using one-tailed tests based on 1000 Monte Carlo randomisations of the fork-length data. The algorithm made the null hypotheses (no differences between pairs of habitats) true by randomly assigning brook trout to flat or riffle, while still maintaining the same number of individuals in each habitat (Minitab Inc. 1992; Command SAMPLE). I repeated the procedure 1000 times to create an empirical distribution for each statistic from which I could calculate a P-value to test the null hypothesis of no difference.

2.3 RESULTS

2.3.1 Habitat

For each enclosure, and for all enclosures combined, Monte Carlo randomisations show that riffles were significantly shallower ($P<0.001$) and had significantly faster currents ($P<0.001$) than flat habitats (Table 2.2). With the exception of one enclosure (Drook Upper), substrate size did not vary between habitats (Table 2.2).

2.3.2 Habitat Preference

In all 4 enclosures, brook trout at low densities exhibited no significant preference for flat or riffle habitat (Table 2.3). Lack of habitat preference at low density suggests that ideal-free or despotic habitat selectors recognise no fitness difference between habitats. With pre-emption, on the other hand, a lack of habitat preference at low density suggests that individuals are selecting high-quality sites in both habitats.

2.3.3 Isodars

Significant isodar regressions described habitat use in each experimental enclosure. The best isodar model was different for each enclosure (a comparison of the linear, logarithmic and best-curved isodar solutions for each enclosure can be found in Table 2.4) but all were curved (Table 2.5, Figures 2.1 and 2.2).

Drook Lower: One of 14 replicates was not included in the analysis because it contained a zero value. A logarithmic model best fit the data (F=40.10, df=1,11, P<0.001, R_1^2 =0.54, AIC=-44.2; Table 2.5) although there was greater variance at higher densities (Figure 2.1). The linear model had arced residual patterns and relatively high AIC value (AIC=-21.1) indicating a poor fit to the data. Other curvilinear models provided good fits to the data (Table 2.4) but unrealistic trajectories in density among habitats. For example, one model showed density in riffle habitat increase from 0 to more than 2, then decline to 1.5, and increase again to 3, as density in flat increased from 0 to 3 m^{-2}.

Drook Upper: Two of 12 replicates were removed because of zero values. Linear, logarithmic, and curved models had acceptable distributions of residuals and realistic trajectories. The best-fit line (F=14.55, df=1, 8, P=0.005, R_1^2=0.65, AIC=-40.2; Table 2.5 Figure 2.1) and several other good models were all curvilinear. The linear model (F=12.34, df=1,8, P=0.008, R_1^2=0.61, AIC=4.5) provided a reasonable, but poorer, fit to the data while the logarithmic model (F=2.36, df=1,8, P=0.163, R_1^2=0.23, AIC=-8.5) was not significant at α=0.05 (Table 2.4).

Bristy Lower: Of 10 replicates none was removed for zero values. A curved model provided the best fit (F=73.06, df=1, 8, P<0.001, R_1^2=0.90, AIC=-24.4; Figure 2.2, Table 2.5) and four other curvilinear solutions provided good fits to the data. Linear (AIC=-17.2) and logarithmic (AIC=-20.3) models had poorly distributed residuals and relatively high AIC values indicating poor fits (Table 2.4).

Bristy Upper: Two of 13 replicates were removed for zero values. Several curvilinear models with multiple variables provided good fits to the data but were relatively complex compared with a simpler curvilinear model that was selected (F=56.3, df=1, 9, P<0.001, R_1^2=0.75, AIC=-41.3; Figure 2.2, Table 2.5). All of these models shared a very similar trajectory and showed minimal pattern in residual plots. Residual plots also showed a good fit for a sigmoidal curve. I discarded that model because of its relative complexity and the inability to generate reliable and comparable estimates for F- and P-values in non-linear regression (e.g. Jennrich 1995). Regardless, fitness-density curves and site-quality distributions were virtually identical for the non-linear and curvilinear solutions. Linear (AIC=-34.8) and logarithmic (AIC=-31.7) models had poorly distributed residuals and relatively high AIC values indicating poor fits (Table 2.4).

All isodars identified density differences between habitats at larger population sizes (Figures 2.1 and 2.2), despite the apparent lack of habitat preference at low density. This change in the distribution of individuals between habitats would be unlikely to occur in ideal-free or despotic habitat selectors, unless density itself somehow changes the quality of the habitats differentially. The more parsimonious interpretation is that site pre-emption, a form of interference competition, most probably controls the habitat distribution of brook trout.

2.3.4 Test of Isodar Analysis

Figures 2.1 and 2.2 illustrate the fitness-density curve and the distribution of habitat quality inferred from each isodar. Predictions of body-size distributions were tested using only the highest-density replicates to ensure that the maximum number of sites was occupied. Randomisation tests of the highest-density replicates confirmed the differences in mean body size predicted from habitat quality for all enclosures (Table 2.6, Figure 2.3). Distributions of habitat quality for Bristy Cove Upper suggested a larger mean body size for trout in riffle habitat, but the difference was expected to be very small. In fact, no difference in mean fork length was detected (P=0.976 for randomisation test of highest-density replicate; Table 2.6). Mean fork length in flat was greater than in riffle for all other enclosures ($P<0.01$ for all other enclosures; Table 2.6), as predicted from the distributions of habitat quality. Note that differences in mean body size between habitats are contrary to the expectation of the ideal-free distribution and also to the despotic distribution when, as is the case here, there is no preference for either habitat at low density.

The predicted variation in body size was confirmed at Bristy Cove Lower where the coefficient of variation for fork length in riffle habitat was significantly greater than in flat habitat (P=0.029, Table 2.6). Bristy Cove Upper also provided support for predicted variation (P=0.054, Table 2.6). Variation in size was also consistent with predicted differences between habitats in the Drook enclosures, although neither was significant at $\alpha=0.05$ (P=0.119, Table 2.6).

2.4 DISCUSSION

Curvilinear isodars suggest that brook trout distributions result from site pre-emption, a form of interference competition, thus providing evidence of site dependent habitat selection in this species. Body-size distributions between habitat pairs bolster this conclusion, suggesting that sites are pre-empted through size-related dominance. My isodar analysis also is consistent with behavioural studies of brook trout and other salmonid species. Prior residence (Jenkins 1969, Bohlin 1977, Glova and Field-Dodgson 1995, but see Newman 1956, Bachman 1984) and dominance-based competition (Newman 1956, Jenkins 1969, Bachman 1984, Heggenes 1988) are both recognised as primary determinants of site selection in salmonids, concordant with the site-dependent model of habitat use (Rodenhouse et al. 1997). In fact, what my isodar analysis reveals about habitat selection in brook trout probably comes as little surprise to those who study salmonid behaviour. This point emphasises one of my own. The isodar analysis allowed me to predict competitive interactions between individuals based only on population census data. Density-dependent habitat selection is a key process linking individual- and population-levels of ecological organisation (Rosenzweig and Abramsky 1985, Morris 1997).

Isodar analysis, with its emphasis on population density, should document the way that individual fish rank sites in the different habitats. The different shapes of my isodars indicate that there may be considerable variation in the distribution of site-qualities among habitats. All 4 isodars, however, do identify the importance of competitive interference and the lack of strong habitat preference at low population densities. Without a carefully replicated survey isodar (e.g., Rodríguez 1995) that examines monospecific brook trout distributions, it is difficult to determine whether my isodars document generalised habitat-selecting behaviour in flat and riffle or simply the distribution of favourable microhabitats in each enclosure.

Given spatial and temporal variability of stream environments, and the phenotypic and behavioural plasticity of salmonid species, it is likely that site dependence oversimplifies salmonid habitat selection. Theories of habitat selection, including site dependence, provide a theoretical context from which to examine issues of salmonid habitat use. First, they emphasise the important effects of conspecific density on the distribution of individuals between habitats. Second, they help to integrate studies of habitat selection at the scale of microhabitats or sites with those at the scale of habitats or reaches. Brook trout actively select and defend the highest-quality site available but their site choice is highly dependent on population density and perhaps other factors associated with the scale of habitats. Third, they suggest directions for future research that may allow us to model salmonid populations at a landscape scale (e.g., Danielson 1991, 1992, Pulliam and Danielson 1991, Dunning et al. 1992).

Was my experimental protocol suitable to detect the behavioural ecology of individuals? Brook trout were captured by electrofishing, introduced into a novel environment, given only 3 days to select preferred sites, and were then recaptured during daylight hours. First, although it is possible that individuals did not have sufficient time to explore fully the enclosures and so may not have acted in an entirely "ideal" (*sensu* Fretwell and Lucas 1970) manner, the enclosures were relatively small (Table 2.1) and it is likely that 3 days would be sufficient for a brook trout to evaluate a substantial portion of each habitat before selecting a site. Second, all individuals were used once only and all were treated the same within and among replicates. Third, although salmonids feed heavily in the early morning and late evening (e.g., Hoar 1942, Kalleberg 1958), they maintain feeding positions throughout daylight hours with little variation in their activity patterns (e.g., Bachman 1984). Fourth, replicates were run in a random order and all were performed in the same manner so that any patterns in population distribution that emerged must have resulted primarily from the interaction of brook trout at different population densities. Finally, the isodar regressions were all highly significant with minimal residual variation despite the short duration of the replicates. If brook trout were not exhibiting consistent habitat-selecting behaviour then population densities in flat and riffle habitats would be expected to fluctuate much more erratically, giving scattered data points instead of four significant regression lines. Sources of additional variation introduced by my experimental protocol would, if anything, make it less likely that I would find consistent and significant patterns in population distribution.

All isodar models for a given enclosure are directly comparable with each other. AIC values allowed me to rank the models regardless of the number of parameters they contained. The best models have the lowest AIC values. Despite testing a number of higher-order polynomials, all isodar equations that I selected were simple linear regression models with a single independent variable. Many polynomials were rejected because they described improbable fluctuations in population density among habitats. In all the models I selected, curvilinearity resulted from standard data transformations (Neter and Wasserman 1974, Draper and Smith 1981, Montgomery and Peck 1992, Sokal and Rohlf 1995), such that the linear, logarithmic, and curvilinear models in Table 2.4 are directly comparable. My ability to select the best model was further enhanced by calculating R_1^2 with backtransformed values.

It is of particular interest that I was able to test the isodar analysis using fork length as an estimate of relative dominance. I interpret the unanimous confirmation of predicted differences in mean body size between habitats (Table 2.6), and the partial agreement between observed and predicted variation in body size (Table 2.6), as support that the brook trout in the enclosures were distributed largely according to a dominance-based occupation of the most profitable sites available. Note, even though the results for the test of predicted variation in body size for Drook enclosures were not significant, all results are in the direction predicted by site-dependent habitat selection. Moreover, detailed observations in a stream tank confirmed three *a priori* predictions of the site-dependent distribution (Chapter 3). Newfoundland brook trout select some sites preferentially over others, sites are occupied in the order of their preference, and large fish occupy higher preference sites than do smaller fish (Chapter 3).

