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**Foraging and Growth in Relation to Habitat Use of
Young-of-the-Year Atlantic Salmon (*Salmo salar*)**

Isabelle Girard

A Thesis

in

The Department

of

Biology

Presented in Partial Fulfilment of the Requirements

for the Degree of Master of Science at

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ABSTRACT

Foraging and Growth in Relation to Habitat Use of Young-of-the-Year Atlantic Salmon (*Salmo salar*)

Isabelle Girard

Using snorkeling observations, I examined the habitat use and preference of 216 individually tagged young-of-the-year Atlantic salmon in their first summer of life, using both a univariate and a multivariate approach. Habitat preference was determined by comparing the habitat used by fish to that available in the stream. The univariate analyses showed that salmon preferentially used a wide range of current velocity (6-48 cm·s⁻¹) and water depth (20-39 cm) and a narrower range of cover (complete cover from aerial predators) and substrate (pebbles). However, a multivariate logistic regression approach showed that only water depth and current velocity were key variables in habitat selection. Indeed, habitat preference of salmon increased with current velocity and water depth and then decreased at water depths above 30 cm. Drift rate within the stream was surveyed in order to predict food abundance for each fish in the study site. Correlates of fitness (i.e. foraging rate and growth rate) were also measured to relate individual fitness of each fish to their habitat choice. The results showed that y-o-y Atlantic salmon did not grow at a faster rate in the preferred habitats, despite the increase in food abundance and a higher foraging rate. I suggest that young-of-the-year salmon can grow reasonably well in a variety of habitat types and that the ideal free distribution may be a better description of their habitat use than the ideal despotic distribution.

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Introduction

A niche represents the range of environmental conditions that are required by an individual or species to survive and reproduce (Ricklefs & Miller 2000). Quantifying the ecological niche has been a fundamental part of ecology ever since Hutchinson (1957) redefined the niche as an “n-dimensional hyper-space”. A multivariate description of the niche has been attempted for a wide variety of organisms including bivalve molluscs (Green 1971), ground-dwelling animals (Krasnov & Shenbrot 1998), invertebrates in prairie wetlands (Zimmer et al. 2000) and birds (Gregory & Gaston 2000). Perhaps the greatest limitation of these descriptions is that they have been based primarily on presence versus absence data (e.g. Green 1971) rather than on a direct measure of fitness across a range of habitat types.

There has been a renewed interest in quantifying the niche with the recognition that the loss of habitat quantity and/or quality plays a major role in the extinction of species (Primack 1998). For example, Cornelius et al. (2000) found that habitat fragmentation drives many bird populations towards extinction. Habitat loss due to pollution or fundamental changes in channel morphology has also been implicated as the major factor causing the extinction or endangerment of freshwater fishes in North America (Meffe et al. 1997). A striking example is the current status of wild Atlantic salmon (*Salmo salar*) in native rivers throughout North America, which is best described by widespread declines and extirpation throughout most of its historical range. Many of these declines can be attributed to the construction of mainstream dams, pollution and dewatering of streams, as well as overfishing (Parrish et al. 1998; COSEWIC 2001).

The Atlantic salmon has attracted considerable research interest because of its cultural and economic value. As well, because of its low tolerance to environmental degradation, this species is a valuable indicator of environmental quality (Wilzbach et al. 1998). Not surprisingly, quantifying the freshwater niche of Atlantic salmon has attracted much effort. Most of the studies have concentrated on young-of-the-year salmonids because the abundance of a year class is thought to be predominantly determined by variability in first-year-survival (Elliott 1994).

Typically, the preferred habitat of juvenile Atlantic salmon has been described as riffles, shallow (<23 cm) and fast-flowing (>15 cm·s⁻¹) areas, with a gravel (2-16 mm), pebble (16-64 mm) or cobble (64-250 mm) substrate (DeGraaf & Bain 1986; Heggenes & Saltveit 1990; Gibson et al. 1993). However, juveniles may also use less typical habitats such as pools, deep (> 46 cm) and slow-flowing (< 15 cm·s⁻¹) areas, and flats, which are intermediate between riffles and pools (Gibson et al. 1993; Bremset & Berg 1999). As they grow, juveniles tend to shift towards deeper and faster waters over a coarser substrate (Symons & Heland 1978).

Habitat preference has been inferred by quantifying the habitat used by salmon in relation to the habitat that is available to them (DeGraaf & Bain 1986; Morantz et al. 1987; Gries & Juanes 1998; Nislow et al. 1999). The three most important variables are water column depth, current velocity and substrate size. For example, DeGraaf & Bain (1986) showed that young-of-year salmon preferred areas 17-45 cm deep, with currents of 9-45 cm·s⁻¹ over a sand (diameter = 0.062-2.0 mm), gravel and pebble (diameter = 2-64 mm) or cobble (diameter = 64-250 mm) substrate.

