

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

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Abstract: The literature on stream fish movement offers diverse views on the patterns (restricted vs. nonrestricted), causes (competition vs. habitat use), and consequences (mobile fish of lower vs. equal fitness) of movement. We tagged 320 young-of-the-year Atlantic salmon (*Salmo salar*) (30.1–55.3 mm), using relatively noninvasive tagging (elastomers) and recovery (snorkeling) techniques, to test these alternative views. Most fish (mean = 63.8%) stayed in the study sites (10–120 m) throughout their respective study season (28–74 days). Of the resighted fish, 61.8% moved less than 1 m up- or down-stream and only three fish moved more than 10 m, causing extremely leptokurtic movement curves. Movement and site fidelity were weakly affected by habitat use and competition. Fish originally found in slow water moved farther 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 grew as fast or faster than more sedentary fish, supporting the idea that movement can be advantageous and is not just a by-product of density-dependent population regulation.

Résumé : La littérature scientifique sur les déplacements des poissons en eau courante fournit des perspectives diverses sur les structures (confinement vs. ouverture), les causes (compétition vs. utilisation de l'habitat) et les conséquences (poissons mobiles de fitness inférieur vs. fitness égal) des déplacements. Nous avons marqué 320 saumons de l'Atlantique (*Salmo salar*) de l'année et utilisé des techniques relativement inoffensives de marquage (élastomères) et de recapture (plongée en apnée) pour évaluer ces différentes perspectives. La plupart des poissons (moyenne = 63,8 %) sont demeurés aux sites d'étude (10–120 m) durant la durée de leur étude respective (28–74 jours). Parmi les poissons retracés, 61,8 % s'étaient déplacés de moins de 1 m vers l'amont ou vers l'aval et seulement trois poissons avaient parcouru plus de 10 m, ce qui a produit des courbes de déplacement à leptocurtose extrême. L'utilisation de l'habitat et la compétition affectent peu les déplacements et la fidélité au site. Les poissons trouvés au départ en eau lente se déplacent plus loin que les poissons provenant d'eau rapide; de même, les poissons originaires de sites à forte densité de population sont plus susceptibles de disparaître que les poissons de sites à faible densité. Enfin, les poissons mobiles croissent aussi rapidement, sinon plus rapidement, que les poissons sédentaires, ce qui laisse croire que les déplacements peuvent apporter des avantages et qu'ils ne sont pas seulement les résultats indirects d'un contrôle de la population relié à la densité.

[Traduit par la Rédaction]

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,

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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), and 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 into 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) and 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 noninvasive 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, and 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). The stream's main channel is about 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). 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). In 2000, movement was monitored within 10 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 single 45- 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). The study sites were selected to represent a wide range of habitats that also were accessible for snorkeling.

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). Fish were tagged at fork lengths between 30.1 and 55.3 mm (1998, 36.6–55.3 mm; 1999, 33.0–51.3 mm; 2000, 30.1–40.9 mm) 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 following eight 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 re-

Fig. 1. The location of the study sites in the lower reach of Catamaran Brook, New Brunswick, Canada. The inset 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 10 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 nontagging 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.