My findings contrast those of Rodríguez's (1995) isodar analysis of brook trout and Atlantic salmon demonstrating that intraspecific competition was not a significant factor controlling population distributions. There are at least three possible explanations for this discrepancy. First, Rodríguez (1995) had only 12 data points available to fit six model parameters. He notes that this lack of statistical power likely resulted in undetected intra- and interspecific effects (Rodríguez 1995). Second, intraspecific habitat preferences are most likely manifested when a species occurs at low densities and when heterospecifics are absent (Fretwell and Lucas 1970, Rosenzweig and Abramsky 1985, Rodríguez 1995). Third, my use of experimental enclosures removed much of the microhabitat variation inherent in sampling geographically separate habitats. This could mean that my analysis was better able to detect differences in density caused by competition.

Brook trout exhibited no strong preference for either habitat at low population densities suggesting that relatively high quality sites existed in both flat and riffle habitats in all of the enclosures. My study, together with the isodar analysis of Rodríguez (1995), contrasts the prevailing view that brook trout prefer pools or flats (Gibson 1966, 1973, Griffith 1972, Cunjak and Green 1983, 1984, Peake et al. 1997). This likely reflects the strong focus on density dependence inherent in isodar theory. Habitat preference is best determined at low population densities when potential interference is minimised. It is likely that flats contain a number of sites that are filled in order of their quality (Hughes and Dill 1990, Hughes 1992a, 1992b, Nakano 1995a, 1995b) relative to the quality of sites contained in neighbouring habitats. Three of my isodars do document an increased use of flat habitat at high densities that could easily be misinterpreted as a distinct preference for flats in field surveys. Instead, high densities of brook trout in flat habitats may reflect the adoption there of less aggressive, more active foraging groups associated with reduced current (Keenleyside 1962, Grant and Noakes 1987, 1988, McLaughlin et al. 1992, 1994, Biro et al. 1997). Stream-dwelling brook trout may adopt this behaviour at high densities when their expectation of net energy gain is greater with active foraging than with defence of a particular site in faster-flowing water. The population size for such a behavioural switch is likely to depend on the relative suitability of sites available in the stream and the densities of conspecific and heterospecific competitors.

My study supports theories of habitat selection as well as our ability to infer mechanisms of habitat selection from the patterns that they create (isodars). There is a clear and reciprocal linkage between the optimal behaviour of individuals and their resulting distribution across habitats.

2.5 SUMMATION

In this chapter I have applied isodar theory to document density-dependent habitat selection of brook trout. I used isodars to infer individual behaviour from field census data gathered from 4 experimental enclosures. Consistent with published accounts of stream salmonid behaviour, curvilinear isodars suggest that brook trout are site-dependent habitat selectors. Body size distributions of brook trout support this conclusion but my predictions rely upon inferred site-quality distributions. I have not confirmed my conclusions with behavioural observations. To further test isodar theory, in the next chapter I test the hypothesis of site dependence by observing individual brook trout in an experimental stream tank.

Table 2.1: Characteristics of habitats contained in experimental stream enclosures at Cape Race, Newfoundland.

River	Enclosure	Habitat	Position	Length (m)	Area (m^2)
Drook	Lower	Flat	Downstream	16.3	52.2
		Riffle	Upstream	15.9	30.4
	Upper	Flat	Upstream	8.4	27.2
		Riffle	Downstream	8.5	13.7
Bristy Cove	Lower	Flat	Downstream	12.2	26.9
		Riffle	Upstream	11.7	24.3
	Upper	Flat	Upstream	13.9	46.4
		Riffle	Downstream	14.5	21.7

Table 2.2: Habitat characteristics of flat and riffle for experimental stream enclosures at Cape Race, Newfoundland. Mean values ± standard errors are shown for water depth, water velocity, and substrate size in each enclosure, and for all enclosures pooled. P-values were calculated from 1000 Monte Carlo randomisations and indicate whether differences between flat and riffle are significant.

Measure	**Location**	**Flat (±SE)**	**Riffle (±SE)**	**P**
Water Depth	Drook Lower	24.4 (±1.29)	10.6 (±0.50)	<0.001
(cm)	Drook Upper	16.2 (±0.77)	8.6 (±0.49)	<0.001
	Bristy Lower	18.7 (±0.94)	7.2 (±0.68)	<0.001
	Bristy Upper	17.0 (±1.36)	9.1 (±0.76)	<0.001
	All	19.5 (±0.64)	9.0 (±0.33)	<0.001
Water Velocity	Drook Lower	2.4 (±0.29)	15.4 (±1.51)	<0.001
(cm s^{-1})	Drook Upper	5.8 (±1.15)	18.0 (±1.68)	<0.001
	Bristy Lower	4.3 (±0.42)	11.3 (±1.53)	<0.001
	Bristy Upper	1.5 (±0.32)	9.4 (±1.70)	<0.001
	All	3.2 (±0.26)	13.2 (±0.84)	<0.001
Substrate Size	Drook Lower	13.1 (±1.12)	12.6 (±1.03)	0.745
(cm)	Drook Upper	4.5 (±0.70)	8.0 (±0.77)	<0.001
	Bristy Lower	12.8 (±1.34)	15.6 (±1.43)	0.155
	Bristy Upper	20.5 (±2.31)	22.6 (±2.29)	0.547
	All	13.7 (±0.88)	15.4 (±0.87)	0.183

Table 2.3: Mean difference in brook trout population density (trout m^{-2}) between flat (N_f) and riffle (N_r) habitats for all replicates at low density (less than 0.5 trout m^{-2}) in the Cape Race stream enclosures. T-tests indicate that the density differences between habitats are not significant for any of the enclosures. Brook trout show no significant preference at these densities for flat or riffle habitat.

Location	**df**	**$N_f - N_r$ (± S.E.)**	**t**	**P**
Drook Lower	7	0.05 (± 0.03)	1.58	0.158
Drook Upper	5	0.19 (± 0.08)	2.26	0.074
Bristy Cove Lower	4	0.19 (± 0.08)	2.19	0.094
Bristy Cove Upper	7	0.03 (± 0.04)	0.69	0.515

Table 2.4: A comparison of the linear, logarithmic and best-curved isodar solutions for the four brook trout enclosures at Cape Race, Newfoundland. The best model relating trout density in flat (N_f) to that in riffle (N_r) was chosen using six screening criteria outlined in section 2.2.5. R_1^2 was calculated from backtransformed values to ensure comparability between models. Patterns in residuals were classified as acceptable (A), when there was no strong pattern in plots of residuals, or not acceptable (NA) together with a description (arc, bowl) of the pattern observed in the residuals plot. The Akaike information criterion (AIC) values provided a measure of the model's likelihood. The model with the lowest AIC value indicated the best fit for each enclosure. Curved isodar plots were also classified as realistic (R) or not realistic (NR). Models were discarded as not realistic if they described a trajectory with large shifts in density back and forth among habitats. Note that multiple models yield acceptable and realistic results for Drook Upper and Bristy Cove Upper (see section 2.3.3).

MODEL	F	df_n	df_d	P	R_1^2	RESID	AIC	ISO
DROOK LOWER								
$N_f=\beta_0+\beta_1 N_r+\varepsilon$	8.37	1	11	0.015	0.43	arc-NA	-21.1	
$\log N_f=\beta_0+\beta_1 \log N_r+\varepsilon$	**40.10**	**1**	**11**	**<0.001**	**0.54**	**A**	**-44.2**	
$\log N_f=\beta_0+\beta_1 N_r+\beta_2 N_r^2+\varepsilon$	27.79	2	10	<0.001	0.72	A	-46.7	NR
DROOK UPPER								
$N_f=\beta_0+\beta_1 N_r+\varepsilon$	12.34	1	8	0.008	0.61	A	4.5	
$\log N_f=\beta_0+\beta_1 \log N_r+\varepsilon$	2.36	1	8	0.163	0.47	A	-8.5	
$N_r=\beta_0+\beta_1 N_f^2+\varepsilon$	**14.55**	**1**	**8**	**0.005**	**0.65**	**A**	**-40.2**	**R**
BRISTY COVE LOWER								
$N_f=\beta_0+\beta_1 N_r+\varepsilon$	31.67	1	8	<0.001	0.80	arc-NA	-17.2	
$\log N_f=\beta_0+\beta_1 \log N_r+\varepsilon$	18.13	1	8	0.003	0.65	arc-NA	-20.3	
$N_f=\beta_0+\beta_1 \log N_r+\varepsilon$	**73.06**	**1**	**8**	**<0.001**	**0.90**	**A**	**-24.4**	**R**
BRISTY COVE UPPER								
$N_f=\beta_0+\beta_1 N_r+\varepsilon$	47.37	1	9	<0.001	0.84	bowl-NA	-34.8	
$\log N_f=\beta_0+\beta_1 \log N_r+\varepsilon$	18.12	1	9	0.002	0.72	bowl-NA	-31.7	
$\log N_f=\beta_0+\beta_1 N_r+\varepsilon$	**56.30**	**1**	**9**	**<0.001**	**0.75**	**A**	**-41.3**	**R**
$N_f=\dfrac{\beta_0}{1+e^{-\beta_1(N_r-\beta_2)}}+\varepsilon$						A		R

Table 2.5: Analysis of variance for best-fit isodars of brook trout density in flat (N_f) and riffle (N_r) habitats from all stream enclosures at Cape Race, Newfoundland. All isodars were calculated with geometric mean regression. Note that all regressions are highly significant and curvilinear.

DROOK LOWER: $\log N_f = -0.15 + 0.58 \log N_r$

Source	df	Mean Square	F	P
Model	1	1.16	40.10	<0.001
Error	11	0.03		
Total	12			

DROOK UPPER: $N_r = 0.17 + 0.02 N_f^2$

Source	df	Mean Square	F	P
Model	1	0.22	14.55	0.005
Error	8	0.02		
Total	9			

BRISTY COVE LOWER: $N_f = 2.16 + 1.74 \log N_r$

Source	df	Mean Square	F	P
Model	1	5.35	73.06	<0.001
Error	8	0.07		
Total	9			

BRISTY COVE UPPER: $\log N_f = -0.88 + 1.07 N_r$

Source	df	Mean Square	F	P
Model	1	1.12	56.30	<0.001
Error	9	0.02		
Total	10			

Table 2.6: Comparison of mean trout size and variation in trout size between flat and riffle habitats for all stream enclosures at Cape Race, Newfoundland. Distributions of habitat quality (Figures 2.1 and 2.2, right) were used to predict which habitat should contain the largest trout and which should have maximum variation in trout size. P-values represent one-tailed tests of the predictions based on empirical distributions from 1000 Monte Carlo randomisations. Top: Mean fork length as index of trout size. Observed fork lengths were consistent with predicted size distributions in all enclosures. The P-value for Bristy Cove Upper (*) is based on a two-tailed test and supports the prediction of no difference in mean fork length between the two habitats. Bottom: Coefficient of variation for trout fork length as an index of variability in dominance. Although only Bristy Cove Lower yielded significant differences between habitats, all other observations are consistent with the qualitative predictions identified in the "prediction" column.

