Patterns, predictors and consequences of space use in individually tagged young-of-the-year Atlantic salmon (*Salmo salar*)

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Abstract

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Movement, at various spatial and temporal scales, plays a major role in shaping the ecology of animals at the individual and the population level. In this study, I applied recently developed tagging methods (visible implant fluorescent elastomers) to examine the space use of Atlantic salmon (*Salmo salar*) during their first growing season. First, I monitored 320 YOY salmon to test alternative views on the patterns (restricted vs. not-restricted), causes (competition vs. habitat use) and consequences (mobile fish of lower vs. equal fitness) of movement in stream fish. Most fish (mean = 63.8%) stayed in the study sites (10-120m) throughout their respective study season (28-74 days), and 61.8% of the re-sighted fish moved less than 1 m up- or downstream. Fish originally found in slow water moved farther than fish from fast water, and fish found at high population density were more likely to disappear than fish from low density. Mobile fish grew as fast, or faster, than more sedentary fish, suggesting that movement can be advantageous. Second, I mapped the daily territories of tagged YOY salmon to test if the typical single-central-place view of territoriality among YOY salmonids holds when fish are followed for longer periods, at low population densities. In contrast to earlier studies, YOY salmon visited several foraging stations (median = 12.5; range = 3-26) within their territories, and showed limited fidelity to any particular station. When mapped around several stations,

rather than assuming one station as is customary, territories of YOY salmon were larger than previous reported (mean = 0.932 m^2), were less circular in shape, and were elongated along the stream length rather than the stream width. Although the study fish used large multiple-central-place territories, aggressive acts directed toward other YOY Atlantic salmon were usually found on the outskirts of these areas, suggesting these were fairly efficiently defended against conspecifics. A literature review suggested that YOY salmonids defend small territories from one central-place foraging station at high population density, but use several stations and large territories at low density. Third, as current velocity, prey abundance and prey mobility increase, stream-fish are predicted to become less mobile, use smaller home ranges, and become more aggressive as they switch from "cruising" to "sit-and-wait" foraging. I tested if these predictions held for YOY Atlantic salmon that specialize as sit-and-wait foragers, but vary in the number of foraging stations visited and the distance traveled within a territory (15.7-95.0 m/40min). As predicted, territory size decreased with increasing current velocity and prey availability. YOY salmon, however, were most mobile and attacked intruders more often at intermediate, optimal, current velocities. These findings, and the fact that fish in slow water do not feed more on benthic prey than fish in fast water, suggest that mobility in YOY Atlantic salmon reflects the patrolling of territories, rather than just the direct exploitation of other food resources than drifting prey.

Acknowledgements

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Contribution of Authors

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General Introduction

Animals exhibit great variability, both within and among species, in how they move about

in their environment (Helfman 1990; Turchin 1998; Kramer and McLaughlin 2001). Over

their lifetime, animals vary in mobility from small mammals, such as red squirrels, which

often remain in a localized area from birth to death (Berteaux and Boutin 2000), to

neotropical passerines, which migrate long distances between two different habitats

several times over their lifespan (Cox 1985), to tunas, which move more continuously

over large geographical areas throughout their adult life (Block 2001). At small spatial

and temporal scales, however, animals may be sedentary and show fidelity for a specific

site, or travel widely as they actively search for resources within a habitat (e.g., McNab

1963; Huey and Pianka 1981). In general, the space use patterns adopted by animals have

important ecological implications, because they may be associated with individual fitness,

affect the abundance and distribution of populations, and influence the persistence of

populations via the rescue effect (Fretwell 1972; Turchin 1998; Hanski 2001).

Space use in territorial animals has received great attention, in part because of the

direct role territoriality and aggression play during resource competition and population

regulation (Patterson 1980; Davies and Houston 1984; Rodenhouse et al. 1997). The

main distinction between a home range, which is an area that an animal uses repeatedly in

the course of its activity (sensu Barrows 1996), and a territory, is that the latter refers to a

"defended area" (Noble 1939; Maher and Lott 1995). In spite of this simple definition,

however, territorial animals exhibit great variability between species in their space use

patterns (Brown 1964). Individuals may defend territories on a temporary basis, such as a

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lek during a breeding season (Brown 1964), may relocate their territory several times over a lifetime (Rayor and Uetz 2000; Whiteman and Côté 2004), or defend a relatively permanent territory for much of their life (Berteaux and Boutin 2000). Similarly, at an intraspecific level, territories vary in size, in the way which animals search for and exploit resources within them, and in the degree to which they are defended (Davies and Houston 1984; Grant 1997). For example, animals may defend only a portion (i.e., a core area) of a home range (Wilson 1975), defend a "partial territory" against smaller individuals only (Newman 1956), defend only against conspecifics, or defend concentric territories against many species (Grant 1997). Although, a vast literature exists on territoriality, the space use patterns of territorial animals and their ecological basis and consequences often remain unclear (see Stamps 1994); this should especially apply to animals that cannot be monitored for long enough time to provide accurate estimates of space use, or to evaluate its consequences for individual fitness.

In general, territoriality is assumed to evolve in situations where aggression leads to increased individual fitness, e.g., through increased growth, survival or reproduction (Brown 1964; Davies and Houston 1984; Grant 1997). Hence, home ranges should be defended only when the cost of defense is outweighed by the benefits of obtaining exclusive access to a given resource or an area. As a result, whether animals choose to defend an area at a given time should depend on ecological conditions, such as whether resources are distributed in a defendable manner (Brown 1964; Grant 1993; 1997).

Whether an animal defends a territory, and how it exploits its territory, may also depend on its social status within a group or a population. Dominant individuals, with

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presumably higher fitness, typically defend small home ranges in preferred habitats where resources are abundant, while subordinates may be forced to settle in poorer habitats or become floaters without a territory (Rodenhouse et al. 1997; Whiteman and Côté 2004). Thus, in terms of space use, subordinates may be viewed as more mobile than dominant animals because they relocate as they are driven out of local habitats (Nakano 1995), or may need to forage more widely on scarce resources (e.g., Ens et al. 1995). Alternatively, however, some studies suggest that more mobile animals in a population may do as well, or better, than sedentary individuals (e.g., Fraser et al. 2001).

Salmonid fishes provide an interesting model system for the study of territoriality and are often used to test general ideas on space use of territorial animals, such as on the effect of food abundance on territory size (Keeley 2000; Imre et al. 2004), the ecological correlates of foraging mode (McLaughlin et al. 1992; Fausch et al. 1997), and the patterns of space use in central-place foragers (Grant et al. 1989; Biro et al. 1997). In part, stream-dwelling salmonids make ideal study animals because they feed on invertebrate drift, which is an easily quantifiable food resource (e.g., Keeley and Grant 1995), defend territories that vary readily in size in response to different environmental conditions (McNicol and Noakes 1984; Keeley 2000), and exhibit great variability in their foraging mode (McLaughlin et al. 1992). Also, because stream-dwelling salmonids remain territorial during their freshwater life and thus defend territories over a large range in body size, they are ideal for examining size-related changes in territory size and habitat use (Morantz et al. 1987; Elliott 1990; Keeley and Grant 1995).

Early life history is a critical period in terms of survival in stream-dwelling

salmonids (Elliott 1994; Metcalfe et al. 1995). However, because of an inability to tag and monitor small fishes in the wild (Barlow 1993), studies of space use in young-of-the-year (YOY) stream fishes suffer from two major drawbacks. First, for movement over longer distances, studies are often confined to a so-called cross-sectional approach, which involves sampling untagged individuals as they pass a fixed point in space or move through a fixed area (also called a Eulerian approach) (Okubo 1980; Folt et al. 1998). For YOY salmonids, this involves sampling fish in drift nets as they move downstream soon after they emerge from the gravel and start feeding (Elliott 1994; Johnston 1997). Second, on a small spatial scale, the typically short observations of untagged fish may result in biases in estimates of territory use toward those YOY fish that remain sedentary and occur at high density, simply because these individuals are easier to monitor.

Currently, the most popular method used to track stream-salmonids is the passive integrated transponder (PIT-tag) technology (Armstrong et al. 1996); however, although very useful, this method often results in mortality in small fish (< 8.4 cm)(Roussel et al. 2000). Recently, however, advances in tagging techniques have allowed biologists to tag smaller fish than previously possible. The method used in this study, the visible implant fluorescent elastomer technique (V.I.F.E.), involves injecting a minuscule amount of fluorescent paint under the skin of the fish (Dewey and Zigler 1996). Different colours and tagging locations can then be used to create unique tags for many individuals (Dewey and Zigler 1996). To date, the V.I.F.E method has been used at an increasing rate to tag several species of coral reef fishes, as well as freshwater fishes (Dewey & Zigler 1996; Skalski and Gilliam 2000). Hence, this method allows YOY salmonids to be tagged on an

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individual basis and monitored for longer than previously possible, during an early life history phase where territoriality plays a major role for competition and survival.

In my Ph.D. thesis, I use repeated observations of individually tagged fish (i.e., a longitudinal approach) to provide new insights on how YOY Atlantic salmon (*Salmo salar*) explore, exploit and defend their environment. Juvenile Atlantic salmon is a convenient study animal because it epitomizes the territorial nature of stream-salmonids (e.g., Kalleberg 1958), and represents well those animals that undergo a gradual shift in their habitat preferences while defending territories over long periods of time. The new insights derived from observing marked individuals allow me to answer four general questions: (*i*) how far individuals relocate their territories or home ranges over the first growing season, (*ii*) how individuals vary in their use of space within a territory or home range, (*iii*) how is the above space-use variability related to potential environmental and ecological determinants, and (*iv*) what are the individual consequences of adopting different patterns of space use in a territorial system. The thesis is organized into three chapters and is based primarily on data collected on a naturally occurring salmon population in Catamaran Brook, New Brunswick, Canada.

The available literature offers very polarized views on the patterns, causes and consequences of larger scale movement and site fidelity in stream-dwelling fish. In terms of patterns, movement is frequently described as either restricted (Gerking 1959), or not restricted (Gowan et al. 1994). Similarly, movement is often suggested to be caused by either competition for space (Chapman 1962), or changes in habitat preferences (Kahler et al 2001). Finally, mobile individuals are reported to be either of smaller size and lower

fitness (Chapman 1962), or to be of equal or greater fitness (Armstrong et al. 1997;

Kahler et al 2001) than resident fish. In chapter 1, I use YOY Atlantic salmon to test these

alternative hypotheses on the patterns, causes and consequences of movement and site

fidelity in stream-dwelling fish.

The size, shape, and defence of territories provide key insights into how animals

exploit their local environment (Covich 1976; Adams 2001). Stream-dwelling salmonids

are frequently used to test general hypotheses on local space use in central-place foragers

(Grant et al. 1989), which are animals that forage from and deliver food to a single central

location (Stephens and Krebs 1986). Some recent studies, however, suggest that stream-

salmonids may alternate among several foraging locations (i.e., central places) within

their territories; this is a characteristic of multiple central-place foraging, an alternative

space use pattern that so far has received very limited attention in mobile animals (e.g.,

Covich 1976; McLaughlin and Montgomerie 1989). In chapter 2, I describe the size,

shape and defence of multiple central-place territories of YOY Atlantic salmon, and test

if and how these patterns vary from the single central-place space-use patterns that are

typically reported for stream-salmonids. Also, I review the literature for estimates of

territory size, the number of foraging stations used, and aggressive behaviour in YOY

stream-dwelling salmonids, and examine if and how these variables are associated with

population density, the most commonly measured correlate of territory size.

Mobile animals typically search for prey via a sit-and-wait foraging mode or by

cruising widely for food over larger areas (McLaughlin 1989; Helfman 1990). In general,

the sit-and-wait mode tends to be associated with low mobility and small home ranges (or

territories), while cruising individuals are viewed as more mobile (Huey and Pianka 1981). Animals typically adopt a sit-and-wait foraging when prey is mobile and abundant, but cruise for food when it is sedentary or in a low abundance (Helfman 1990). To date, relatively few studies examine the association among foraging mode, mobility and territory size, while asking how these space use variables are shaped by environmental factors (but see e.g., Katano 1996). In the third and final chapter, I apply predictions from the foraging mode and the territoriality literature to examine the environmental correlates of territory use in multiple-central-place foragers and stream-dwelling salmonids. More specifically, I test how current velocity, which is directly linked to the availability and mobility of drifting prey, affects territory size, foraging behaviour, mobility and aggression in YOY Atlantic salmon.

Chapter 1. Patterns and correlates of movement and site fidelity in individually tagged young-of-the-year Atlantic salmon (*Salmo salar*)

Introduction

Animal movement provides a behavioural link between individuals and higher-level population processes (Turchin 1998). For individuals, the choice between showing site fidelity or moving longer distances has direct consequences in terms of energetic costs (Forseth et al. 1999), growth (Fraser et al. 2001), susceptibility to predation (Gilliam and Fraser 2001) and mortality (Elliott 1994). At the population level, movement plays a role in the regulation of local density (Chapman 1962), determines the spatial scale over which population regulation occurs (Ray and Hastings 1996), shapes the geographical distribution of populations (Hanski 1998), and indicates to what degree populations are divided into smaller evolutionary units (Fausch and Young 1995).

Because streams can be conceptualized as one-dimensional habitats, stream fishes are good candidates for a quantitative examination of the shape of movement curves (Skalski and Gilliam 2000). Early studies on the movement of stream fishes noted that many fish are sedentary (e.g., Gerking 1959). Recently, however, this 'restricted movement paradigm' has been questioned by Gowan et al. (1994), who pointed out that the conclusion of restricted movement is often based on only a fraction of the original fish that are recaptured within small study sites. Hence, studies should also examine movement at larger spatial scales, or monitor fish that immigrate into the study sites, to ensure that mobile fish are represented (Gowan et al. 1994).

Although movements of stream fishes have been studied extensively, the literature has a few notable weaknesses. First, only few studies examine movement curves quantitatively (Harcup et al. 1984; Heggenes 1988; Gowan and Fausch 1996), and modeling of these curves is rare (but see Skalski and Gilliam 2000; Rodríguez 2002; Zabel 2002). Second, these studies rely invariably on invasive methods, e.g., electrofishing, that can promote relocation out of study sites (Nordwall 1999); we are not aware of any study in which fish are carefully observed as they are released back onto their home range. Third, although dispersal has major implications for the survival of young-of-the-year (YOY) salmonids (Elliott 1994), the methodological problem of tagging small fish has led to a bias in the movement literature towards larger fish. To date, most studies on dispersal of YOY salmonids sample fish as they drift by a fixed point in space (e.g., Johnston 1997), but rarely follow tagged individuals over time (but see Shirvell 1994; Kahler et al. 2001).

An examination of the causes and consequences of mobility is necessary for the prediction and interpretation of movement patterns (Gilliam and Fraser 2001). For salmonids, the conventional view suggests that competition causes small, subordinate individuals to emigrate during episodes of density-dependent population regulation (Chapman 1962; Elliott 1994). This scenario predicts that (*i*) mobile fish will be smaller and grow slower than resident fish, and (*ii*) they will be more likely to abandon areas of high population density where competition is greater. Alternatively, some studies suggest that larger, presumably dominant, fish are more mobile than smaller fish (Armstrong et al. 1997; Gowan and Fausch 2002), and that mobile individuals grow faster than resident

fish (Kahler et al. 2001; see Fraser et al. 2001 for a non-salmonid example). In this case, mobility is often thought to be caused by ontogenetic changes in habitat preferences rather than density-dependent competition. Hence, this scenario predicts that (*i*) mobile fish will be larger and grow faster than residents, and (*ii*) as fish grow and shift their habitat preferences (see Morantz et al. 1987), they will be more likely to abandon shallow, slow running waters. Rarely are both scenarios examined simultaneously (but see Kahler et al. 2001).

This study describes the patterns of movement and site fidelity in individually tagged YOY Atlantic salmon (*Salmo salar*) in a natural stream. Unlike previous studies on stream fish movement, we rely on relatively non-invasive techniques for the capture and release of fish; individuals were caught with dipnets and carefully released via snorkeling within their original territory. Also, to ensure that mobile individuals are represented along with sedentary fish, we conducted this study at three spatial scales (10, 45, 120 m), and tagged and monitored fish that immigrated into the study area. Finally, we test simultaneously the two alternative scenarios on the causes and consequences of movement in stream salmonids.

Materials and methods

Study area and study population

Data on movement of YOY Atlantic salmon were collected in 1998, 1999 and 2000, at Catamaran Brook, a third-order tributary of the Little Southwest Miramichi River in central New Brunswick, Canada (Fig. 1.1). The stream's main channel is about

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20.5 km long (mean width = 7.2 m), and it is the subject of a long term study on the effect of logging on the stream and its biota (Cunjak et al. 1993). The adult Atlantic salmon spawn in late-October and November each fall (Cunjak et al. 1993). YOY salmon emerge from the gravel and start foraging in mid-June at about 26 mm in length (Randall 1982). Juvenile salmon remain in the stream for 2-3 years, foraging mainly (> 99%) on drifting invertebrates (Keeley and Grant 1995). Because of beaver activity, and its influence on the spawning migration of adult fish, YOY salmon were only found in the lowest 7 km of the stream in the three study years (Richard A. Cunjak; Department of Biology and the Faculty of Forestry and Environmental Management, University of New Brunswick, Bag Service 45111, Fredericton, NB E3B 6E1, Canada; Personal communication).

All data were collected in the lower reach (Cunjak et al. 1993), the 2 km section upstream from the mouth of Catamaran Brook (Fig. 1.1). The spatial scale (i.e., spatial extent) of the study area, in this case defined as the continuous stream length over which movement was monitored, varied among the three years (Fig. 1.1). In 2000, movement was monitored within ten study sites with a median length of 10 m (range: 6-11 m). Because no systematic attempts were made to locate fish in areas between the sites, the spatial scale was deemed 10 m. In 1998 and 1999, movement was monitored within a single 45 m, and 120 m, long study sites, respectively; i.e. the spatial scale was 45 m and 120 m. Notice that in 1999, fish were not tagged in the whole 120 m study site, but the spatial scale was judged to be 120 m because recapture attempts were made in both the tagging and non-tagging zones of the study site (Fig. 1.1). The study sites were selected to represent a wide range of habitats that also were accessible via snorkeling.

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Sampling and tagging protocol

A total of 320 YOY Atlantic salmon were individually tagged over the three study seasons, ranging from 40 fish in 1998, when the tagging protocol was developed, to 216 fish in 1999 (Table 1.1). Fish were tagged at fork lengths between 30.1-55.3 mm (1998, 36.6-55.3 mm; 1999, 33.0-51.3 mm; 2000, 30.1-40.9) and as early as 2-3 weeks after emergence. The initial survey each year was conducted according to the following procedure. An observer (author S.Ó. Steingrímsson) snorkeled upstream through the study site and when a fish was observed at a foraging station, it was caught using two aquarium dipnets, and the location was marked by embedding a numbered flag in the substrate. Each fish was anaesthetized using clove oil (Keene et al. 1998) and fork length was measured with calipers to the nearest 0.05 mm. Fish were then tagged by a subcutaneous injection of a minute amount of fluorescent red, green or orange elastomer (Dewey and Zigler 1996). Each fish was tagged in two of the eight following positions: the operculum (left and right); the base of the dorsal fin (anterior and posterior); the caudal peduncle (dorsal and ventral); and the base of the pectoral fin (left and right) (positions 1-8, respectively). In 2000, when fish were tagged at a relatively small size, tagging positions on the operculum (1 and 2) were omitted. Upon recapture any fish with fading tags were retagged to minimize tag loss. After fish had recovered from anaesthesia for 5-15 minutes, they were returned in dipnets to their foraging station via snorkeling, which allowed for observation of the fish during their release. Most fish immediately resumed their natural feeding behaviour when returned to the stream. A few fish,

however, appeared disturbed upon release, and either hid in, or rested on the substrate at the point of release, or in several cases (<10%) showed bursts of upstream swimming. Fish that swam away were immediately recaptured and placed back on their station to minimize tagging-induced movement; in no case were more than two recaptures necessary.

Data on the location of the tagged fish were collected repeatedly during several sampling surveys conducted from early July to late September (Table 1.1). The surveys were categorized as (1) capture, (2) observation, and (3) electrofishing surveys (Table 1.1). In capture surveys, which included the initial tagging effort each year, fish were located via snorkeling, captured, measured, tagged if necessary, and released (see above). In observation surveys, fish were also recognized via snorkeling but only the location was marked. In both these types of surveys, Steingrímsson snorkeled repeatedly through each study site (or a subsection of a site) and often on consecutive days to ensure that a high proportion of the fish were observed (Table 1.1). However, the time and effort devoted to locating and catching fish varied considerably among the surveys and the study years. Most importantly, in 1999, 13 days were allocated towards the initial tagging effort in an attempt to tag every YOY Atlantic salmon in the tagging zones of the study site; each zone was snorkeled through repeatedly until no new individuals had been found on at least two consecutive occasions. Consequently, later in 1999, untagged individuals observed in the tagging zones were tagged and classified as putative immigrants (Table 1.1). In 1998 and 2000, less time was devoted to the initial tagging survey as no plans were made to tag all fish in the study sites; e.g., in 2000 only six to eight fish were tagged

in each study site. Snorkeling observations were conducted between 10:00 and 22:00, with over 90% of observations between 13:00 and 19:00; the mean water temperature in these surveys was 18.8°C (range: 15-26°C). Because of low water temperatures, electrofishing was used to catch the study fish in the final survey of the 1999 season. The 120-m study site was divided into eight, 10-20 m long zones, which were blocked with barrier nets. Each zone was sampled by a four-person crew, using a Smith-Root Model 12A electrofisher (500 V; Smith-Root Inc., 14014 NE Salmon Creek Ave. Vancouver, WA 98686, USA), a dipnet and a seine, held immediately downstream from the shocking area. Three consecutive sweeps were completed for each zone and the final fish number was adjusted for sampling efficiency (Zippin 1958). The study period, from the first day of tagging to the last day of final recaptures, was 30 days in 1998, 87 days in 1999 and 63 days in 2000 (Table 1.1).

Movement, site fidelity, ecological correlates and growth

Measurements of individual movements were facilitated by making detailed habitat maps of each study site using an x-y coordinate system. First, spray-painted nails (25 cm) were driven into both riverbanks at 2- or 2.5-m intervals, linearly along the site length (i.e., y-transect). After each snorkeling survey, a measuring tape was stretched across the stream, between the matching nails on the two riverbanks, thus creating an x-transect at a fixed y-value (at 0, 2, 4 m, etc.). The x-y location of each fish was then measured by extending a meter stick at a 90° angle from the measuring tape to the fish location. This method provided accurate (±5 cm) estimates of the x-y coordinates. Maps,

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with the location of each fish, were created for each study site by transferring the data to ArcView GIS 3.2 software. The distance a fish moved between surveys was measured both as the up- and downstream distance (along the y-axis), and as the actual displacement between the two coordinates, a method which also incorporates potential habitat-related movement along the stream width. Because of the length of the study sites in 1998 and 1999, coordinates were recorded in two and three contiguous sections, respectively, which were later transformed into one x-y surface by applying simple geometric calculations. For each spatial scale, we created movement histograms showing the proportion of the population moving a given distance. Such curves often have to be corrected for the so-called distance-weighting effects as longer distances are less likely to be detected than short movements (Porter and Dooley 1993). However, because we found no statistical difference between the original and the weighted curves (Kolmogorov-Smirnov test, $P > 0.95$ in all cases), and because each pair of corresponding curves looked identical, we only report the original unweighted curves.

Our analysis of the ecological correlates of movement and site fidelity was limited to 1999, because this study season yielded the most comprehensive data in terms of sample size and the number of correlates measured (i.e., population density, fork length, water depth and current velocity). For each fish, the local population density was estimated by viewing the distribution of individuals in ArcView GIS, and was calculated as the number of YOY salmon within a 2-m radius from the fish, divided by the circle area within the stream boundaries. The body size estimate was also obtained at a local scale, as the relative fork length of the focal fish compared to the average fork length of

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its four nearest neighbors (fork length $_{focal\ fish}$ × fork length $_{neighbors}^{-1}$ × 100). The water depth and the current velocity were measured for each fish at the exact location of capture; the current was measured at 40% of the water column depth using a Marsh-McBirney meter (Model 201D; Marsh-McBirney Inc., 4539 Metropolitan Ct. Frederick, MD 21704 USA). The four correlates, as measured in the initial survey, were tested for an association with two dependent variables, the seasonal displacement distance and the site fidelity. The seasonal displacement distance was estimated for fish that remained in the study sites throughout the study season, and was simply the distance between the first and last location at which a fish was found. The relationship between the correlates and the displacement distance was examined using a linear regression, a curvilinear (i.e., quadratic) regression and a backwards step-wise regression analysis with all four correlates (and their quadratic terms). Because the three analyses yielded the same results, only the linear regression statistics are reported. In terms of site fidelity, fish were categorized as those that remained in the study site throughout the season (score = 0) or those that disappeared from the sites during the study season via emigration or mortality (score = 1). Logistic regression was used to test for correlates of site fidelity; again the correlates were tested both in a uni- and multi-variate analyses and because both yielded the same results, only the former is reported. Because the initial survey in 1999 lasted for 23 days, fork length estimates for these analyses were adjusted for date by regressing the fork length on the day of year, and adding the residual length of each fish to the mean fork length (44.7 mm, reached on 15 July) for the survey. Because fork length of YOY fish increased, in all three years, linearly from the time of tagging to early September,

growth rates were calculated as (Fork length$_{final}$ - Fork length$_{initial}$) × (Day of year$_{final}$ - Day of year$_{initial}$)$^{-1}$ (unit = mm/day).

The total number of tagged fish in each survey was calculated as: $N = N_{fish\ found} + N_{not\ found}$, where $N_{not\ found}$ refers to fish that were not found in the survey itself, but were found in both a previous and a subsequent snorkeling survey; these extra fish were thus presumed to be in the study site, but inactive, during the survey. The decline in the numbers of tagged fish in the study sites was calculated as the instantaneous daily loss rate (Z') according to the following formula

$$Z' = - \ln(N_t / N_0)/\Delta t$$

where N_0 and N_t refer to the number of fish at the beginning and the end of the period of interest and Δt is the number of days between the two estimates. In this case, Z' incorporates losses resulting from mortality along with losses such as emigration and tag loss (Ricker 1975). Finally, we had access to water discharge data for Catamaran Brook, collected every hour via a hydrometric gauge maintained by Environment Canada (Cunjak et al. 1993).

Results

Patterns of movement and site fidelity

Despite the small spatial scale, our observations on movement are based on a majority of the tagged fish in our study. Of the 291 YOY Atlantic salmon that were tagged at the beginning of the three study seasons (i.e., original residents), 246 fish were

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re-sighted at least once during their respective season. Also, of the 29 immigrants tagged in the study site in mid-August 1999 (i.e., early immigrants), 27 fish were re-sighted at least once during the rest of the season. In addition to these tagged fish, we also caught a total of 30 untagged fish (i.e., late immigrants) in the tagging zones of our study site, during the final electrofishing survey in 1999. It is possible that some fish were inactive in the initial 1999 survey and thus wrongly classified as immigrants. However, based on the proportion of fish not found (13.8%) in the other capture survey in 1999 (survey no. 3), and the fact that we put 1.86 times more effort (13 vs. 7 days) into the initial survey compared to survey no. 3 (Table 1.1), we estimate that we missed only $(0.138)^{1.86} = 2.5\%$ of the YOY salmon (4.8 fish) in the initial survey.

Of the original residents, the re-sighted fish showed remarkably restricted movement; on average 61.8% of these fish moved less than 1 m up- or downstream from their original tagging location, whereas 96.9% moved less than 5 m in either direction (Fig. 1.2). The proportion of fish remaining within a given distance was similar for the three study years, irrespective of the spatial extent of the sites; i.e., 97.8%, 96.6% and 96.4% of the fish moved less than 5 m up- or down-stream at a spatial scale of 10, 45 and 120 m, respectively (G-test: $G = 0.10$, df $= 2$, $P > 0.9$). Still, the movement curves, and their statistical parameters, varied among the study years, mainly because of three fish (one in 1998 and two in 1999) that moved farther than 10 m downstream (Fig. 1.2; Table 1.2). First, at a spatial scale of 10 m, where no long movement distances could be detected, no clear pattern emerged in terms of skewness of the movement curves; i.e., after 40 days the curve was skewed towards upstream movements ($P < 0.01$) whereas

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after 20 and 61 days, skewness was not detected ($P > 0.05$) (Table 1.2). At 45 m and 120

m, however, all curves were significantly skewed toward downstream movement (all

cases: $P < 0.001$). Second, the movement curves were generally leptokurtic, i.e., they had

significantly higher peaks and longer tails compared to a normal distribution, and as with

skewness, this pattern was clearer at larger spatial scales. Hence, at 10 m, kurtosis ranged

from 1.56 to 3.31 ($P < 0.05$), whereas at 45 m and 120 m, kurtosis ranged from 9.41 to

110.40 ($P < 0.001$) (Table 1.2).