There are, however, a number of limitations to the previous descriptions of

juvenile salmon habitat use and preference. First, a multivariate approach is preferable to the univariate approach that has been used, because of the well-known correlation among many habitat variables in streams (Hynes 1970; Bardonnnet & Bagliniere 2000). Indeed, a univariate approach may not fully reflect the interdependence among the variables. This was demonstrated by Guay et al. (2000) who showed that a multivariate approach (i.e. multivariate logistic regression) was a better predictor of Atlantic salmon parr habitat selection, than a univariate approach (i.e. habitat suitability index). It is important to note that studies using a multivariate approach are relatively rare, in part due to the inherent complexity of the statistics involved (but see Heggenes & Saltveit 1990; Nakano & Kaeriyama 1995; Bremset & Berg 1999).

Second, the optimal habitat is identified by using the ratio of habitat use to habitat availability rather than by a direct measure of fitness across habitat types (e.g. Morantz et al. 1987). Nislow et al. (1998) is a rare exception; they showed that fish occupying faster current velocities experienced a greater food abundance, leading to higher foraging rates and greater first-year survival. Unfortunately, they did not measure the growth rate of fish.

Third, previous studies have not dealt with differences between individuals even though individual salmon differ markedly in their mobility and habitat use (Armstrong et al. 1999). Unfortunately, few studies have individually tagged juvenile salmon in order to follow them in natural conditions, primarily because of the difficulty in tagging small individuals (Dewey & Zigler 1996; but see Einum & Fleming 2000).

Finally, previous studies have described the habitat use for separate age classes of salmon, but ignored the important variation that could potentially occur within an age class. Some studies even combine age classes when describing the habitat used by

juvenile salmon (e.g. Heggenes & Saltveit 1990). As well, most studies do not show how habitat preference may vary over a growing season. Therefore, there has been no detailed study of the gradual change in habitat use and preference within a single age class of Atlantic salmon.

My goal was to describe the gradual change in habitat use of young-of-the-year Atlantic salmon (hereafter, y-o-y salmon) during their first summer of life in relation to likely correlates of their individual fitness. Preferred habitat was quantified by the ratio of habitat use to availability using a multivariate logistic regression. Individual foraging and growth rates were used as correlates of fitness, and measured by repeatedly monitoring tagged individuals. Food abundance was also measured in order to link habitat use and food abundance to the rate of foraging and growth.

Materials and methods

Study site and species

I collected data at Catamaran Brook, a third order tributary of the Little Southwest Miramichi River (46°52.7' N, 66°06.0' W) in central New Brunswick, Canada. This stream has a large population of anadromous Atlantic salmon (*Salmo salar*) and is relatively unaffected by human activity (Cunjak et al. 1990). Adult Atlantic salmon return to spawn in the river between late September and early November, lay their eggs in gravel nests, and then emigrate from the stream (Cunjak et al. 1993). Y-o-y salmon emerge from these nests the following June, at about 2.6 cm in length, and remain in the stream for 2-3 years, actively feeding in the water column until they emigrate to sea (Randall 1982; Cunjak et al. 1993; Keeley & Grant 1995). Fifteen other species of fish are also found in

the watershed, including brook trout (*Salvelinus fontinalis*), blacknose dace (*Rhinichthys atratulus*) and white sucker (*Catostomus commersoni*) (Cunjak et al. 1993). For a more detailed description of the stream, see Cunjak et al. (1990, 1993), Keeley & Grant (1995, 1997) and Steingrímsson & Grant (1999).

Total watershed area is about 50 km² and contains a wide range of habitat-types: flats, shallow (< 46 cm) and slow-flowing (< 15 cm·s⁻¹); runs, deep (> 23 cm) and fast-flowing (> 15 cm·s⁻¹); riffles, shallow (< 23 cm) and fast-flowing (> 15 cm·s⁻¹); and pools, deep (> 46 cm) and slow-flowing (< 15 cm·s⁻¹) habitats (Cunjak et al. 1993; Gibson et al. 1993). Five study sites were chosen in the 750 m reach immediately upstream from the mouth of the brook, based on two criteria: the combined sites included all four habitat-types, and the sites were all located within a 110 m reach in order to detect habitat shifts in individuals that moved between sites. On average the sites were 16.25 m ± 0.97 (range = 15-20 m) in length and 5.88 m ± 0.26 (range = 3.30-9.20 m) in width (Fig. 1). All sites were repeatedly sampled from 2 July to 4 September 1999 to obtain measurements of the habitat used by and available for the tagged individuals within the sites (Table 1).