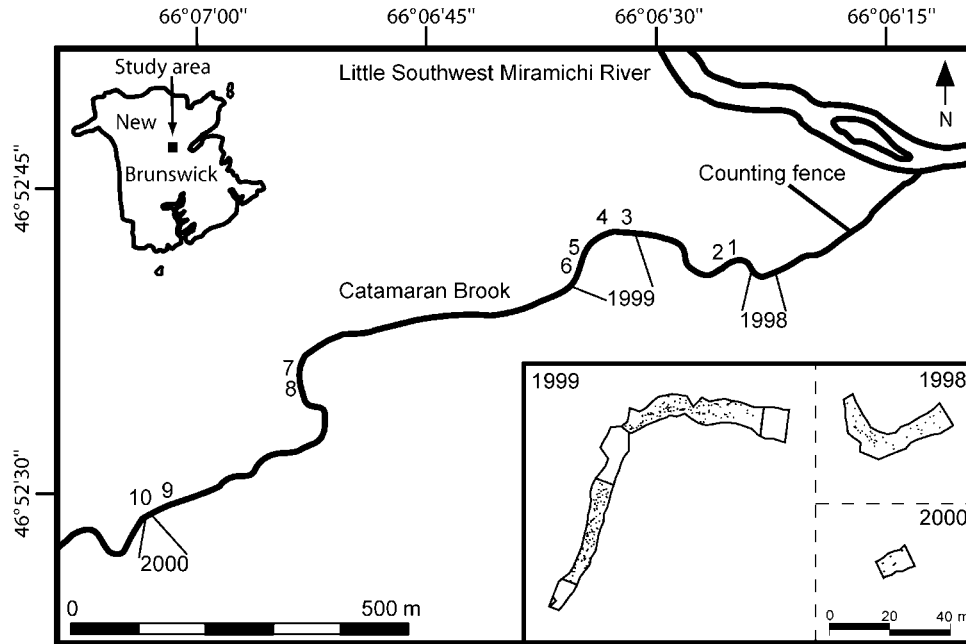


Table 1. Summary of the sampling effort and sampling methods used to monitor movement of young-of-the-year (YOY) Atlantic salmon in Catamaran Brook in 1998–2000.

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 m, 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 m, 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

^aTwenty-nine immigrants were tagged in 1999; no attempt was made to tag immigrants in 1998 and 2000.

^bThe 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) that each section of the respective study sites was visited (or sampled) during the survey.

capture any fish with fading tags were retagged to minimize tag loss. After fish had recovered from anaesthesia for 5–15 min, 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 recap-

tured 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). The surveys were categorized as (1) capture, (2) observation, and (3) electrofishing surveys (Table 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). 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). 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 1000 and 2200, with over 90% of observations between 1300 and 1900; 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- to 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, 14014 NE Salmon Creek Ave., Vancouver, WA 98686, U.S.A.), 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).

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 were then measured by extending a metre 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 with the location of each fish were created for each study site by transferring the data to ArcView GIS 3.2 software. The distance

that a fish moved between surveys was measured both as the up- and down-stream 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 with the average fork length of its four nearest neighbors ($\text{fork length}_{\text{focal fish}} / \text{fork length}_{\text{neighbors}} \times 100$). 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, 4539 Metropolitan Ct., Frederick, MD 21704, U.S.A.). 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 $(\text{Fork length}_{\text{final}} - \text{Fork length}_{\text{initial}}) \times (\text{Day of year}_{\text{final}} - \text{Day of year}_{\text{initial}})^{-1}$ (unit = mm·day⁻¹).

The total number of tagged fish in each survey was calculated as $N = N_{\text{found}} + N_{\text{not found}}$, where $N_{\text{not found}}$ 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

$$(1) \quad Z' = -\ln(N_t/N_0)/\Delta t$$

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 resighted 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 resighted 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 3) and the fact that we put 1.86 times more effort (13 vs. 7 days) into the initial survey compared with survey 3 (Table 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 resighted fish showed remarkably restricted movement; on average 61.8% of these fish moved less than 1 m up- or down-stream from their original tagging location, whereas 96.9% moved less than 5 m in either direction (Fig. 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. 2; Table 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 after 20 and 61 days, skewness was not detected ($P > 0.05$; Table 2). At 45 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 with 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 and 120 m, kurtosis ranged from 9.41 to 110.40 ($P < 0.001$; Table 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 2). The median displacement was low, ranging from only 0.86 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 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. 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. 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. 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 further 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 indica-

Fig. 2. Movement of YOY 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 days), respectively. Notice that even though the x axes range from -100 to 20 m, the probability of detecting a given movement distance decreases gradually in the upstream 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).