MEAN FORK LENGTH (mm)

River	Enclosure	Prediction	Flat (n)	Riffle (n)	P
Drook	Lower	Flat > Riffle	107.1 (98)	96.3 (56)	<0.001
	Upper	Flat > Riffle	117.6 (142)	97.2 (9)	0.005
Bristy Cove	Lower	Flat > Riffle	121.3 (61)	102.7 (31)	<0.001
	Upper	Flat ≤ Riffle	117.2 (68)	117.1 (19)	*0.976

COEFFICIENT OF VARIATION FOR LENGTH

River	Enclosure	Prediction	Flat (n)	Riffle (n)	P
Drook	Lower	Flat > Riffle	22.7 (98)	19.7 (56)	0.119
	Upper	Flat < Riffle	20.6 (142)	24.8 (9)	0.119
Bristy Cove	Lower	Flat < Riffle	12.9 (61)	16.8 (31)	0.029
	Upper	Flat > Riffle	24.1 (68)	16.9 (19)	0.054

Figure 2.1: Brook-trout isodars from Cape Race, Newfoundland for two enclosures on Drook River (left) with inferred fitness-density curves (middle), and expected distributions of habitat quality (right). Isodar densities are calculated as the number of trout m^{-2}. Density pairs containing zero values are shown in the isodar plots but were not used to estimate the regression lines. Both isodars are curvilinear (Table 2.5) suggesting site-dependent habitat selection. The inferred distributions of habitat quality were used to predict differences in body size between habitats.

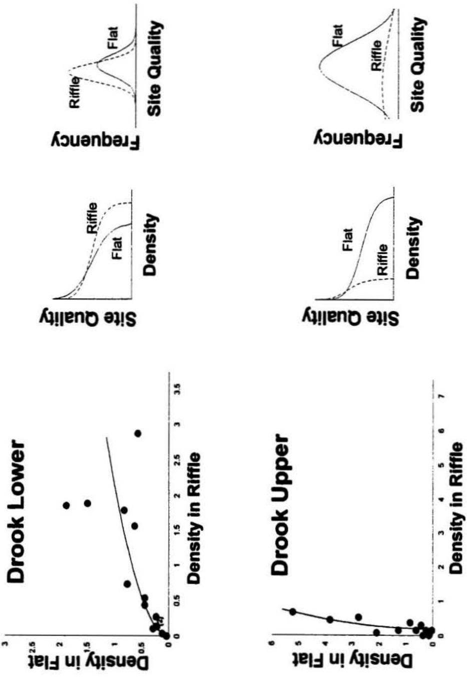

Drook Lower
Density in Flat
0
0.5
1
1.5
2
2.5
3
Density in Riffle
0
0.5
1
1.5
2
2.5
3
3.5
Drook Upper
Density in Flat
0
1
2
3
4
5
6
Density in Riffle
0
1
2
3
4
5
6
7
Site Quality
Density
Flat
Riffle
Frequency
Site Quality
Riffle
Flat
Site Quality
Density
Flat
Riffle
Frequency
Site Quality
Flat
Riffle

Figure 2.2: Brook-trout isodars from Cape Race, Newfoundland for Bristy Cove River enclosures (left) with inferred fitness-density curves (middle), and expected distributions of habitat quality (right). Isodar densities are calculated as the number of trout m^{-2}. Density pairs containing zero values are shown in the isodar plots but were not used to estimate the regression lines. The curvilinear isodars suggest site-dependent habitat selection. The inferred distributions of habitat quality were used to predict differences in body size between habitats.

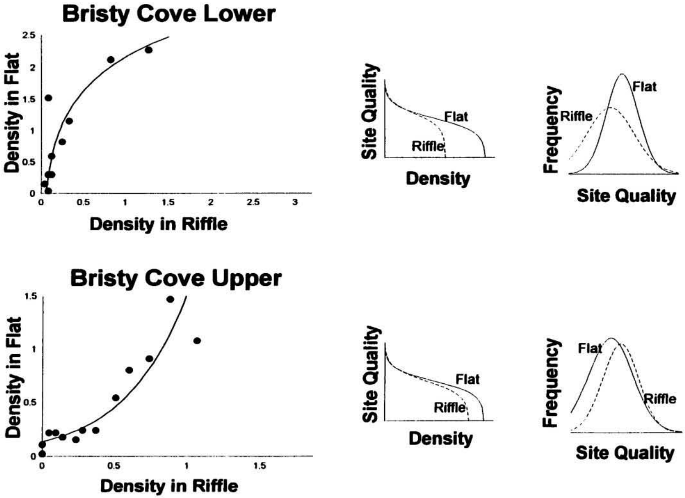
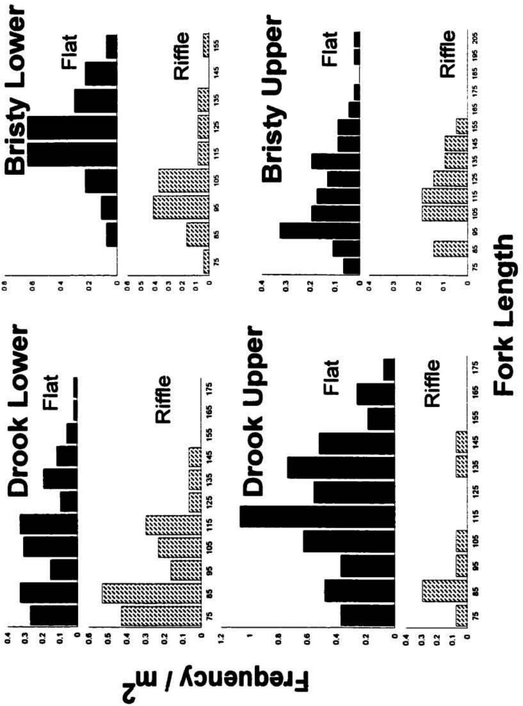

Bristy Cove Lower
Density in Flat
2.5
2
1.5
1
0.5
0
0
0.5
1
1.5
2
2.5
3
Density in Riffle
Site Quality
Flat
Riffle
Density
Frequency
Riffle
Flat
Site Quality
Bristy Cove Upper
Density in Flat
1.5
1
0.5
0
0
0.5
1
1.5
Density in Riffle
Site Quality
Flat
Riffle
Density
Frequency
Flat
Riffle
Site Quality

Figure 2.3: Body-size distributions of Cape Race brook trout in flat and riffle habitats of each enclosure, taken from replicates at highest population density. If brook trout are ideal pre-emptive habitat selectors, then these body-size distributions are predicted to approximate the habitat-quality curves (Figures 2.1 and 2.2; right) for each enclosure. Statistical tests of differences in mean body size and variation in body size are given in Table 2.6.


Drook Lower
Flat
Riffle
Drook Upper
Flat
Riffle
Bristy Lower
Flat
Riffle
Bristy Upper
Flat
Riffle
Frequency / m^2
Fork Length

Chapter 3

TESTING THE HYPOTHESIS OF SITE-DEPENDENT REGULATION

3.1 INTRODUCTION

3.1.1 Overview

In Chapter 2 I constructed isodars from field data at Cape Race. The isodars were curved, suggesting that brook trout behave as site-dependent habitat selectors. In this chapter, I use density-dependent habitat selection theory to make three *a priori* predictions about the habitat-selecting behaviour of brook trout, and then test those predictions by observing Cape Race brook trout in an experimental stream tank. My results support the hypothesis of site dependence in this species and highlight the link between competitive interactions at the individual level and population distribution patterns. Confirmation of habitat-selecting behaviour inferred from population census data further supports isodar theory.

3.1.2 Testing Isodar Theory

Recall that all four best-fit isodar solutions from Chapter 2 were curvilinear, implying site-dependent habitat selection (Morris 1994). Site pre-emption is consistent with published accounts of dominant (e.g., Jenkins 1969, Heggenes 1988, Hughes 1992a) or resident (Jenkins 1969, Heggenes 1988) salmonids maintaining feeding sites (e.g., Fausch and White 1981, Bachman 1984, Fausch, 1984) or territories (e.g., Gerking 1953, Lindroth 1954, Miller 1957, Kalleberg 1958, Griffith 1972, McNicol and Noakes 1981, Grant and Noakes 1988, Grant et al. 1989, Grant and Kramer 1990) that maximise potential energy profit (Hughes and Dill 1990). If brook trout are indeed site-dependent habitat selectors, then the following three predictions should be supported:

1. Brook trout should occupy some sites preferentially to others.
2. Individuals should fill sites sequentially in order of relative site quality.
3. When all animals have simultaneous access to sites of varying quality, dominant, larger brook trout should occupy the highest quality sites.

To develop tests for the three predictions, imagine that we have a section of stream containing flat and riffle habitats with variable depth, cover, and current velocity. Assume that we can identify individual sites based on spatial co-ordinates of a grid system in the stream. Each site would have a particular quality based on its suite of microhabitat characteristics. Imagine then that we can introduce trout at different population densities, observe the habitat-selecting behaviour of individuals, and record their exact locations at regular intervals throughout several days.

We can test the first 2 predictions by comparing the actual distribution of trout in our stream to a large number of computer-generated random distributions at the same sample size. To test prediction 1, that brook trout occupy some sites preferentially to others, we can compare the frequency distribution of site use for a given experiment with the random distributions. If brook trout exhibit non-random site use then some sites should be used often while others are seldom or never used, giving a frequency distribution with a large coefficient of variation (Figure 3.1, bottom). Otherwise, if trout exhibited no site preference, frequency of use would be similar amongst all sites resulting in a frequency distribution with a relatively small coefficient of variation (Figure 3.1, top). A coefficient of variation that was greater than 95% of the coefficients from the random distributions would demonstrate a significant preference for some sites over others.

Testing prediction 2 requires that we manipulate population densities. A single fish in the stream should occupy the best sites. At higher population densities dominant fish would still occupy the highest-quality sites while subordinate fish would be forced into lower-quality sites, particularly if fish were introduced into the stream simultaneously at the beginning of a replicate. If brook trout fill sites sequentially, in order of relative quality, then high-quality sites should be ranked highly (used frequently) regardless of density while lower-quality sites should be used only at higher densities. There should be a high degree of concordance in the ranks given to sites by trout at different densities. We can calculate the degree of agreement amongst different density treatments by calculating Kendall's coefficient of concordance (Zar 1996). As above, if Kendall's coefficient for the experiment was greater than 95% of the coefficients calculated for our randomised distributions, then there is evidence that brook trout fill sites in order of relative quality.

Testing prediction 3, that larger brook trout occupy the highest quality sites, requires that we establish a significant, positive relationship between trout size and the quality of site it occupies. If we measure site quality as the number of times a site was occupied during the course of the experiments, then the largest trout should be found consistently in the sites that were most commonly occupied.