Habitat availability

The habitat available for y-o-y salmon was assessed at each site in early (24 July), middle (21-22 August) and late (3 September 1999) summer, yielding 3 rounds of habitat availability (Table 1). Within each site, transects were established perpendicular to the current at 2.5 m intervals, using a 30 m long measuring tape. At 1-m intervals along each transect, measurements of current velocity, water depth, substrate size and the degree of overhead cover were obtained. A portable Marsh-McBirney meter (Model 201D) was

used to measure current velocity ($\pm 0.5 \text{ cm}\cdot\text{s}^{-1}$) at the bottom (2 cm above the substrate following DeGraaf & Bain, 1986), at the mean distance of the fish's "nose" above the substrate, while holding position in the water column at a particular site and time (see "habitat use" below), and at 40 % of the water column depth (i.e. mean water column velocity, Hynes 1970; hereafter, mean current velocity). A meter stick and a 30-m long measuring tape were used to measure water depth ($\pm 0.5 \text{ cm}$) and distance from shore ($\pm 2.5 \text{ cm}$), respectively. Cover was estimated visually from approximately 30 cm above the water surface and categorized as: 0 = none (fish is fully visible), 1 = partial (fish is partly visible), or 2 = complete (fish is not visible). Water temperature was measured in each site on all three sampling occasions (early, middle and late), using a hand-held thermometer at a haphazard location ($\pm 0.25^\circ\text{C}$). Substrate size was measured only once, early in the summer (2 July), as it does not vary significantly over the season (DeGraaf & Bain 1986; Morantz et al. 1987). At 1-m intervals along the transect, the dominant substrate along a 10-cm line (i.e. 5 cm left and right of each 1-m mark on the measuring tape) was visually estimated and subsequently coded from 1 to 7 using a modified Wentworth scale of particle size similar to the one used by DeGraaf & Bain (1986) (Table 2).

Tagging individuals and measurements of length and mass

All visible y-o-y salmon in each site were marked from 6-27 July 1999. A few individuals may have avoided capture if they rarely came out of hiding. A total of 193 fish were captured, using two dipnets and by repeatedly snorkeling through each site. Five fish were caught at a time and placed in buckets containing stream water. Each individual was then anesthetized in a mixture of 3-4 drops of clove oil and approximately 800 ml of

water (Keene et al. 1998), and tagged using a 1-cc hypodermic syringe containing fluorescent elastomer paint (Dewey & Zigler 1996).

Individuals were marked using 1-2 colors out of 3 (red, green and orange), at 2 out of 8 possible locations on the fish (Fig. 2), creating a distinctive tag for each individual. Immediately after tagging, the fork length (± 0.025 mm) of each individual was measured using a caliper. The fish were allowed to recover in a bucket of water for 5-10 minutes, and then released within 0.5 m of their original location of capture. Between 10-19 August 1999, 160 tagged individuals and 29 new individuals, were retagged or tagged using the same procedure as above. Immediately after tagging, individuals were measured for fork length and mass (± 0.005 g) using a lightweight portable scale, before being released within 0.5 m of their location of capture. A total of 6 individuals out of the 222 tagged (2.7 %) during the summer, did not survive the tagging process. All individuals caught during an electrofishing sweep of all sites between 21-30 September 1999 were measured for fork length and mass.

Habitat use

For each of five rounds of habitat use measurements, tagged fish were found by repeatedly snorkeling through each of the five sites until no new fish was located in the last two runs through each site. Each site was consequently sampled about 10 times per round to ensure a good capture efficiency, as up to 45% of y-o-y salmon may be found sheltering during the day, in summer (Gries & Juanes, 1998). Once a fish was identified, the location where it was first observed that day was marked with a numbered flag buried in the substrate. The distance of the fish's "nose" above the substrate while holding position in the water column was estimated visually and recorded, as well as the time of

day. Water temperature was measured arbitrarily, once every 30 minutes, in each site while fish were being identified.

Once all visible individuals were found, current velocity (bottom, “nose” and mean), water depth, distance from shore, and cover were measured for each numbered flag, using the same method described for habitat availability (see above). Substrate size was estimated visually in a 100 cm² quadrat around each flag and coded using the same method as above.

Sampling all sites took between 5-14 days, and yielded five rounds of habitat use measurements for each site (Table 1).

Food abundance

After each of the five rounds of habitat measurements, a drift sample was taken to assess the food available for the fish in each site, and whether food abundance affected their habitat selection. Benthic samples were not taken, as most of the foraging attempts are directed at drifting invertebrates present in the water column, and less than 1% of all foraging attempts are directed towards the benthos or the surface of the water column (Keeley & Grant 1995). A 1-m long drift net with an opening of 15.2 × 23 cm and a 300 μm mesh size was used to obtain 25 drift samples (i.e. 5 rounds * 5 sites). This net is effective since it maintains a laminar flow at the mouth of the net and prevents back-washing (Field-Dodgson 1985). For each of these five sampling rounds, the drift nets were alternated between a slow current station (range: 2-8 cm·s⁻¹) and a fast current station within each site (range: 5-58 cm·s⁻¹). To obtain an adequate sample, the drift nets were left longer in slow current areas (\bar{x} = 99 min) than in fast current areas (\bar{x} = 61.5 min). Immediately before each drift sample, the following measurements were taken

directly in front of the drift net: bottom, “nose” (i.e. mean height above the substrate of all fish measured in each site and in each round) and mean current velocity, current velocity at ½ of drift net height (i.e. 12 cm), water temperature and water depth, using the methods as described for habitat availability. Time of day was taken at the beginning and at the end of each drift sample.