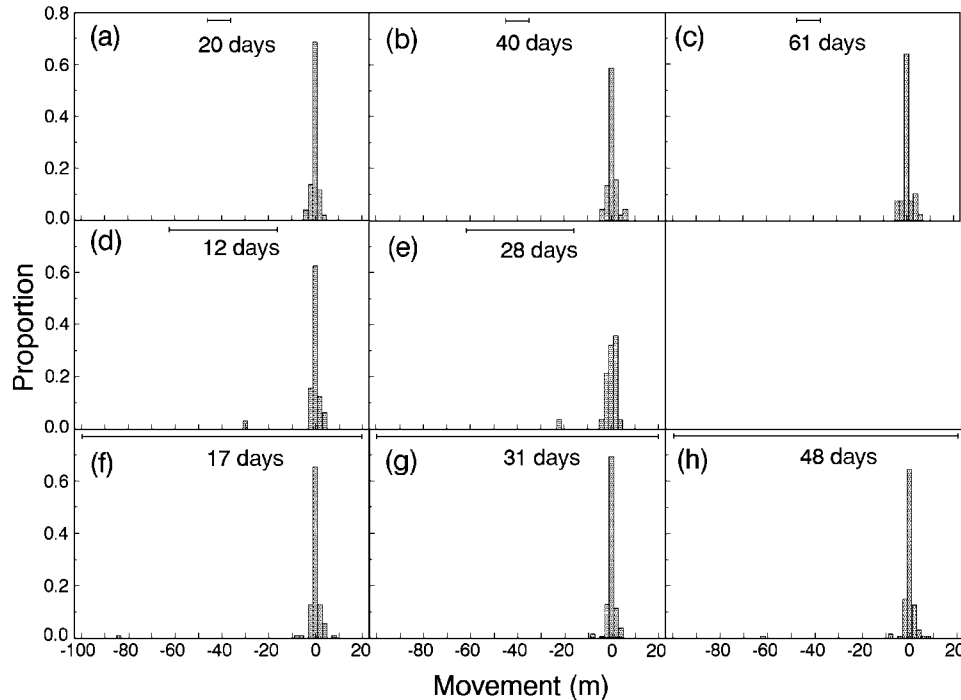


Table 2. Quantitative description of the movement patterns of YOY Atlantic salmon examined at three spatial scales.

Spatial scale (m)	Days from tagging	$N_{\text{found}}/N_{\text{not found}}^a$	Displacement (m)		Shape of curve ^b		
			Median	Maximum	Skewness (g_1)	Kurtosis (g_2)	
Year 2000							
10	20	51/2	0.86	4.22	-0.44ns	2.66***	
10	40	44/1	1.03	7.34	1.03**	3.31***	
10	61	39/1	1.17	6.50	0.67ns	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_{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.

^bSkewness (g_1) and kurtosis (g_2) were calculated and tested for normality using Sokal and Rohlf (1981). Significance level: ns, $P > 0.05$; *, $0.05 > P > 0.01$; **, $0.01 > P > 0.001$; ***, $P < 0.001$.

^cThe only curve that is not depicted in Fig. 2.

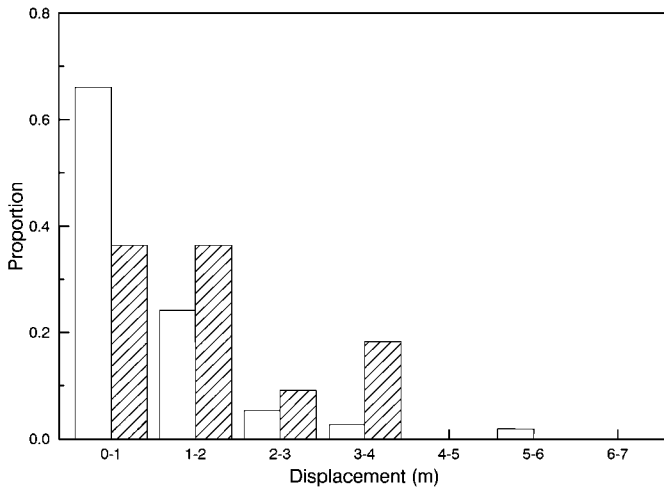
tor of the frequency of movement outside of the study sites, our data suggest, at least qualitatively, that the majority of the fish were lost to mortality rather than emigration.

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 current velocity (slope = -0.315, $r^2 =$

0.085, $P = 0.004$; Table 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 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 3). Fish

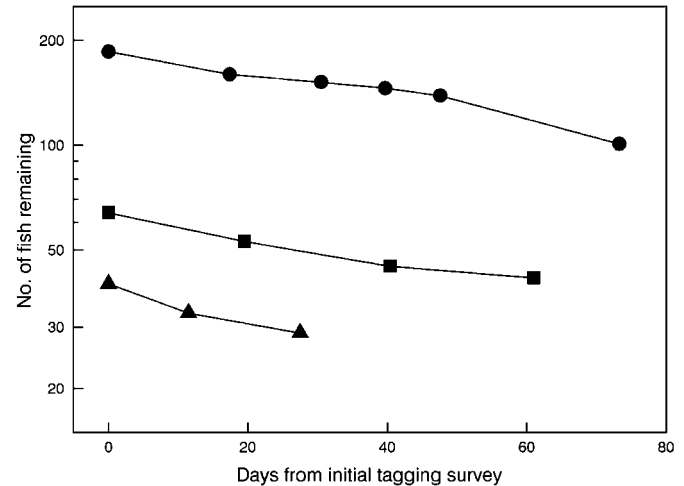
Fig. 3. The displacement of the original resident YOY Atlantic salmon (*Salmo salar*) (open bars, $n = 112$) and the early immigrants (hatched bars, $n = 22$) from mid-August to early September in 1999.