Not surprisingly, the maximum dispersal distance of the original residents

increased with the spatial extent of the study site, ranging from 6.5 m at a spatial scale of

10 m, to 31.0 m at 45 m and to 84.9 m at a site length of 120 m (Table 1.2). The median

displacement was low, ranging from only 0.86 m to 1.65 m. The median displacement

also appeared to increase with time (i.e., days from tagging), but this trend was not

significant (Spearman's $r = 0.59$, $n = 9$, $P = 0.094$), perhaps because the pattern was

inconsistent among the study years, i.e., there was a significant interaction between time

and the study year (Analysis of covariance, ANCOVA, $F_{2,3} = 14.84$, $P = 0.028$) (Table

1.2). In 1999, the early immigrants moved farther (mean = 1.14 m) than the original

residents (mean = 0.66 m) over the last month of the study season (Fig. 1.3)(t-test: $t =$

2.45, df = 132, $P = 0.016$).

The number of the original resident fish, tagged at the beginning of each study

season (n = 291), declined during the three seasons at an instantaneous daily loss rate (Z')

of 0.0078; hence, on average, 99.22% of the fish remained in the study sites from one day

to the next (Fig. 1.4). For each of the three years, Z' ranged from 0.0118 in 1998, to

0.0083 in 1999 and to 0.0071 in 2000, but the slopes did not differ significantly (ANCOVA: $F_{2,7} = 1.34$, $P = 0.322$) (Fig. 1.4). Because of the low loss rates, 72.3%, 54.0% and 65.0% of the original residents remained in the study sites at the end of the 1998, 1999 and 2000 season, respectively. The proportion of early immigrants that remained in the study site from tagging in mid-August in 1999 to the end of the season (21 of 29 fish, $Z' = 0.0077$), was identical to the proportion of the original residents retained over the same period (101 of 152 fish, $Z' = 0.0096$) (G-test: $G = 0.203$, df = 1, $P > 0.5$). Thus, immigrants were not more likely to disappear from the study site than the original resident fish.

The loss of tagged fish from our sites can be due to tag loss, mortality or emigration. First, it is unlikely that tag loss contributed much to the overall loss of the tagged fish. In the six surveys in which fish were recaptured, only 2.9% (range: 0-4.4%) of the tagged fish were missing a tag from one of the two positions. If we assume that the probability of losing both tags is $(0.029)^2$, then only 0.084% of the fish lost both tags between consecutive capture surveys, and only 0.46 of the 320 tagged fish disappeared as a result of tag loss. Of the 119 tagged YOY salmon that were lost over the three study seasons, we cannot estimate accurately how many fish disappeared as a result of mortality or emigration. However, even the distance-weighted curves, which take into account the low probability of detecting longer movement (Porter and Dooley 1993, see methods) suggest that only about 2.7 and 2.0 individuals moved farther than 10 m, but remained within a distance of 45, and 120 m, in 1998 and 1999, respectively. Hence, if this low frequency is an indicator of the frequency of movement outside of the study sites, our

data suggest, at least qualitatively, that the majority of the fish were lost to mortality rather than emigration.

Ecological correlates and growth consequences

Of the original residents that remained within the study site throughout the 1999 season, the seasonal displacement was weakly related to one of the four variables, i.e., current velocity (Slope = -0.315, $r^2 = 0.085$, $P = 0.004$) (Table 1.3). Hence, fish in slow water in the initial tagging survey moved farther from their original location than fish from faster water. The other three variables, population density, relative fork length and water depth were not significantly related to seasonal displacement (Table 1.3). Similarly, only one of the four variables contributed to whether the original residents remained within, or disappeared from the study site during the season (Table 1.3). Fish found at high population densities in the initial survey were more likely to disappear from the study site than fish from low-density areas (logistic regression: $B = 1.43$, $P = 0.032$). At a population level, the daily loss rate (Z') calculated between subsequent surveys in the three study years was correlated with the mean water discharge in Catamaran Brook during the corresponding periods (Pearson's $r = 0.814$, $n = 10$, $P = 0.004$); i.e., the original resident fish disappeared faster from the study sites during periods of high discharge (Fig. 1.5).

Fork length of the original residents increased linearly from the time of tagging to early September each year, and the mean growth rate during this period was 0.295, 0.238 and 0.290 mm/day in the 1998, 1999 and 2000, respectively. In 1999, the study season

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extended to the end of September whereas growth leveled off sharply in early September; in this case individual growth rates were based only on the original linear increase, and no growth was assumed to have occurred after early September (Girard 2002). For the original residents that stayed in the study sites throughout each of the three seasons, no association was found between individual growth rates and seasonal displacement (all cases: Pearson's correlation, $P > 0.2$). The immigrants found in 1999 provide an alternative view on the growth consequences of movement. When first tagged in mid-August, the early immigrants were slightly, but not significantly, smaller (mean = 51.3 mm) than the original residents (mean = 52.4 mm) (t-test: $t = 1.87$, df = 166, $P = 0.063$); a similar pattern was seen for the late immigrants, which were significantly smaller (mean = 53.3 mm) than the original residents (mean = 57.1 mm) when caught at the end of the season (t-test: $t = 5.52$, df = 124, $P < 0.001$). In terms of growth, however, early immigrants grew faster (mean = 0.271 mm/day) than the original residents (mean = 0.237 mm/day) in the latter part of the 1999 season (t-test on residual growth rate: $t = 2.65$, df = 105, $P = 0.009$) (Fig. 1.6). In fact, 16 of the 20 immigrants grew faster than the average growth rate predicted for any given initial fork length. Hence, at the end of the season, the early immigrants had reached a similar size (mean = 56.9 mm) to the original residents (mean = 57.1 mm) (t-test: $t = 0.48$, df = 113, $P < 0.63$).

Discussion

The shape of movement curves has been described in several studies on stream-dwelling fish, focusing mostly on salmonids (e.g., Harcup et al. 1984; Heggenes 1988;

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Gowan and Fausch 1996), cyprinids and centrarchids (i.e., chub, dace and sunfish) (Smithson and Johnston 1999; Skalski and Gilliam 2000). In this study, most re-sighted YOY Atlantic salmon moved extremely short distances over their critical first summer of feeding (61.8% < 1 m, 96.9% < 5 m). For periods where longer movements (>10 m) were detected, the movement curves were extremely leptokurtic ($g_2 = 21.41-110.40$), characterized by high peaks and long tails. Although leptokurtosis is a common feature of movement curves reported in the stream-fish literature, the frequency of mid- to long-distance movements is higher and kurtosis is less extreme ($g_2 = 1.55-7.34$) than observed in our study (Heggenes 1988; Heggenes et al. 1991; Skalski and Gilliam 2000). As in other studies on YOY salmonids (Hume and Parkinson 1987; Webb et al. 2001), movements were skewed towards downstream in our study.

There are potential methodological reasons for the restricted movement and the extreme leptokurtosis found in our study. First, some of the fish that disappeared in this study may have emigrated out of the study sites, because (*i*) the maximum distance detected each year increased with the spatial extent of the sampling effort, (*ii*) fish moved (immigrated) into the study area in 1999, and (*iii*) because the maximum dispersal distance of YOY salmonids is likely about 1 km (Hume and Parkinson 1987; Webb et al. 2001). However, although our movement curves may underestimate longer movements (Porter and Dooley 1993), it is unlikely that further sampling up- and downstream would have yielded many fish, especially considering the low frequency of movement over 10 m. This view is consistent with electrofishing data collected in 1998-2000 at Catamaran Brook, which show an overall decrease in the mean number of YOY Atlantic salmon

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from 36.4 to 21.2 per 10 m stream length from July to late October, respectively ($Z' =$ 0.50) (based on 13-19 study sites where YOY were found each year; Richard A. Cunjak; Department of Biology and the Faculty of Forestry and Environmental Management, University of New Brunswick, Bag Service 45111, Fredericton, NB E3B 6E1, Canada; Personal communication). Hence, if we assume that this loss rate indicates the overall mortality rate in the stream, and also applies to our study sites, then 78 of the 119 missing fish would be assigned to mortality and only 41 to emigration. Importantly, if fish had been found outside the study sites, the movement curves would have become even more leptokurtic (via longer tails), relative to the curves described in the literature.

Another methodological reason for the low frequency of mid- to long-distance movement observed in our study, may be our relatively non-invasive capture and release techniques. In previous studies, fish were often captured via invasive methods, such as electrofishing (Nordwall 1999), and released into the original capture section, the size of which was usually much larger than home range areas of stream fishes, and in particular, those of stream-dwelling salmonids (Nakano 1995). Consequently, many fish were released outside their familiar space; a practice that could promote exploratory behaviour (Armstrong et al. 1997). Occasionally, fish were released close to the site of capture (e.g., Heggenes et al. 1991), but even in these studies fish were not observed upon their release. In contrast, fish in this study were released at the exact location of capture, and the influence of stress-related movement at the time of release was minimized by catching fish again and bringing them back to their original location.

The classic view of the ecological causes and consequences of movement in YOY

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salmonids suggests that small, subordinate fish emigrate from areas of high population density (Chapman 1962; Elliott 1994). Our study does not support this view; population density was not related to the seasonal displacement of fish, and was only weakly correlated with whether or not fish disappeared over the season. Hence, if density induced movements, it did so only by causing movement out of the study site, a process also influenced by density-independent events such as changes in water discharge (Shirvell 1994). In our study, however, the initial local densities ranged from 0.08 to 1.19 fish/m^2, which suggests that territories of the original residents occupied only 1.6-24.5% of the local stream area (Keeley and Grant 1995), a percent habitat saturation (PHS) at which density-dependent emigration, growth, or mortality, is only detected in 0.7-46.1% of salmonid populations (see Grant and Kramer 1990 for details on PHS). Consequently, low population densities and low levels of competition may in part explain why the majority of the original residents were sedentary, and why the more mobile residents were similar in body size, and grew at a rate similar to that of the more sedentary ones.

Alternatively, we suggested that ontogenetic changes in habitat preferences, and seasonal habitat changes (e.g., droughts), can cause movement out of areas that become unfavourable, and that mobile fish may be larger, and grow faster than sedentary fish (Armstrong et al. 1997; Kahler et al. 2001). Thus, YOY Atlantic salmon may leave shallow, slow running waters as they grow (see Morantz et al. 1987). In this study, fish found in slow currents, moved farther from their original location than fish from faster waters, suggesting habitat selection can induce movement. However, current velocity explained only 8.5% of the variation in the displacement distance, and did not contribute

to whether fish remained in the study area or disappeared. These weak effects can be explained by a parallel study focusing on the habitat use of our study fish in 1999, which showed negligible ontogenetic changes in habitat selection over the first growing season (Girard 2002). Hence, the lack of movement found in this study may reflect the fact that most fish did not outgrow their habitat during the study period. Finally, growth rates of the original residents were independent of how far they moved within the study areas, whereas the immigrants tagged in 1999 grew faster than the original residents from the time they were tagged in mid-August. Hence, our study supports the idea that fish moving longer distances are not necessarily of lower fitness, and that movement of stream fish can be advantageous (Fraser et al. 2001; Rodríguez 2002).

Clearly, the perception of mobility depends on the time and space over which movement is monitored. Hence, although the local movement patterns of the original residents changed little over time, there was a gradual increase in the proportion of immigrants in the 1999 study site (to 33.6% of the final fish number), suggesting that on a stream-wide basis a substantial number of fish may relocate longer distances. Similarly, although movement of YOY stream salmonids is often affected by population density (Elliott 1994) and habitat use (Kahler et al. 2001), these effects may vary seasonally, from being minimal when movement is restricted in mid-summer, to being more profound during periods of intense competition in the days after emergence (Elliott 1994), during drastic habitat changes in early winter (Whalen et al. 1999), or during severe fluctuations in stream discharge (Shirvell 1994). Finally, the restricted movement observed can partly be due to variability among species; Atlantic salmon move shorter distances than many

other salmonids, such as brook charr (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) (Rodríguez 2002).

The literature on movement in stream fish frequently classifies individuals as mobile or sedentary based on how far they move, or on whether they leave a study site or not. Although this dichotomy is useful for modeling movement (Skalski and Gilliam 2000; Rodríguez 2002), the classification is often arbitrary and may not always reflect fixed differences among individuals in a population (but see Harcup et al. 1984 and Fraser et al. 2001). In our study, there may be inherent differences between mobile and sedentary fish, as immigrants moved longer distances, and grew faster than the original residents after their arrival in the study site. However, the mobility of the immigrants can also be caused by exploratory behaviour as fish settle in new habitats (Armstrong et al. 1997), whereas the fast growth can be due to compensatory growth because the immigrants were slightly smaller than the residents at their arrival in the study site (Maclean and Metcalfe 2001). Finally, although this study suggests that most YOY Atlantic salmon adopt restricted movement soon after emergence, it should be emphasized that mobility of stream fishes varies considerably among life stages and species (Rodríguez 2002). We agree with recent studies that suggest a more rigorous quantitative modeling of movement curves is needed, along with an understanding of the social and environmental conditions that shape these curves in natural habitats (Skalski and Gilliam 2000; Fraser et al. 2001; Rodríguez 2002).

Table 1.1. Summary of the sampling effort and sampling methods used to monitor movement of young-of-the-year Atlantic salmon in Catamaran Brook in 1998-2000.

Survey no.	No. of fish tagged[a]	Survey dates	Sampling effort[b]		Mean water temperature, °C	Survey type
			No. of days	Repeats		
Spatial scale = 10 m, Year 2000						
1	64	12-13 July	2	1-3	18.7	Capture
2	-	13 July-17 Aug.	21	3-5	19.8	Observation
3	-	20-23 Aug.	4	3-5	16.5	Capture
4	-	11-12 Sept.	2	3-5	16.0	Capture
Spatial scale = 45, Year 1998						
1	40	4-6 Aug.	3	3-5	21.0	Capture

2	-	16-17 Aug.	2	3-5	19.5	Capture
3	-	1-2 Sept.	2	3-5	17.0	Capture

Spatial scale = 120, Year 1999

1	187	6-28 July	13	5-7	20.5	Capture
2	-	27 July-7 Aug.	5	1-3	19.4	Observation
3	29	10-22 Aug.	7	3-5	18.4	Capture
4	-	23-25 Aug.	3	1-3	21.1	Observation
5	-	30 Aug.-10 Sept.	7	3-5	18.5	Observation
6	-	20-30 Sept.	5	3	11.7	Electrofishing

[a] 29 immigrants were tagged in 1999; no attempt was made to tag immigrants in 1998 and 2000.

[b] The sampling effort is indicated both as the total number of days allocated towards seeking out YOY salmon, and as the estimated number of times (repeats) each section of the respective study sites was visited (or sampled) during the survey.

Table 1.2. Quantitative description of the movement patterns of young-of-the-year Atlantic salmon examined at three spatial scales.

Spatial scale (m)	Days from tagging	$N_{\text{fish found}}$ / $N_{\text{not found}}$[a]	Displacement (m)		Shape of curve[b]	
			Median	Maximum	Skewness g_1	Kurtosis g_2
Year - 2000						
10	20	51/2	0.86	4.22	-0.44^{ns}	2.66^{***}
10	40	44/1	1.03	7.34	1.03^{**}	3.31^{***}
10	61	39/1	1.17	6.50	0.67^{ns}	1.56^{*}
Year - 1998						
45	12	32/1	1.16	31.00	-5.14^{***}	28.11^{***}
45	28	28/1	1.65	23.00	-4.37^{***}	21.41^{***}
Year - 1999						
120	17	110/50	0.91	84.85	-9.77^{***}	99.97^{***}
120	31	131/21	0.96	8.71	-1.66^{***}	9.41^{***}
120[c]	40	136/10	0.89	62.70	-9.99^{***}	110.40^{***}
120	48	127/12	1.03	61.40	-9.61^{***}	102.56^{***}

[a] $N_{\text{fish found}}$ is the number of original residents found in each survey and is used to establish

the movement curves; $N_{\text{not found}}$ is the estimated number of original residents in the site, but inactive, during the survey.

[b] skewness (g_1) and kurtosis (g_2) were calculated and tested for normality via Sokal and Rohlf (1981). Significance level is symbolized as: [ns] $= P > 0.05$, [*] $= 0.05 > P > 0.01$, [**] $= 0.01 > P > 0.001$, [***] $= P < 0.001$.

[c] the only curve that is not depicted in Figure 1.2.

Table 1.3. Ecological correlates of seasonal displacement and site fidelity of young-of-the-year Atlantic salmon in Catamaran Brook, in 1999.

Predictor	Range		Displacement[a]			Site fidelity[b]		
	(min, max)	Slope	r^2	P	% Correct	B	P
Population density (fish/m^2)	0.08, 1.19	-0.001	0.000	0.994	62.57	1.430	0.032
Relative fork length (%)	-27.8, 28.2	-0.009	0.023	0.140	48.13	0.005	0.821
Current velocity (m/s)	0.00, 0.35	-0.315	0.085	0.004	51.34	0.202	0.638
Water depth (cm)	7, 79	0.066	0.001	0.768	50.80	-0.034	0.966

Note: Minimum, min.; maximum, max.

[a] results from a linear regression analysis; n = 95 in all four cases. Displacement, current velocity and water depth were $\log_{10}$ transformed for the analysis.

[b] results from a logistic regression analysis; site fidelity was scored either as 0 (fish that remained in the study site throughout the study

period, n = 95) or 1 (fish that disappeared from the site over the study period, n = 92). Unavoidably, some remaining fish not caught in

the final electrofishing survey may be wrongly classified among the disappeared fish; however, a Zippin (1958) estimate of the final

number of original residents in the site (n = 101) suggests that this number is low (n = 6).

Fig. 1.1. The location of the study sites in the lower reach of Catamaran Brook, New Brunswick, Canada. The embedded map in the top left corner shows the location of Catamaran Brook within New Brunswick; the enlarged maps in the bottom right corner of the figure show the study sites in 1998 and 1999, and one of the ten study sites used in 2000 (labeled 1-10). In 1999, the 120-m-long site consisted of tagging zones in which all fish were tagged and non-tagging zones in which fish were only recaptured. The dots show the original location of tagged fish in the three enlarged study sites. The values for the latitude and longitude refer to the main map of the lower reach in Catamaran Brook.

66°07'00"   66°06'45"   66°06'30"   66°06'15"

Study area

New

Brunswick

46°52'45"

Little Southwest Miramichi River

Counting fence

4 3

5

6

2 1

Catamaran Brook

1999

1998

7

8

46°52'30"

10 9

2000

0

500m

1999

1998

2000

0   20   40m

35
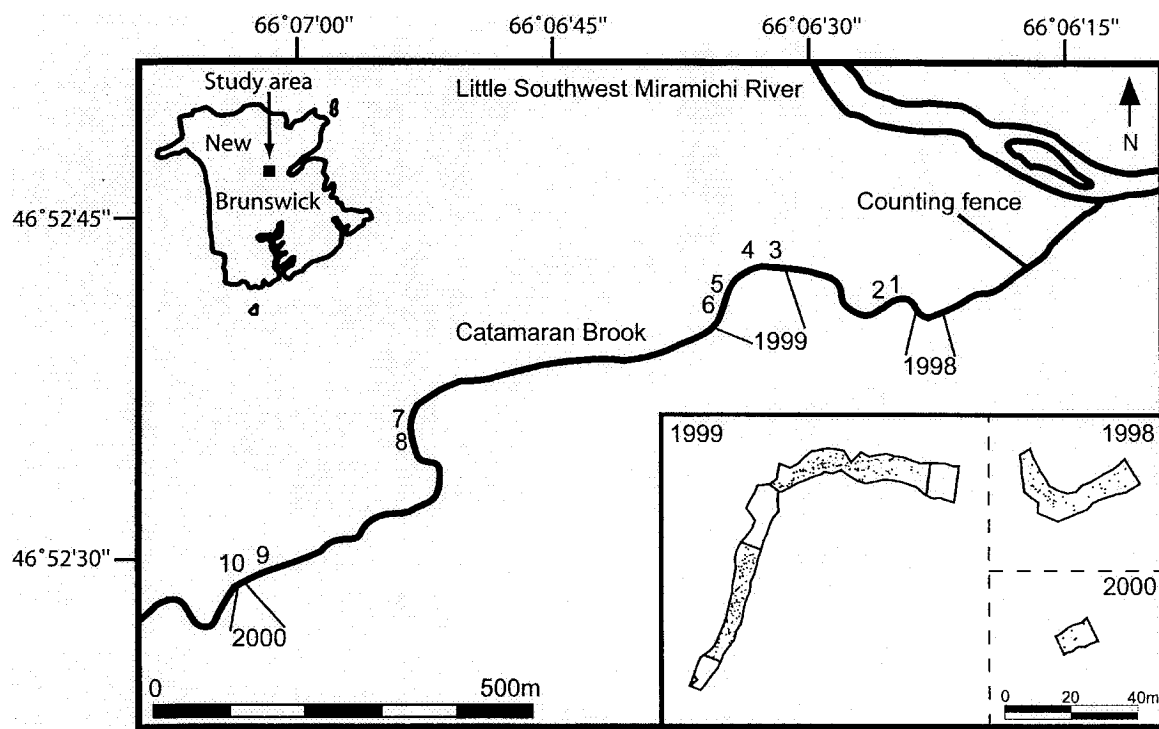
Fig. 1.2. Movement of young-of-the-year Atlantic salmon (*Salmo salar*) in Catamaran

Brook monitored at a spatial scale of 10 m (a, b, c; 2000), 45 m (d, e; 1998) and 120 m (f,

g, h; 1999). Positive and negative values on the x-axes refer to upstream and downstream

movement, respectively. The horizontal line and the number at the top of each graph

indicates the spatial extent of the study site, and the number of days from the initial

tagging survey (e.g., 20 d), respectively. Notice that even though the x-axes range from -

100 m to 20 m, the probability of detecting a given movement distance decreases

gradually in the up- and downstream direction, from 100% at 0 m, to 0% at the maximum

detectable movement distance of 10, 45 and 120 m (see Porter and Dooley 1993).
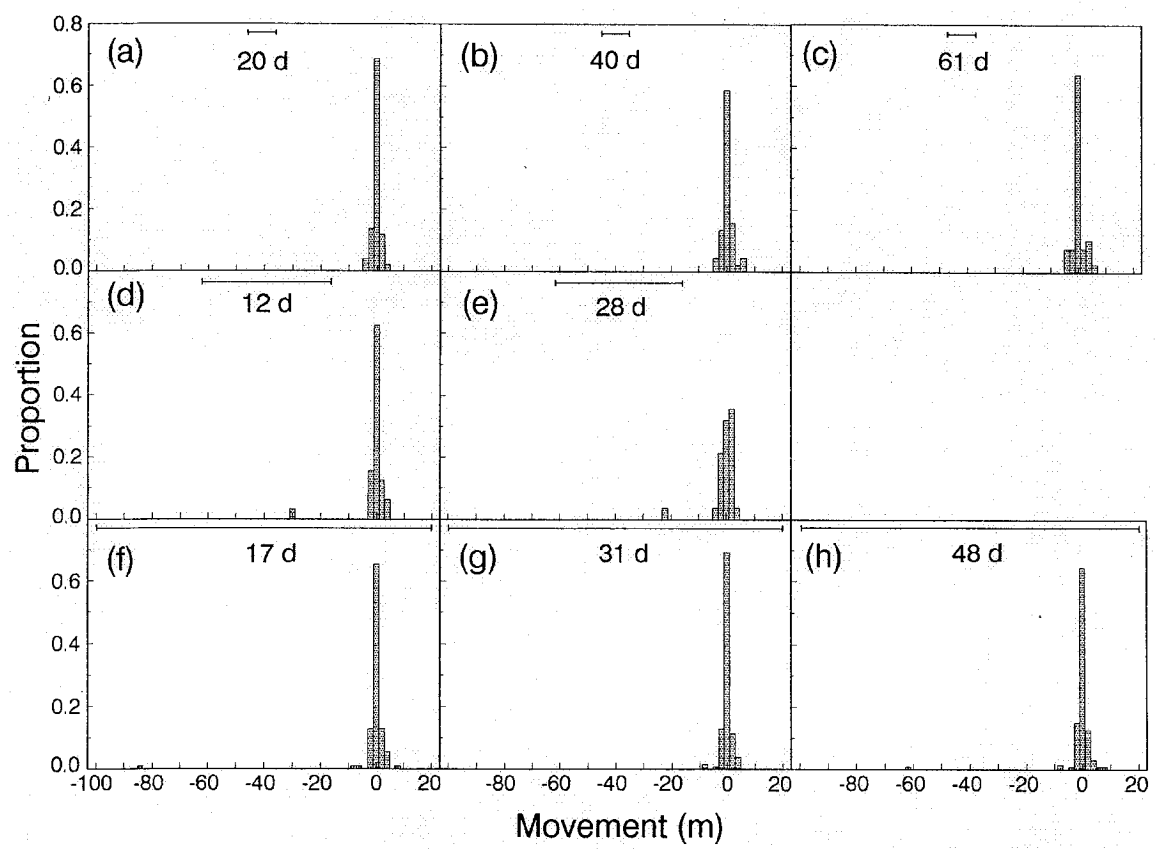
Fig. 1.3. The displacement of the original resident young-of-the-year Atlantic salmon

(*Salmo salar*) (open, n = 112) and the early immigrants (hatched, n = 22) from mid-

August to early September in 1999.
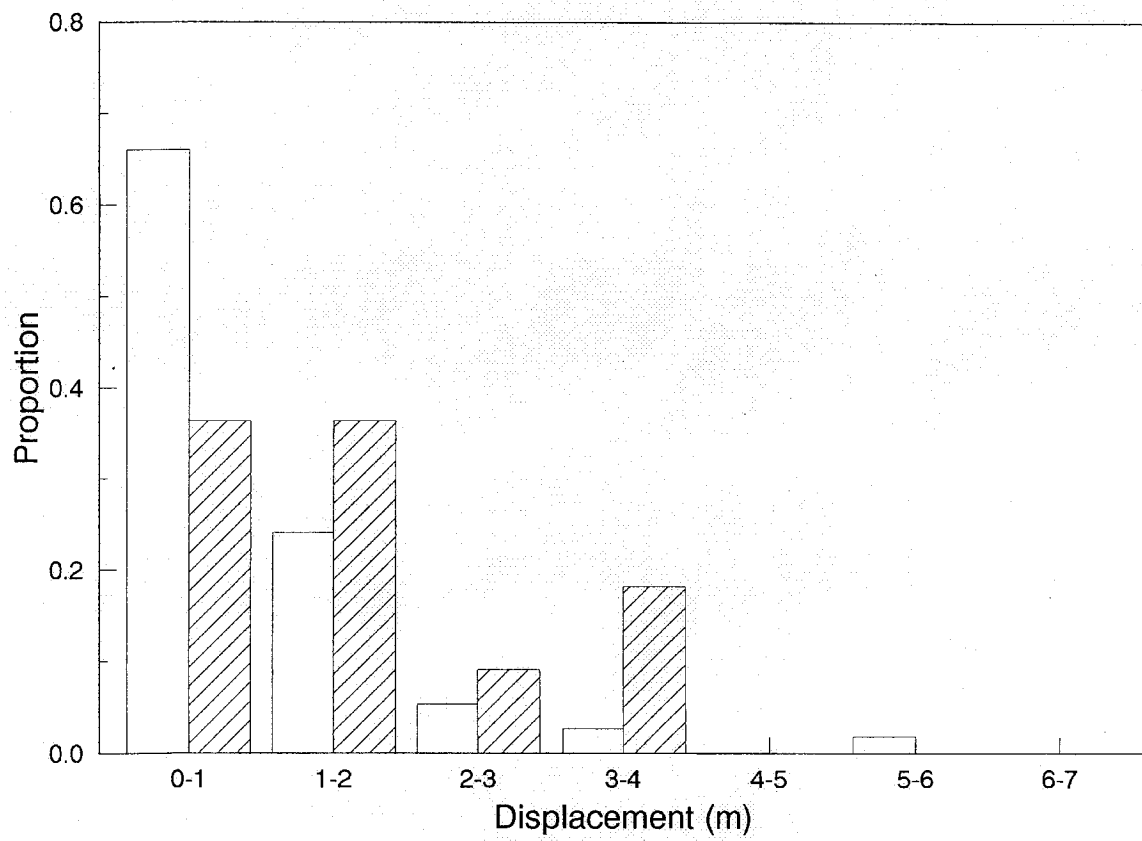
Fig. 1.4. The retention of tagged young-of-the year Atlantic salmon (*Salmo salar*) in the

study sites during the three consecutive study seasons, 1998 (▲), 1999 (●) and 2000 (■).