All drift samples were preserved in 10 % buffered formalin and sorted back at Concordia University, once the field season was over. Each sample was processed by removing inedible material such as insect exuviae and plant material. Food items that were considered much too big for y-o-y salmon to eat (i.e. > 5 mm in length; Keeley & Grant 1997) were also removed from the sample before counting the number of food items. The drift rate at each station and date was expressed as the number of organisms per 20 minutes. When water depth was less than the depth of the net (23 cm), this rate was prorated to the area of the drift net opening ($15.2 \times 23 \text{ cm} = 349.6 \text{ cm}^2$).

Foraging rate

The foraging rate of 43 individuals was measured on 26-27 August 1999 between 15:00 and 19:30, as fish are most active in the afternoon (Nislow et al. 1998). Once a tagged individual was located via snorkeling, the tag of the fish was noted and the fish was allowed to acclimate to the observer’s presence (i.e. downstream of the fish), for five minutes before any measures were taken (Heggenes & Saltveit 1990; McLaughlin et al. 1994). Each individual was then observed for 10 minutes to count the number of foraging attempts, i.e. rapid movements towards a potential food item (Grant & Noakes 1987).

Statistical analysis

In order to meet the assumptions of parametric testing, current velocity, water depth, number of organisms·20 min⁻¹ and foraging rate were log₁₀ transformed before analyses. In a few areas of the stream, the current velocity meter did not detect any current (i.e. 0.0 cm·s⁻¹); these were scored as 0.5 cm·s⁻¹ to facilitate the log₁₀ transformation.

An index of habitat preference was created by plotting frequency distributions of the habitat used by salmon versus the habitat available in the stream. Goodness of fit tests (Sokal & Rohlf 1995) were used to test for overall differences between the distributions of use and availability for each variable. Chi-squares tests identified significant differences between use and availability for each category of the variable. Habitat preference was defined as a significant overuse of a category whereas habitat avoidance was defined as a significant under use of a category.

Guay et al. (2000) concluded that a multivariate approach may be more powerful than a univariate approach for predicting local variations in fish density. Therefore, I used multivariate logistic regression analysis to determine the key variables that distinguished between used and available habitat in early, middle and late summer. The probability that y-o-y salmon used a habitat was then plotted to show the relative importance of each variable, throughout the summer. A probability of 1.0 was not expected as the used habitat is a subset of the available habitat. Measures of used habitat versus unused habitat would, potentially, have yielded a probability of 1.0.

Individual growth rate was calculated as: (final- initial fork length) / (final- initial date of fork length measure). Because fork length was measured in three separate rounds (Table 1), two measures of growth rate were calculated: early in the summer (i.e. between

rounds 1 and 3) and late in the summer (i.e. between round 3 and electrofishing).

Results

Out of the 216 y-o-y salmon measured, 86.6 % of them were relocated sometime throughout the summer. Specifically, 68.6%, 86.2 %, 89.5% and 78.0% of fish, for which habitat use was measured, were relocated in rounds 2, 3, 4, and 5, respectively. This percentage was based on the efficiency of recapture, and was calculated as: number of tagged fish found in round (x) / number of fish found in round (x+1) + number of fish not found in round (x+1), but found in a later round. In reality, 90.1% of fish were relocated in round 5, but due to bad weather, habitat use measurements were obtained for only 128 out of the 149 fish.

Habitat availability

The average current velocity available in the stream changed significantly over the summer (Table 3). All three current velocity measurements increased from early to mid-summer, and then decreased until late summer. The average water column depth available in the stream also changed significantly over the summer, and showed the same seasonal patterns as current velocity.

The average discharge of the stream during the study period (2 July-4 Sept. 1999) was only $0.1215 \text{ m}^3 \cdot \text{s}^{-1}$, the third lowest of the last 10 years (D. Cassie, Department of Fisheries and Oceans, P.O. Box 5030, Moncton, N.B., E1C 9B6, unpublished data). Hence, current velocities and water depths in 1999 were lower than average. The dominant substrate available in the stream was pebble (16-64 mm), while the predominant cover was a partial or complete cover (Table 3).

Habitat use

The average current velocity used by y-o-y salmon changed significantly over the summer (Table 4). All three current velocity measurements increased from early to mid-summer and then decreased until late summer. The average water column depth used by fish in the stream also changed significantly over the summer, exhibiting the same seasonal patterns as current velocity.

The dominant substrate size used by fish, namely pebble, did not change significantly over the summer. The dominant cover used by fish changed significantly over the summer ($X^2 = 14.52$, $df = 4$, $P < 0.01$), but because cover was grouped into only three categories, fish always favored a complete cover (Table 4).