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. 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 $\text{mm}\cdot\text{day}^{-1}$ in the 1998, 1999, and 2000, respectively. In 1999, the study season 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 $\text{mm}\cdot\text{day}^{-1}$) than the original residents (mean = 0.237 $\text{mm}\cdot\text{day}^{-1}$) in the latter part of the 1999 season (t test on residual growth rate, $t = 2.65$, $df = 105$, $P = 0.009$; Fig. 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

Fig. 4. The retention of tagged YOY Atlantic salmon (*Salmo salar*) in the study sites during the three consecutive study seasons: 1998 (\blacktriangle), 1999 (\bullet), and 2000 (\blacksquare). 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 relabeled with the corresponding arithmetic values.



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; 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 resighted 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 are 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) 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 down-stream would have yielded many fish, especially

Table 3. Ecological correlates of seasonal displacement and site fidelity of YOY Atlantic salmon in Catamaran Brook in 1999.

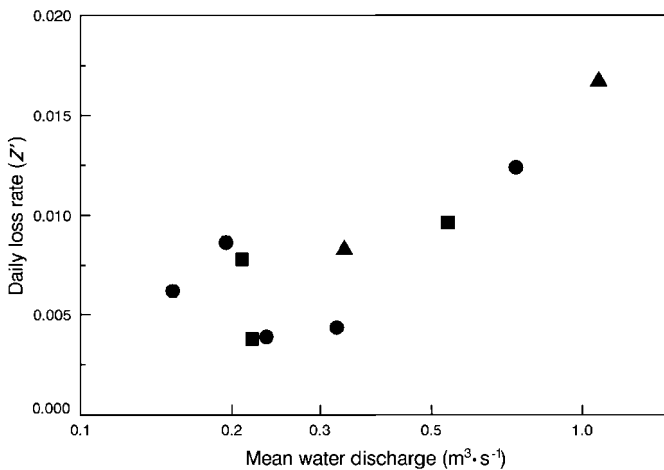
Predictor	Range (min., max.)	Displacement ^a			Site fidelity ^b		
		Slope	r^2	P	B	% correct	P
Population density (fish·m ⁻²)	0.08, 1.19	-0.001	0.000	0.994	1.430	62.57	0.032
Relative fork length (%)	-27.8, 28.2	-0.009	0.023	0.140	0.005	48.13	0.821
Current velocity (m·s ⁻¹)	0.00, 0.35	-0.315	0.085	0.004	0.202	51.34	0.638
Water depth (cm)	7, 79	0.066	0.001	0.768	-0.034	50.80	0.966

Note: min., minimum; max., maximum.

^aResults from a linear regression analysis; $n = 95$ in all four cases. Displacement, current velocity, and water depth were log₁₀ transformed for the analysis.

^bResults 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 ($n = 6$).

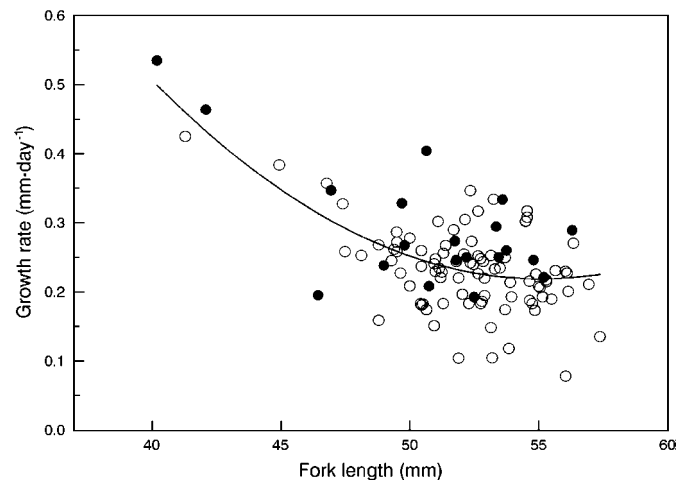
Fig. 5. The influence of water discharge in Catamaran Brook on the instantaneous daily loss rate (Z') calculated for tagged YOY Atlantic salmon (*Salmo salar*) in the study sites in 1998 (▲), 1999 (●), and 2000 (■). The Z' values are calculated based on the decline in the numbers of fish between each of the consecutive snorkeling surveys.



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 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 disappeared 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 noninvasive capture and release techniques. In previous studies, fish were often captured via invasive

Fig. 6. Growth rate of the original resident YOY Atlantic salmon (*Salmo salar*) (○) and the early immigrants (●) in Catamaran Brook in 1999. Growth rate for all fish was estimated from the time that 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⁻¹) = 4.050 - 0.139Fork length (mm) + 0.00126(Fork length²) (mm) ($r^2 = 0.404$, $n = 107$, $P < 0.001$).



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 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).

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