The overall loss rate (Z) for the three years was 0.0078 (i.e., slope = -0.0078). For the

ease of presentation, the logarithmic y-axis is re-labeled with the corresponding

arithmetic values.

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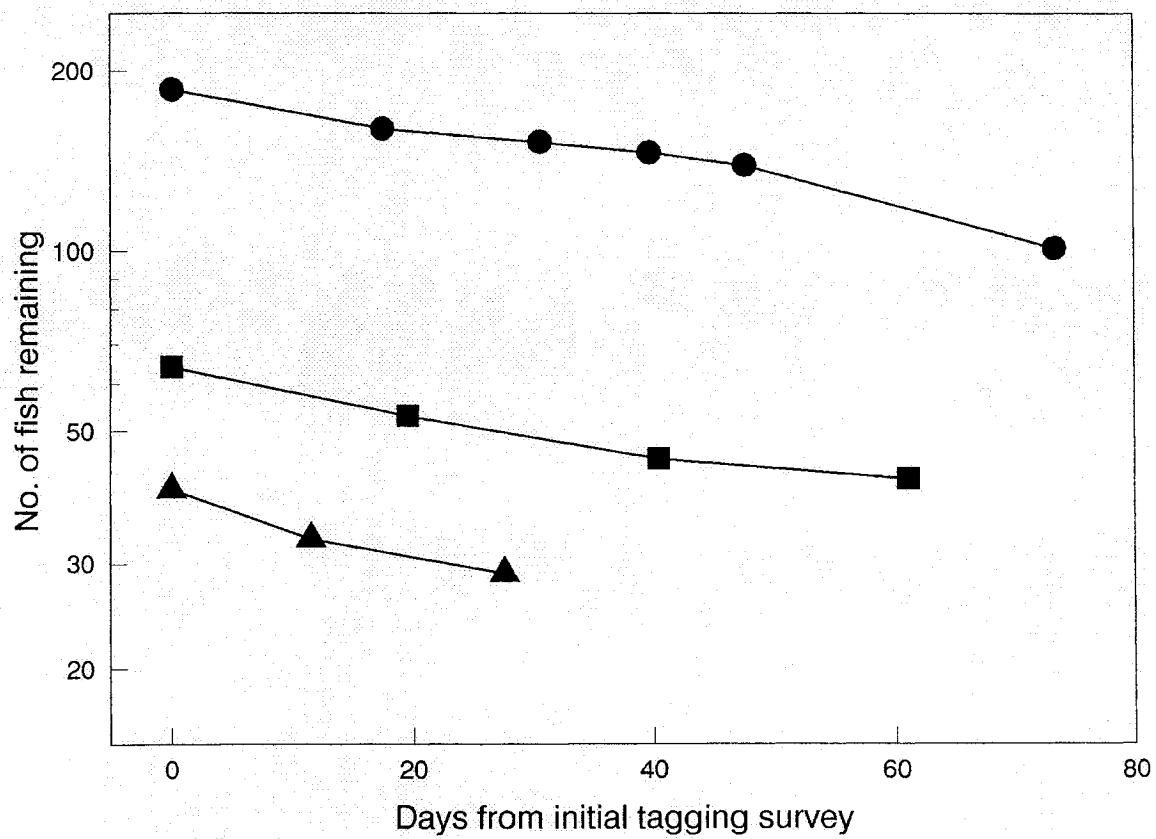
Fig. 1.5. The influence of water discharge in Catamaran Brook on the instantaneous daily

loss rate (Z') calculated for tagged young-of-the-year Atlantic salmon (*Salmo salar*) in the

study sites in 1998 (▲), 1999 (●) and 2000 (■). The Z' values are calculated based on the

decline in the numbers of fish between each of the consecutive snorkeling surveys.

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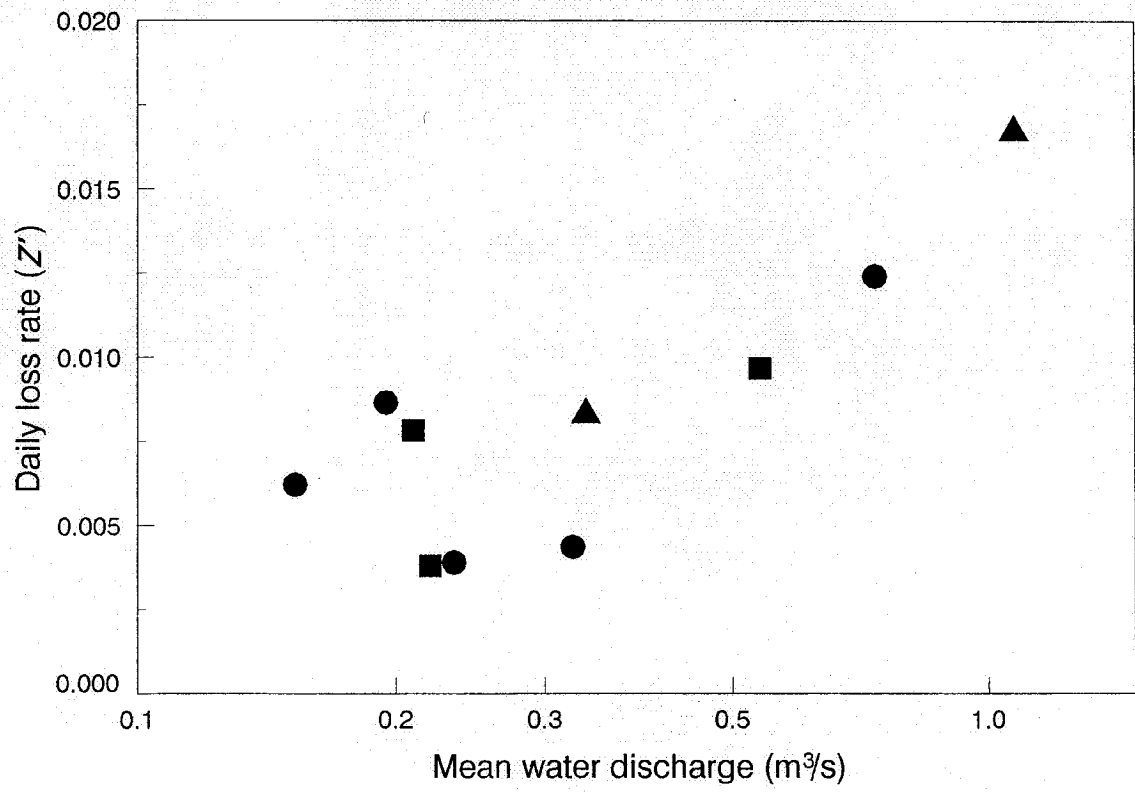
Fig. 1.6. Growth rate of the original resident young-of-the-year Atlantic salmon (*Salmo salar*) (○) and the early immigrants (●) in Catamaran Brook in 1999. Growth rate for all fish was estimated from the time the early immigrants were tagged (10-22 August), until growth had leveled off (5 September). The x-axis refers to the fork length at the beginning of this growth period. The solid line shows the predicted growth rate for any initial fork length and is described by the formula: Growth rate (mm/day) = 4.050 - 0.139 Fork length (mm) + 0.00126 (Fork length)^2 (mm) ($r^2 = 0.404$, $n = 107$, $P < 0.001$).
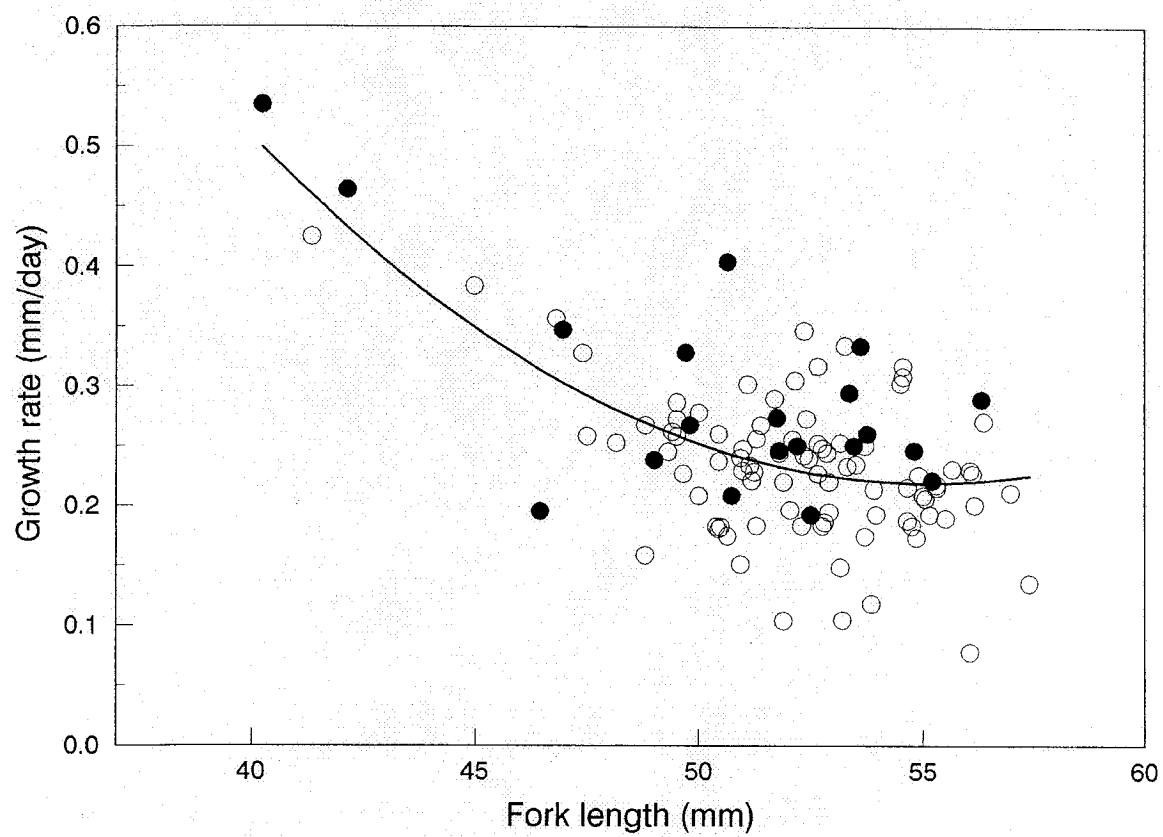
Chapter 2. Size, shape and defence of multiple central-place territories in wild young-of-the-year Atlantic salmon (*Salmo salar*)

Introduction

The size and shape of home ranges, and the degree to which these areas are defended, provide key insights into how animals exploit their environment (Covich 1976; Adams 2001), and have an effect on the distribution and the abundance of populations (Patterson 1980). Central-place foraging, a common pattern of local space-use, occurs when animals forage from or deliver food to a single central location, such as a nest or a burrow (Stephens and Krebs 1986). Central-place foragers are often territorial because of their sedentary nature and because the central place is often valuable (e.g., Getty 1981a; Brown and Gordon 2000).

Although numerous studies exist on the patterns of foraging and aggression around a central place (e.g., Getty 1981a; 1981b; Ford 1983), this central-place framework has rarely been expanded to foragers that switch among a limited number of central-place foraging stations (i.e., multiple central-place foraging; Fig. 2.1) (Covich 1976; Chapman et al. 1989; McLaughlin and Montgomerie 1989). Based on the few available studies, however, animals may adopt multiple central-place foraging to increase their prey encounter rate, reduce travel cost, or reduce predation risk (Covich 1976; Chapman et al. 1989; McLaughlin and Montgomerie 1989).

Juvenile salmonid fishes in streams have emerged as a classic case of encounter-at-a-distance foragers (sensu Stephens and Krebs 1986), that conform to the so-called

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central-place territorial model (CPTM). Hence, these fish typically initiate all aggressive acts and foraging attempts from a single central-place, and each foraging attempt involves an attack on a single prey and a return to the same central-place (Grant et al. 1989; Elliott 1990; Keeley 2000; but see Keeley and Grant 1995, Nakano 1995). In general, studies of the size and shape of territories defended by stream-dwelling salmonids that conform to the CPTM have been remarkably consistent. First, the territories of stream-salmonids are small compared to the home ranges of most freshwater fishes (Minns 1995). Second, studies typically suggest that body size is the strongest predictor of territory size; i.e., the foraging and the aggressive radii around the central station increase as fish grow (Grant et al. 1989; Elliott 1990; Keeley and Grant 1995). Third, the aggressive distance moved to defend the territory is typically greater than the foraging radii, causing most aggressive acts to be located on the outskirts of the foraging area (Grant et al. 1989; Keeley 2000). Fourth, the central-place space-use patterns can be described as a cardioid (Noakes and McNicol 1982), teardrop-like (Dill et al. 1981) or elliptical in shape (Elliott 1990), although the area can often be calculated by assuming a simple circular shape (Grant et al. 1989). Finally, territoriality is thought to play a role in limiting or regulating population density (Grant and Kramer 1990; Elliott 1994; Grant et al. 1998), even though territory size typically decreases with increasing food abundance (Slaney and Northcote 1974), intruder pressure (Keeley 2000), and visual isolation (Kalleberg 1958; Imre et al. 2002).

Despite the dogma that juvenile salmonids conform to the CPTM, several studies have demonstrated considerable variability in local space-use behaviour, where individuals range from sit-and-wait to widely cruising foragers (Grant and Noakes 1987;

McLaughlin et al. 1999), and may defend (territorial fish), or not defend (non-territorial fish and floaters) their foraging areas (Puckett and Dill 1985; Nakano 1995). In part, the notion that territorial fish comply with the CPTM stems from early influential studies which found that (*i*) stream-salmonids forage for drifting invertebrates and defend territories from one primary station (Kalleberg 1958; Keenleyside and Yamamoto 1962; but see Bachman 1984), and (*ii*) sedentary fish are more aggressive than those which forage widely (i.e., non-territorial) (Puckett and Dill 1985). However, the emphasis on the CPTM, particularly for YOY salmonids, may also reflect the inability to tag and follow small fish in natural habitats. Hence, to date, most studies have mapped territories of YOY fish at high population densities, where individuals using a single foraging station may be easiest to monitor (e.g., McNicol and Noakes 1981; Elliott 1990; Keeley 2000). Similarly, studies examining foraging, mobility, and aggression of YOY fish that do not conform to the CPTM, tend to focus on the time allocated to the different activities, rather than their distribution in space (Grant and Noakes 1987; McLaughlin et al. 1999; see Biro et al. 1997 for an example in lakes). In summary, very limited effort has been directed toward systematically mapping the space-use of YOY salmonids that do not conform to the CPTM (but see Bachman 1984; Nakano 1995 for studies on older fish). This trend is unfortunate because space-use behaviour can have particularly strong effects on individual fitness and the population regulation of young salmonids at high population densities (Elliott 1994). At low population densities, however, it is possible that territory size may be a function of population density rather than the reverse.

In this study, I adopt recent improvements in tagging techniques to examine the

daily space-use patterns of YOY Atlantic salmon (*Salmo salar*) in a natural stream. Atlantic salmon are ideal challenging the current view of territoriality in stream-salmonids because they, on one hand, epitomize the central-place-territorial nature of stream-dwelling salmonids (Kalleberg 1958), but alternatively, appear to occasionally use more than one foraging station (Keeley and Grant 1995; Armstrong et al. 1999). Hence, following tagged fish enables me to quantify the space-use behaviour of fish that could not be studied previously, i.e., individuals of greater mobility, found at lower densities, and occupying a greater range in environmental conditions. First, I verify if, and to what degree, YOY Atlantic salmon use single versus multiple central-place territories. Second, I examine if multiple central-place space-use patterns differ in size, shape and defence from the typical CPTM documented previously. I compare these patterns both by superimposing all foraging data obtained for each focal fish onto one foraging station (i.e., mapping via the CPTM), and by comparing my findings with published descriptions of territorial behaviour. The single central-place paradigm predicts that (*i*) the size of multiple central-place home ranges will be positively related to body size, (*ii*) these areas will be close to circular in shape, and (*iii*) that fish that forage from multiple stations will defend their home ranges less intensely than single central-place foragers. Finally, I use literature data to test if population density predicts whether the space-use of YOY stream-dwelling salmonids conforms to the CPTM or to a multiple-central-place territorial model; this comparison is important to determine whether the current view of territorial behaviour in stream-dwelling salmonids may be due to a bias toward observations conducted at high densities in the field and in laboratories.

Materials and methods

Study area and Study population

I collected data on YOY Atlantic salmon at Catamaran Brook, a tributary of the Little Southwest Miramichi River in New Brunswick (see Cunjak et al. 1993 and Chapter 1 for more details on the study population and the stream biota). I collected all the data at 10 study sites (6-11 m in length) in the lower reach, a 2-km reach immediately upstream from the mouth of Catamaran Brook (see Chapter 1, Fig. 1.1). To ensure that space use was observed over a large range of environmental conditions, I alternated the sites among relatively slow and fast running waters (Range in mean current velocity = 0.045-0.178 m/s, overall range = 0-0.66 m/s), which included habitats as deep as 105 cm (Table 2.1).

Capture and Tagging surveys

I individually tagged a total of 90 YOY Atlantic salmon (6-11 per study site) in two snorkeling surveys, conducted on 25 June-2 July, and on 12-13 July, 2000. In the former survey fish were tagged at fork lengths ranging from 27.30 to 36.35 mm (n = 60), whereas in the latter survey fork length ranged from 30.15 to 40.60 mm (n = 30). I snorkeled upstream through the study sites, caught each fish with two dipnets, and embedded a labeled flag at the capture location. I anaesthetized each fish separately using clove oil (Keene et al. 1998), measured fork length (i.e., body length) with calipers to the nearest 0.05 mm, and tagged it with subcutaneous injections of a small amount of fluorescent red, green or orange elastomers (Northwest Marine Technology, Inc., P.O.

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Box 427, Ben Nevis Loop Road, Shaw Island, WA 98286, U.S.A.) in two of six potential

positions (see Chapter 1 for details). After fish recovered from anaesthesia (5-15 min), I

returned them in dipnets, via snorkeling, to the exact place of capture. Following all

space-use observations (see below), I recaptured all tagged fish still remaining in the

study sites and measured their fork length, in two snorkeling surveys conducted on 20-23

August and 11-12 September. Because, fork length increased fairly linearly during the

study season, I estimated the fork length of each fish, on the day of its space-use

observation, by assuming a linear increase in fork length between its two closest dates of

capture, one before and one after the observation. For five fish, not recaptured after their

space-use observation, I estimated fork length by using the mean daily length increase

exhibited by all recaptured fish over the observation period.

Estimates of Space use and Population density

      I observed daily space-use patterns for 50 of the tagged individuals (1-3 fish per

day) between 3 July and 17 August, 2000; data were not collected on any fish until at

least 24-h after tagging. In general, I monitored each fish over four 10-min periods on the

same day (between 1330-1850 h), yielding 20-min of observations in early and late

afternoon, respectively. The only exceptions to this rule were three fish that I observed for

a total of only 30-min, and four fish where the last 20-min were obtained on the

subsequent day.

      To quantify space-use I first identified each fish from downstream (via

snorkeling), and then waited at least five minutes before each 10-min observation period.

Second, I drew a schematic map of the local streambed around each fish on a water resistant mylar sheet. Third, I monitored the fish over each 10-min period, during which I mapped the location of each foraging station, noted switches between stations, and recorded the direction (1-12 o'clock, with 12 o'clock as directly upstream) and the distance (in body lengths) of foraging attempts and aggressive acts initiated from each station. The foraging mode of juvenile Atlantic salmon is a distinct and easily recognizable behaviour, where fish hold their position against the current by hovering above, or laying on the streambed, and occasionally dart up into the water column as they intercept prey (Kalleberg 1958). In contrast to this foraging behaviour, individuals switched between stations via steady directional swimming or by using currents to glide between stations. I defined foraging stations as locations where fish held its position against the current for at least 5 seconds. After observing a fish, I embedded a flag into the stream substrate at the exact location of each station.

I created a digital map of each study site, and the space-use patterns of each fish, using ArcView GIS 3.2, in conjunction with the Animal Movement extension (Hooge and Eichenlaub 2000). For each site, I created a simple x-y coordinate system by embedding a series of nails (25 cm) along each riverbank at 2-m intervals (y-axis), and stretching a measuring tape between matching nails on the two riverbanks (x-axis). For the multiple central-place areas, I measured the x-y coordinates of all foraging stations (± 5 cm) by extending a meter stick at a 90° angle from the tape to the station. I then calculated the x-y coordinate for each foraging and aggressive event based on the vector (i.e., direction and distance) of each act, and the coordinate of the station from which it was initiated.

Because of the sometimes rapid changes in behaviour, I was not always able to record the direction and the distance of all foraging attempts obtained for each fish. For these fish, I simulated vectors for foraging attempts that were only counted, by a random sampling from those foraging attempts (obtained for the same individual) where I measured both the direction and the distance (see below). Finally, I mapped single central-place space-use patterns by superimposing foraging attempts from all stations onto a single station; this was achieved by setting the x and y for all stations to zero.

To estimate the multiple central-place home range size, I applied the minimum convex polygon (MCP) method to the coordinates of all foraging attempts (both recorded and simulated), stations, and aggressive acts (Schoener 1981). For comparison, I also removed spatial outliers (5%) from each home range via the harmonic mean method and estimated the MCP area for the remaining 95% of the data points (Hooge and Eichenlaub 2000). Because the 100% and 95% estimates were highly correlated (linear regression: $\log_{10}MCP_{100\%}$ (m^2) = 0.088 + 0.857 $\log_{10}MCP_{95\%}$ (m^2), r^2 = 0.781, n = 50, P < 0.001), I only report $MCP_{100\%}$ hereafter; on average, $MCP_{100\%}$ were 1.29 times greater than $MCP_{95\%}$. Because aggressive acts were rare, and each act had a much greater effect on the single-central-place space-use estimate than on the corresponding multiple-central-place estimate, I estimated the size of the single central place areas based only on the foraging attempts (simulated attempts excluded). As before, I estimated the size of the single central place areas using both 100% and 95% MCP estimates, and because there was a good agreement between the two estimates (linear regression: $\log_{10}MCP_{100\%}$ (m^2) = 0.261 + 1.015 $\log_{10}MCP_{95\%}$ (m^2), r^2 = 0.865, n = 50, P < 0.001) I report only the former; on

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average, $MCP_{100\%}$ were 1.72 times greater than $MCP_{95\%}$.

I examined and compared the shape of single versus multiple central-place space-use patterns by using Jennrich and Turner's (1969) home range estimates (hereafter, JT-estimates), which assume space use follows a bivariate normal distribution (Hooge and Eichenlaub 2000). The JT-method has been criticized as a method for estimating the size of areas (e.g., Schoener 1981), but provides two valuable indicators of territory shape: (*i*) eccentricity, which indicates to what degree territories deviate from a circle, and (*ii*) the angle along which territories are elongated. Eccentricity is based on the ratio between the vectors of the major (a) and minor (b) axis of the JT home range and is calculated as:

$$Eccentricity = \sqrt{(a/b)}$$

Hence, the length of the major (a) and the minor (b) axis represent the length and width of the JT estimate, and are statistically identical to the first and second eigenvectors of the bivariate normal distribution, respectively (Sokal and Rohlf 1981). Consequently, eccentricity = 1, when home ranges are circular (i.e., a = b), and then increases in value as the shape becomes more elliptical (i.e., a >> b). I used the angle of the major axis of the JT-estimate to determine whether home ranges were elongated along the stream length (absolute value of the angle = 45-90°; where +90° and -90° represent the upstream and downstream directions, respectively) or along the stream width (absolute value of the angle = 0-45°, where 0° is perpendicular to the water flow; Fig. 2.2)(Hooge and Eichenlaub 2000).

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I examined the defence of the corresponding multiple- and single-central-place areas, against intra- and interspecific intruders, by comparing the spatial distribution of aggressive acts to the spatial distribution of foraging attempts. Hence, for each fish, I plotted MCP areas based only on the foraging attempts, where I removed 0%, 25%, and 50% of the outliers, resulting in three core areas based on 100%, 75%, and 50% of the foraging attempts, respectively. For each fish, I counted the number of aggressive acts that fell outside and inside the boundaries of the three core areas; I excluded from this analysis six aggressive acts for which I did not record the direction or the distance.

I estimated population density in the 10 study sites during snorkeling surveys conducted between 1500 and 1800 on 2-3 September 2000, at water temperatures of 16.5-17.0°C. On 1 September, I divided each site into a series of 4-m^2 quadrats by marking the four corners of each quadrat. In each survey, I entered the water immediately downstream of each site, waited for 5 min, and then snorkeled gradually upstream through the site, counting all fish in each quadrat along the way. I estimated the population density of potential intruders around each home range by averaging the numbers of fish from all 4-m^2 quadrats that were within a 1-m distance from, or were in contact with the MCP boundaries of the home range. On average, I counted the number of fish over an area of 17.5 m^2 (range: 4-42 m^2) for each home range.

Literature data

I obtained estimates of fork length, territory size, the number of foraging stations used, the frequency and radii of aggressive acts, and population density, from the

available studies on territory size of YOY stream-dwelling salmonids. For each study I

obtained from one to three estimates (the mean or median value) for a given variable (if

studies reported the findings from several separate experiments or treatments). For studies

that reported an estimate of territory size at one fixed point in time, I extracted values for

other variables using those estimates that were closest in time. For studies that examined

the relationship between territory size and fork length, I obtained the mean (or the

median) fork length and then predicted the territory size from the reported relationship. If

studies repeatedly estimated territorial behaviour and population density for a given

treatment, or for the same population of fish, I averaged these estimates over time. For

two studies (Keeley and Grant 1995; Keeley and McPhail 1997), values differ slightly

from those previously published because I had access to original data specifically for

YOY fish (Ernest R. Keeley, Department of Biological Sciences, Idaho State University,

Pocatello, ID 83209, U.S.A., personal communication).

Results

General information

For the 50 YOY Atlantic salmon monitored in this study, I recorded a total of

6912 foraging attempts, 171 aggressive acts initiated by the focal fish, and 44 occasions

where the focal fish were chased or displaced by another fish during 1970 min of direct

observations. For 4225 foraging attempts (61.1%), I recorded both foraging direction and

distance; these data were then used to simulate values for the remaining 2687 attempts,

which were included for the multiple central-place estimates (see methods). Of 171

aggressive acts initiated by the focal fish, the vast majority were directed toward

blacknose dace (*Rhinichthys atratulus* (Hermann)) (110 acts, 64.3%) and other YOY

Atlantic salmon (58 acts, 33.9%), whereas only 1.2% (2 acts) were directed toward

Atlantic salmon parr and in one case (0.6%) the intruder type was not recorded.

The mean population density of intruders was 0.68 fish/m^2 for blacknose dace

(47.6% of the total fish count), 0.43 fish/m^2 for YOY Atlantic salmon (30.0%), 0.20

fish·m^2 for Atlantic salmon parr (13.9%), and a cumulative 0.12 fish/m^2 for all other

species (8.5%). Although the proportion of aggression directed towards the three most

common intruders ranked the same as their relative abundance, more aggressive acts were

directed toward blacknose dace and fewer toward Atlantic salmon parr than expected (*G*-

test of independence, Williams' correction: G_{adj} = 42.82, df = 2, $P < 0.001$). Of the 44

intruders that displaced the focal fish, more than expected (63.6%, n = 28) were other

YOY Atlantic salmon and Atlantic salmon parr (18.1%, n = 8), whereas fewer than

expected (11.4%, n = 5) were blacknose dace (*G*-test of independence, Williams'

correction: G_{adj} = 29.85, df = 2, $P < 0.001$); in three cases (6.8%) the intruder type was

not recorded.