Our test of site dependence relies on the appropriateness of the null model. In comparing actual distributions to randomised ones, we make two implicit assumptions: 1) brook trout would potentially use any of the sites identified in the stream section, and 2) individuals could move between any two sites in the section during the interval between observations. If we assume that population size is low relative to the number of sites available, then it is possible that almost all distributions could appear non-random when compared to a the null model with all sites included. For this reason, I develop a null model whose randomisation routine includes only those sites that were actually occupied in a given replicate. Assumption 1 of the null model, therefore, becomes that we expect brook trout would use any of the sites observed to be occupied in a given replicate.

3.2 METHODS

3.2.1 Experimental Methods

Brook trout were captured from Cape Race River (46°40' N, 53°05' W; Figure 1.2) with a Smith-Root (Vancouver, Washington, USA) Model 12 backpack electrofisher and transported to a large holding tank at the indoor aquarium facility of the Department of Fisheries and Oceans, St. John's, Newfoundland. Cape Race River is a short (3 km axial length), shallow, and fast-flowing stream. Mean density of brook trout older than age 1 is approximately 0.3 m^{-2} (Hutchings 1990). The population is comprised of individuals up to four years of age with mean fork lengths ranging from 84.5 to 160.0 mm for 1+ to 4+ age classes respectively (Hutchings 1990). A small population of threespine stickleback also inhabits the river (Hutchings 1990).

Experiments were conducted in a 14.2 m^2 flow-through stream tank (Figure 3.2). The stream tank contains three distinct sections: one flat section that is relatively slow-flowing and deep, and two riffle areas that are shallow with moderate to fast current (Table 3.1). Substrate was coarse gravel throughout. I used white gravel to divide the tank into 164 30x30 cm squares. Each square was considered an individual site. I distributed 30 opaque-grey Plexiglas covers on the substrate throughout the stream tank. The covers were C-shaped. The base was buried in gravel, leaving a 15 cm high vertical wall that supported a 20 cm long overhead ceiling. The covers were oriented with their open side facing upstream. They varied in width from 2.5 to 12.5 cm, thereby providing different amounts of current break and overhead cover. Variation in depth, current, and cover provided a range of site qualities from which trout could choose.

Single replicates were conducted at 6 densities (1, 4, 8, 12, 16, 20 fish) and at two depths (shallow and deep) giving a total of 12 experimental treatments. Individual trout were used in 1 treatment only. For each treatment, trout were drawn equally from 4 size classes (90-102.49, 102.5-114.99, 115-127.49, 127.5-139.99 mm fork length), a range that included trout from 1+ to 3+ years of age (Hutchings 1990). Individuals were measured, weighed, and marked with small coloured beads attached behind their dorsal fin with nylon suture material. To ensure consistency among replicates, all food was withheld during the experimental period. For each replicate all fish were simultaneously introduced into the flat section of the stream tank and left for one day to explore. Each day during the second, third, and fourth days, the exact location of each individual was noted every 15 min over a 6 hr period. Observations for treatments with 20 fish were taken only every 1/2 hr. I classified individuals as moving, stationary, or positioning (maintaining a general position but moving about that position slightly). Two treatments, 4 and 20 fish in shallow water, were discontinued after the third day because of mechanical problems.

3.2.2 Statistical Analysis

Did brook trout exhibit non-random site occupancy? For each of the 12 treatments, I created a frequency distribution summarising site use in the stream tank over the period of observation (SAS Institute 1990c; Proc FREQ), excluding all sites that were not occupied. I then calculated the corresponding coefficient of variation for each distribution (SAS Institute 1990c; Proc SUMMARY). Exclusion of unoccupied sites provided a conservative estimate of variation because unoccupied sites were assumed to be unavailable / unacceptable to the trout. I then repeated this procedure with 1000 randomised replicates of the original experimental treatments. Trout were assigned to randomly selected sites by replacing observed site selections with randomly generated site numbers selected from a univariate normal distribution (SAS Institute 1990b; Proc DATA, Command RANUNI) containing only the site numbers occupied for that replicate in the original data set. To determine whether the observed coefficient of variation was significantly larger than predicted by chance alone, I determined the number of times the coefficient from a random distribution was greater than or equal to that of the actual distribution.

An observed coefficient of variation that is larger than coefficients from random distributions would always indicate non-random site use. Exclusion of unoccupied sites in my analyses, however, introduces the risk that very strong site selection could result in a distribution with a small coefficient of variation, i.e., a few sites used many times and no other sites occupied. In this case, an unambiguous test for non-random site use would require inclusion of all sites in the stream tank.

Did individuals fill sites sequentially in order of relative site quality? Separate analyses were conducted for shallow- and deep-water replicates, allowing me to control for possible changes in site quality associated with the different water-depth treatments. Analyses were based on the total number of sites occupied over the 6 density treatments for each depth. The relative qualities of the sites were ranked for each of the 6 density treatments based on the number of times a fish was observed occupying a given site (SAS Institute 1990c; Proc RANK). Ties were assigned the mean of corresponding ranks such that the sum of all ranks was the same in each of the 6 density treatments for a given depth. This provided a site by density-treatment matrix of site ranks for each of shallow and deep- water treatments. I used the resulting matrix to calculate Kendall's coefficient of concordance, using the correction for tied ranks (Zar 1996, p. 437-441). Kendall's coefficient of concordance would have a maximum value of 1 if all sites were ranked in the same order at all densities, and a minimum value of 0 if there was no agreement in site rankings among density treatments. I then repeated this procedure with 1000 randomised data sets and compared the actual and randomised values as above. Randomisations were based on two different null models. The first model is identical to the one described above used to calculate the coefficient of variation. Trout were assigned to randomly selected sites by replacing observed site selections with randomly generated site numbers. In the second null model the frequencies of site use within replicates (i.e., site ranks) were reassigned to different sites in a Monte Carlo randomisation. In this more conservative null model I assume that site use can be non-random, testing only whether brook trout rank sites in the same order among replicates.

Did larger brook trout occupy the highest quality sites? The analyses of brook trout size included only observations for which trout were classified as stationary or positioning. Moving individuals could not be considered as occupying a site. Within each treatment, fish were ranked based on fork length; ties were broken by fish mass (SAS Institute 1990c; Proc RANK). As above, sites were ranked based on the number of times they were occupied. Overall site rank was calculated separately for shallow- and deep-water replicates as the mean of ranks assigned to a site in the 6 different density treatments (SAS Institute 1990c; Proc RANK, Proc SUMMARY). For each fish, I then determined the mean rank of all sites the individual occupied throughout the course of the experiment (SAS Institute 1990c; Proc SUMMARY). Finally, I tested whether larger brook trout occupy the highest quality sites. I used a randomised complete block design (RCBD) in which the mean rank of all occupied sites was explained by fish ranked by body size, blocked for water treatment (SAS Institute 1990c; Proc GLM). Residuals of the RCBD were normally distributed so it was not necessary to use nonparametric statistics to test these ranked values.

3.3 RESULTS

Brook trout exhibited non-random site use. Even with a conservative null model incorporating only those sites actually occupied, in all 12 treatments the coefficient of variation for the actual data was greater than that for the corresponding 1000 random distributions (Table 3.2). Site use, therefore, is decidedly non-random ($P<0.001$); trout were using particular sites in the stream tank much more frequently than others. Figure 3.3 provides an illustration of the actual distribution of trout (bottom) compared with one of the randomised distributions (top) for the treatment with shallow water and 8 fish. It is striking to note the magnitude of the non-random pattern. Actual coefficients of variation were approximately 2 to 5 times greater than the largest coefficients of variation generated from the random distributions (Table 3.2).

Brook trout used the same set of preferred sites in different experiments. Kendall's coefficient of concordance was 0.45 for deep-water replicates and 0.56 for shallow-water replicates (Table 3.3). For both null models, none of the coefficients of concordance calculated from the corresponding randomised distributions was greater than or equal to these values ($P<0.001$). The largest coefficients of concordance from the conservative null model were approximately 3/4 the value of the coefficients calculated from the actual data (Table 3.3) while those of the less conservative model were somewhat less (0.29 for both shallow and deep water replicates). Brook trout appear to recognise and show preference for the same sites, regardless of density.

Larger brook trout occupied the highest quality sites. Brook trout fork length was a significant predictor of the mean rank of all sites occupied by an individual trout (Tables 3.4, 3.5; F=3.45, df=19, 121, P<0.001). Larger, presumably higher-ranking trout occupied the highest quality sites (Figure 3.4).

3.4 DISCUSSION

Habitat selection theory provides us with the opportunity to infer optimal behaviours from population distributions. It is particularly encouraging, therefore, that my laboratory experiments have supported the theoretical isodar models developed by Morris (1994) and the interpretation of empirical isodars constructed for Cape Race brook trout (Chapter 2). The results are even more striking when one considers the dynamic nature of lotic systems, the phenotypic plasticity of salmonids, and the influence of processes other than density-dependent habitat selection on population distributions. To my knowledge, only one other study has documented optimal behaviour of individuals to test competitive interactions inferred from an isodar. Foraging patterns of deer mice (*Peromyscus maniculatus*), measured by giving-up densities of resources (GUD's), were shown to be consistent with the ideal-free distribution (Morris 1997). Results of these two studies demonstrate that population distributions among habitats are linked to individual competitive behaviours through density-dependent habitat selection.

Habitat selection behaviour in brook trout is consistent with the principal aspects of site dependence (Pulliam 1988, Pulliam and Danielson 1991, Rodenhouse et al. 1997). Brook trout recognise sites of different quality (prediction 1) and attempt to occupy the best site possible (prediction 2), given their presumed relative position in a dominance hierarchy (prediction 3). My results are similar to those of Bohlin (1977) who found that 1+ sea trout occupied the most suitable sites while smaller 0+ individuals were forced into less suitable sites as population density was experimentally increased. Although I did not test whether preferred sites conferred higher fitness to their occupants, other studies (e.g., Fausch 1984, Hughes 1992b, Nakano 1995a) have demonstrated that salmonids occupying preferred sites have better access to drifting invertebrate prey resulting in faster growth rates. Similarly, indirect evidence suggests that high-quality sites are not negatively affected as population density increases. Dominant individuals generally occupy upstream positions within habitats, forcing subordinates into downstream or distant lateral positions where they are unable to interfere with the delivery of drifting prey (Fausch 1984, Hughes 1992a, Nakano 1995a, 1995b). At high population densities, increased numbers of subordinates must, to some degree, negatively impact high-quality sites. It is likely, however, that either all sites would be impacted equally or that poor-quality sites, occupied by lower-ranking individuals, would be affected more than high-quality sites. A complete test of site dependence (e.g., Morris 1991) would require demographic measures of fitness for individuals occupying known sites.