Univariate analysis of habitat preference

My three measures of current velocity (i.e. bottom, “nose” and mean) were highly inter-correlated, both for the habitat used by fish (r 's > 0.58 ; $n = 737$, P 's $\ll 0.001$) and available in the stream (r 's > 0.81 ; $n = 603$, P 's $\ll 0.001$). Also, a multivariate analysis (shown below) showed that the mean current velocity was the most important of the three in distinguishing between what y-o-y were using and what was available for them. Consequently, I present data only for mean current velocity.

Y-o-y generally avoided slow currents ($< 3 \text{ cm}\cdot\text{s}^{-1}$) and seemed to prefer moderate currents ($> 6 \text{ cm}\cdot\text{s}^{-1}$) (Fig. 3). The distribution of current velocities used by fish differed significantly from that available to them in early, middle and late summer (Goodness of fit tests: early: $X^2 = 112.61$, $df = 5$, $P \ll 0.001$; middle: $X^2 = 110.39$, $df = 5$, $P \ll 0.001$; late: $X^2 = 105.41$, $df = 5$, $P \ll 0.001$). Early (Fig. 3a) and late (Fig. 3c) in the summer, fish significantly preferred current velocities between $6\text{-}24 \text{ cm}\cdot\text{s}^{-1}$, and significantly

avoided current velocities below $1.5 \text{ cm}\cdot\text{s}^{-1}$ (Chi-square tests: $df = 1$, P 's < 0.005). In mid-summer (Fig. 3b), y-o-y significantly preferred current velocities between $12 - 48 \text{ cm}\cdot\text{s}^{-1}$, and significantly avoided current velocities below $3 \text{ cm}\cdot\text{s}^{-1}$. Y-o-y salmon were always found less often than expected in currents velocities greater than $48 \text{ cm}\cdot\text{s}^{-1}$.

The distribution of water column depths used by fish differed significantly from that available to them in all three time periods (Goodness of fit tests: early: $\chi^2 = 101.22$, $df = 7$, $P \ll 0.001$; middle: $\chi^2 = 173.58$, $df = 7$, $P \ll 0.001$; late: $\chi^2 = 133.53$, $df = 7$, $P \ll 0.001$) (Fig. 4). Early (Fig. 4a) and late (Fig. 4c) in the summer, y-o-y salmon significantly preferred water depths between 20-39 cm, and avoided water depths below 12 cm (Chi-square tests: $df = 1$, P 's < 0.005). In mid-summer (Fig. 4b), water depths between 26-31 cm were significantly preferred whereas water depths below 15 cm were significantly avoided.

Because the availability of substrate and cover were measured only once during the summer, the use of all three time periods were combined and then compared with availability. The distribution of substrate and cover used by fish differed significantly from that available to them in the summer of 1999 (Goodness of fit tests: substrate: $\chi^2 = 60.31$, $df = 3$, $P \ll 0.001$; cover: $\chi^2 = 25.12$, $df = 2$, $P \ll 0.001$). Fish significantly preferred a pebble substrate, and significantly avoided boulders and substrate smaller than gravel (Chi-square tests: $df = 1$, P 's < 0.01) (Fig. 5a). As well, y-o-y salmon significantly preferred a complete cover, and significantly avoided areas with a partial cover (Chi-square tests: $df = 1$, P 's < 0.01) (Fig. 5b).

Multivariate analysis of habitat preference

A forward stepwise multivariate logistic regression was used to identify the key

habitat variables that best predicted the habitat used by salmon versus the habitat available in the stream over the summer. A multivariate logistic regression was performed on each time period separately to explore differences over time. In addition, the statistical significance of all variables raised to a power of up to 2, as well as all interactions terms were assessed. Only two key variables contributed significantly to the model for each time period: mean current velocity and water column depth (early: $X^2 = 89.94$, $df = 3$, $P \ll 0.001$, 67.2 % correct classification, Fig. 6a; middle: $X^2 = 126.60$, $df = 3$, $P \ll 0.001$, 74.7 % correct classification, Fig. 6b; late summer: $X^2 = 115.27$, $df = 3$, $P \ll 0.001$, 74.1 % correct classification, Fig. 6c). Current velocity and water depth alone, explained 27.3, 38.8 and 40.9 % of y-o-y habitat choice in early, middle and late summer respectively. Habitat preference, of y-o-y salmon, was consistent throughout the summer; probability of y-o-y using a habitat increased with current velocity and water depth until a water depth of about 30 cm, at which time probability of use decreased with increasing water depth (Fig. 6).

The probability of y-o-y using a particular habitat was used subsequently as a multivariate index of habitat preference to test for the fitness consequence of habitat choice (i.e. relationship between habitat preference and food abundance, foraging rate and growth rate).