In order to compare various components of territorial behaviour of my study fish

with previous studies, I reviewed the 13 available studies on territory size in YOY

stream-dwelling salmonids; seven of these were laboratory studies in stream tanks,

whereas six were conducted under natural conditions (Table 2.2). The 13 studies yielded

25 estimates of territory size (1-3 estimates per study), 22 estimates of the number of

foraging stations used by territorial fish, 18 and 14 estimates of aggressive frequency and

radii, respectively, and 21 estimates of the population density under which the behavioural variables were estimated.

Multiple central-place home ranges?

In general, the 50 focal fish can be described as using multiple, rather than single central-place home ranges. First, over the 40-min observation period, the fish visited between 3 and 26 foraging stations (median = 12.5 stations), and no fish remained at one station for the entire 40 min (Fig. 2.2). During this time, the typical (i.e., the median) individual visited each of its foraging stations on average 4.0 times (range in the mean number of visits per station for the 50 fish = 1.3-11.5 visits $\times$ station^{-1} $\times$ 40-min^{-1}). In spite of limited observation time, the 50 fish visited 68.5% of their stations more than once.

Second, in agreement with typical patterns of home range use, focal fish limited their space use to a set of foraging stations, and traveled repeatedly over the same area. This trend is reflected in asymptotic curves of the accumulated number of stations visited (Fig. 2.3a; Repeated measures analysis of variance, ANOVAR; quadratic polynomial contrast: $F_{(1, 46)} = 21.32, P < 0.001$) and the estimated home range size (Fig. 2.3b; ANOVAR; quadratic polynomial contrast: $F_{(1, 46)} = 23.67, P < 0.001$), versus sample size over the four 10-min study periods.

Third, because of the large number of foraging stations used, most fish have limited fidelity to one particular station. On average, 34.7% (11.5-97.9%) of the foraging attempts were initiated from the primary (i.e. most used) station, whereas 18.2% (1.4-

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36.7%), 12.6% (0.7-25.5%), and 34.5% (0-67.3%) were from secondary, tertiary, and all

other stations, respectively (Fig. 2.4a). In contrast, in the two previous studies which

report the use of different stations among YOY stream-dwelling salmonids, 72% and

80% of all foraging attempts were initiated from primary stations and only 8% and 2%

were not from the three most used stations (Keeley and Grant 1995; Keeley and McPhail

1998, respectively; see Table 2.2 for more details on each study). Not surprisingly, the

proportion of foraging attempts initiated from the primary station decreased with the total

number of stations individuals visited over the observation period (Fig. 2.4b).

Finally, apart from the number of stations used, the YOY salmon showed typical

central-place behaviour; i.e., all foraging attempts and a vast majority (> 95%) of

aggressive acts directed toward intruders, were initiated while the fish held position on a

foraging station but not when a fish cruised between stations.

Size and shape of multiple vs. single central place areas

The multiple-central-place territories of YOY Atlantic salmon in Catamaran

Brook in 2000, were larger than previous estimates of territory size for YOY stream-

salmonids (Fig. 2.5). First, all 50 data points were above the allometric regressions from

five previous studies (Sign test, $P < 0.001$). Second, although the 50 multiple-central-

place territories (range = 0.268-4.469 m^2) overlapped with territory size in the five

allometric studies (range = 0.002-0.489 m^2), the multi-central areas were on average 8.1

times larger (mean, back-transformed from $\log_{10} = 0.932$ m^2) than found for the five

studies, when territory size was predicted for the average-sized fish (4.3 cm) in my study

(mean = 0.107 m^2). Unlike all previous studies that measured territory size in YOY salmonids over a comparable range in size, I found no relationship between territory size and body size (log$_{10}$ multiple central place area (m^2) = -0.373 + 0.531 log$_{10}$ fork length (cm), r^2 = 0.010, P = 0.497)(Fig. 2.5).

For comparative purposes, I also calculated territory size when data were superimposed onto a single station for each fish (Fig. 2.6.); because I did not detect aggression for all fish, these alternative estimates were only based on foraging attempts. In this case, territory size increased with body size (log$_{10}$ single central place area (m^2) = -3.072 + 2.743 log$_{10}$ fork length (cm), r^2 = 0.268, P < 0.001), and was more similar in size (mean, back-transformed from log$_{10}$ = 0.045 m^2; range = 0.013 - 0.364 m^2) to territories described earlier for YOY salmonids (Fig. 2.5; see previous paragraph).

The shape of the multiple central-place areas differed from the shape when the data were superimposed onto a single central place. The multiple central place areas were significantly more elongated (median eccentricity = 1.285, range = 1.052-2.668) than the patterns of foraging around each central place station (Wilcoxon signed-ranks test: Z = 4.368, n = 50, P < 0.001), which were much closer to being circular in shape (median eccentricity = 1.148, range = 1.005-1.385) (Fig. 2.7a). Moreover, the multiple central place areas were elongated along the stream length (i.e., absolute angle > 45°) for 32 of the 50 fish, whereas 33 of the foraging areas around each station were elongated along the stream width (i.e., absolute angle < 45°) (Fig. 2.7b); overall, there was a significant difference in the angle of the primary axis (categories: < or > 45°) between the multiple- and the single-central-place areas (G-test of independence, Williams' correction: G_{adj} =

9.009, df = 1, $P < 0.005$). Hence, YOY used a multi-central area, which was typically elongated along the stream length, and was 65% longer than wide, whereas the foraging area around each focal point, was typically elongated from side-to-side, and was 32% wider than long.

Defence of multiple and single central-place areas

Aggression was detected for 41 of the 50 focal fish over the 40-min observation period. Twenty-two fish were aggressive toward other YOY Atlantic salmon (maximum 8 acts), and 31 fish showed aggression toward blacknose dace (maximum 10 acts)(Fig. 8). Although, the rate of aggression varied considerably among individuals (range = 0-11 acts/40-min), the mean rate of aggression (3.4 acts/40-min = 5.1 acts/h), was only 6.4-65.4% of the rate reported in earlier studies (Table 2.2; mean = 36.6 acts/h, range = 7.8-79.4 acts/h).

In agreement with typical patterns of territorial defence, the mean aggressive radius (3.6 body lengths) for the focal fish was significantly greater than the corresponding mean foraging radius (1.25 body lengths) (paired t-test: $t = 10.50$, df = 39, $P < 0.001$) (Fig. 2.9). However, in spite of their large home ranges, the aggressive radius found for the study fish falls within the range of radii reported in previous studies (Fig. 2.9; Table 2.2; mean = 3.2 body lengths, range = 1.7-5.8 body lengths). Also, the mean aggressive distances for the focal fish were significantly shorter than found in Keeley and Grant's (1995) study on the same population (mean = 5.4 body lengths), during which fish used much smaller areas (Fig. 2.9)(two-sample t-test; $t = 4.94$, df = 65, $P < 0.001$.

Finally, the aggressive radii for the focal fish did not differ significantly between attacks directed toward YOY Atlantic salmon (mean = 3.5 body lengths) and blacknose dace (mean = 3.6 body lengths) (two-sample t-test: $t = 0.264$, df = 51, $P = 0.792$).

Because my study fish occupied large home ranges and engaged in lower rates of aggression than reported previously, they may defend their home range less exclusively than fish defending single central-place territories. I assessed the exclusivity of the areas used by comparing the spatial distribution of aggression to the distribution of foraging attempts. Because comparable data were not available for previous studies, I used the spatial distribution of behaviour of my study fish when superimposed onto a single central-place as an approximation of a typical single central-place territory; this assumption seemed reasonable given the similarity in aggressive distances between my study and previous studies (Fig. 2.9).

First, a significantly lower proportion of aggression directed toward YOY Atlantic salmon occurred outside the 100% core foraging area when I mapped space use via the multiple (39.1%) rather than the single (70.9%) central-place approach (Wilcoxon paired sign rank test: $Z = 2.296$, $n = 22$, $P = 0.022$)(Table 2.3); the same comparison, however, did not reveal significant differences at core areas of 50% and 75% (Wilcoxon signed-ranks test: $Z = -0.422$ and 1.364, $n = 22$, $P = 0.673$ and 0.172, respectively). Hence, the outskirts of the multi-central territories appear to be defended less exclusively against YOY salmon than for the single central-place territories.

Second, the spatial patterns of aggression towards blacknose dace were similar to, but clearer than the patterns observed for YOY Atlantic salmon. Hence, independent of

size of the core area (50%, 75%, 100%), the proportion of aggressive acts found outside of the boundaries were consistently, and significantly lower for the multiple central-place areas than for the single central-place areas (Wilcoxon signed-ranks test: Z = 2.932-3.261, n = 31, P = 0.001-0.003)(Table 2.3). Hence, the multiple central-place territories as a whole, appear to be defended less exclusively against blacknose dace, than the typical single central-place territories.

Third, the difference in defence against the two intruder types was also revealed by a more direct comparison. For the multi-central territories, the percent of aggressive acts outside the core area was greater for YOY salmon than for blacknose dace at the 50% and 75% boundaries (Mann-Whitney U-test: P = 0.025 and 0.022, respectively), but not significantly so for the 100% core area (Mann-Whitney U-test: P = 0.140) (Table 2.3; see Fig. 2.8a and 2.8b for an example of the distribution of aggressive acts). Meanwhile, the percent of aggressive acts found outside of the 50%, 75% and 100% core areas did not differ between the two intruder types for the single central-place-areas (Mann-Whitney U-test: P = 0.458-0.794). Hence, multiple central-place territories are defended more exclusively against other YOY salmon than blacknose dace.

A comparative analysis of territorial behaviour and population density

In relation to previous studies on YOY stream-salmonids, several unique aspects of territorial behaviour described in this study appear to be associated with population density. First, territory size decreased with population density (linear regression: $\log_{10}$ territory size (m^2) = -0.284 - 0.808 $\log_{10}$ population density (no. fish/m^2), r^2 = 0.714, n =

22, $P < 0.001$) (Fig. 2.10a). Across studies, territory size also increased with fork length (linear regression: $\log_{10}$ territory size (m^2) = -3.248 + 3.388 $\log_{10}$ fork length (cm), r^2 = 0.520, $n = 25$, $P < 0.001$). However, fork length explained only 7.7% of the variance over and above population density when both were included in the model (multiple regression: $\log_{10}$ territory size (m^2) = -1.445 - 0.629 $\log_{10}$ population density (no. fish/m^2) + 1.612 $\log_{10}$ fork length (cm), r^2 = 0.791, $n = 21$, $P < 0.001$; partial $P < 0.001$ for population density, partial $P = 0.018$ for fork length). Finally, when I added the study type (field study vs. experiment) as a categorical variable to the above multiple regression model, territory size (*i*) differed between the study types (ANCOVA: Partial $P = 0.022$), and (*ii*) decreased faster with increasing population density in field studies than in experiments (ANCOVA: Interaction$_{\text{population density} \times \text{study type}}$, partial P-value < 0.001).

Second, the median number of foraging stations reported in a given study was negatively associated with population density (Spearman's $r = -0.564$, $n = 21$, $P = 0.008$) (Fig. 2.10b). Notice, however, that the studies listed in Table 2.2 rarely provide an accurate estimate of the number of stations used, but simply assume the use of a single station is the typical behaviour.

Third, across studies, the mean aggressive frequency increased with population density (linear regression: $\log_{10}$ aggressive frequency (no./h) = 0.975 + 0.398 $\log_{10}$ population density (no. fish/m^2), r^2 = 0.536, $n = 19$, $P < 0.001$)(Fig. 2.10c). Hence, even though aggressive frequency is considerably lower in this study, compared to most previous studies, this may be partly due to a much lower intrusion rate for a given area. When the study type was added as a categorical variable to the above model, aggressive

frequency (*i*) differed between the two types (ANCOVA: Partial $P = 0.004$), and (*ii*)

increased faster with increasing population density in field studies than in experiments

(ANCOVA: population density $\times$ study type, partial P-value < 0.001).

Fourth, across studies, the mean aggressive radius was negatively related to

population density (linear regression: $\log_{10}$ aggressive radius (body lengths) $= 0.734 -$

$0.227 \log_{10}$ population density (no. fish/m^2), $r^2 = 0.635$, $n = 15$, $P < 0.001$)(Fig. 2.10d);

but was not related to fork length (linear regression: $\log_{10}$ aggressive radius (body lengths)

$= -0.002 + 0.805 \log_{10}$ fork length (cm), $r^2 = 0.150$, $n = 15$, $P = 0.154$). Furthermore,

study type did not influence the aggressive radius over and above the effects detected for

population density (ANCOVA: study type, Partial $P = 0.853$; population density $\times$ study

type, partial P-value $= 0.917$). Importantly, unlike previous studies, where aggressive

distance is either used to determine, or is strongly linked with territory size, the mean

aggressive radius in my study (3.6 body lengths $= 15.5$ cm) is seven times shorter than the

average diameter (109.0 cm) of the median territory. Thus, the study fish do not appear to

actively exclude intruders from the whole territory at any given time.

Discussion

Challenging the single-central-place paradigm

The CPTM has proven very useful for determining the minimum spatial

requirements of stream-dwelling salmonids (Grant et al. 1989), and for examining how

these requirements vary across ecological conditions (McNicol and Noakes 1984; Keeley

2000). To date, however, a few studies show that the single central-place framework does

not apply to all salmonids, particularly for larger fish that coexist in dominance

hierarchies. For example, Bachman (1984) and Nakano (1995) demonstrated the use of

multiple focal points for stream-dwelling brown trout (*Salmo trutta*) (estimated total

length = 8-33 cm, 1-32 stations) and masu salmon (*Oncorhynchus masou masou*)

(standard length = 7.1-20.4 cm, 1-15 stations), respectively. In both studies, however,

data on each territory were gathered over several weeks to months, and the number of

stations may be inflated by territory relocation, e.g., due to changes in stream discharge

(e.g., Shirvell 1994), or to gradual changes in habitat preferences (Morantz et al. 1987).

Also, in agreement with the notion that single central-place space-use is primarily

adopted by territorial fish, (*i*) Nakano (1995) showed that the use of multiple foci was

more common among subordinate, non-territorial fish that could not defend a single

favourable focal point, and (*ii*) Bachman (1984) suggested that although his fish used

multiple foraging stations, they should rather be described as using home ranges, than

actively defending territories.

A few field studies on YOY stream-dwelling salmonids suggest that territorial

fish visit several foraging stations within their territory (Table 2.2). However, even these

studies either do not quantify the number of stations (Dill et al. 1981), or focus on the

single central-place estimate of territory size even if fish visit several foraging stations

(Keeley and Grant 1995; Keeley and McPhail 1998). In part, the latter tendency is due to

the low number of stations used by most fish (Keeley and McPhail 1998), and the absence

of a significant difference in the mean territory size between the single- and multiple

central-place areas (Keeley and Grant 1995).

Consequently, this study is the first to examine in detail the distinct multiple central-place nature of the daily space-use patterns exhibited by YOY Atlantic salmon. All 50 fish used more than one foraging station (median = 12.5 stations), visited most stations repeatedly, showed limited fidelity to any one particular station, and foraged only when they held their position at a station. Interestingly, their typical sit-and-wait foraging, and the absence of feeding as fish cruised between stations, suggest that the behaviour of Atlantic salmon is somewhat less flexible than for brook trout, which are frequently observed to use either a sit-and-wait (stayers) or a cruising (movers) foraging tactic (Grant and Noakes 1987; McLaughlin et al. 1992).

Why use large multiple central-place territories?

As in previous studies on stream-salmonids, the size and shape of the spatial patterns of foraging, when superimposed onto one central place, can be explained based on their reliance on drifting invertebrates (e.g., >99% of prey items for juvenile Atlantic salmon; Keeley and Grant 1995). As fish grow, they gradually increase their foraging radius, which allows them to intercept a greater number of invertebrates drifting downstream (Grant et al. 1989; Keeley and McPhail 1998). Similarly, a slight side-to-side elongation of the central-place foraging area enhances the cross-sectional area of the water column over which fish intercept their prey (Grant et al. 1989). However, it is less obvious why a drift-feeding fish would forage from multiple central-places, over large areas which tend to be elongated along the stream length and much wider than the transect over which prey is intercepted from each station.

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To date, multiple central-place foraging has been documented for several animals that utilize depletable food resources. For example, studies on primates and birds suggest that as food is depleted around one central place (sleeping sites and chicks, respectively), foragers increase their prey encounter rate, and reduce their total travel costs, by switching to another central place (Chapman et al. 1989; McLaughlin and Montgomerie 1989). Similarly, Covich (1976) suggested that by using several connected openings, burrowing mammals can exploit larger areas without an increase in predation risk. Initially, these ideas do not seem to apply directly to multi-central drift-feeding in stream-salmonids, primarily because drifting invertebrates are often viewed as a non-depletable resource (Allan 1982). Hence, prey availability is unlikely to decline at a station as a result of drift-feeding of the territory holder; meanwhile, however, fish are likely to suffer from increased travel costs.

However, the benefit of multiple central-place foraging in stream-salmonids may be very subtle. By patrolling large areas, YOY salmon likely exclude competitors from areas immediately upstream of many of its focal points. Because a large portion of invertebrates drift short enough distances to originate from within a multi-central territory (McIntosh and Townsend 1998; Elliott 2002a), the prey encounter rate at these foraging stations may be greater if the traffic of intruders through the territory is suppressed. If true, this idea may help explain why multiple central-place territories tend to be elongated along the stream length, a shape for which any local increase in drifting prey would affect more stations in the downstream direction. Obviously this idea remains to be tested, but fewer competitors immediately upstream of a foraging station is suggested as the reason

why the radius and the frequency of aggressive acts for a typical central-place territory is greater in the upstream, than in the downstream direction (Grant et al. 1989). Finally, this idea is consistent with the finding that in groups of stream-living brown trout, an upstream competitor may reduce the feeding rate of fish holding station downstream (Elliott 2002b).

Are multiple central place areas really defended?

Not surprisingly, multi-central territories are not defended as exclusively as typical single central-place territories. For my fish, the mean aggressive radius (15.5 cm) is similar to that detected for the much smaller single-central-place territories, which suggests that large multi-central areas are only partly defended at any given moment. The frequency of aggression initiated by these fish is also lower than in other studies on territoriality in YOY stream-salmonids. For several reasons, however, these findings do not necessarily mean that aggression does not reduce the traffic of intruders through multi-central home ranges.

First, the two studies that report the greatest aggressive distances for YOY stream-salmonids, also reported the use of multiple foraging stations (Keeley and Grant 1995; Keeley and McPhail 1998; Table 2.2). However, the typical fish in these studies used only 2-3 stations, and defended territories smaller than reported for my study fish, but larger than for most single central-place territories (Table 2.2). Hence, when YOY salmon use a low number of stations, they chase intruders from farther away, perhaps to defend the whole multiple central-place area. This idea is supported by the fact that Keeley and

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Grant (1995) did not find a significant difference in the territory size of their fish when mapped in a single versus multiple central-place manner. My study, however, suggests that YOY salmon cease to defend all areas of their home range simultaneously as they increase the size of their multi-central areas.

Second, the low rates of aggression observed in this study appear to be consistent with Nakano's (1995) study on masu salmon, where the use of multiple focal points was primarily associated with small, less aggressive individuals, within a dominance hierarchy that spanned a large range in body size (standard length = 7.1-20.4 cm). However, this view may not hold for my study fish, because (*i*) all 50 fish used more than one station, (*ii*) the social structure of wild YOY Atlantic salmon is described as a territorial mosaic rather than as a space-related dominance hierarchy (Kalleberg 1958; Slaney and Northcote 1974), and (*iii*) the low aggressive rate appears to be due to a low density of intruders. Hence, future space-use studies may benefit from correcting for the opportunity for aggression (e.g., intrusion rate) when testing if single and multiple central-place foragers differ in aggressiveness.

Third, based on the spatial distribution of aggressive acts, multi-central territories seem to be defended more exclusively against other YOY salmon than against blacknose dace; this likely reflects the different behaviour of the two intruder types. Because YOY Atlantic salmon typically move very short distances over the first summer (61.8% move < 1m up- or downstream)(Chapter 1), they likely retain their territories and their conspecific neighbors, over long periods of time. In this case, an occasional aggressive encounter between familiar neighbors could be sufficient to maintain boundaries of large multi-

central territories. Alternatively, YOY salmon may be inefficient in defending large areas

against blacknose dace, which usually cruise widely (alone or in small groups) for benthic

invertebrates, without much apparent regard to the long-term boundaries of the multi-

central territories (personal observation).

Density-dependent space-use?

Territorial behaviour of YOY stream-dwelling salmonids appears to be highly

associated with population density. At high densities, numerous studies suggest that

territorial fish forage, and initiate aggression from one central-place (McNicol and

Noakes 1981; Keeley 2000), but most of these observations are of untagged fish. By

using tagged fish, however, it may turn out that some fish use multiple stations even at

high population densities, and these fish should not be automatically classified as non-

territorial or floaters. Alternatively, very limited data is available on the space-use

patterns of stream-salmonids at low population densities, partly because territoriality is

more likely to contribute to the regulation of population numbers at high densities (Slaney

and Northcote 1974; Grant and Kramer 1990). Hence, although this study clearly shows

that at least some populations of YOY Atlantic salmon switch to using multi-central

territories at low population densities, further research is needed on the patterns and

benefits of this behaviour, especially because changes in population density have a greater

impact on the growth rate of stream-salmonids at low rather than at high densities (Crisp

1993; Jenkins et al. 1999; Imre 2003).

Obviously, a range of ecological variables other than population density can affect

the space-use patterns of mobile animals (Adams 2001). For example, the behaviour of YOY brook trout appears to be consistent with the CPTM in fast-running waters, but not in slow-running waters or in lakes (Grant et al. 1989; McLaughlin et al 1992; Biro et al. 1997). Similarly, Nakano (1995) clearly demonstrated that social status can affect the number of foraging stations used; i.e. dominant fish typically use fewer stations than subordinates. In chapter 3, I will analyse further the 50 YOY Atlantic salmon tagged and followed in this study, and examine how the multiple central-place behaviour and social behaviour is associated with environmental factors.

In summary, by following individually tagged YOY Atlantic salmon in the wild, this study clearly demonstrates that at low population densities, YOY salmonids may repeatedly visit many foraging stations within their territories. Furthermore, when territories are mapped around several stations, rather than just around a single station, several dogmas about the territorial behaviour of stream-salmonids are challenged. Hence, in this study, territories of YOY Atlantic salmon are larger than previously established, they are not as circular in shape as thought earlier, they tend to be elongated along the stream length rather than the stream width, and although these fish do not comply with the CPTM and visit several stations within their home ranges, these areas still appear to be fairly efficiently defended against other YOY salmonids.

Table 2.1. Summary of habitat characteristics for the 10 study sites in Catamaran Brook, measured on 18th and 19th of August, 2000.

Site	Site dimensions[a]		Habitat characteristics, mean (range)[b]			
	Length, m	Width, m	Water velocity, m/s	Water depth, cm	Substrate size	n
1	10.0	5.0	0.086 (0 - 0.18)	32.3 (1 - 59)	4.5 (1 - 6)	30
2	9.0	5.3	0.088 (0 - 0.35)	22.1 (1 - 47)	3.9 (1 - 6)	27
3	8.5	8.8	0.045 (0 - 0.14)	34.5 (1 - 76)	4.8 (2 - 6)	44
4	10.0	4.2	0.155 (0 - 0.66)	23.4 (2 - 52)	5.0 (3 - 6)	27
5	10.0	5.4	0.063 (0 - 0.17)	33.0 (2 - 66)	4.4 (1 - 6)	32
6	9.0	4.8	0.178 (0 - 0.42)	18.4 (1 - 43)	5.1 (4 - 6)	22
7	6.0	4.9	0.058 (0 - 0.11)	47.1 (3 -105)	4.7 (4 - 6)	19
8	11.0	5.4	0.070 (0 - 0.34)	34.4 (1 - 69)	4.5 (2 - 6)	32
9	11.0	8.6	0.054 (0 - 0.21)	28.5 (1 - 82)	4.8 (2 - 6)	50
10	11.0	6.7	0.078 (0 - 0.38)	22.6 (2 - 47)	4.7 (1 - 6)	39

[a] The site width is an average based on 4-6 transects located at every 2 m along the stream length.

[b] Habitat variables were measured at 2 m intervals across 4-6 transects in each study site. Current velocity was measured at 40% depth (from the substrate), using a Marsh-

McBirney meter (model 201D; Marsh-McBirney Inc., 4539 Metropolitan Ct., Frederick, MD 21704, U.S.A.). I scored substrate particle size based on a modified Wentworth scale from DeGraaf and Bain (1986) [1, < 0.004 mm (plant detritus, clay); 2, 0.004-2.0 mm (silt, sand); 3, 2-16 mm (gravel); 4, 17-64 mm (pebble); 5, 65-256 mm (cobble); 6, > 256 mm (boulder); 7 (bedrock)].

Table 2.2. Review of published studies on territory size, the number of foraging stations, aggression, and population density in YOY stream-dwelling salmonids.

No.	Specie[a]	Conditions	Fork length (cm)	Territory size (m²)	Foraging stations (no.)[b]	Aggressive frequency (acts/h)	radii (body lengths)	Population density (no./m²)	Source
1a	S.s.	Stream tank	2.5	0.011	1	-	-	-	Kalleberg 1958, page 91
1b	S.s.	Stream tank	4.5	0.030	1	-	-	-	Kalleberg 1958, page 91
1c	S.s.	Stream tank	-	0.027	1	-	-	49.5	Kalleberg 1958, page 66-67
2a	O.k.	Stream tank	5.6	0.135	1	32.4	-	8.8	Mason 1969, Population 2, left aquarium
2b	O.k.	Stream tank	5.8	0.190	1	32.4	-	5.2	Mason 1969, Population 2, right aquarium
3a	O.m.	Stream tank	2.5	0.037	1	30.0	-	31.5	Slaney and Northcote 1974, Exp. 2, L-prey[c]
3b	O.m.	Stream tank	2.5	0.018	1	57.0	-	67.6	Slaney and Northcote 1974, Exp. 2, I-prey[c]
3c	O.m.	Stream tank	2.5	0.010	1	45.0	-	112.6	Slaney and Northcote 1974, Exp. 2, H-prey[c]

	Species	Type							Source
4a	*O.k.*	Natural	4.5	0.131	Several	-	-	-	Dill et al. 1981, high intruder pressure
4b	*O.k.*	Natural	4.5	0.199	Several	-	-	-	Dill et al. 1981, low intruder pressure
5	*S.f.*	Stream tank	5.4	0.110	1	19.5	3.0	16.7	McNicol and Noakes 1981
6a	*S.f.*	Stream tank	4.6	0.036[d]	1	25.7	2.2	41.7	McNicol and Noakes 1984, Exp. I.
6b	*S.f.*	Stream tank	4.7	0.079	1	-	2.8	18.2	McNicol and Noakes 1984, Exp. II.
6c	*S.f*	Stream tank	4.6	0.095	1	-	-	18.2	McNicol and Noakes 1984, Exp. III.
7	*S.f.*	Natural	4.6	0.340	1 (1-2)	7.8	4.8	2.5	McNicol et al. 1985
8	*S.f.*	Natural	4.0	0.028	1	45.8	2.2	6.0[e]	Grant et al. 1989
9	*S.t.*	Natural	3.7	0.037	1	44.3	3.9	5.9	Elliott 1990
10	*S.s.*	Natural	4.1	0.187	3 (1-30)	8.6	5.4	3.3	Keeley and Grant 1995
11	*O.m.*	Natural	3.8	0.175	2 (1-5)	20.3	5.8	3.2	Keeley and McPhail 1998
12a	*O.m.*	Stream tank	4.0	0.054	1	47.8	3.1	27.8	Keeley 2000, low density[f]

12b	*O.m.*	Stream tank	3.8	0.032	1	64.7	2.6	48.4	Keeley 2000, med. density[f]
12c	*O.m.*	Stream tank	3.7	0.024	1	79.4	2.1	83.6	Keeley 2000, high density[f]
13a	*O.m.*	Stream tank	2.9	0.016	1	25.8	2.5	46.6	Imre et al. 2002, control
13b	*O.m.*	Stream tank	3.0	0.008	1	37.8	1.7	49.3	Imre et al. 2002, divider
13c	*O.m.*	Stream tank	2.9	0.010	1	34.8	2.0	38.1	Imre et al. 2002, cobble

[a] *S.s.* = Atlantic salmon (*Salmo salar*), *S.f.* = brook charr (*Salvelinus fontinalis*), *S.t.* = brown trout (*Salmo trutta*), *O.k.* = coho salmon (*Oncorhynchus kisutch*), *O.m.* = rainbow trout (*Oncorhynchus mykiss*).