Were the null models realistic? Only one site of the 164 was never occupied during the course of the experiment and individual brook trout were seen to swim around the entire 14.2 m^2 tank several times between observations. It is likely that all 164 sites were equally available and that brook trout could easily move among all sites between observation periods. By excluding sites that were not occupied in a given replicate, I minimised the likelihood of erroneously detecting a non-random pattern of site use. Limited movement of individuals could result in non-random site use (prediction 1) but it is highly unlikely to generate concordant site rankings (prediction 2) or consistent use of favoured sites by dominant individuals (prediction 3). Without selection for particular sites, there would be little reason to expect the significant and consistent deviations from random distributions that I found.

It is also unlikely that the significant positive relationship between trout size and the mean occupied-site quality (prediction 3) simply reflects differential site preference by small and large fish. Equal numbers of fish were drawn from each size class for each replicate and rankings of site quality were based on the number of times a site was occupied. As such, site ranks were equally influenced by trout of all sizes. If small and large fish were simply expressing different site preferences, then sites preferred by small fish would be occupied just as frequently as, and therefore be ranked identically to, sites preferred by large fish. In this case we would not predict the significant relationship observed between an individual's size and the rank of sites it occupied (Table 3.5).

Grand (1997) demonstrated that juvenile coho salmon in an artificial stream channel exhibit ideal-free distributions of unequal competitors based on the input-matching prediction (Parker and Sutherland 1986). Our results are not mutually exclusive. Grand (1997) reported that individuals exhibited "apparent territoriality" before the feeding trials; they maintained relatively stationary positions, engaged in occasional aggressive interactions with neighbours, and divided themselves unequally among habitats. When food was introduced from two point sources, all of the fish moved to the upper end of the channel and engaged in scramble competition at the two points. Most prey was consumed within 20 cm of the mesh barrier. While I do not disagree with Grand's (1997) methods or conclusions, I believe the documented distribution inherently ignores habitat. Sixteen individuals appear to be selecting between two precise sites based on the amount of food available, the number of competitors at the site, and their relative competitive abilities. In this, and other input-matching studies (e.g., Harper 1982, Milinski 1984, Inman 1990), differences among individuals are not due to their relations to particular habitats but to their ability to capture food particles (Łomnicki 1988). Although input matching helps us to understand the way individuals assess the potential costs and payoffs with feeding at a given site, its restrictive conditions are probably seldom fulfilled under natural conditions (Milinski 1994) and it does not describe density-dependent habitat selection of individuals in a realistic landscape (Lima and Zollner 1996). The documented distribution of coho salmon may reflect habitat-selecting behaviour in slow-flowing glides and pools where territoriality tends to break down and dominance hierarchies predominate (Grand 1997) but the "apparent territoriality" displayed by the unfed coho juveniles distributed throughout the stream channel probably represents a more realistic distribution of fish across habitats. Prey distributions in natural streams are unlikely to originate as point sources.

Unquantified observations of behaviour during the course of my experiment suggest that brook trout maintain sites through agonistic interactions, as expected with site dependence, but many did not appear to defend strictly defined territories. It is possible that my experimental protocol may have biased trout behaviour toward greater movement than would be normal for natural populations; individuals were introduced into a foreign environment and were not fed during the experimental period. Other authors, however, have reported a lack of strict territoriality in stream salmonids, arguing that each fish defends a temporarily chosen spot against subordinates (Newman 1956, Chapman 1962, Jenkins 1969, Bachman 1984). In some cases, subordinates are known to switch to a non-territorial or transient foraging behaviour (Kalleberg 1958, Jenkins 1969, Nakano 1995a, 1995b), perhaps the ecological equivalent of surplus individuals in nesting bird populations (e.g., Krebs 1971). What emerges is a process of site-dependent habitat selection in which individuals will use aggression to occupy and maintain the highest quality site possible given their relative rank in a dominance hierarchy.

The mechanism of habitat selection I describe for brook trout is similar to the unnamed distribution of *Pemphigus* aphids documented by Whitham (1978, 1980). Survival, growth, and reproductive success of *Pemphigus* aphids depend on a female's position on a leaf, with basal positions conferring higher fitness than distal positions. Females compete with each other through shoving and kicking contests in which dominant, larger females win the superior basal positions. Subordinates occupying distal positions do not affect the quality of more basal individuals. Once settled, the aphids form galls and direct competition ceases. Brook trout, however, exist in a dynamic and heterogeneous environment in which competitive interference among individuals is continuous through much of the feeding season. Site occupancy may be relatively temporary, changing as an individual grows and with other factors such as variations in population density, season, and stream conditions. It is likely that many environments with unidirectional flows of food select for individuals with limited home ranges that compete for specific sites or territories in locations of high and predictable food delivery. Environments without such flows may select for non-aggressive habitat selection at larger spatial scales (Grant and Noakes 1987, 1988). Juvenile brook trout, for example, are active foragers and rarely aggressive in stillwater side-pools (McLaughlin et al. 1992, 1994) or lakes (Biro et al. 1997) but are sedentary and aggressive in running water (Grant and Noakes 1987, 1988).

Similar results could also be generated by ideal despotic habitat selectors. Despots may defend individual sites within habitats but their decision would be based on the mean fitness of a habitat rather than on the quality of individual sites. All individuals occupying the best habitat would have higher fitness than those in the poorer habitat. For Cape Race brook trout there appears to be no clear habitat preference at low densities (Chapter 2) so it is unlikely that either habitat that has a consistently higher mean site quality. Under these circumstances, the differences between site-dependence and despotism begin to disappear. The only predictable difference would be that increasing density should have minimal impact on the fitness of site holders in the case of site dependence. Even this dichotomy, however, can be expected to break down at some density. As population size increases, a population of surplus individuals must, to some degree, begin to affect the fitness of site holders, whether a result of competition for resources or a requirement for increased vigilance.

The key point is that brook trout are recognising differences in site qualities and are competing for high-quality sites with agonistic behaviour. This interference competition for sites was predicted by isodar theory based on only comparison of population density estimates among habitats. Site dependence is likely an oversimplification of population regulation in stream salmonids but it is clear that the optimal behaviour of brook trout is consistent with the fundamental assumptions of site pre-emption by dominant individuals. Habitat selection theory highlights a strong and reciprocal linkage between the nature of competitive interactions and the resulting population distribution they create.

3.5 SUMMATION

In this chapter I tested the hypothesis of site-dependent habitat selection in brook trout by observing individuals in an experimental stream tank. Three *a priori* predictions of site dependence were supported; individual brook trout recognise sites of different quality (prediction 1), and they occupy the best site possible (prediction 2), given their presumed relative position in a dominance hierarchy (prediction 3). My results add support to theories of density-dependent habitat selection, and further highlight the reciprocal linkage between individual behaviour and population density.

Table 3.1: Mean (and range) of water velocity and depth for 164 30x30 cm sites in three sections of the stream tank (Figure 3.2) used to test site dependence in brook trout. Values were calculated for deep- and shallow-water treatments.

		Velocity (cm/s)		**Depth (cm)**	
Section	**n**	**Deep**	**Shallow**	**Deep**	**Shallow**
Riffle 1	76	16.1 (3-28)	12.4 (3-25)	27.6 (26-31)	16.6 (15-20)
Flat	60	9.1 (0-25)	5.2 (0-18)	55.7 (31-63)	44.7 (20-52)
Riffle 2	28	34.0 (23-47)	26.4 (16-35)	27.4 (24-29)	16.4 (13-18)

Table 3.2: Coefficients of variation (C.V.) calculated from site-use frequency distributions for brook trout in all experimental treatments. In all cases, C.V.'s for observed data are greater than those for 1000 randomised distributions indicating that brook trout are using some sites more frequently than predicted by chance alone (Figure 3.3).

Number of fish	C.V. observed data	P	Largest C.V. from 1000 randomised distributions
DEEP WATER			
1	150.3	<0.001	71.6
4	180.4	<0.001	59.4
8	206.9	<0.001	51.9
12	191.1	<0.001	44.8
16	273.4	<0.001	44.9
20	237.5	<0.001	43.3
SHALLOW WATER			
1	141.9	<0.001	81.1
4	105.3	<0.001	65.9
8	138.6	<0.001	46.9
12	182.2	<0.001	42.8
16	195.5	<0.001	40.3
20	127.9	<0.001	49.5

Table 3.3: Kendall's coefficient of concordance (W) for shallow- and deep-water treatments compared with the largest W for 1000 randomised distributions. Larger coefficients for observed data indicate that brook trout rank and occupy sites in a similar order as population densities are increased. Sites appear to fill sequentially, in order of relative site quality.

Water level	**Kendall's *W* observed data**	**P**	**Largest *W* from 1000 randomised distributions**
Deep	0.44	<0.001	0.31
Shallow	0.54	<0.001	0.33

Table 3.4: Mean rank of sites occupied by Cape Race brook trout of a given rank. Site ranks are based on frequency of occupation. Trout ranks are based on fork length and weight. Lower numbers represent better sites and larger trout. The number of replicates available to calculate the ranks is given by *n*. Larger, presumably dominant, brook trout occupy the highest quality sites (Table 3.5).

Trout Rank	Mean Site Rank	Std. Dev.	n
1	16.6	4.0	12
2	13.0	3.5	10
3	14.9	3.7	10
4	13.6	2.4	10
5	15.9	2.2	8
6	16.6	3.4	8
7	16.9	4.6	8
8	17.2	3.0	8
9	15.2	5.4	6
10	16.9	4.8	6
11	18.8	4.3	6
12	19.7	6.7	6
13	16.2	7.9	4
14	23.6	9.5	4
15	19.6	8.8	4
16	13.0	4.2	4
17	12.8	0.6	2
18	11.9	2.6	2
19	28.0	3.3	2
20	31.0	9.3	2

Table 3.5: ANOVA table for randomised complete block design (RCBD) illustrating that a brook trout's size (rank) is a significant predictor of the mean quality of sites it occupies. A trout's rank could only be as low as the number of trout in a given replicate. The relationship was not significantly different for shallow- or deep-water treatments.

Source	df	SS	MS	F	P
Trout Rank	19	1389.8	73.2	3.45	<0.001
Water Level	1	68.7	68.7	3.24	0.075
Error	101	2144.4	21.2		
Total	121	3602.9			

Figure 3.1: Hypothetical example of relatively uniform site use where individuals show little or no site preference (top left) compared with a distribution in which some sites are used preferentially to others (bottom left). Spatial co-ordinates of each site are on the X and Y axes. The height of each column represents the number of times a given site is occupied. Corresponding frequency distributions illustrate that a lack of site preference results in a relatively small coefficient of variation (C.V., top right), while distinct site preferences result in a relatively high coefficient of variation (C.V., bottom right).