Food abundance

The number of organisms captured in a drift net ($\bar{x} \pm SE = 42.32 \pm 11.11$, range 4-186) was positively correlated to current velocity (*partial r* = 0.93, $n = 21$, $P \ll 0.001$) and negatively correlated to water depth (*partial r* = -0.45, $n = 21$, $P < 0.05$) and Julian date (*partial r* = -0.60, $n = 21$, $P < 0.005$). When all three variables were included in a

stepwise multiple regression, food abundance in the stream at one time was best predicted by: \log_{10} number of organisms \cdot 20 minutes $^{-1}$ = 1.38 \log_{10} current velocity (m \cdot s $^{-1}$) - 0.0083 Julian date -0.94 water depth (cm) + 5.48 (r^2 = 0.96, n = 25, P << 0.001). This model was then used to predict the number of organisms flowing through the width of a drift net (15.2 cm) for the location of each fish in the stream in early (6-23 July), middle (10-20 August) and late (30 Aug.-2 Sept.) summer. The predicted drift rate was then prorated to the height of the water column experienced by each fish in each time period. This measure of food availability was then compared to the multivariate habitat preference for fish in early, middle and late summer.

Over the summer, food abundance was always positively correlated to the probability of y-o-y using a habitat (early: r = 0.83, n = 193, P << 0.001; middle: r = 0.84, n = 160, P << 0.001; late summer: r = 0.75, n = 126, P << 0.001). The regression model that best described food abundance was: early, Log_{10} number of organisms \cdot 20 minutes $^{-1}$ = 3.17 probability of y-o-y using a habitat in early summer - 0.97 (r^2 = 0.69, n = 193, P << 0.001, Fig. 7a; middle, Log_{10} number of organisms \cdot 20 minutes $^{-1}$ = 2.37 probability of y-o-y using a habitat in mid-summer - 0.40 (r^2 = 0.71, n = 160, P << 0.001, Fig. 7b; and late summer, Log_{10} number of organisms \cdot 20 minutes $^{-1}$ = 2.031 probability of y-o-y using a habitat in late summer - 0.66 (r^2 = 0.57, n = 126, P << 0.001, Fig. 7c). Throughout the summer, more food was available for fish in the preferred habitats.

Correlates of Fitness

Foraging

Foraging rate of fish ($\bar{x} \pm \text{SE} = 3.22 \pm 0.27$, range = 0.80-10.10 attempts \cdot min $^{-1}$) increased with current velocity (Ancova: $F = 8.93$, $df = 1,39$, $P < 0.005$) and was highest

when fish experienced a partial cover (Ancova: $F = 4.00$, $df = 2,39$, $P < 0.05$; Fig. 8). Current velocity and cover combined, explained 37.4 % of the variation in foraging rate. Foraging rate was not correlated to any other habitat variable (*partial r*'s < 0.28 , *n*'s = 43, *P*'s > 0.05).

Foraging rate was compared to early and late summer growth separately (see below). Foraging rate was negatively correlated with late summer growth ($r = -0.48$, $n = 28$, $P < 0.01$), but was uncorrelated with early summer growth rate ($r = -0.21$, $n = 42$, $P = 0.18$). It was probably not surprising that foraging rate was not correlated with growth rate early in the summer, because foraging rate was measured only in late summer (i.e. 26-27 August).

Foraging rate was positively correlated to the probability of y-o-y using a habitat ($r = 0.44$, $n = 43$, $P < 0.005$). The regression model that best described the relationship was: Log_{10} foraging rate (attempts \cdot min. $^{-1}$) = $0.646 \cdot$ average probability of y-o-y using a habitat (between middle and late summer) + 0.056 ($r^2 = 0.20$, $n = 43$, $P < 0.005$; Fig. 9). Consequently, foraging rate was highest in the preferred habitats.

Growth

Fork length of fish ($\bar{x} \pm \text{SE} = 50.35 \pm 0.26$, range = 33.05-63.00 mm) increased over time until it leveled off towards the end of the summer (Fig. 10). In order to simplify calculations, I assumed that growth rate had ceased by the time fish were electrofished (i.e. Julian date = 264 - 273). A date for when growth ceased was estimated as the intersection between a linear regression of fork length on date prior to electrofishing (i.e. Julian date < 241) and the mean fork length of fish during electrofishing (i.e. fork length = 57.1 mm). The intersection point was found on Julian date 248 (i.e. 5 Sept.) (Fig. 10).

Since the two relationships in Fig. 10 differed little, I made the simplifying assumption that growth rate was linear over the season and ceased on day 248.

Growth rate decreased with increasing initial body size in both early ($\bar{x} \pm SE = 0.24 \pm 0.005$, range = 0.14-0.54 mm·day⁻¹; Fig. 11a) and late summer ($\bar{x} \pm SE = 0.25 \pm 0.007$, range = 0.079-0.54 mm·day⁻¹; Fig. 11b). In order to control for the effect of fork length on growth rate, the residuals from the quadratic relationships (Fig. 11) were used as an estimate of early and late growth rate in further analyses. Fish that grew relatively fast for their length in early summer, also tended to grow relatively fast late in the summer ($r = 0.26$, $n = 86$, $P < 0.05$). But because the correlation was so weak, growth rate was analyzed separately for early and late summer.