[b] Median number of stations (and range); most studies map territories from one station but note that not all fish remain at one station.

[c] From experiment 2, L-prey = low prey, I-prey = intermediate prey, H-prey = high prey.

[d] Not in the original paper, territory size estimated via the circular method (territory size = aggressive distance$^2 \times \pi$)

[e] Estimate of population density obtained from Grant and Kramer 1990.

[f] Estimates of fork length and population density obtained from Keeley 2001.

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Table 2.3. Summary of the spatial distribution of aggressive acts directed toward intra-
and interspecific intruders by 40 YOY Atlantic salmon in Catamaran Brook, New
Brunswick.

Core foraging area (% MCP)[a]	Aggression vs. YOY Atlantic salmon		Aggression vs. blacknose dace	
	n	% outside core area	n	% outside core area
Multiple central place mapping				
50%	22	92.8	31	83.7
75%	22	79.5	31	57.3
100%	22	39.1	31	21.9
Single central place mapping				
50%	22	90.9	31	97.0
75%	22	90.2	31	88.5
100%	22	70.9	31	62.2

[a] The boundaries of the three core areas (50, 75, and 100%) were established via the
minimum convex polygon (MCP) method, after omitting 50, 25, and 0% of the outlying
foraging attempts, respectively.

Fig. 2.1. Schematic representation of space use of a central-place forager (CPF) and a

multiple central-place forager (MCPF). The central stations are represented by a fish (or

⊕), a solid arrow and (●) indicates foraging or aggressive acts, whereas arrows with

dashed lines represent shifts between stations.
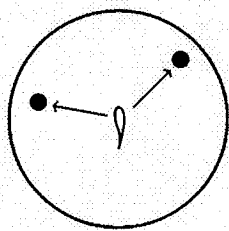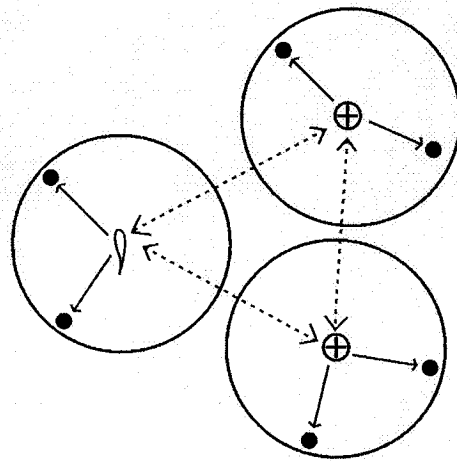
CPF   MCPF

Fig. 2.2. Variability in the number of foraging stations visited in 40 min by 50 YOY

Atlantic salmon in Catamaran Brook, in 2000. The 100% minimum convex polygon

(solid line), encircles the location of all aggressive acts and foraging attempts (●), and

foraging stations (⊕) for the fish with (a) fewest (n = 3) and (b) most (n = 26) foraging

stations, whereas (c) shows the frequency distribution of the number of stations visited by

each fish over the 40-min observation period. In accordance with the methods used to

estimate territory shape, the angles indicate the upstream (90°), downstream (-90°), and

riverbank-to-riverbank (0°) direction.

Fig. 2.3. Influence of sample size and time on (a) the total number of foraging stations visited and (b) the multiple-central-place estimate of daily territory size for YOY Atlantic salmon in Catamaran Brook. The sample size for each individual refers to the total number of foraging and aggressive acts recorded, along with recorded switches between foraging stations. The four consecutive symbols on each figure represent the mean values for the two dependent variables (± 95% C.I.) based on 47 study animals after accumulative 10, 20, 30 and 40 minutes of observations, respectively.

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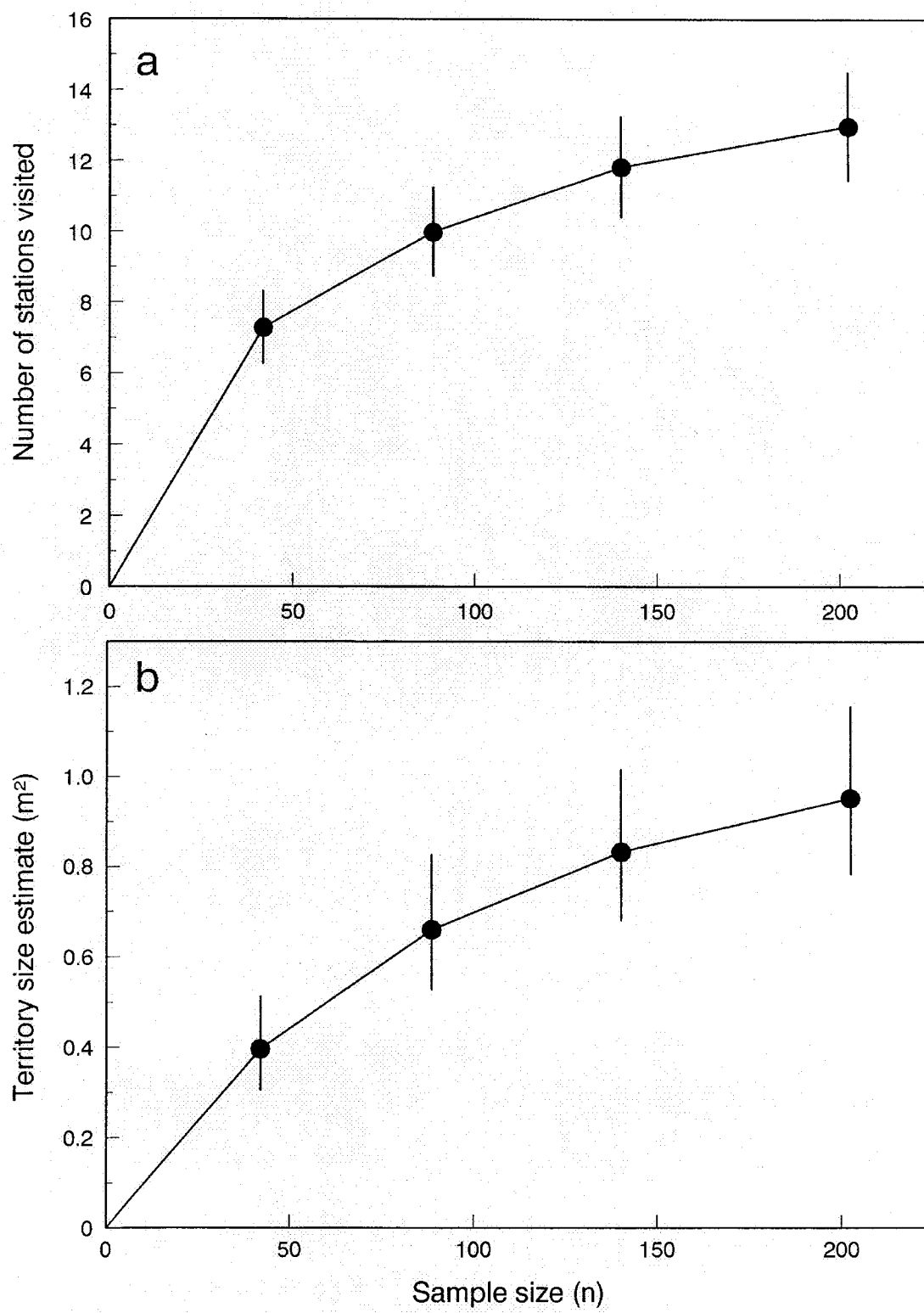
Fig. 2.4. The relationship between (a) the rank of foraging station and the mean percent of foraging attempts initiated from stations of a given rank by YOY Atlantic salmon in Catamaran Brook, 2000, and (b) the association between the number of foraging stations visited, and the relative use of the primary station (Spearman's $r = -0.673$, $n = 50$, $P < 0.001$). Station rank was determined by how often foraging occurred from a particular station (1 = primary station, most forages, etc). The sample size (a; number above the line at every fifth rank) declined with increasing rank because fewer fish used more stations; estimates of 0 (for stations ranked 24th - 26th) were placed on the x-axis. The points labeled 1 and 2 in (b) indicate the two fish depicted in Fig. 2.2a, and 2.2b, which visited the fewest and most foraging stations, respectively.
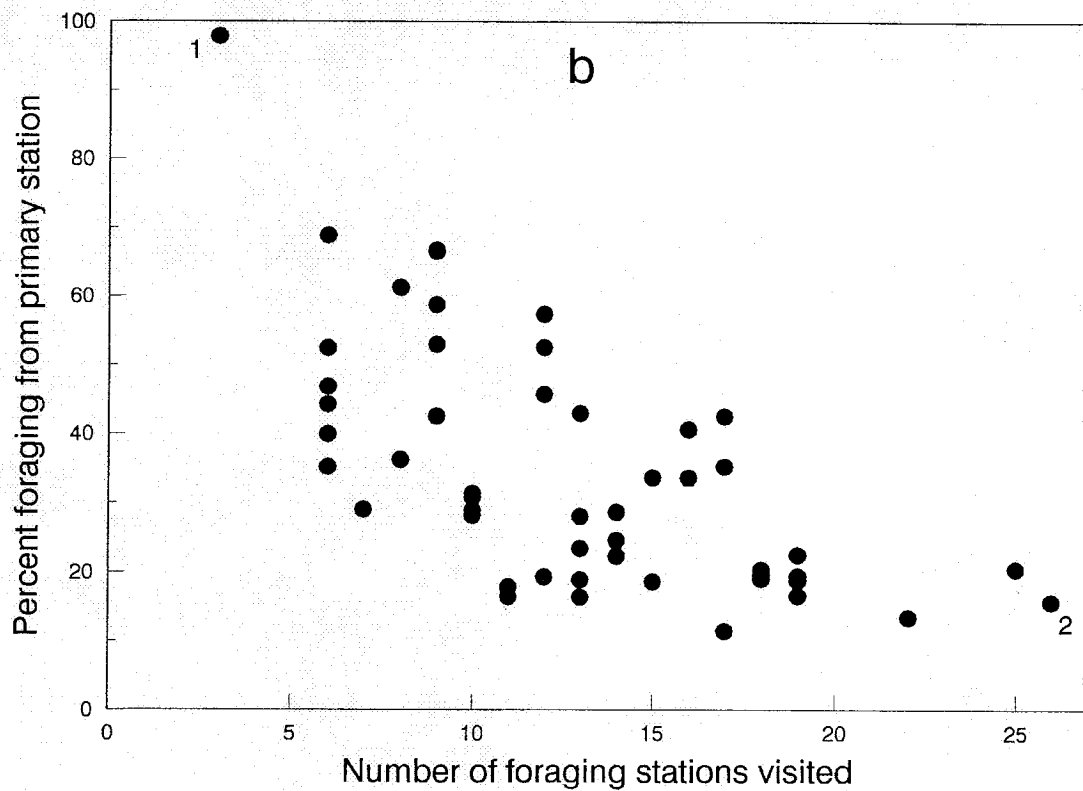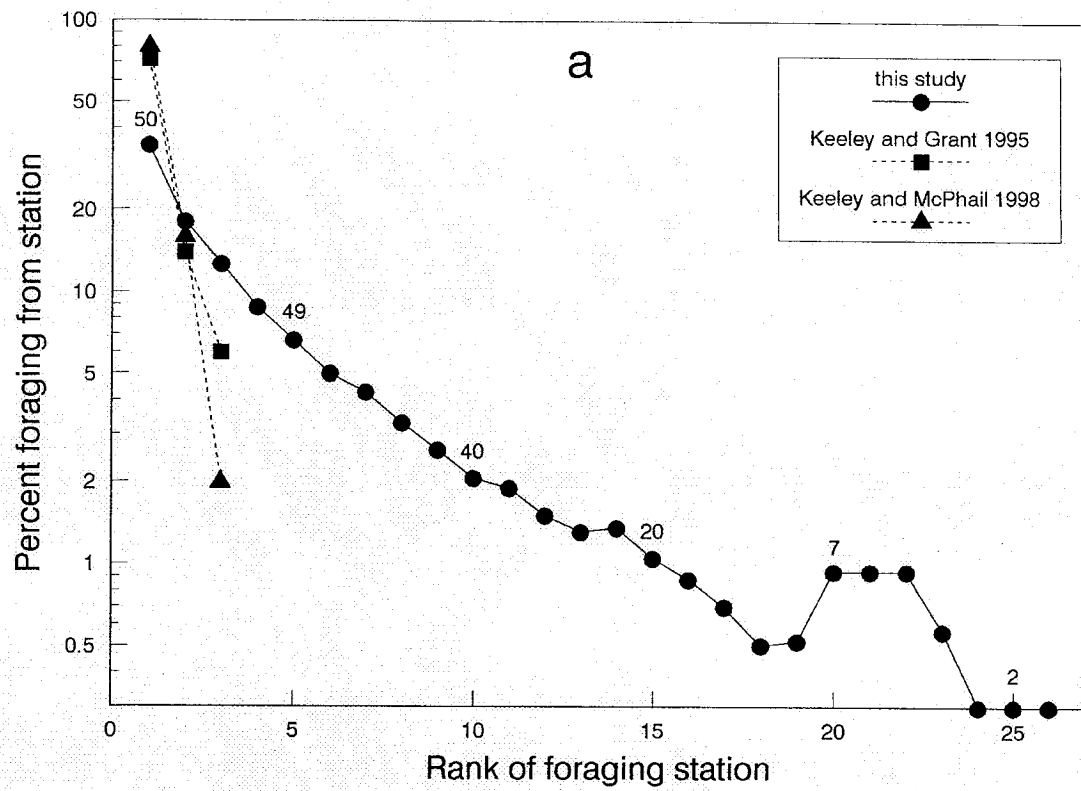
Fig. 2.5. An allometric comparison between the multiple central-place territories for

YOY Atlantic salmon in Catamaran Brook, 2000, territory size when the same data are

superimposed on a single central-place, and published estimates of territory size in YOY

stream-dwelling salmonids. The solid circles and the two solid lines represent the

multiple-central-place territory size for the 50 study animals, and the regressions for the

multiple- and single- central-place areas, respectively. The dashed lines (numbered as in

Table 2.2) represent the relationships found in four previous allometric studies of

salmonid territory size: 8 = Grant et al. (1989), *Salvelinus fontinalis*; 9 = Elliott (1990),

Salmo trutta; 10 = Keeley and Grant (1995), *Salmo salar*; and 11 = Keeley and McPhail

(1998), *Oncorhynchus mykiss*. The dotted line represents Grant and Kramer's (1990)

interspecific territory-size relationship, which incorporates most other estimates of

territory size for salmonids.
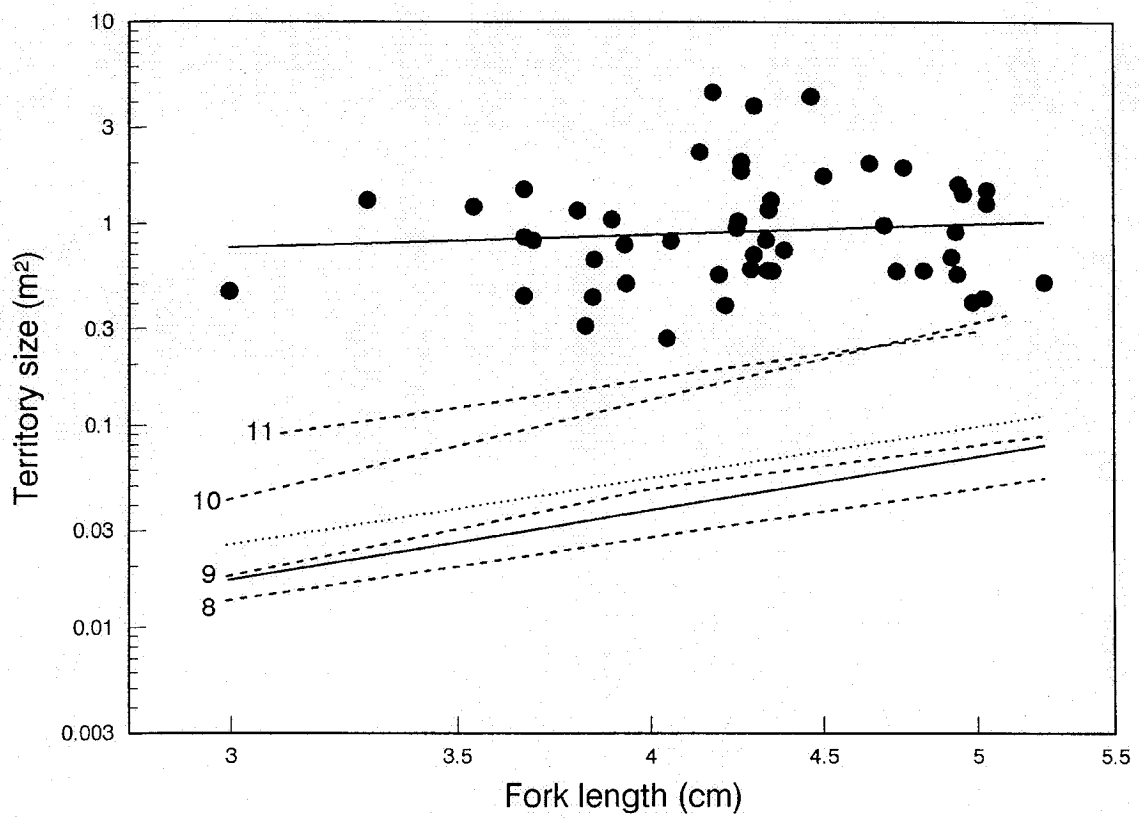
Fig. 2.6. An example of the central-place space-use patterns which emerge for YOY

Atlantic salmon in Catamaran Brook, New Brunswick, when all foraging attempts (●) are

superimposed onto a single central-place station (⊕). The two 100% minimum convex

polygons (solid line), encircle the single central-place-areas for the fish which visited (a)

fewest (n = 3) and (b) most (n = 26) foraging stations, and for which the multiple central-

place territories are depicted in Fig. 2.2a and 2.2b, respectively. In accordance with the

methods used to estimate territory shape, the angles indicate the upstream (90°),

downstream (-90°), and bank-to-bank (0°) direction.

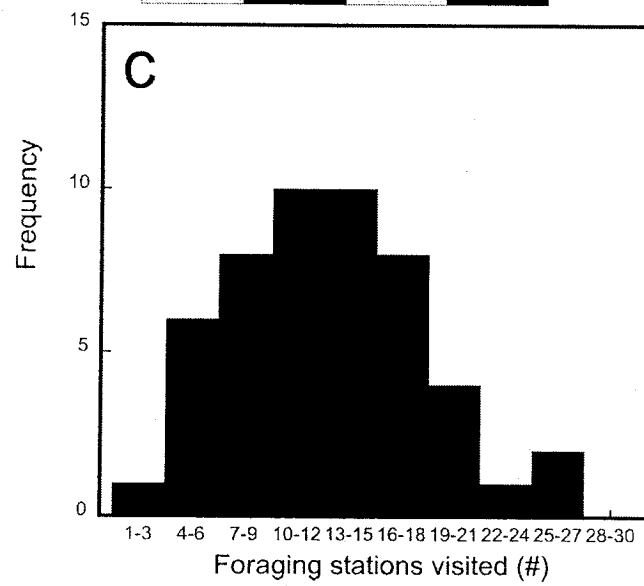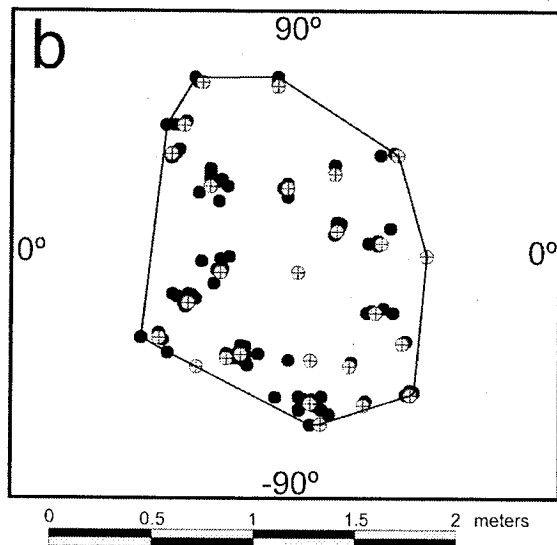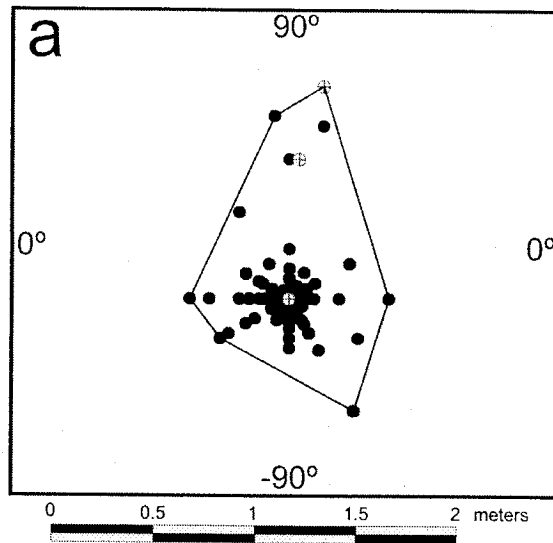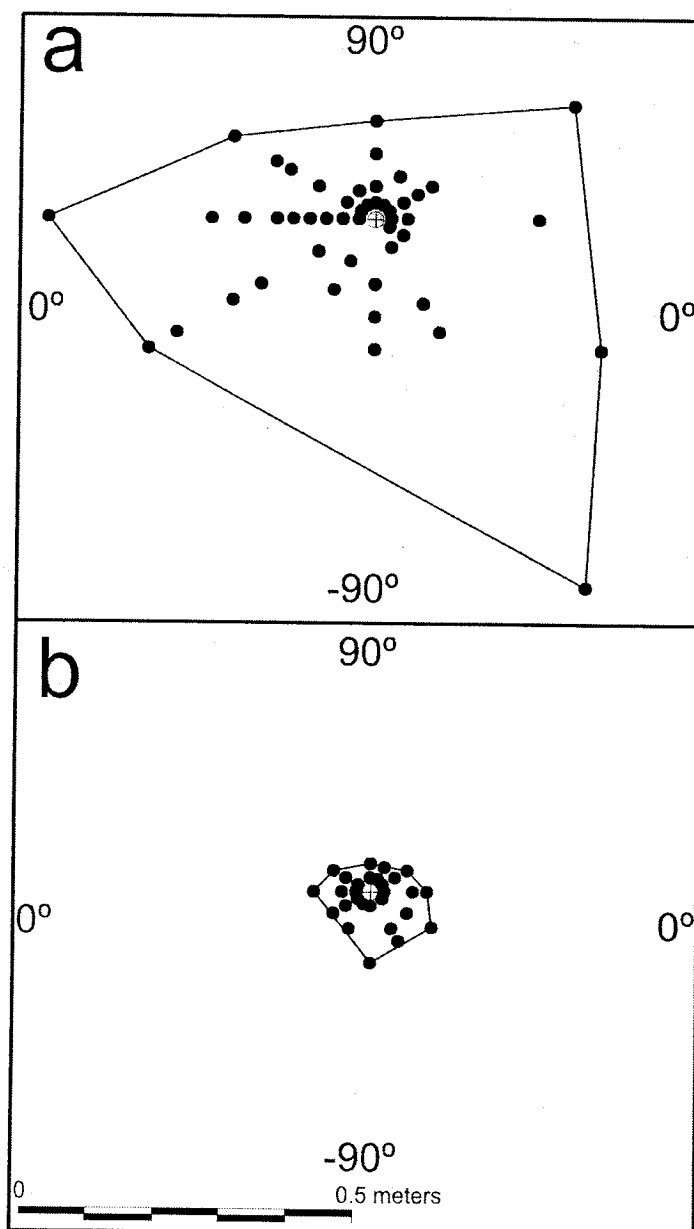Fig. 2.7. Shape of the multiple central place territories, and territories when the same data are superimposed onto a single central place for 50 YOY Atlantic salmon in Catamaran Brook, New Brunswick, 2000. Eccentricity (a) indicates to what degree home ranges are elongated (1 = circular), and (b) the absolute value of the angle along which territories are elongated. The angle indicates if the areas are elongated along the stream length (absolute angle = 45-90°; where + and - 90° equals the up-downstream direction, respectively) or along the stream width (absolute angle = 0-45°, where 0° is perpendicular to the water flow)(see Fig. 2.2 and Fig. 2.6).
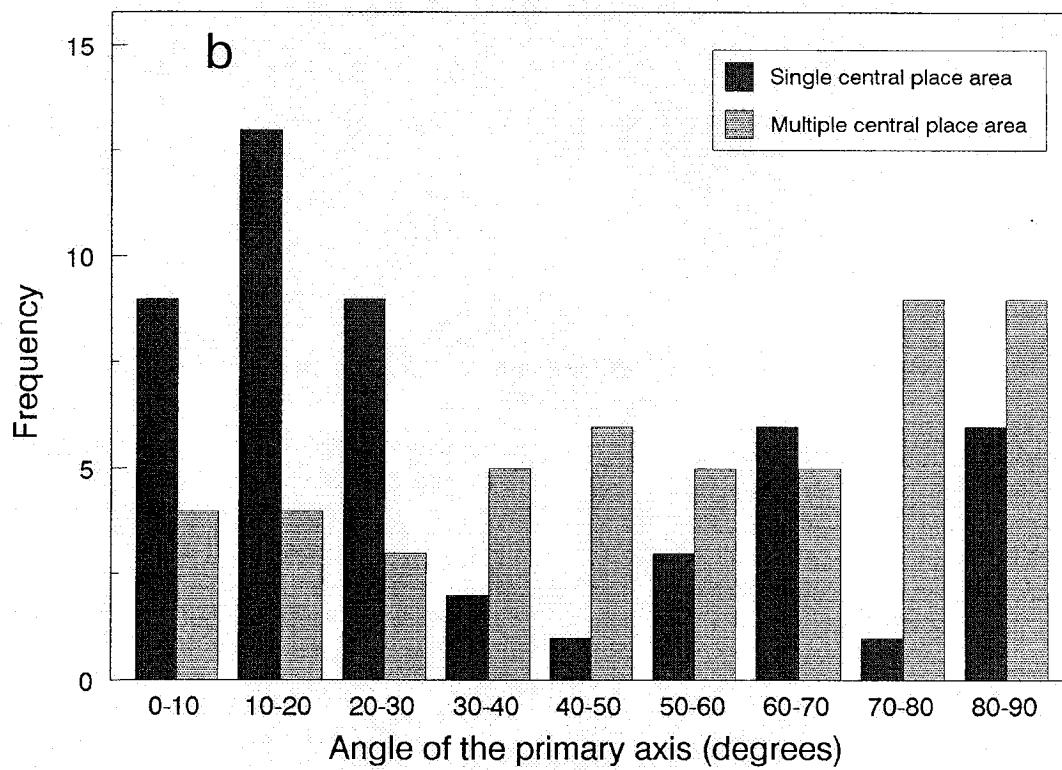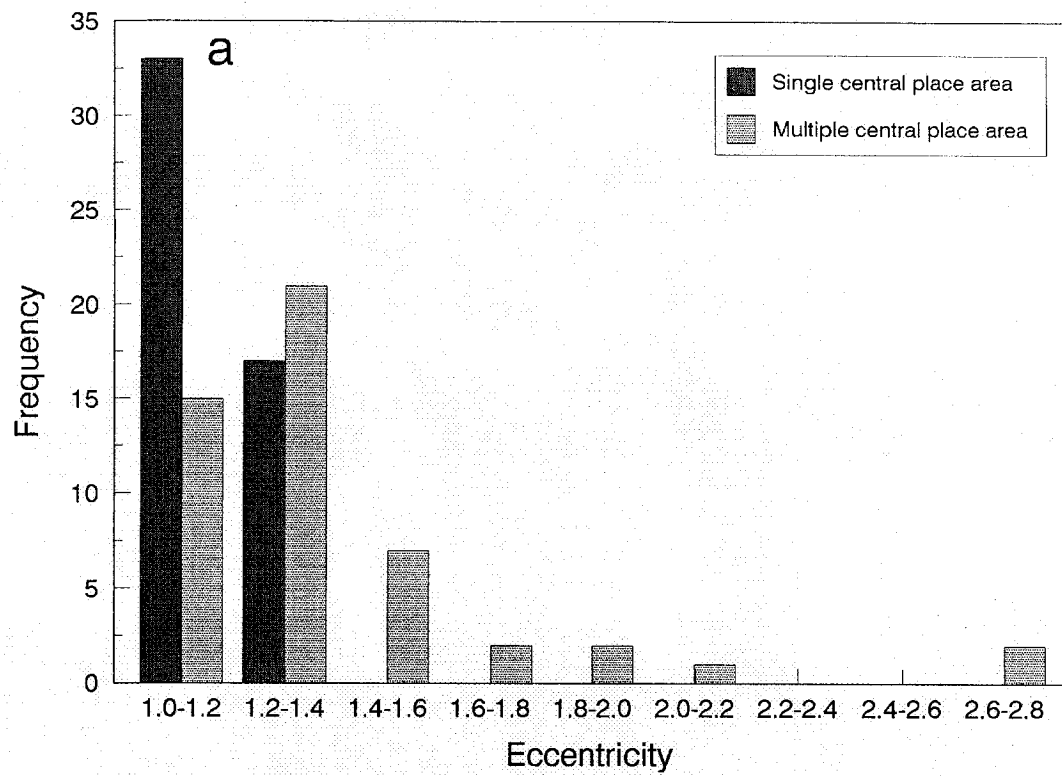
Fig. 2.8. Variability in the frequency of aggression for 50 YOY Atlantic salmon in

Catamaran Brook, in 2000. The three graphs depict the multiple central-place territories

of the fish that was most aggressive toward (a) other YOY Atlantic salmon and (b)

blacknose dace, and (c) a frequency plot for the total number of aggressive acts initiated

by each fish over the 40-min observation. In (a) and (b), the minimum convex polygon

(dashed line), encircles the location of all aggressive acts directed toward YOY salmon

(☆), and blacknose dace (△), and all foraging attempts (●) and foraging stations (⊕).