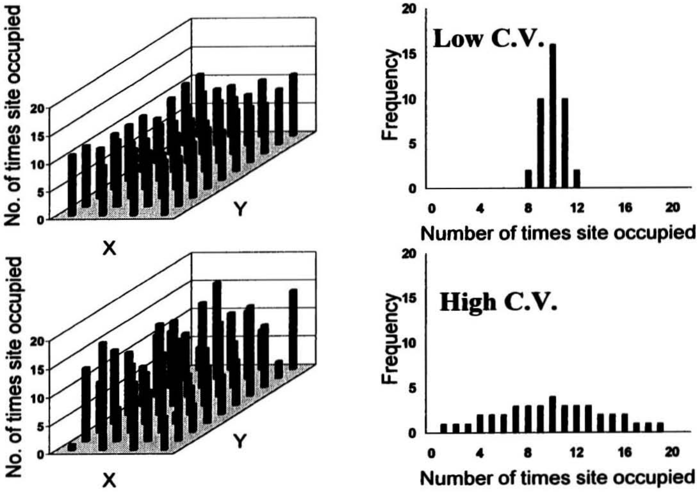

No. of times site occupied
0
5
10
15
20
X
Y
Low C.V.
Frequency
Number of times site occupied
0
4
8
12
16
20
High C.V.

Figure 3.2: Schematic illustration of stream tank area available to fish. Screens at either end separate fish from a paddle wheel that provides current. Shallow, faster-flowing sections (riffles) are stippled and the deeper, slow-flowing (flat) section is white. The grid divides the stream tank into 164 30x30 cm sites. Black rectangles represent opaque-grey Plexiglas covers of varying width. Table 3.1 provides water velocities and depths for the three stream tank sections.

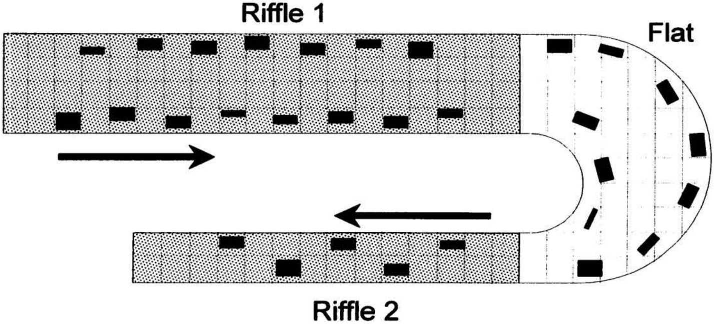
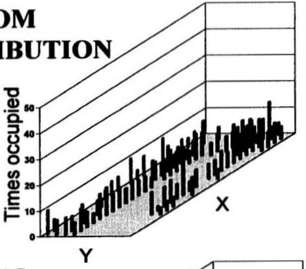
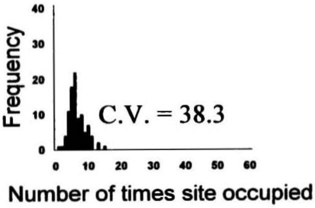

Riffle 1
Flat
Riffle 2

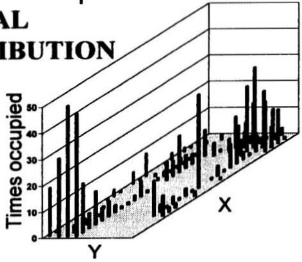
Figure 3.3: One of 1000 computer-generated random distributions (top left) and the actual distribution of brook trout in the experimental stream tank over 3 days of observation (bottom left) for the 8-fish, shallow-water treatment. Note that only sites occupied in the actual distribution were used in the randomisations and that all zero values were excluded from calculations. The coefficient of variation (C.V.) for the random distribution (top right) is substantially lower than the C.V. for the actual distribution (bottom right). For this, and all other treatments, all of the randomised distributions had smaller C.V.'s than the actual distributions (Table 3.2).

RANDOM DISTRIBUTION





ACTUAL DISTRIBUTION



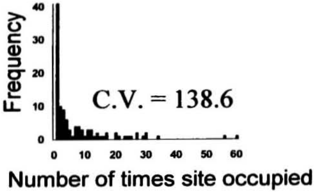
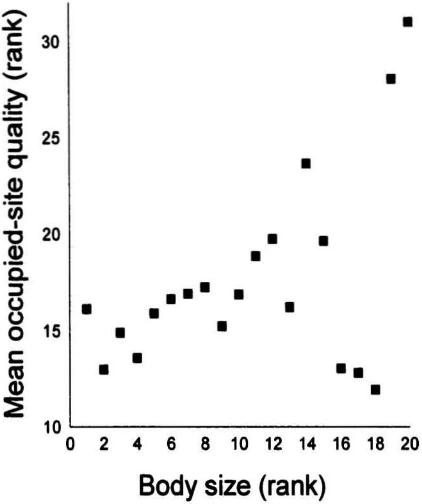


Figure 3.4: Body size (rank) is a significant predictor of the mean quality (rank) of the sites occupied by individual brook trout from Cape Race, Newfoundland (Tables 3.4, 3.5). Large, high-ranking individuals are shown to the left of the X-axis. Higher mean site qualities are to the bottom of the Y-axis.


Mean occupied-site quality (rank)
10
15
20
25
30
0
2
4
6
8
10
12
14
16
18
20
Body size (rank)

Chapter 4:

LANDSCAPE-DEPENDENT HABITAT PREFERENCE

4.1 INTRODUCTION

4.1.1 Overview

Isodars constructed in Chapter 2 identified differential use of habitats among enclosures. It is unclear how much of the variation in habitat use results from different site-quality distributions among enclosures versus among-population variation in habitat preference. Habitat preference has a considerable effect on individual fitness and, therefore, is likely a highly adaptive trait, perhaps evolving differently among populations. I examine two Cape Race brook trout populations inhabiting different rivers for potential differences in habitat preference. The populations probably share a common ancestry but have been isolated in two adjacent rivers, each with very different habitat compositions. By moving individuals from each river to a common stream tank, I was able to observe habitat-selecting behaviours under identical conditions. My results support an *a priori* prediction that habitat preferences in each population should reflect the habitat composition of the river from which it comes.

4.1.2 Evolution of Habitat Preference in the Landscape

Habitat preference is assumed to be adaptive such that when fitness is higher in preferred habitats, natural selection moulds and maintains the preferences if they have a genetic basis (Jaenike and Holt 1991, Martin 1998). There is considerable evidence that genetic variation for habitat preference (e.g., Christensen 1977, Rausher 1982, Byers 1983, Jaenike and Grimaldi, 1983, Hoffmann et al. 1984, Jaenike 1985, Rice 1985, Taylor 1986, 1987, Rausher and Englander 1987, Jaenike and Holt 1991) is common for many invertebrate species in which habitat-selecting behaviour is relatively simple. In species with more complex behaviours, we generally see the evolution of reaction norms [defined as the set of phenotypes expressed by a single genotype across a range of environmental conditions (Stearns et al. 1991)], that may obscure genetic links to habitat preference (Rausher and Englander 1987). Optimality models used to study these more complex behaviours incorporate the assumption that natural selection favours the evolution of habitat-selecting behaviours that maximise fitness under the most common environmental conditions encountered (Dawkins 1982).

In the context of a landscape, we can imagine that evolutionary response depends on the relative frequency of different habitats and their relative influence on overall fitness (Levins 1962, 1968, Houston and McNamara 1992, Kaweki and Stearns 1993, Gotthard and Nylin 1995, Sibly 1995). We can apply the concept of phylogenetic envelopes to evolution in landscapes such that a population today is simply the last pass of a phylogenetic lineage through past environments (Holt and Gaines 1992). Consider a simple landscape composed of source and sink habitats (where, respectively, $r > 0$ and $r < 0$; Pulliam 1988). Adaptation within the realised niche (source and sink) is weighted toward the fundamental niche (source) in which population abundance and reproductive output are usually greatest (Holt and Gaines 1992, Kaweki 1995). Individuals in the sink habitat are largely dispersed descendants of source populations and, as such, are possibly maladapted to their environment. In this way, natural selection acts as a conservative force, inhibiting the expansion or shifting of the fundamental niche (Holt and Gaines 1992, Kaweki 1995). Changes in the fundamental niche (source) would be expected only when reproductive contributions from the combined sinks are greater than those from the sources. This could occur when the greatest number of individuals is found in sink habitat as would be the case when high quality sink habitat makes up a large portion of the landscape (Holt and Gaines 1992, Kaweki 1995, Holt 1996). Alternatively, density-dependent dispersal driven by interference also could favour improved adaptation in the sink and, hence, expansion of the fundamental niche (Holt 1996).

Landscape structure, even at small spatial scales, can have profound effects on adaptive response. Blue tit (*Parus caeruleus*) populations on the French mainland and the island of Corsica inhabit heterogeneous landscapes composed of deciduous and evergreen woodlands. The mainland landscape is composed primarily of deciduous woodlands while the Corsican landscape is primarily evergreen. Mainland individuals exhibit adaptive life-history traits for the deciduous habitats and are apparently maladapted to the evergreen woodlands (Blondel et al. 1992, Dias and Blondel 1996, Lambrechts et al. 1997), a result of gene flow from the high-quality habitats to the lower-quality ones (Dias et al. 1996). The opposite is true in the Corsican population. Each population is well adapted to the conditions of the predominant habitat in the local landscape. Individuals from another Corsican population inhabiting a large and isolated patch of deciduous habitat are not maladapted. It appears that the physical isolation of the two Corsican landscapes has minimised gene flow between them (Lambrechts et al. 1997). Response to selection pressures in a heterogeneous landscape is a function of all habitats occupied by a population but is particularly influenced by abundant (Dias and Blondel 1996) and high-quality ones (Kaweki and Stearns 1993).

Studies of salmonid fish indicate that most species appear to have characteristic habitat preferences that are adaptive. Brook trout, for example, are generally considered as flat or pool dwellers (Chapter 1) but clearly use sites within both flat and riffle habitats (Chapters 2 and 3). If habitat preference in brook trout is adaptive and under genetic control, then we might expect that populations evolve preferences that reflect the habitat composition of the watersheds (landscapes) they inhabit. When a large proportion of the population occupies lower-suitability sites, either as a result of landscape composition or interference, we may see expansion or shifting of the fundamental niche to include more marginal habitat. Fish inhabiting fast-flowing mountain streams with few pools, for example, may evolve behavioural and morphological adaptations to better utilise riffle habitats.

4.1.3 Salmonid Adaptive Response

Brook trout are a polytypic species with a wide geographical distribution throughout eastern North America (Power 1980). Most salmonids, including brook trout, are renowned for their extreme interpopulation variability in a number of fundamental characters such as morphology, growth, and life history (e.g., Power 1980, Northcote 1988, Elliott 1994). Cape Race brook trout populations inhabiting different rivers in close proximity, for example, have evolved extensive differences in life-history characteristics including age at maturity, egg size, fecundity, reproductive effort, and costs of reproduction. Variation in life history for these brook trout is an adaptive response to differences in growth rate, ultimately controlled by differences in food abundance among rivers, and appears linked to genetic differences among populations (Hutchings 1990, 1993, 1994, 1996, Ferguson et al. 1991). Similar life-history differences have been documented for trout populations inhabiting stream reaches above and below impassable waterfalls (e.g., Northcote and Hartman 1988).