Growth rate early and late in the summer were not correlated to the probability of y-o-y using a habitat (early: $r = -0.06$, $n = 137$, $P \gg 0.05$; late: $r = -0.11$, $n = 81$, $P \gg 0.05$). Habitat preference was not a good predictor of growth rate in early (Fig. 12a) or late summer (Fig. 12b). If anything, fish seemed to grow slightly faster in the least preferred habitats.

Discussion

This is one of the rare studies to mark and follow the habitat use of small fish over most of a growing season. Surprisingly, I found only weak evidence of an ontogenetic niche shift in habitat use or preference of y-o-y Atlantic salmon towards deeper and faster waters from June to September 1999. For example, the preferred current velocity, of y-o-y Atlantic salmon, increased from 6-24 cm·s⁻¹ in early summer to 12-48 cm·s⁻¹ in mid-

summer then decreased again to 6-24 cm·s⁻¹ in late summer. This lack of a continuous shift towards deeper faster waters does not necessarily imply that such a shift is unimportant. Rather, it may be due to the low discharge in 1999 (D. Cassie, Department of Fisheries and Oceans, P.O. Box 5030, Moncton, N.B., E1C 9B6, unpublished data). Therefore, there may not have been a sufficient range of current velocities and water depths required to demonstrate a continuous shift of salmon, towards deeper and faster waters.

Notwithstanding these results, the overall trend showed that larger fish tended to be found in deeper and faster waters (correlation between mean current velocity and fork length: $r = 0.33$, $n = 362$, $p < 0.001$; correlation between water column depth and fork length: $r = 0.22$, $n = 362$, $p < 0.001$). Other studies have also found some evidence of a niche shift in y-o-y salmon. For example, Nislow et al. (1999) found that y-o-y salmon preferred slower water currents ($< 18 \text{ cm}\cdot\text{s}^{-1}$) early in the summer than later in the summer ($> 21 \text{ cm}\cdot\text{s}^{-1}$).

Throughout the summer of 1999, y-o-y salmon in Catamaran Brook used slower and slightly shallower waters than previously reported in the literature (Table 5). The low discharge in 1999 may also explain this result. While calculations of preference may vary slightly from one study to another, the preferred ranges in our study, were well within the ranges reported in earlier studies (Table 5). The wide range of current velocities and water depths preferred by y-o-y salmon, implies that juveniles can survive in a broad range of conditions.

A multivariate logistic regression showed that mean current velocity and water

column depth were the key variables that distinguished between the habitat used by y-o-y salmon and available for them in the stream. Therefore, water column depth and mean current velocity combined were better predictors of habitat selection, throughout the summer, than each variable separately (Fig. 6). As well, variables that were apparently preferred by y-o-y, in the univariate analysis were shown to be unimportant to habitat selection in the multivariate analysis. These results demonstrate the importance of using a multivariate technique in order to predict fish habitat selection. Guay et al. (2000) also used a multivariate logistic regression to predict the distribution of juvenile Atlantic salmon (1+ and 2+ parr; FL = 50-100 mm) in a river. They found that the probability of observing vs. not observing a juvenile was dependant on water depth, current speed and substrate composition ($\ln(p / 1-p) = 8.461 \text{ water depth (m)} + 2.86 \text{ current velocity (m}\cdot\text{s}^{-1}) + 0.093 \text{ substrate composition (D50)} - 6.203 \text{ current velocity}^2 \text{ (m}\cdot\text{s}^{-1})^2 - 3.067$). The importance of substrate in their model suggests that juvenile salmon may become more specialized in their habitat demands as they grow. Heggenes & Saltveit (1990), also used a multivariate analysis (i.e. principal component analysis) to show that current velocity, water depth and to some extent substrate and cover have an effect on habitat selection by juveniles Atlantic salmon (1+ and 2+ parr; FL = 80-90 mm).

From previous univariate results (e.g. Morantz et al. 1987), one might have expected habitat preference to increase with current velocity and then decrease once current velocity exceeded $50 \text{ cm}\cdot\text{s}^{-1}$. Such a trend has usually been explained by the increased costs of swimming and decreased feeding efficiency experienced by fish at high current velocities (Hill & Grossman 1993; Fausch 1984). We found no such trend in our

multivariate results, perhaps because of the scarcity of fast current velocities in our study sites. Alternatively, juveniles were often observed resting on the bottom or behind a rock when currents exceeded 15-20 cm·s⁻¹. This may have decreased energetic costs while maintaining their feeding efficiency. Indeed, Nislow et al. (1999) suggest that the cost of swimming in high currents may not be of importance in habitat selection by y-o-y Atlantic salmon.