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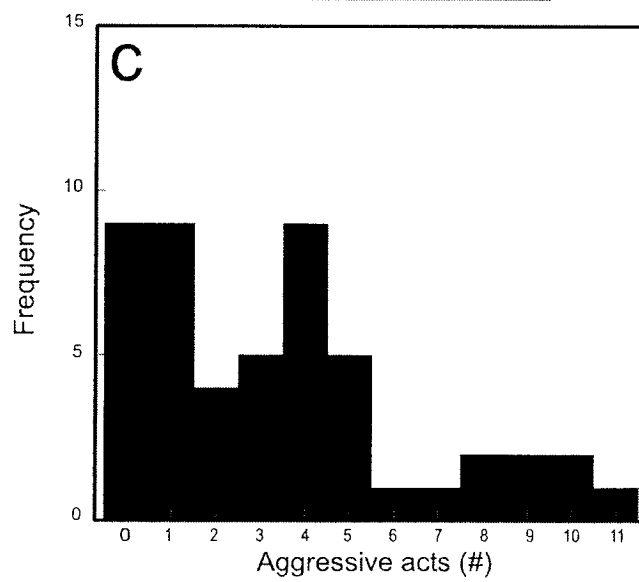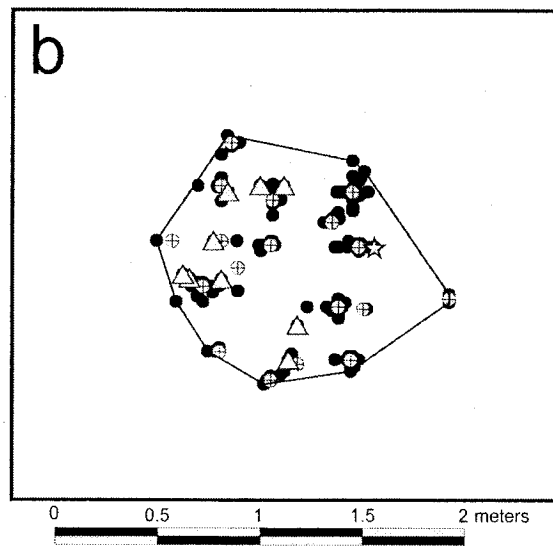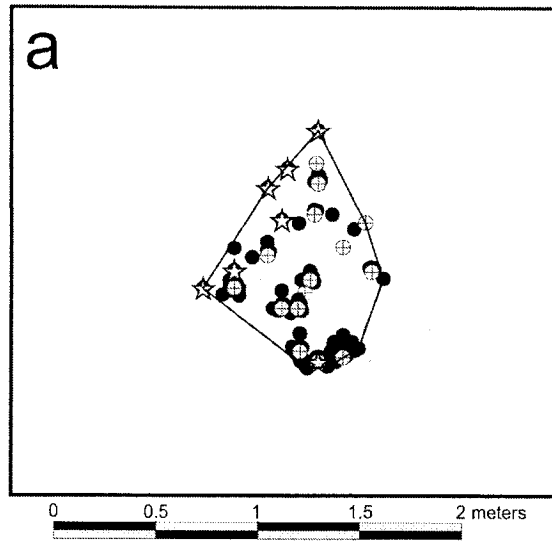
Fig. 2.9. Frequency of all foraging and aggressive distances for (a) the 50 YOY Atlantic salmon monitored in Catamaran Brook, New Brunswick, 2000 (foraging, n = 4225; aggression, n = 165), and for (b) 27 YOY salmon monitored in the same stream in 1992 (Keeley and Grant 1995; foraging, n = 2433; aggression, n = 463). Each bar represents the two length categories indicated on the x-axis (± 0.25 body lengths). The arrows point to the mean aggressive distance for (a) the 50 focal fish, and (b) the previous studies on YOY stream-dwelling salmonids (the numbers refer to studies listed in Table 2.2).
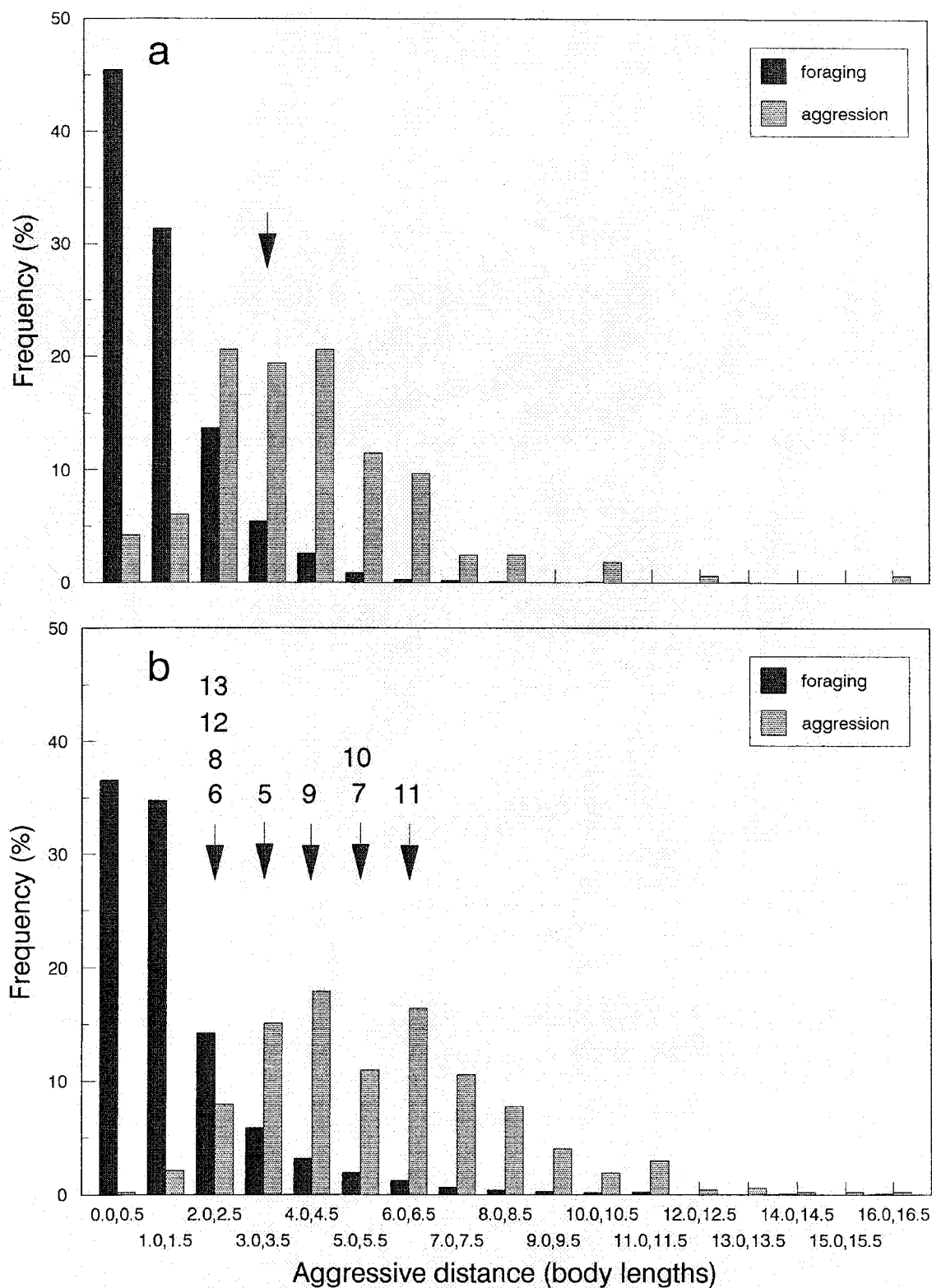
Fig. 2.10. The association between population density and (a) territory size, (b) the number of foraging stations used, (c) the rate of aggression, and (d) the mean aggressive radii obtained from this study (see arrows) and previously published studies on territory size in YOY stream-dwelling salmonids (listed in Table 2.2). The studies are classified as observational studies conducted in a natural stream (●) or as experimental studies conducted in a artificial stream tank (□).

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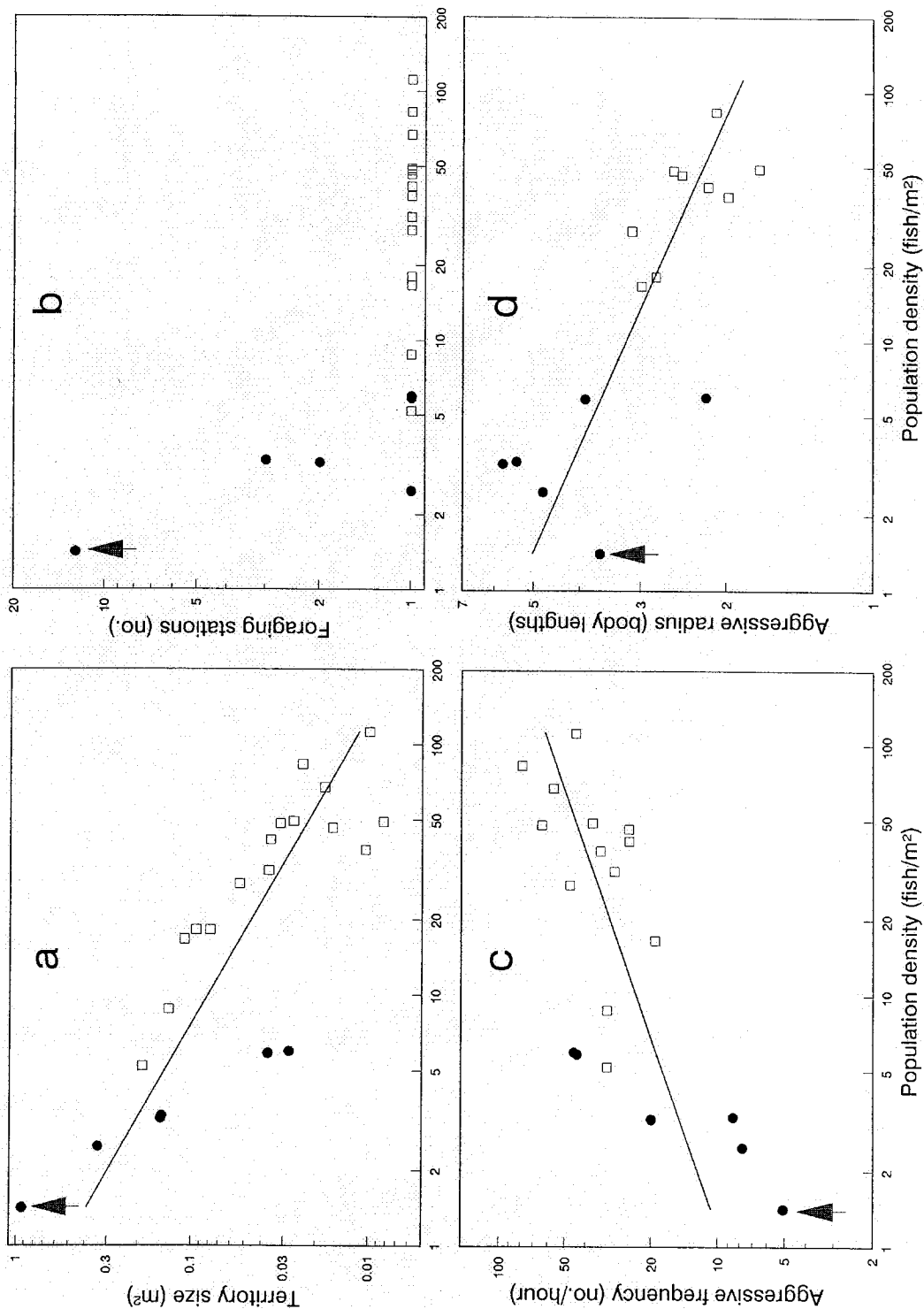
Chapter 3. Ecological determinants of territory use in a multiple central-place forager, the young-of-the-year Atlantic salmon (*Salmo salar*)

Introduction

Animals exhibit great variability, both within and between species, in how they search for food and attack prey (Helfman 1990). As an example, animals may vary from being sit-and-wait foragers, which search for prey from a stationary position, to being cruising foragers, which actively search for food (Pianka 1966; Schoener 1971; McLaughlin 1989). Individuals may even switch foraging mode depending on the distribution of food resources (Helfman 1990; Fausch et al. 1997). Typically, animals adopt a sit-and-wait foraging mode when prey are mobile or spatially predictable, but are likely to become cruising foragers when prey are sedentary or spatially unpredictable (Huey and Pianka 1981). Similarly, it has been suggested that at a high and low prey density, ectothermal animals adopt a sit-and-wait and cruising foraging mode, respectively (Helfman 1990; but see Huey and Pianka 1981).

In general, foraging mode is believed to be closely linked to mobility and home range size; e.g., cruising individuals are likely to be more mobile and use larger home ranges than sit-and-wait foragers. However, although cruising foragers are frequently shown to be more mobile (Huey and Pianka 1981; Katano 1996), and are often said to travel more 'widely' than sit-and-wait foragers (e.g., Huey and Pianka 1981), surprisingly few studies actually examine how foraging mode or mobility are related to home range size. The available studies, however, tend to support the above idea that more mobile

animals that cruise for food have larger home ranges (e.g., Ford 1983; Katano 1996).

In addition, the territory size literature suggests animals use smaller areas when prey is dense and rapidly renewable (Davies and Houston 1984), the same conditions in which animals are predicted to adopt a sit-and-wait foraging mode (Ford 1983; Katano 1996). Also, because small home ranges are more easily defended than large ones (e.g., Grant et al. 1992), animals should be likelier to defend their home ranges at higher prey densities (Davies and Houston 1984; Carpenter 1987). Hence, a synthesis of the foraging mode and territoriality literatures suggest a positive association between mobility and home range size, and that territorial defence should decrease as these two components of space-use increase.

Freshwater fish, and salmonids in particular, may be used as a model system for studying the effects of environmental factors on local space-use, because they can exhibit a wide spectrum of foraging tactics in the wild (Grant and Noakes 1987; Katano 1996; Fausch et al. 1997). In fast-running waters, where drifting invertebrates provide a spatially predictable, rapidly renewing, and abundant prey resource, stream-dwelling fish typically adopt a sit-and-wait tactic and intercept the mobile prey from a centrally-placed foraging station (Kalleberg 1958; Grant et al. 1989). Intuitively, because the space-use of these fish is constrained by repeated returns to the same central-place location, they are often viewed as sedentary and as using small territories. In slow-running waters and lakes, however, fish may cruise over large areas, as they specialize on sedentary or patchy food, such as benthic or planktonic invertebrates (Minns 1995; Katano 1996; Biro et al. 1997). Often, the space use of stream-salmonids also appears to be associated with social status.

Hence, more dominant individuals adopt sit-and-wait foraging tactics as they defend the best feeding positions where high current velocities consistently provide more drifting prey, while subordinate fish travel widely where fewer drifting prey are available (Grant and Noakes 1988; Nakano 1995; but see Martin-Smith and Armstrong 2002).

For salmonids, the above variability in foraging mode has been demonstrated between species (Ferguson and Noakes 1983), between lake and stream populations of the same species (Biro and Ridgway 1995), and between conspecific individuals found in slow- and faster-running waters of the same stream (Grant and Noakes 1987; McLaughlin et al. 1992). Similarly, a number of studies show that the territories of stream-salmonids tend to be smaller where current velocity is faster and drifting prey is more abundant (McNicol and Noakes 1984; Keeley and Grant 1995; but see Dill et al.1981). As with other animals, however, studies on salmonids rarely examine how foraging mode and mobility relate to territory size, in part because estimates of territory size are typically confined to sit-and-wait individuals that forage from a single central-place (see Chapter 2). This is especially true for YOY fish, which so far have been difficult to tag and follow in natural settings (see Bachman 1984; Nakano 1995 for studies on older fish).

Understandably, most studies on foraging mode in juvenile salmonids focus on species that exhibit flexible behaviour, where individuals adopt either a sit-and-wait or cruising foraging mode. YOY Atlantic salmon, however, differ from this dichotomy because although they resemble cruising foragers as they swim between foraging stations, they are rarely, if ever, moving when initiating an attack on their prey and are best defined as sit-and-wait, multiple-central-place foragers (Chapter 2; for examples of multiple

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central-place foraging among other animals see Covich 1976; Chapman et al. 1989; McLaughlin and Montgomerie 1989). Juvenile Atlantic salmon, however, exhibit variability in the numbers of foraging stations they visit (Chapter 2), and may switch toward more benthic prey when drifting prey are scarce (Armstrong et al. 1999; for another salmonid example see Fausch et al. 1997). Hence, YOY Atlantic salmon may offer new insight into the relationships among foraging mode, mobility and territory size in stream-salmonids, and in multiple central-place foragers in general.

In this paper, I adapt general predictions on how space use and social behaviour relate to current velocity, prey abundance and prey mobility in stream-dwelling salmonids, and apply them to multiple-central-place space-use in YOY Atlantic salmon (Fig. 3.1). Based on this foraging-mode framework, fish should (*i*) inhabit smaller home ranges, (*ii*) visit fewer foraging stations, and (*iii*) be less mobile, as current velocity and thus the abundance and mobility of drifting invertebrates available to fish increase (Fig. 3.1). Second, with an increasing current velocity and drift abundance, fish will (*i*) forage more frequently, (*ii*) travel shorter distances on each foraging attempt, and (*iii*) be less likely to adopt benthic feeding. Finally, YOY inhabiting areas with preferred current velocity (6-48 cm/s, Girard 2002) should be dominant, more aggressive, and grow faster than fish in slower waters (< 6 cm/s, Girard 2002; see Grant and Noakes 1988; but see Martin-Smith and Armstrong 2002).

To test these predictions, I monitored space-use for 50 individually tagged YOY Atlantic salmon in a natural stream, and measured habitat features of their territories. Below, I first describe the variability in space-use behaviour detected among my study

fish, and examine whether and how various aspects of foraging behaviour and mobility are related to territory size. I then test if, and how, space-use behaviour, is affected by current velocity and prey availability. Because several other ecological variables (e.g., water depth and body size) may influence space use, and because I did not always expect linear relationships between current velocity and space use, I also test for the effect of current velocity in a multi-variate and quadratic manner.

Materials and methods

Study population, sampling surveys, body size and growth

I studied YOY Atlantic salmon at 10 study sites in Catamaran Brook in central New Brunswick in 2000 (see Cunjak et al. 1993, Chapter 1, and Chapter 2 for more details). Ninety fish (fork length = 27.30-40.60 mm) were initially captured, tagged and measured for fork length in two snorkeling surveys on 25 June to 4 July, and 12-13 July. Once I completed the space-use observations for all focal fish (see below), I recaptured, and measured all tagged fish found in the study sites in two final snorkeling surveys on 20-23 August and 11-12 September. I analysed the movement of the same study fish in Chapter 1, and initially described their patterns of home range behaviour in Chapter 2.

Because I did not measure fish, on the exact day of their space-use observation, I typically estimated fork length of each fish on the day of observation by assuming a linear increase in fork length between the capture surveys closest in time, one preceding and the other subsequent to the observation date (see Chapter 2). Growth rate was measured as (Fork length$_{final}$ - Fork length$_{initial}$) × (Day of year$_{final}$ - Day of year$_{initial}$)$^{-1}$ (unit = mm/day).

Because most fish were observed between the second (12-13 July) and the third (20-23 August) capture survey, and because growth rate varied slightly between the different time periods, only fish found in both these surveys were used to test if and how growth changed across current velocities.

Observations of space use

I observed the territory use of 50 tagged individuals via snorkeling from 3 July to 17 August, 2000. Typically, fish were monitored for two 10-min periods in the early afternoon, and another two 10-min periods later that same afternoon, yielding 40-min of observations for each fish collected between 1330-1850 h (see Chapter 2 for details). For each territory, I recorded the location of foraging stations, the direction (1-12 o'clock) and the distance (in body lengths) of foraging attempts, the location of aggressive acts, and recorded if an intruder chased the focal fish. I estimated various components of space use by creating a simple x-y coordinate system for each study site, and mapping each territory using an ArcView GIS 3.2 software in conjunction with the so-called Animal Movement extension (Hooge and Eichenlaub 2000). Territory size was estimated via the minimum convex polygon method based on all spatial coordinates ($MCP_{100\%}$) (Schoener 1981). More general details on the measurement and estimation of space use can be found in Chapter 2.

Because of rapid changes in the behaviour of my study fish, I could not record every behavioural event for all 50 fish. Consequently, I gave priority to recording the location of all foraging stations visited (because these greatly affected each estimate of

territory size), and the location of all aggressive acts (because these events were rare); this behaviour was thus recorded consistently throughout the 40-min of observation. Furthermore, because foraging was very frequent compared to other events, I estimated the distance and direction of as many foraging attempts as possible during the first 30 minutes, whereas during the last 10-min period I estimated foraging rate. I estimated the number of switches and the mean and total distance allocated toward switching for fish using only those 10-min periods in which I recorded all switches between stations. For 25 fish all four periods were used, while for 11, 12, and 2 fish, three, two and one of the 10 min periods were used for estimation, respectively.

Movement within territories was associated with four different activities; (*i*) foraging at a station, (*ii*) switching between foraging stations, (*iii*) attacking intruding fish, and (*iv*) fleeing from an intruder. First, the distance traveled while foraging at a station was calculated as the number of foraging attempts × 2 × the mean foraging radius; hence, I assumed each foraging bout included a direct return to the same station. Second, I estimated the distance traveled while switching based on the number of switches × the mean distance traveled between consecutive stations. Finally, the distance traveled while chasing and fleeing from an intruder was calculated as the frequency of these events × 2 × the mean aggressive distance. Hence, because I rarely witnessed a focal fish fleeing from an intruder, and because I did not estimate the mean fleeing distance, I assumed it equaled the mean aggressive distance. The distance allocated toward the four movement activities was prorated to a total of 40 minutes based on those 10-min periods that were useable.

Habitat and food abundance

For each fish, current velocity and water column depth were measured at, and averaged across those five stations where most foraging attempts were recorded. If a fish visited fewer than five foraging stations, I measured the habitat variables at all stations visited. I measured current velocity with a Marsh-McBirney meter (Model 201D; Marsh-McBirney, 4539 Metropolitan Ct., Frederick, MD 21704, U.S.A.), at 40% of the total depth at each station (measured from the bottom). Water temperatures were measured before and after the 20 min of observation conducted in the early and late afternoon, respectively.

Because of time constraints, I did not sample invertebrate drift at the 50 territories on the day of the space-use observation. Instead, I predicted food density at each territory, using a multiple regression model which I established based on a total of 30 drift samples, collected in the 10 study sites on three occasions (22-23 July, 8-9 August, and 4-5 September) over the season. I collected the samples by placing a 1-m long drift net (mesh size = 300 μm) attached to a metal frame opening (15.2 × 23 cm), in the water, haphazardly at one of the marked locations in each site (i.e., where the 90 YOY salmon were found initially); no location was sampled more than once. I varied the sampling time depending on how fast drift accumulated in the net (mean = 49 min, range = 15-120 min). For each sample, I recorded the time and day of sampling, water temperature, and the current velocity (measured in the center of the net opening) and water depth at the sampling location. Samples were collected between 1325h and 1845h, and always at least two hours before dusk.

Each drift sample was preserved in 10% buffered formalin and processed at Concordia University. First, I separated intact organisms from other drifting material and debris. Second, I counted all organisms (>99% of the total number) judged to be within the size range of edible prey for YOY Atlantic salmon (Keeley and Grant 1997). Third, I measured the dry weight of each sample by placing it in an oven at 50°C for 72 h (Merritt and Cummins 1978). Each sample was then placed in a desiccator, and weighed once on each of three consecutive days until the weight was stable ($\pm$ 0.0001 g). Both the numbers and dry weight of drifting organisms were prorated to the area of the drift net frame (if net was not completely submerged), and to a fixed time of 20 minutes. Because there was a good correspondence between numbers and dry weights for the drift samples [linear regression: $\log_{10}$ drift dry weight (mg/20min) = -1.710 + 1.032 $\log_{10}$ drift number (no./20min), $r^2 = 0.881$, $n = 30$, $P < 0.001$] I only report the numbers hereafter. Finally, I used multiple regression based on the sampling date, and the habitat features measured for each drift sample, and at each territory, to predict the invertebrate drift rate (no. organisms/area of the drift net opening/20min) at the 50 territories.

Statistical analysis

To facilitate the analysis, I applied a few general rules and simplifying assumptions. First, because drift rate was derived from, and strongly related to current velocity (see results), and because space use changed in an identical manner in response to both variables, I focused on current velocity as an independent variable in most analyses, and report the influence of drift rate more selectively. Second, because a linear

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relationship between current velocity (or drift rate) and space use was not always expected, I tested for the effect of current velocity (and drift rate) via both a simple linear regression, and by adding a quadratic component to the model. If neither regression model was significant, I reported the simple model, unless the quadratic model had a much lower P-value and was close to being significant ($P < 0.15$). Third, because ecological variables other than current velocity and drift rate may influence space use (i.e., water depth, water temperature and fork length), I tested for their effect by adding them to a multiple regression model along with current velocity. Overall, these additional variables had only minor influence on the P-value obtained for current velocity and drift rate, and never changed whether current velocity and drift rate were more strongly associated with space use in a linear or curvilinear manner. Because I do not put forward any a priori hypotheses on the influence of water depth and water temperature on space use in stream-dwelling salmonids, and rarely do so for fork length, I also compared the partial P-values for these variables to a Bonferroni corrected significance level (P-value) of 0.006 (i.e., unplanned tests for nine space use variables for each correlate = 0.05/9).

Finally, where necessary to meet the assumptions for parametric tests, dependent and independent variables were either $\log_{10}$- or square-root transformed. However, because current velocity and drift rate were square-root transformed, the squared term added to curvilinear relationships is automatically reversed to its original form and reported as such (e.g., current velocity$^{1/2}$ × current velocity$^{1/2}$ = current velocity).