Adaptive behavioural responses are also common among populations. Response to current, a proximate component of habitat selection for stream-dwelling salmonids, is different for genetically separate populations of rainbow trout above and below impassable waterfalls, probably a response to the net loss of individuals that are swept over from upstream populations (Northcote 1969, Northcote et al. 1970, Northcote and Kelso 1981). Population-level differences in aggressiveness have been identified in laboratory-reared chinook salmon (*Oncorhynchus tshawytscha*; Taylor 1988, 1990) and related to differences in food availability in isolated populations of brook trout (Dunbrack et al. 1996). Other behaviours such as migration (e.g., Northcote 1992, Elliott 1994) and instream movements (Riley et al. 1992) also differ among salmonid populations. In all cases, behavioural differences appear adaptive in response to local environmental conditions.

If brook trout exhibit adaptive habitat preference, then individuals coming from populations exposed to different landscape structures should exhibit different habitat-selecting behaviours. I test this prediction with brook trout from two isolated Cape Race rivers.

4.2 MATERIALS AND METHODS

4.2.1 Study Rivers and Field Methods

I studied populations from Cape Race River (46°40' N, 53°05' W) and a small unnamed stream referred to as Whale Pond River (46°38' N, 53°12' W) at Cape Race, Newfoundland (Figure 1.2). Both of these small-order rivers terminate in impassable waterfalls that plunge approximately 20 to 30 m over sea cliffs into the Atlantic Ocean. The rivers, separated by 10 km and with no sea linkage, contain reproductively isolated populations of brook trout. Brook trout populations in similar rivers at Cape Race were found to be distinguishable at several enzyme loci (Ferguson et al. 1991) with distinct life-history characteristics (Hutchings 1990, 1993, 1994), probably caused by divergent evolution since isolation after the last glaciation some 10,000 to 12,000 years before present (Rogerson 1981, Hutchings 1994).

Cape Race River is relatively large (3 km length) and fast flowing, containing primarily riffle habitat. Whale Pond River, on the other hand, is very small (1 km length) with a low gradient and is composed primarily of flat habitat. Except for a small population of threespine stickleback in Cape Race River, brook trout are the only fish in the two rivers. Size distributions are similar for both rivers with maximum-recorded fork lengths of 160 mm for Cape Race River (Hutchings 1990) and 180 mm for Whale Pond River. Mean density of brook trout older than age 1 is approximately 0.3 m^{-2} in Cape Race River (Hutchings 1990) and 1.7 m^{-2} in Whale Pond River.

Habitat composition was measured in the two rivers by visually dividing them into alternating sections of flat and riffle habitat. Minimum length for a section was 3 m. A section was considered to be flat when most of its surface was unbroken by current. The length of each habitat was measured and its area determined by measuring stream width every 5 m, or in shorter sections, at a minimum of 3 equally spaced locations. Width transects were run at 1/3 and 2/3 the section length. Depth, substrate size and current velocity at 2/3 depth (Flo Mate Velocity Meter, Marsh-McBirney, Frederick, MD, USA) were measured at 3 equally-spaced stations along each width transect yielding a total of 450 microhabitat stations.

I used a backpack electrofisher (Smith-Root Model 12, Vancouver, Washington, USA) to capture equal numbers of brook trout from flat and riffle habitats in each river. At time of capture, I anaesthetised fish with benzocaine and measured fork length, keeping only those fish between 100 and 120 mm. Brook trout captured in flat habitat were given adipose-fin clips for identification. Fish from the two rivers were then transported in separate tanks to holding facilities at the Department of Fisheries and Oceans, St. John's, Newfoundland, Canada.

4.2.2 Habitat Preference Experiment

Habitat selecting behaviour of brook trout was observed in a 14.22 m^2 flow-through stream tank (Figure 4.1). A grid of 164 30 x 30 cm squares was outlined with white gravel. Substrate was gravel throughout. Depth and current velocity at 2/3 depth (Flo Mate Velocity Meter) were measured at the centre of each square. The tank has three areas: one that is relatively deep and slow-flowing flat habitat, and another two that are relatively shallow and fast-flowing riffle habitat (Figure 4.1). Each replicate consisted of placing 6 trout from one river, 3 captured from each of flat and riffle habitat, into the stream tank and allowing them 2 days to explore. On the third day, the exact location and the habitat of origin for each individual was noted every 15 min for 2, 2-hour periods separated by 1 hour. All food was withheld during the experiment. This protocol provided 18 locations for each of 6 fish per replicate. It was repeated 5 times for each river. Technical difficulties limited one Whale Pond River replicate to just 13 observation periods.

4.2.3 Habitat Analysis

I documented potential landscape differences between Cape Race River and Whale Pond River with the field measures of habitat. Section length and width measures were used to calculate the area and proportion of flat and riffle habitat in each river. Analyses of variance confirmed significant differences among rivers and among habitats in depth, substrate size, and velocity (SAS Institute 1990c, Proc GLM). Significant river x habitat interactions for depth and substrate required that I consider only simple effects. I performed unplanned multiple comparisons among means with Tukey's honestly significant difference test for unequal sample sizes (Zar 1996). I also confirmed differences between flat and riffle sections of the stream tank with t-tests of depth and velocity measures using Satterthwaite's approximation for unequal variances (SAS Institute 1990c, Proc TTEST; Zar 1990).

4.2.4 Analysis of Brook Trout Habitat Preference

For each replicate, I calculated the mean population density in flat habitat to generate 5 independent estimates of habitat use for brook trout from each river (SAS Institute 1990b; Proc FREQ, Proc MEANS). I then used t-tests to determine whether fish from either river showed a distinct preference for flat or riffle habitat by comparing the mean density observed in flat habitat against the null model of equal density in the two habitats (SAS Institute 1990c; Proc TTEST). Next, I tested for possible differences in habitat selecting behaviour between the two populations and within each population.

Analysis of variance (ANOVA) identified whether population density in flat habitat was significantly related to the river or habitat of origin (SAS Institute 1990c; Proc GLM).

4.3 RESULTS

4.3.1 Habitat Comparison

Cape Race River is 72.8% riffle and 27.2% flat habitat with a total area of 0.48 km^2. Whale Pond River is a much smaller (7.11×10^{-4} km^2), predominantly flat habitat (77.1%) river with only 22.9% riffle habitat. Mean current is faster in riffle habitats than in flats (22.6 vs. 8.6 cm s^{-1}, F=43.5, df=1,449, $P<0.001$) and faster in Cape Race River than in Whale Pond River (19.9 vs. 7.8 cm s^{-1}, F=63.3, df=1,449, $P<0.001$). Tukey's honestly significant difference test confirmed that Cape Race River also is deeper than Whale Pond River in both flat (21.6 vs. 12.9 cm, q=11.6, $P<0.05$) and riffle habitats (15.9 vs. 10.7 cm, q=7.0, $P<0.05$). Within Cape Race River, flats are deeper than riffles (21.6 vs. 15.9 cm, q=9.2, $P<0.05$) and substrate in riffles is larger than substrate in flats (22.5 vs. 16.9 cm, q=4.5, $P<0.05$). There were no other measured differences between habitats or rivers. Stream tank conditions mimicked natural ones. Flat habitat was deeper (38.0 vs. 10.5 cm, t=21.5, df=60, $P<0.001$) and had slower current (1.7 vs. 8.8 cm s^{-1}, t=13.0, df=146, $P<0.001$) than riffle.

4.3.2 Habitat Preference

Whale Pond River trout appear to prefer flat habitat to riffle (t=2.78, df=4, P=0.050, Figure 4.2) while Cape Race River trout show equal preference for the two habitats (t=-0.57, df=4, P=0.600, Figure 4.2). As predicted, brook trout from Whale Pond River occupied the flat habitat in the stream tank more frequently than those from Cape Race River (F=4.49, df=1,16, P=0.050, Table 4.1, Figure 4.2). There was no difference in habitat preference among trout captured in flat or riffle habitat (F=0.01, df=1,16, P=0.927, Table 4.1).

4.4 DISCUSSION

Predictable differences in habitat use for these two brook trout populations highlight the importance of landscape composition to the evolution of habitat preference in salmonids. It appears that habitat preference is at least partly a function of the relative reproductive contributions of individuals among habitats in a landscape. Given that the streams exist in the same climatic and geological environment, it is unlikely that there are unique environmental factors that would explain the observed differences in habitat use. The fact that habitat of origin for individual fish had no influence on habitat preference reinforces the likelihood that there are real between-population differences in habitat preference.

The lack of a distinct preference for flat or riffle habitat in Cape Race River brook trout is consistent with my findings from experimental enclosures in Drook and Bristy Cove rivers (Chapter 2). All three rivers are relatively large and deep with fast currents compared to Whale Pond River and likely contain many high-quality sites within riffle habitats. It appears that habitat preference in Whale Pond River trout may have shifted relative to these other populations. I suspect that Whale Pond River is somewhat unique as a salmonid stream in that it has such a high proportion of flat habitat within a very small system yet still supports a small and reproductively isolated population of brook trout. Populations isolated above waterfalls, in most cases, experience the opposite extreme: a landscape composed largely of riffle habitat with frequent extremes in flow (e.g., Northcote and Hartman 1988, Elliott 1994). Regardless, the variation in habitat use that I documented for these geographically adjacent populations highlights the potential risk of applying habitat-based models across large areas without consideration of the landscape that a population inhabits.

A complete test for landscape-dependent habitat preference should include both fitness and genetic components. Although habitat preference is assumed to be adaptive, few studies of salmonid fish document the fitness consequences associated with the occupation of a given habitat or site (e.g., Fausch 1984, Hughes 1992b, Nakano 1995a). Field-based studies that track habitat-selecting behaviour and life-history characteristics of individuals throughout their lifetimes would perhaps be the most effective way of linking fitness to habitat (Hutchings 1996). Genetic control of habitat preference could be implicated after conclusive tests with laboratory-reared brook trout. It might still remain unclear, however, whether laboratory-reared individuals exhibited normal habitat-selecting behaviour for their respective populations.

I have assumed that trout are using sites within the habitats in the order of their relative suitability (Chapters 2 and 3), that interference among individuals is minimal, and that any interference is more significant at the scale of sites than habitats. Casual observations of individual behaviours support these assumptions. First, the relatively low density of trout used in the experiment (0.42 trout m^{-2}) minimised interference among individuals. This was particularly true because the tank's shape created partial visual isolation between habitats. Second, all individuals were approximately the same size (100 to 120 mm) thus reducing the likelihood of strong size-dependent dominance hierarchies emerging. Finally, apparently dominant trout rarely attempted to exclude subordinates from entire habitats. Aggression appeared to be utilised to maintain a preferred position within a habitat. Under these conditions, it is likely that population density reflected actual habitat preferences and was not a misleading indicator of individuals' assessments of habitat quality (cf. van Horne 1983).