Results

Variability in local space-use patterns

The 50 YOY Atlantic salmon monitored in this study (mean fork length = 4.30 cm, range = 2.99-5.24) can all be classified as sit-and-wait predators that forage from multiple central-places (Chapter 2). However, in spite of this apparent lack of flexibility in foraging mode, the focal fish exhibited considerable variability in their local space-use patterns. Most strikingly, over the 40-min of observation, focal fish used territories $(MCP_{100\%})$, which ranged 16.7 fold in size, from 0.268 m² to 4.469 m² (mean, back-calculated from log_{10} = 0.932 m²) (Fig. 3.2abc), visited as few as 3, and as many as 26 foraging stations (median = 12.5 stations) (Chapter 2, Fig. 2.2), and traveled within their territory, a total distance ranging from 15.7 m to 95.0 m (median = 39.3 m) (Fig. 3.2def).

Further variability is revealed when the total distance traveled by each fish is divided into its four behavioural components; i.e., the distance traveled while (*i*) foraging from a station, (*ii*) switching between foraging stations, (*iii*) chasing intruding fish, and (*iv*) fleeing from intruders (Fig. 3.3). The distance traveled during foraging attempts varied 6.0 fold, from 8.2 m to 49.6 m (mean = 19.4 m; % of the total distance: mean = 48.9%, range = 14.8-91.4%). The distance traveled while switching stations, which is the best indicator of the effort the study fish allocated towards "cruising" over their territory, ranged 33.7 fold, from 2.4 m to 79.2 m traveled over 40 minutes (mean = 23.8 m; % of the total distance: mean = 47.8%, range = 4.6-84.3%) (Fig. 3.3). On average, foraging and switching stations accounted for 96.6% of the total distance, whereas very limited effort was allocated toward chasing (mean = 3.0%, range = 0-20.3%) and fleeing from (mean =

0.4%, range = 0-1.8%) intruders (Fig. 3.3).

The variability in the distance traveled during foraging bouts is due to differences in the foraging frequency (range = 19-93 attempts/10 min), and differences in the mean foraging radius (range = 3.6-12.2 cm). Similarly, the variability observed in the distance traveled while switching can be traced to how often YOY switched between foraging stations (range = 1-46.5 switches/10 min) and to a lesser degree to the mean distance traveled between consecutive stations (range = 22.3-117.0 cm) (Table 3.1). Hence, on average, YOY Atlantic salmon switched between stations as infrequently as once every 10 minutes, and as frequently as once every 12.9 seconds. In addition, YOY salmon foraged, on average, 0.85 to 48 times at each station before switching to another. Finally, in spite of the relatively short overall distance traveled during chases directed toward intruding fish, fish varied considerably in their aggressive frequency (range = 0-11 chases/40min) and the mean aggressive radius (range = 1.9-31.8 cm).

The 50 focal fish directed a vast majority of their foraging attempts toward prey drifting in the water column (mean = 91.2%: range = 75.0-99.1%). Meanwhile, benthic foraging (mean = 7.5%; range = 0.0-25.0%) and foraging attempts directed toward the water surface (mean = 1.3%; range = 0.0-12.1%) were infrequent.

Behavioural and structural correlates of territory size

Unlike those salmonids that use only one central-place station, the size of the multiple central-place territories of YOY Atlantic salmon in Catamaran Brook was primarily affected by the mean distance traveled between consecutive foraging stations (P

< 0.001), and the total number of stations visited over the observation period ($P < 0.001$) (Table 3.2). Hence, the mean switching distance likely indicated the proximity of foraging stations, which along with the number of stations visited, affected the area occupied. Consistent with previous studies, however, territory size was also positively related to the mean foraging radius ($P = 0.019$). Often, estimates of area use increase with the number of spatial positions recorded (Schoener 1981; Chapter 2). In this study, sample size was significantly correlated with territory size ($P = 0.047$); however, this result did not confound our analysis because sample size added little to the step-wise regression model, and because the association was negative (Table 3.2). Meanwhile, neither foraging rate nor the rate at which individuals switched stations were related to territory size ($P = 0.352$ and 0.373, respectively).

Finally, in this study, more mobile individuals appeared to occupy larger territories. However, whether this association was significant depends on my measure of mobility; i.e., territory size was significantly correlated with the distance traveled while switching stations (Pearson's $r = 0.308$, $n = 50$, $P = 0.030$; both variables $\log_{10}$ transformed) but not with the total distance traveled (Pearson's $r = 0.206$, $n = 50$, $P = 0.151$; both variables $\log_{10}$ transformed).

Environmental variability

The habitat of the 50 territories varied widely in both current velocity (mean = 0.159 m/s, range = 0.012-0.362) and water depth (mean = 34.4 cm, range 14.6-78.7). Water temperature during the space use observations varied between 17.5 and 22.5°C

(mean = 19.8 °C).

The number of invertebrate prey caught at the 30 drift sampling locations increased with current velocity, but decreased as the summer progressed [multiple regression: $\log_{10}$ invertebrate drift (no./drift net/20min) = 4.431 + 1.1345 $\log_{10}$ current velocity (m/s) - 0.009 day of year, $r^2 = 0.918$, $n = 30$, $P < 0.001$]. When added to the model, neither water temperature (partial $P = 0.231$) nor depth (partial $P = 0.727$) added significantly to explain the drift rate. Consequently, I estimated the drift rate at each territory based on the mean current velocity at the territory, and the day of year at which the observation was made. The predicted drift rate at the 50 territories varied between 0.9 and 89.7 invertebrates (mean = 30.0) drifting through an area equivalent to the drift net frame (15.2 × 23 cm = 349.6 cm^2) in 20 minutes.

Environmental determinants of space use

Current velocity and drift rate of prey were related to several components of space use in YOY Atlantic salmon, but not always in the predicted manner (Fig. 3.4). First, as predicted, territory size generally decreased with increasing current velocity ($P = 0.014$) and drift rate ($P = 0.029$) (Fig. 3.4ad). Second, contrary to the foraging predictions, the number of foraging stations visited within the territory did not increase with decreasing current velocity ($P = 0.202$) or drift rate ($P = 0.096$) (Fig. 3.4be); in fact, if anything there was a trend for fish to visit more stations in faster water where drifting invertebrates were more abundant. Third, the total distance traveled within the territory was best described by a curvilinear relationship ($P < 0.001$ and $P = 0.003$ for current velocity and drift rate,

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respectively), where fish traveled most at intermediate current velocities. In contrast, distance traveled was predicted to increase in slow waters where drifting prey is less abundant (Fig. 3.4cf). Overall, the univariate results reported above, were supported when the effects of current velocity (and drift rate, though not reported) on space use were examined via multiple regression analysis (Table 3.3). Hence, in no case did the inclusion of water depth, water temperature and fork length, affect whether current velocity was significantly associated with a given space use component, or whether this relationship was better described in a linear or curvilinear manner. Water depth was the only other correlate that was related to the above space use components (Table 3.3); fish in deep waters used significantly larger territories than those found in shallower waters (partial P = 0.005); this relationship is also marginally significant when compared to a Bonferroni-corrected significance level of P = 0.006 (see methods). Interestingly, the total distance traveled was not related to the size of the focal fish (partial P = 0.315) (Table 3.3).

The influence of current velocity on space use can be explored further by examining the foraging and switching behaviour exhibited by the focal fish (Fig. 3.5). Overall, these two components of behaviour showed a similar response to current velocity (and drift rate, not shown), even though this was not always predicted. First, as expected based on the increased availability of drifting prey and increased swimming costs, the mean foraging radius and the mean distance traveled between consecutive stations decreased as current velocity increased (Fig. 3.5ad.; P = 0.023 and < 0.001, respectively). Second, with increasing current velocity, both the foraging frequency and the rate at which fish switched between stations, increased initially and then leveled off and

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decreased slightly (Fig. 3.5be; $P < 0.001$ and $P = 0.011$, respectively). Interestingly, these findings were not expected for the switching behaviour because drift-feeding fish should be likelier to remain at one station in fast waters, where drifting prey is abundant. Third, as in the case of the total distance traveled within the territory, the overall distance due to foraging attempts is greatest at intermediate current velocities (Fig. 3.5c; $P < 0.001$; see Fig. 3.4c for comparison). Similarly, the total distance moved while switching between foraging stations tended to be greatest at intermediate current velocities, although this was not a significant relationship (Fig. 3.5f; $P = 0.147$); most importantly, none of my measures of mobility suggested that YOY Atlantic salmon were most mobile in slow-running waters as expected based on the foraging-mode literature. Finally, fish were not more likely to feed on benthic invertebrates in slow running waters where fewer drifting prey were available, than in faster waters; I detected no association, either linear ($P = 0.780$) or curvilinear ($P = 0.293$), between the percent of foraging attempts directed toward the benthos (arcsine transformed) and current velocity (square-root transformed).

A multiple-regression approach did not alter how foraging and switching behaviour were associated with current velocity (or drift rate, not shown), even though this behaviour occasionally appeared to be affected by other ecological correlates (Table 3.4). First, when relationships between current velocity and different components of space use were accounted for, YOY in deep waters tended to travel a greater mean distance on each foraging bout (partial $P = 0.047$) and during switches between consecutive stations (partial $P = 0.016$) than fish in shallower water (Table 3.4); however, these associations are not significant if compared to a Bonferroni-corrected significance level of $P = 0.006$.

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Second, fork length was positively related to both the mean foraging radius (partial $P <$ 0.001) and also appears to be associated with the total distance traveled during foraging attempts (partial $P = 0.010$). In terms of water temperature, fish tended to travel farther between consecutive stations at higher temperatures (partial $P = 0.023$), but this is not significant when compared to a significance level of $P_{Bonferroni} = 0.006$ (Table 3.4). In general, foraging and switching behaviour responded similarly to drift rate (not shown), as they did to current velocity, irrespective of whether these determinants were examined separately, or in a multiple regression along with other potential determinants.

My results were equivocal regarding the hypothesis that more aggressive individuals, with greater growth potential, inhabit and defend territories in faster waters where drifting prey is more abundant. For example, based on the few observed chases directed toward intruding fish, aggressive acts were slightly more common at intermediate current velocities than in slow-running waters, but decreased again as current velocity increased further ($P = 0.041$) (Fig. 3.6a). But, territory holders inhabiting fast water grew more slowly than those found in slow water ($P = 0.006$) (Fig. 3.6b).

Discussion

Environmental correlates of territory use

Similar to many generalist foragers, stream-fish may adopt alternative foraging tactics; they switch between being mobile as they actively cruise for benthic or patchy prey items (movers), or relatively sedentary as they ambush mobile prey via sit-and-wait foraging tactics (stayers) (Grant and Noakes 1987; Katano 1996; McLaughlin et al. 1999).

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However, the YOY Atlantic salmon monitored in this study do not appear to exhibit the behavioural flexibility underlying this general framework, but rather specialize as central-place foragers. First, all 50 focal fish are best described as sit-and-wait foragers, which visit a number of foraging stations, but rarely if ever attack their prey while swimming between stations (see Chapter 2). Also, in sharp contrast to predictions, fish in slow waters where drifting prey were scarce were not more mobile, did not visit more stations, and did not forage more from the benthos than fish in faster-running waters. In fact, the most mobile fish were found at intermediate current velocities and prey availability. Less surprisingly, however, as current velocity and the prey drift rate increased, both territory size and foraging radii decreased as predicted, whereas foraging rate initially increased and then leveled off (see also Grant and Noakes 1988; Grant et al. 1989; Keeley 2000).

Ecological variables, other than current velocity and the availability of drifting prey, had limited effects on the space use of YOY Atlantic salmon. Foraging radius and the total distance traveled by the focal fish during foraging attempts are positively related to fork length. These findings are not surprising; larger fish are better swimmers and may see farther, causing body size typically to be associated with foraging radius (e.g., Grant et al. 1989; Elliott 1990), which along with foraging rate determined the total foraging distance (see methods). Finally, the focal fish did use larger territories in deeper water, in part because they tend to attack prey at a greater distance, and travel longer distances between consecutive stations under these conditions; at this point in time, however, any explanations on the ultimate causes for this trend would be highly speculative.

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Mobility and foraging in stream-dwelling fishes

Patterns of mobility exhibited by YOY Atlantic salmon in this study were quite interesting. For example, in spite of specializing as sit-and-wait foragers, the study fish were surprisingly mobile, traveling a total distance of 15.7 m to 95.0 m (median = 39.3 m = 914 body lengths/40 min), of which 47.8% (4.6-84.3%) was allocated toward switching between foraging stations. In comparison, based on the mean radii and the frequency of aggressive acts and foraging attempts initiated by a territorial stream-dwelling fish from a single foraging station, I estimate that YOY brook charr (Grant et al. 1989) and YOY rainbow trout (Keeley 2000), traveled a mean distance of 501 and 722 body lengths in 40 minutes, respectively. In comparison, YOY brook trout in two lakes, most of which were cruising foragers, traveled a mean distance of 890 and 1187 body lengths in 40 minutes, while searching for prey (calculated from Biro et al.1997). Hence, MCPF drift-feeding fish are likely more mobile than single CPF and may in some cases travel similar distances as cruising fish. Unfortunately, although many studies on stream-dwelling salmonids focus on the energetic basis of drift feeding from one location (e.g., Enders et al. 2003; Hughes et al. 2003), potential costs associated with switching between stations among drift-feeding fish have received limited attention.

The most mobile fish were found at intermediate current velocities, rather than in slow-running waters where drifting food is scarce. Most surprisingly, this trend emerged when I examined specifically the rate at which YOY Atlantic salmon switched between stations (i.e., rate of movement, sensu Ford 1983), and the overall distance traveled while switching. These findings, along with the fact that fish in slow waters did not divert their

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foraging efforts toward the benthos (sensu, Fausch et al. 1997), suggest that mobility in

YOY salmon was not primarily associated with seeking out alternative prey in areas

where drifting invertebrates were rare. However, the proportion of foraging bouts directed

toward the benthos in this study was greater (7.5%) than previously reported for juvenile

salmon (< 1%; Keeley and Grant 1995), suggesting that salmon may encounter more

benthic prey when they rotate among several focal points.

Why YOY Atlantic salmon travel more between stations at intermediate current

velocities remains unclear, but one potential explanation emerges from their habitat use.

First, although YOY salmon in Catamaran Brook use a wide range of habitats, they show

consistent preferences for current velocities of 12-24 cm/s (Girard 2002; see also Morantz

et al. 1987 for similar results), which match the intermediate current velocities used by

the most mobile fish in this study (Fig. 3.5ef). Second, among drift-feeding fish, preferred

current velocities generally represent higher quality habitats, which are believed to be of

greater value than other habitats, e.g., in terms of energetic gain (Hill and Grossman

1993). Third, Johnsson et al. (2000) showed that brown trout in preferred habitats defend

their territories more intensively than those in lower quality habitat; similar trends are

revealed in this study as aggression is slightly more pronounced at intermediate current

velocities. Consequently, because the study fish rarely chased intruders across the large

multiple central-place areas (see Chapter 2), rapid switching between stations at optimal

water currents may indicate a greater effort toward patrolling and defending territories.

Although patrolling increases travel costs of territory holders, it could reduce the traffic of

intruders immediately upstream of the many foraging stations, especially because a large

portion of the invertebrates drift very short distances once they emerge from the benthos (Elliott 2002a; McIntosh and Townsend 1998; see discussion in chapter 2). Obviously, the above ideas need to be developed and verified in future studies.

Based on the sit-and-wait nature of the study fish, it was less surprising that the distance traveled while foraging at a station is greatest at intermediate current velocities. In slow-running waters, YOY salmon travel far on each foraging attempt but rarely attack prey, resulting in a short overall foraging distance. As current velocity increases, foraging rate initially increases rapidly, yielding a greater overall foraging distance, but then levels off (see similar results in Grant and Noakes 1988), possibly because of an increased prey selectivity or time constraints caused by prey handling; this leveling off then leads to a shorter overall foraging distance as prey are attacked at a gradually shorter distance in faster water. Because foraging rate and mean radii typically respond to current velocity in a similar manner among other drift-feeding fish (e.g., Grant and Noakes 1988), it is likely that stream-salmonids associated with only one foraging station are often most mobile at intermediate current velocities.

The current findings highlight the habitat-related differences in the behaviour of stream-salmonids, where species differ in the foraging mode they adopt most often, and in the flexibility they exhibit in their foraging mode. Some species, such as brook charr (*Salvelinus fontinalis*) (Grant and Noakes 1987; Biro and Ridgway 1995; McLaughlin et al 1999), Dolly Varden charr (*Salvelinus malma*) (Fausch et al. 1997) and coho salmon (*Oncorhynchus kisutch*) (Puckett and Dill 1985) can clearly adopt either a sit-and-wait or an active foraging mode, where the latter is associated with utilizing benthic (Fausch et al

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1997) or pelagic (McLaughlin et al 1999) prey in slow waters where drifting prey is rare. Other species, such as white spotted charr (*Salvelinus leucomaenis*) (Fausch et al. 1997) and Atlantic salmon (Nislow et al. 1998) respond to reduced drift density via increased benthic feeding, but appear to do so while retaining a sit-and-wait position and without switching to active search for prey. Interestingly, however, this study also suggests that although YOY Atlantic salmon are typically sit-and-wait foragers, which prefer relatively fast waters (Kalleberg 1958; Armstrong et al 2003), they may grow faster, or as fast (Girard 2002), in slow-running waters where drift-feeding is presumably less beneficial.

Space use in multiple central-place foragers

To date, multiple central-place foraging has been studied in animals that depend on food resources that gradually become depleted around each central-place during foraging. In this situation, mobile animals, such as brood-splitting birds (McLaughlin et al. 1989), and spider monkeys (Chapman et al. 1989) respond to decreasing food abundance, by switching to another central-place, which in turn allows them to maintain a higher foraging rate. Other benefits from switching among stations is that animals can harvest food over a large area at a lower overall travel cost than if all foraging bouts were initiated from a single location in the area's center (Chapman et al. 1989; McLaughlin et al. 1989). In contrast to the above situations, YOY Atlantic salmon forage on drifting prey that is often viewed as a non-depletable resource (Allan 1982). More specifically, because the current continuously brings new invertebrates, the territory holder's prey encounter rate should not decline at a given station as a result of its foraging efforts.

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Hence, multiple central-place foraging is not confined to animals that harvest obviously depleting food resources, but may also occur in species that harvest rapidly renewable food resources. In these situations, this study suggests that mobility may be linked to foraging in a less direct manner, and may also reflect how, and how intensively, home ranges are patrolled and defended (see e.g., Mitani and Rodman 1979; Paton and Carpenter 1984).

Table 3.1. Behavioural variability in the traveling distance associated with foraging from a station, switching between foraging stations, and chasing intruding fish, by 50 young-of-the-year Atlantic salmon (*Salmo salar*) in Catamaran Brook, New Brunswick.

Variable	Mean	Median	Range	CV
Distance traveled foraging (m/40min)	19.4	15.6	8.2-49.6	0.507
- Foraging rate (no. attempts/10min)	44.9	42.3	19.0-93.0	0.349
- Mean foraging radius (cm)	5.3	4.9	3.6-12.2	0.285
Distance traveled switching (m/40min)	23.5	16.3	2.4-79.2	0.852
- Switching frequency (no./10min)	14.4	9.7	1.0-46.5	0.805
- Mean switching distance (cm)	43.0	41.0	22.3-117.0	0.382
Distance traveled during chases	1.3	1.0	0-6.1	1.089
- Aggressive frequency (chases/40min)	3.4	3	0-11	0.886
- Mean aggressive radius	15.9	15.2	1.9-31.8	0.409

Table 3.2. Summary of the stepwise regression statistics for the behavioural and methodological determinants of $\log_{10}$ territory size (m^2) in young-of-the-year Atlantic salmon (*Salmo salar*) using multiple foraging stations in Catamaran Brook, New Brunswick, Canada.

Correlate	Slope	r^2	P-value
Log_{10} mean switching distance (cm)	1.2407	0.622	< 0.001
Stations visited (no./40 min)	0.0273	+0.171	< 0.001
Log_{10} mean foraging radius (cm)	0.5225	+0.013	0.019
Total number of observations (n)	-0.0007	+0.016	0.047
Log_{10} foraging attempts (no./10 min)	0.1826	+0.004	0.352
Log_{10} station switches (no./10 min)	0.0926	+0.003	0.373
Full model (all significant correlates)	na[b]	0.822	<0.001

[a] correlates are ranked from the top based on their contribution to a stepwise regression model. For the four significant correlates (above the dashed line), I report the slope and the P-value when all four are included in the model, whereas the r^2 shows the increase as these variables were gradually added to the model. For the two non-significant variables, which I removed based on backwards stepwise regression, the table shows the slope, the P-value, and how much these variables added (not significantly) to the r^2 at the time of

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their removal.

[b] not applicable

Table 3.3. Multiple regression analysis describing the influence of current velocity, water depth, water temperature, and fork length on territory size, the number of foraging stations visited, and the total distance traveled within a territory for 50 YOY Atlantic salmon in Catamaran Brook, New Brunswick, Canada.

Space use[a]	Determinant[a]	Slope/Intercept	t	Partial P
Territory size (m^2); r^2 = 0.301, P = 0.002[b]				
	Constant	-1.918	-1.988	0.053
	current velocity (m/s)	-0.787	-2.088	0.042
	water depth (cm)	0.096	2.966	0.005
	water temperature (°C)	0.070	1.847	0.071
	fork length (cm)	0.392	0.581	0.564
Foraging stations (no.); r^2 = 0.101, P = 0.299[b]				
	Constant	-0.005	-0.001	0.999
	current velocity (m/s)	9.767	1.254	0.216
	water depth (cm)	0.849	1.268	0.211
	water temperature (°C)	0.711	0.913	0.366
	fork length (cm)	-15.744	-1.128	0.265

Total distance traveled (m); $r^2 = 0.372$, $P < 0.001$[b]

Constant	-0.712	-0.976	0.334
current velocity (m/s)	6.054	4.563	< 0.001
current velocity^2 (m/s)	-7.867	-4.457	< 0.001
water depth (cm)	0.040	1.654	0.105
water temperature (°C)	0.035	1.247	0.219
fork length (cm)	0.509	1.016	0.315

[a] Territory size, total distance traveled and fork length were $\log_{10}$ transformed for this analysis. Current velocity and water depth were square-root transformed.

[b] Statistics for the complete model, with both significant and non-significant variables.

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Table 3.4. Multiple regression analysis describing the influence of current velocity, water depth, water temperature, and fork length on the foraging and switching behaviour of 50 young-of-the-year Atlantic salmon (*Salmo salar*) in Catamaran Brook, New Brunswick.

Space use[a]	Determinant[a]	Slope/Intercept	t	Partial P
Mean foraging radius (cm); $r^2 = 0.499$, $P < 0.001$[b]				
	Constant	0.153	0.502	0.618
	Current velocity (m/s)	-0.386	-3.243	0.002
	water depth (cm)	0.021	2.046	0.047
	water temperature (°C)	-0.007	-0.574	0.569
	fork length (cm)	1.143	5.359	< 0.001
Foraging attempts (no./10 min); $r^2 = 0.354$, $P = 0.001$[b]				
	Constant	0.786	1.514	0.137
	current velocity (m/s)	4.288	4.543	< 0.001
	current velocity^2 (m/s)	-5.238	-4.172	< 0.001
	water depth (cm)	-0.009	-0.542	0.591
	water temperature (°C)	-0.001	-0.038	0.970
	fork length (cm)	0.154	0.434	0.667

Distance traveled foraging (m); $r^2 = 0.379$, $P < 0.001$[b]

Constant	-0.284	-0.421	0.676
current velocity (m/s)	4.882	3.979	< 0.001
current velocity^2 (m/s)	-6.572	-4.026	< 0.001
water depth (cm)	0.013	0.607	0.547
water temperature (°C)	-0.009	-0.334	0.740
fork length (cm)	1.253	2.707	0.010

Mean switching distance (cm); $r^2 = 0.508$, $P < 0.001$[b]

Constant	0.672	1.611	0.114
current velocity (m/s)	-0.700	-4.396	< 0.001
water depth (cm)	0.035	2.492	0.016
water temperature (°C)	0.039	2.362	0.023
fork length (cm)	0.381	1.306	0.198

Station switches (no./10 min); $r^2 = 0.205$, $P = 0.065$[b]

constant	-0.841	-0.557	0.581
current velocity (m/s)	7.256	2.640	0.011

current velocity^2 (m/s)	-7.940	-2.171	0.035
water depth (cm)	-0.023	-0.470	0.641
water temperature (°C)	0.048	0.831	0.411
fork length (cm)	-0.781	-0.753	0.456

Distance traveled switching (m); $r^2 = 0.126$, $P = 0.293$[b]

|			
Constant	-1.167	-0.778	0.441
current velocity (m/s)	5.745	2.105	0.041
current velocity^2 (m/s)	-6.861	-1.889	0.065
water depth (cm)	0.019	0.390	0.698
water temperature (°C)	0.079	1.385	0.173
fork length (cm)	-0.646	-0.628	0.533

[a] Mean foraging radius, No. of foraging attempts, distance traveled foraging, mean switching distance, No. of station switches, distance traveled switching, and fork length were all $\log_{10}$ transformed for this analysis. Current velocity and water depth were square-root transformed.

[b] Statistics for the complete model, with both significant and non-significant variables.

Fig. 3.1. Schematic representation of predicted links between various components of space use, and their key environmental determinants, current velocity, prey abundance and prey mobility. Typically, stream-dwelling salmonids vary from being sit-and-wait, central-place foragers (CPF) to cruising foragers. YOY Atlantic salmon, however, are exclusively sit-and-wait predators but vary from using one foraging station (CPF) to visiting multiple focal points (multiple central place foragers = MCPF). Note that the prediction about either an increase or decrease in behaviour are not necessarily linear; e.g., foraging rate is generally higher in faster waters, but levels off with increasing current velocity.

Behaviour

small ←———	Home range size	———→ large
one ←———	No. of foraging sites	———→ many
low ←———	Mobility	———→ high
high ←———	Foraging rate	———→ low
short ←———	Foraging radius	———→ long
low ←———	% Benthic foraging	———→ high
high ←———	Dominance rank	———→ low
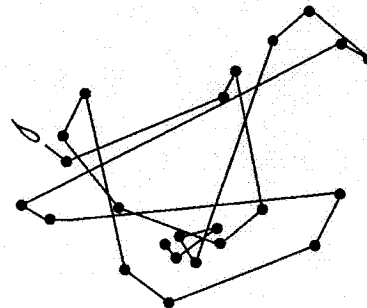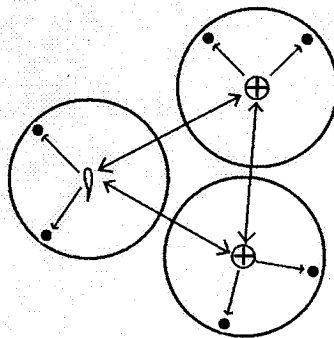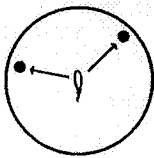
CPF   MCPF   Cruising

	Current velocity	
high ←——	Prey abundance	——→ low
	Prey mobility	

Environment

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Fig. 3.2. Variability in the local space-use patterns of YOY Atlantic salmon (*Salmo salar*). The wide solid line shows the 100% minimum convex polygon, which marks the boundary of the multiple-central-place territory, and is based on the location of all aggressive acts and foraging attempts (●), and the foraging stations visited (⊕). The upper row depicts (a) the smallest and (b) the largest territory, and (c) the frequency distribution of territory sizes. The second row depicts the individuals which traveled (d) least and (e) most (travel pattern = thin solid line), and (f) the frequency of the total distances traveled within the 50 home ranges.
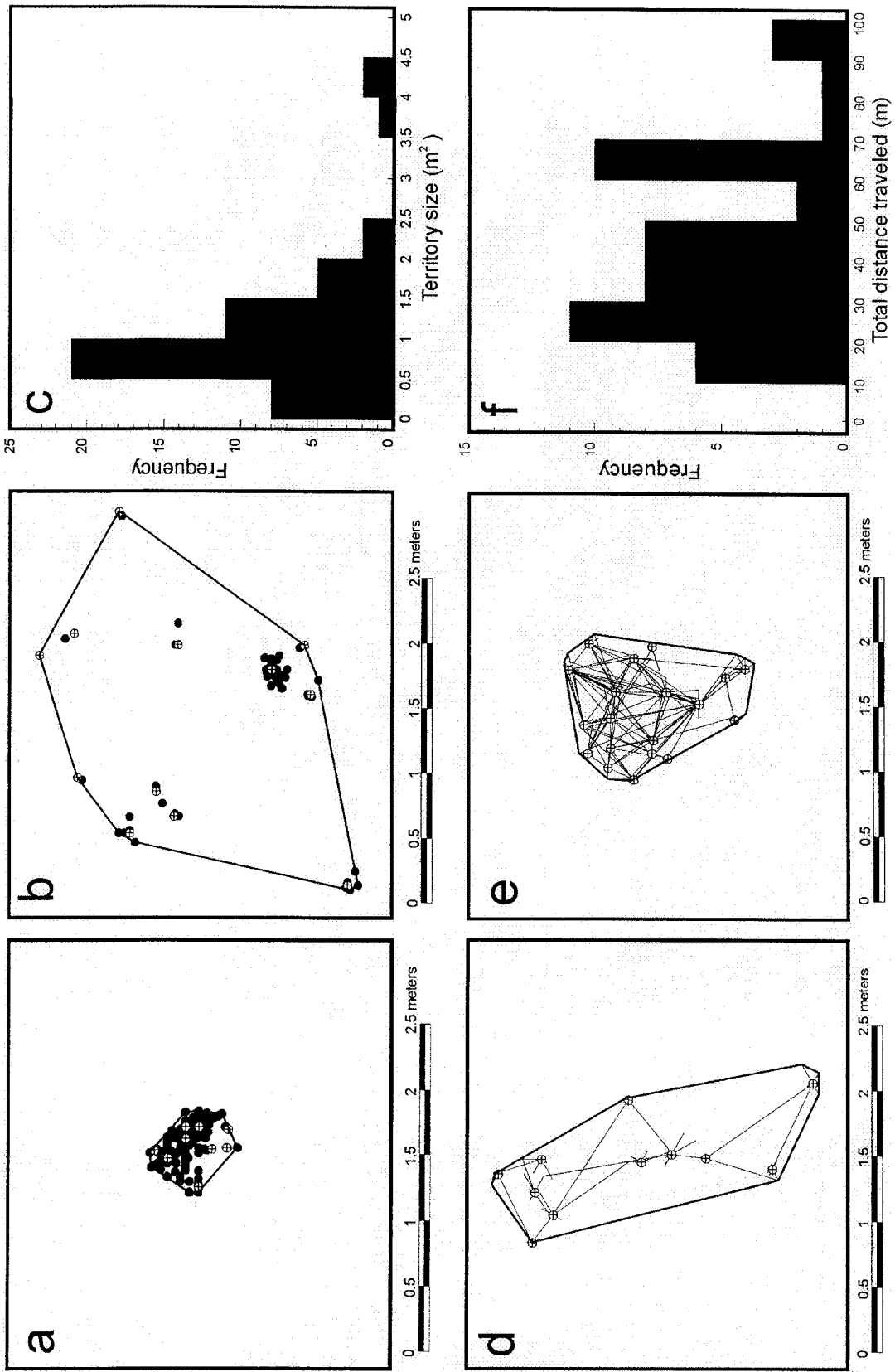
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Fig. 3.3. Individual variability in the total distance traveled within the territories of the 50

YOY Atlantic salmon (*Salmo salar*) in Catamaran Brook, New Brunswick. Each column

represents one fish (individuals 1-50), and indicates (a) the distance, and (b) the

percentage of the total distance, allocated toward switching between stations (grey),

foraging attempts (empty), aggression toward intruding fish (hatched), and fleeing from
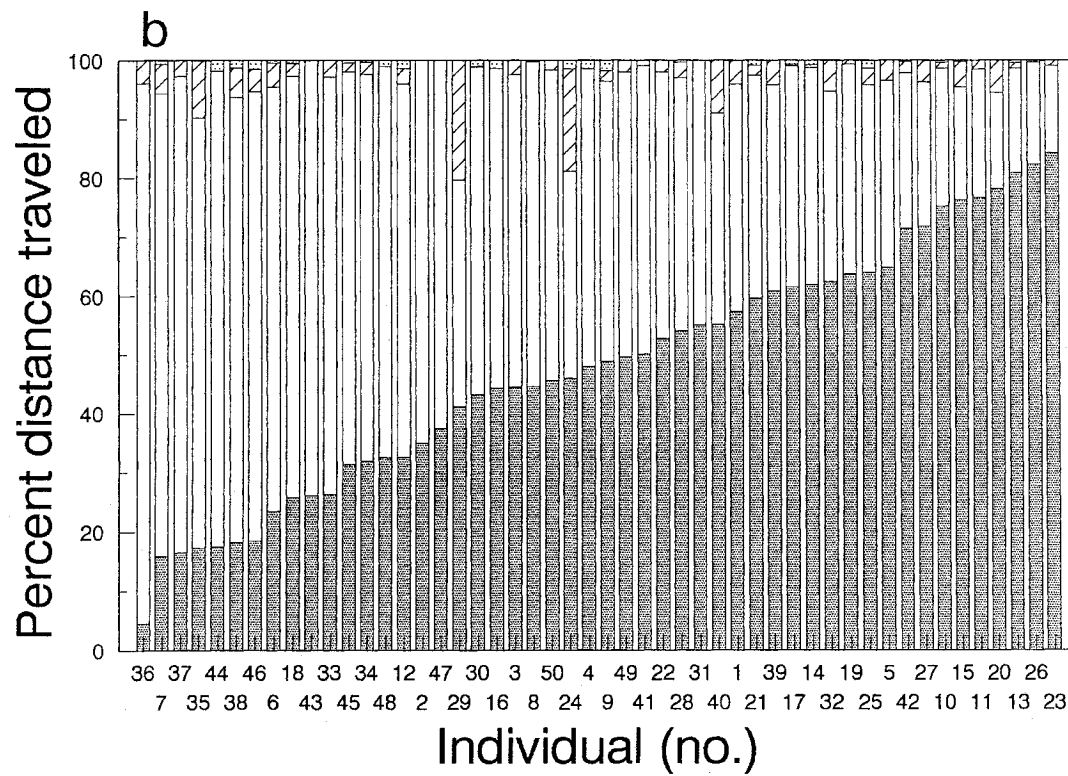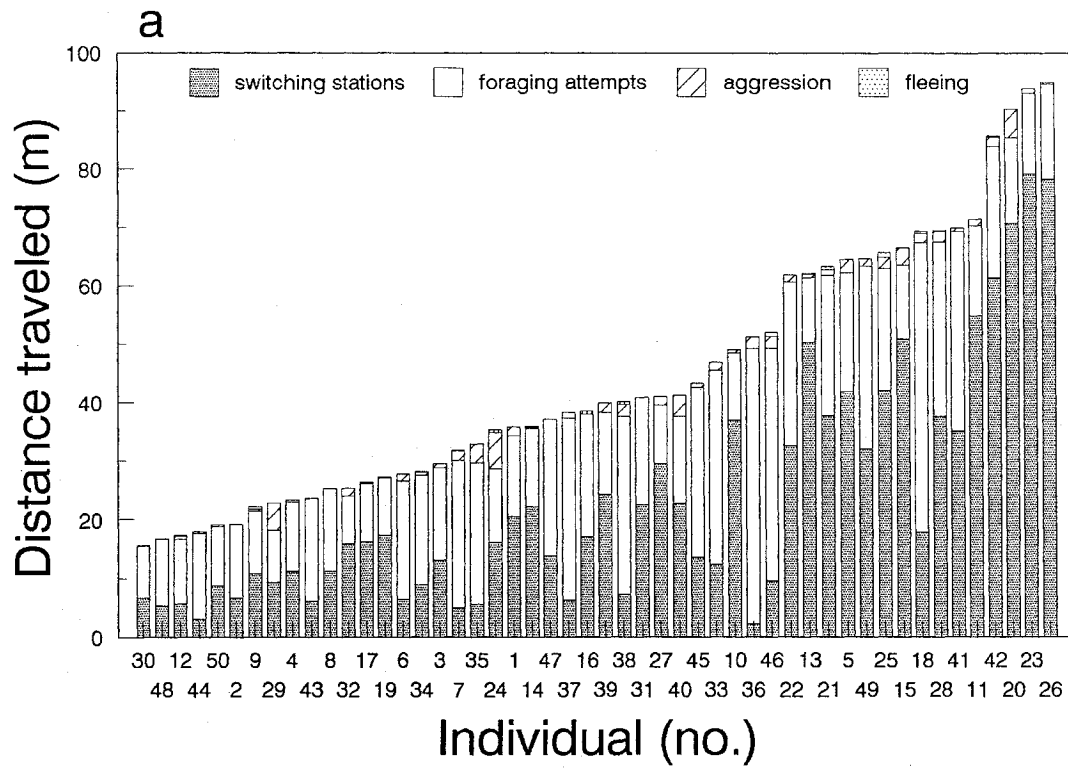
intruders (dotted).

Fig. 3.4. The effect of current velocity (a, b, c) and prey availability (d, e, f) on the territory size, the number of foraging stations visited, and the total distance traveled within territories of 50 young-of-the-year Atlantic salmon in Catamaran Brook, New Brunswick, Canada. The equations best describing these relationships are represented either by a solid (significant) or dashed line (not significant), and are as follows; (a) $\log_{10}$ territory size (m^2) = 0.301 - 0.886 current velocity$^{1/2}$ (m/s), r^2 = 0.119, P = 0.014; (b) foraging stations (no.) = 9.516 + 8.573 current velocity$^{1/2}$ (m/s), r^2 = 0.034, P = 0.202; (c) $\log_{10}$ total distance traveled (m) = 0.547 + 6.010 current velocity$^{1/2}$ - 7.907 current velocity (m/s), r^2 = 0.298, P < 0.001; (d) $\log_{10}$ territory size (m^2) = 0.190 - 0.045 drift rate$^{1/2}$ (no./net/20 min), r^2 = 0.096, P = 0.029; (e) foraging stations (no.) = 9.643 + 0.616 drift rate$^{1/2}$ (no./net/20 min), r^2 = 0.055, P = 0.099; (f) $\log_{10}$ total distance traveled (m) = 1.040 + 0.243 drift rate$^{1/2}$ - 0.023 drift rate (no./net/20 min), r^2 = 0.225, P = 0.003. For visual clarity, all $\log_{10}$- and square-root-transformed values on both axes were replaced with their original, back-transformed values. Note that all dependent variables were estimated over a span of 40 minutes, and that the area of drift net opening = 15.2 × 23 cm = 349.6 cm^2.

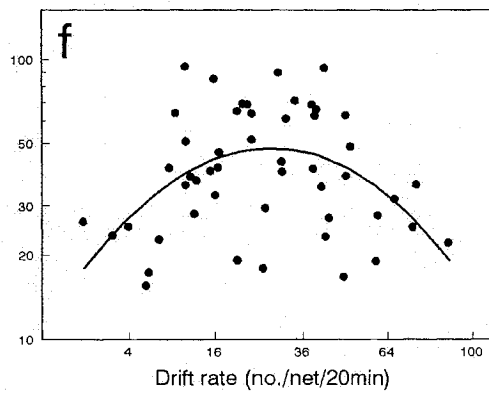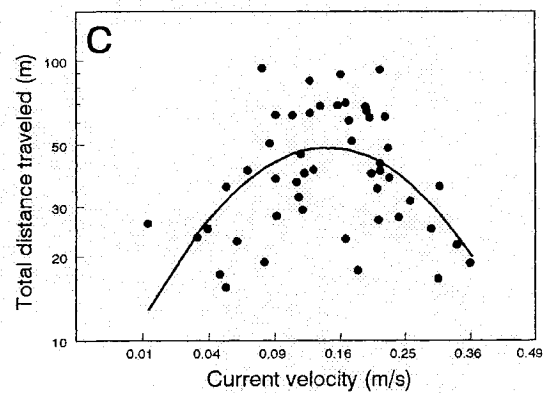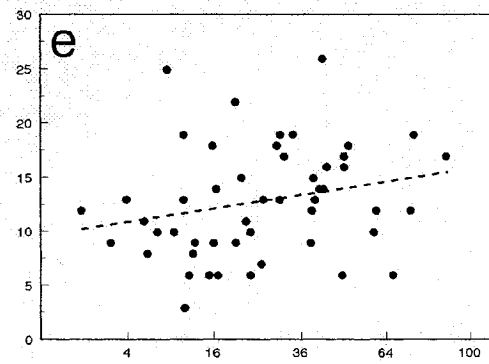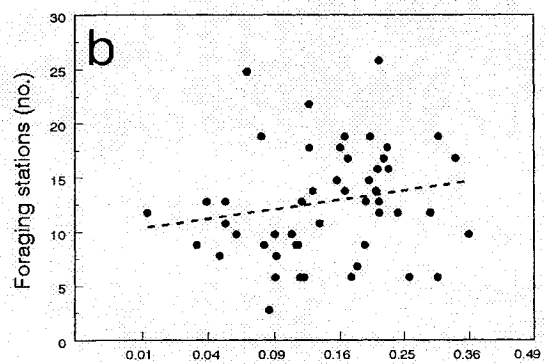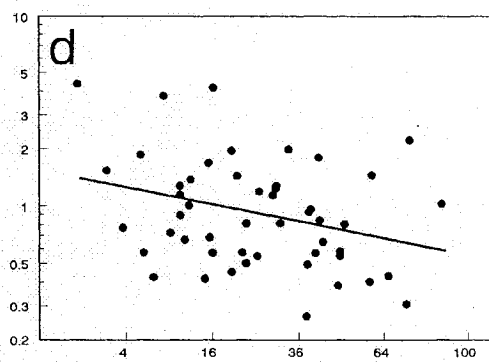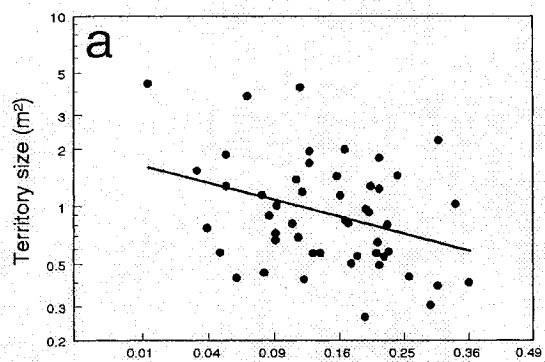**Fig. 3.5.** The influence of current velocity on foraging behaviour (a, b, c) and switching between foraging stations (d, e, f) of 50 young-of-the-year Atlantic salmon in Catamaran Brook, New Brunswick, Canada. The equations best describing these relationships are represented either by a solid (significant) or dashed line (not significant), and are as follows; (a) $\log_{10}$ mean foraging radius (cm) = 0.828 - 0.306 current velocity$^{1/2}$ (m/s), r^2 = 0.102, P = 0.023; (b) $\log_{10}$ foraging attempts (no./10 min) = 0.809 + 4.355 current velocity$^{1/2}$ - 5.359 current velocity (m/s), r^2 = 0.348, P < 0.001; (c) $\log_{10}$ distance traveled foraging (m/40 min) = 0.342 + 5.215 current velocity$^{1/2}$ - 6.928 current velocity (m/s), r^2 = 0.262, P < 0.001; (d) $\log_{10}$ mean switching distance (cm) = 1.916 - 0.804 current velocity$^{1/2}$ (m/s), r^2 = 0.370, P < 0.001; (e) $\log_{10}$ station switches (no./10 min) = -0.409 + 6.980 current velocity$^{1/2}$ - 7.966 current velocity (m/s), r^2 = 0.174, P = 0.011; (f) $\log_{10}$ distance traveled switching (m/40 min) = 0.251 + 5.323 current velocity$^{1/2}$ - 6.752 current velocity (m/s), r^2 = 0.078, P = 0.147.
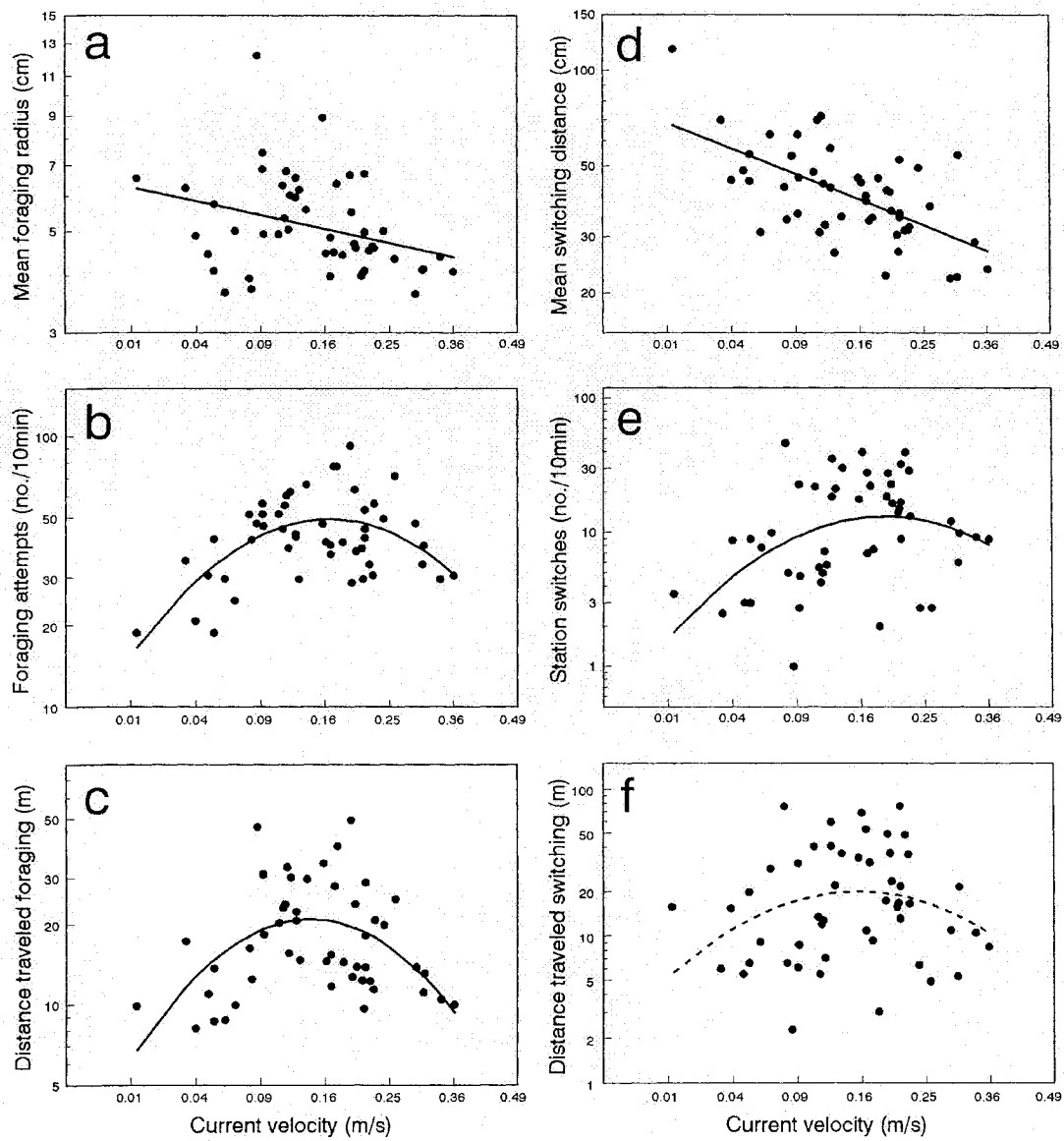
Fig. 3.6. The association between current velocity and (a) the number of aggressive acts directed toward intruding fish and (b) the growth rate of territorial YOY.Atlantic salmon in Catamaran Brook, New Brunswick, Canada. The equations best describing these relationship are depicted by a solid line, and are as follows; (a) $\log_{10}$ chase frequency (no.+1/40min) = -0.390 + 5.843 current velocity$^{1/2}$ - 8.189 current velocity (m/s), r^2 = 0.128, n = 50, P = 0.041 and (b) growth rate (mm/day) = 0.448 - 0.184 current velocity$^{1/2}$ (m/s), r^2 = 0.191, n = 38, P = 0.006. Growth rate is measured between snorkeling surveys conducted on 12-13 July and 20-23 August, 2000, and is thus only reported for fish caught on both occasions.
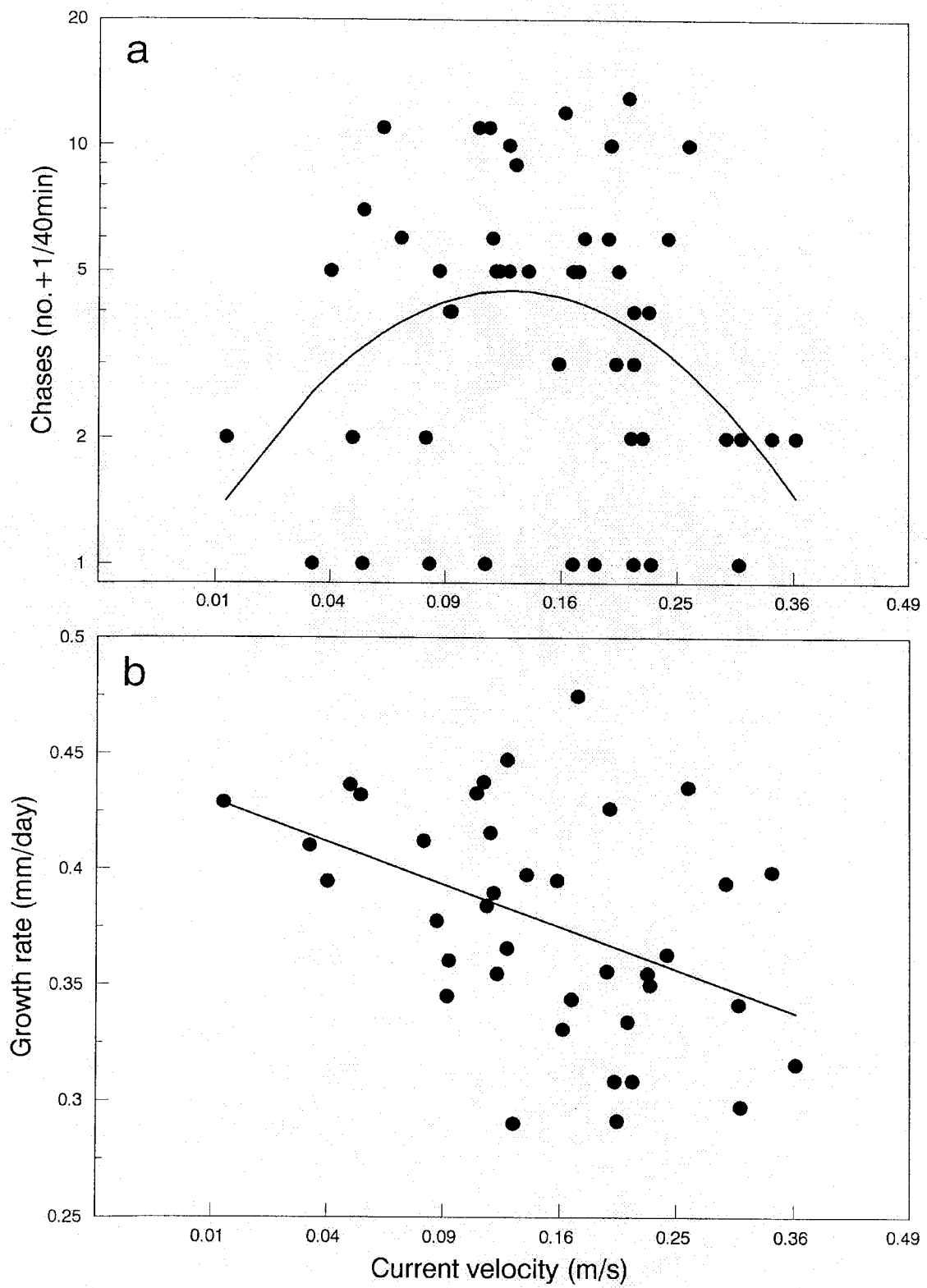
General Conclusions

Ecological processes and ecological studies vary tremendously in terms of their duration and spatial extent (Allen & Hoekstra 1992). Consequently, estimates of many important ecological variables, and space use and abundance in particular, depend largely on the scale over which they are measured (Lewontin & Levins 1989; Swihart & Slade 1985). Therefore, ideally, studies should be conducted at different temporal and spatial scales to recognize inconsistencies among scales (i.e. if different scales produce different answers to the same question) and, ultimately, to determine the scales appropriate for the ecological question of interest (Folt et al. 1998; Lewis et al. 1996; Ray & Hastings 1996).

Territoriality and foraging behaviour play an important role in the ecology of stream-dwelling salmonids, especially for YOY fish that have limited energetic reserves and frequently face intense competition for limited space (Chapman 1962; Elliott 1994). Although, to date, numerous studies exist on space use of YOY salmonids, this literature is limited to short observations of untagged individuals. The common theme of my Ph.D. thesis was to reexamine the patterns, causes and consequences of space use in YOY stream-dwelling salmonids by applying a tagging method which allows for the behaviour of small fish to be monitored on an individual basis over longer periods of time (i.e., at a different temporal scale) than previously possible in natural situations.

Chapter 1 revealed that most YOY Atlantic salmon show extremely restricted movement over their first growing season, independent of the spatial scale (10m, 45m, 120m) over which the movement is measured. This finding, coupled with an occasional fish that moved longer distances, resulted in movement curves that were much more

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leptokurtic than reported in previous studies on stream fish. In addition, movement and site fidelity of YOY salmon did not provide conclusive evidence for the hypotheses that movement in stream-dwelling salmonids is due to either ontogenetic changes in habitat preferences or competition for space. However, fish originally found in slow water did move slightly farther from their tagging location than fish from fast water, whereas fish found at high population densities were more likely to disappear than fish from low densities. Finally, mobile fish did not grow more slowly than more sedentary fish, supporting the idea that movement via the relocation of territories can be advantageous, and is not necessarily a result of subordinate individuals being unable to retain territories in good habitats and being forced into lower quality habitats.

Chapter 2 revealed that by mapping local space use of individuals for longer than previously possible, the daily territories of YOY Atlantic salmon are very different than typically reported in the salmonid literature. First, this chapter demonstrates that in the wild, YOY stream-dwelling salmonids may repeatedly visit many foraging stations within their territories and show limited fidelity to one particular station. Furthermore, when the territories are mapped around several stations, rather than just around a single station as is customary, territories of YOY Atlantic salmon are larger than previously established, they are not as circular in shape as thought earlier, they tend to be elongated along the stream length rather than the stream width, and although the tagged fish did not comply with the single-central-place territorial model and visited several stations within large territories, these areas still appeared to be fairly efficiently defended against other YOY salmonids. Finally, when put in context with earlier studies on territorial behaviour in YOY stream-

salmonids, it appears that the space use of YOY salmonids is highly related to population density. At high population densities, fish defend small territories from a single centrally-place foraging station, but at low density, fish use large territories and forage from several stations.

The YOY salmon examined in Chapter 2, remained sit-and-wait foragers, even though they traveled between several foraging stations within their territories. Chapter 3 revealed that these fish exhibited greater mobility than typically reported for sit-and-wait YOY salmonids, and that they allocated, on average, as much of the total distance they traveled within a territory toward switching between foraging stations, as they did darting for prey. Interestingly, mobility in these multiple central-place foragers was associated with current velocity, prey abundance and prey mobility in a different way than expected from salmonid species that exhibit both sit-and-wait and cruising foraging mode. Hence, instead of being most mobile in slow-running water, where drifting prey is less abundant and less mobile, YOY salmon were most mobile at intermediate, presumably optimal, current velocities. These findings, along with the fact that fish in slow water do not feed more on benthic prey than fish in fast water, may suggest that mobility in YOY Atlantic salmon reflects the patrolling of territories, rather than just the direct exploitation of other food resources than drifting prey.

Obviously, monitoring individually tagged animals over appropriate periods of time and over large enough areas provides valuable information on the consequences of space use at the population and individual level. For YOY salmonids, this study clearly demonstrates that our knowledge of many key aspects of space use may benefit from new

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techniques, which allow us to monitor individuals over longer periods of time, and in situation where behavioural observations have until now been difficult to obtain. Overall, this approach is likely, not only to bring us new insights on space use in stream-fish, but also to open up new possibilities for the continued use of stream-dwelling salmonids to test and advance general theories on territoriality and in ecology in general.

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