It is possible that differences in habitat use between these two populations result from differences in some other habitat-selecting behaviour, e.g., levels of aggression (e.g., Dunbrack et al. 1996). One can imagine a scenario in which Whale Pond River trout exhibited a less territorial, more active foraging tactic mimicking that of brook trout inhabiting lentic habitats (Keenleyside 1962, Grant and Noakes 1987, 1988, McLaughlin et al. 1992, 1994, Biro et al. 1997), thereby permitting many individuals to occupy the preferred, flat habitat. To be consistent with my results, Cape Race River brook trout would also require a preference for sites in flat habitat that was masked by interference from dominant individuals forcing subordinates into riffle. Although low current velocities often induce a behavioural switch to more mobile and less territorial foraging activities within salmonid populations, differences among populations that are tested in the same stream tank must still be explained. Conditions of lower current velocities that might confer short-term benefits to phenotypes with lowered aggression in Whale Pond River would have to be persistent in the long term to generate consistent and predictable differences in habitat use. Individual differences in habitat use among populations exposed to identical experimental conditions indicate real population-level variation in habitat selecting mechanisms.

4.5 SUMMATION

I have demonstrated that brook trout from two isolated populations exhibit different patterns of habitat use. When placed in an experimental stream tank, individuals from a river composed largely of flat habitat occupied flat habitat more frequently than individuals coming from a river composed largely of riffle habitat. Although I have not demonstrated a genetic link to these interpopulation differences, they are consistent with the hypothesis that habitat preference evolves in response to the relative availability of habitats in the landscape a population inhabits.

Table 4.1: Analysis of variance showing that populations from Cape Race and Whale Pond rivers have significantly different preferences for flat and riffle habitats. The habitat from which an individual was captured had no effect on habitat use.

Source	**df**	**Mean Square**	**F**	**P**
River	1	0.0464	4.49	0.050
Habitat of Origin	1	0.0000	0.01	0.927
River x Habitat of Origin	1	0.0074	0.72	0.410
Error	16	0.0104		
Total	19			

Figure 4.1: Schematic illustration of stream tank area available to fish. Screens at either end separate fish from a paddle wheel that provides current. Shallow, faster-flowing sections (riffles) are stippled and the deeper, slow-flowing section (flat) is white. The grid divides the tank into 164 30x30 cm sites. Note that Plexiglas covers were not distributed through the tank (c.f. Chapter 3).

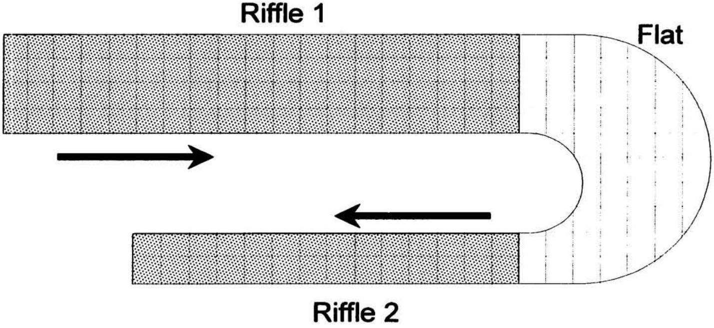
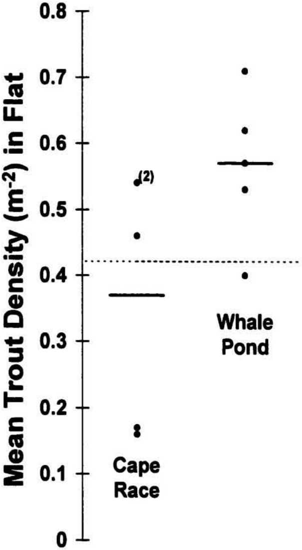

Riffle 1
Flat
Riffle 2

Figure 4.2: Habitat use by Cape Race River and Whale Pond River brook trout in an experimental stream tank. Each point represents the mean population density in flat habitat for one replicate with 6 brook trout from one of the rivers. The horizontal line at 0.42 m^{-2} indicates the density of equal use for flat and riffle habitats. Values above and below that line indicate preference for flat and riffle habitat respectively. Means for each column are shown with short horizontal lines. Whale Pond River trout have a distinct preference for flat habitat while Cape Race River trout show no significant difference in use of both habitats. The difference between rivers is significant (Table 4.1).


0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Mean Trout Density (m^{-2}) in Flat
(2)
Cape Race
Whale Pond

Chapter 5

SUMMARY

I have used field and laboratory experiments to document and test habitat-selection in brook trout. My results support theoretical models of habitat selection, they are consistent with models of landscape-dependent evolution among populations, and they reflect published accounts of habitat use by brook trout and other salmonid fish.

Isodars created in the field were curvilinear; Cape Race brook trout are site-dependent habitat selectors (Chapter 2). The implication is that dominant or early colonising individuals pre-empt sites of highest quality such that the distribution of brook trout reflects the distribution of site 'qualities' among habitats. I confirmed the field experiments by observing the behaviour of individuals in a laboratory stream (Chapter 3). Brook trout behaviour was consistent with three *a priori* predictions of site dependence: 1) brook trout recognise and respond to differences in site quality; 2) individuals select the highest quality site available; 3) larger, presumably dominant, individuals occupy the best quality sites. My results point to a clear linkage, mediated by density-dependent habitat selection, between individual behaviour and distribution.

I also documented apparent landscape-dependent differences in habitat preference among populations of brook trout (Chapter 4). Observations of Cape Race brook trout from two populations that share otherwise identical climate and geology show differences in habitat use within the same experimental stream tank. Individuals from a river primarily composed of flats had a distinct preference for flat habitat in the stream tank, while individuals from a river composed primarily of riffles showed equal use of flat and riffle. No differences in habitat use within populations were found regardless of the habitat from which a fish was captured, suggesting that the influence of an individual's immediate previous experience may have been minimal. Although no genetic link was tested, my results are consistent with the idea that evolved differences in habitat preference reflect the relative proportions and availability of habitats.

Thus, I now have direct evidence linking the behaviour of individuals, their population response to habitat, and ultimate adaptive differences in behaviour among populations. Though not tested here, the implication is that one can use isodars to not only capture the habitat selection behaviour of individuals, but also to identify differences in habitat preference induced by landscape composition.

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APPENDIX 1

Summary tables of replicates for each brook trout enclosure used in experiment 1 at Cape Race, Newfoundland (Chapter 2). The tables provide, for each replicate, the date of trout removal, the number of trout introduced into the enclosure, the number of trout removed at the end of the replicate, and the population density at removal for the entire enclosure. Replicates, performed in random order for each pair of enclosures, are listed in order of the number of trout introduced. Note that the number of replicates varies among enclosures because of time and logistical constraints.

DROOK LOWER

Replicate	Date (mm/dd/yy)	Number Introduced	Number Captured At Completion	Enclosure Density (m^{-2})
1	08/23/94	2	2	0.02
2	08/14/94	5	7	0.08
3	06/30/94	10	15	0.18
4	07/10/94	16	16	0.19
5	06/25/94	18	18	0.22
6	07/13/94	20	20	0.24
7	08/05/94	36	36	0.44
8	07/17/94	40	39	0.47
9	08/08/94	60	62	0.75
10	07/20/94	80	80	0.97
11	08/11/94	100	97	1.18
12	08/17/94	120	117	1.42
13	08/27/94	140	135	1.64
14	07/23/94	160	154	1.87

DROOK UPPER

Replicate	Date (mm/dd/yy)	Number Introduced	Number Captured At Completion	Enclosure Density (m^{-2})
1	08/23/94	2	3	0.07
2	07/10/94	4	4	0.10
3	08/14/94	5	9	0.22
4	07/20/94	10	10	0.24
5	07/17/94	16	16	0.39
6	07/13/94	20	19	0.46
7	08/05/94	28	28	0.68
8	08/08/94	40	37	0.90
9	08/17/94	60	58	1.42
10	08/11/94	80	82	2.00
11	08/27/94	120	110	2.69
12	07/23/94	160	151	3.69

BRISTY COVE LOWER

Replicate	Date (dd/mm/yy)	Number Introduced	Number Captured At Completion	Enclosure Density (m^{-2})
1	08/15/94	2	3	0.06
2	07/24/94	5	5	0.10
3	06/16/94	10	11	0.21
4	08/23/94	10	10	0.20
5	06/19/94	20	19	0.37
6	07/07/94	28	28	0.55
7	06/24/94	40	39	0.76
8	08/27/94	52	47	0.92
9	06/28/94	80	77	1.50
10	08/11/94	100	92	1.79

BRISTY COVE UPPER

Replicate	Date (dd/mm/yy)	Number Introduced	Number Captured At Completion	Enclosure Density (m^{-2})
1	08/15/94	2	1	0.01
2	07/24/94	5	5	0.07
3	06/12/94	10	11	0.16
4	08/23/94	10	11	0.16
5	08/05/94	12	12	0.18
6	07/07/94	17	17	0.25
7	06/16/94	20	12	0.18
8	06/19/94	20	19	0.28
9	06/24/94	40	36	0.53
10	08/27/94	52	50	0.73
11	08/08/94	60	58	0.85
12	06/27/94	80	73	1.07
13	08/18/94	100	87	1.28

APPENDIX 2

List of all models tested to determine best-fit isodar regressions for each brook trout enclosure used in experiment 1 at Cape Race, Newfoundland (Chapter 2).

$N_f=\beta_0+\beta_1 N_r+\varepsilon$

$\log N_f=\beta_0+\beta_1 \log N_r+\varepsilon$

$N_f=\beta_0+\beta_1 \log N_r+\varepsilon$

$\log N_f=\beta_0+\beta_1 N_r+\varepsilon$

$N_f=\beta_0+\beta_1 N_r^2+\varepsilon$

$N_f=\beta_0+\beta_1 N_r^3+\varepsilon$

$N_f=\beta_0+\beta_1 N_r+\beta_2 N_r^2+\varepsilon$

$N_f=\beta_0+\beta_1 N_r+\beta_2 N_r^2+\beta_3 N_r^3+\varepsilon$

$\log N_f=\beta_0+\beta_1 N_r+\beta_2 N_r^2+\varepsilon$

$\log N_f=\beta_0+\beta_1 N_r+\beta_2 Nr^2+\beta_3 N_r^3+\varepsilon$

$$N_f=\frac{\beta_0}{1+e^{-\beta_1(N_r-\beta_2)}}+\varepsilon$$

$Nr=\beta_0+\beta_1 N_f^2+\varepsilon$

$Nr=\beta_0+\beta_1 N_f^3+\varepsilon$

$N_r=\beta_0+\beta_1 N_f+\beta_2 N_f^2+\varepsilon$

$N_r=\beta_0+\beta_1 N_f+\beta_2 N_f^2+\beta_3 N_f^3+\varepsilon$

$\log N_r=\beta_0+\beta_1 N_f+\beta_2 N_f^2+\varepsilon$

$\log N_r=\beta_0+\beta_1 N_f+\beta_2 N_f^2+\beta_3 N_f^3+\varepsilon$

$$N_r=\frac{\beta_0}{1+e^{-\beta_1(N_f-\beta_2)}}+\varepsilon$$