Our measurements of food abundance and correlates of fitness (i.e. foraging rate and growth rate) lead to some contradictory and even counter-intuitive results. First, foraging rate was positively correlated with current velocity and cover, contradicting earlier findings (Nislow et al. 1998) that foraging rate of y-o-y salmon was unrelated to either food abundance or current velocity. Nislow et al. (1998) suggested that foraging rate is related more directly to overall prey density at the site level rather than to food abundance in high velocity, high drift rate habitats. Our study provides one of the few clear links between foraging rate and food abundance at the microhabitat level.

Second, growth rate was found to decrease with increasing initial fork length both early and late in the summer. This may be explained by the lower metabolic rates (Fivelstad & Smith 1991) of smaller fish. As prey density was lower in my study than in previous years (see Keeley & Grant 1997; Steingrimsson & Grant 1999), fish that were initially larger may not have been able to meet their higher metabolic demands, and consequently grew slower than fish that were initially smaller. While studying Atlantic salmon parr, Armstrong et al. 1999, found that growth rate was inversely related to body size. They concluded that dominance of larger individuals may have a higher price than

anticipated when populations are at high densities. Alternatively, as late-emerging juveniles are smaller than early-emerging juveniles at a subsequent date (Einum & Fleming 2000), smaller salmon may try to compensate by increasing foraging rate and time spent foraging as well as decreasing their aggressive encounters (Nicieza & Metcalfe 1997).

Third, y-o-y salmon did not grow at a faster rate in the preferred habitats, despite the increase in food abundance and a higher foraging rate. Similarly, Nislow et al.(1999) found no difference in the growth rate of stocked y-o-y Atlantic salmon between preferred versus not preferred current velocities. These results show the importance of measuring correlates of fitness in studies of habitat selection. Earlier studies have often assumed that the growth and survival of fish is higher in preferred habitats (e.g. Bremset and Berg 1997; Martin 1998). In contrast, our study showed y-o-y salmon can grow well in a wide variety of habitat types. Furthermore, our results suggest that y-o-y salmon may follow an ideal free distribution (IFD) (Fretwell & Lucas 1970), so that equal growth rates are expected across habitat types and no individual can increase its fitness by switching habitat. Indeed, there were 3.67 times more food and 6.90 times more y-o-y salmon in preferred areas (i.e. > 50% probability of y-o-y using the habitat) than in less preferred areas (i.e. < 50% probability of y-o-y using the habitat). This trend does not support the ideal despotic distribution, which predicts fewer fish than expected in the preferred habitats.

The well known territorial behavior of Atlantic salmon (Kalleberg 1958) and other juvenile salmonids in streams have led some to expect an ideal despotic distribution

(Grant & Kramer 1990). But, territorial behavior may simply be the mechanism by which juvenile salmonids achieve an ideal free distribution. Despite the extensive literature involving ideal free distribution, few studies have looked at the potential value of using ideal free distribution to explain the distribution of drift-feeding fish in the wild. However, there have been a few laboratory experiments (Giannico and Healey 1999; Grand 1997; Grand & Dill 1997). Interestingly, Giannico and Healey (1999) found that fish distributed themselves according to food levels in a laboratory experiment. However, as structural complexity of the stream increased, fish tended to deviate somewhat from the IFD, as other factors also became important in habitat selection. Field tests of IFD theory would be a useful addition to studies of habitat use and selection in stream salmonids.

Table 1. Schedule of activities that were conducted during the 1999 field season in Catamaran Brook, New Brunswick.

Round	Dates	Activities	Sites
	25-26 June	Site mapping	1,2,3,4,5
	2 July	Availability of substrate and cover	2,3,4,5
1	6-7 July	Tagging and measurement of fork length	2
	8 July	Habitat use measurements	2
	9-14 July	Tagging and measurement of fork length	5
	15 July	Habitat use measurements	5
	18-27 July	Tagging and measurement of fork length	1,3,4,5
	22-23 July	Habitat use measurements	1,3,4
	23 July	Drift samples	1,2,3,4,5
	24 July	Habitat availability measurements	1,2,3,4,5
	24 July	Availability of substrate and cover	1
2	25-27 July	Locate tagged fish	1,2,3
	28 July	Habitat use measurements	1,2,3
	4-6 Aug.	Locate tagged fish	3,4,5
	6-7 Aug.	Habitat use measurements	3,4,5
	8 Aug.	Drift samples	1,2,3,4,5

3	10-19 Aug	Tagging and measurement of fork length and mass	1,2,3,4,5
	20 Aug.	Habitat use measurements	1,2,3,4,5
	21-22 Aug.	Habitat availability measurements	1,2,3,4,5
	22 Aug.	Drift samples	1,2,3,4,5
4	23-25 Aug.	Locate tagged fish	1,2,3,4,5
	25 Aug.	Habitat use measurements	1,2,3,4,5
	26-27 Aug.	Foraging rates of 43 tagged fish	1,2,3,4,5
	28 Aug.	Habitat use measurements	1,2,3,4,5
	29 Aug.	Drift samples	1,2,3,4,5
5	30 Aug.-2 Sept.	Locate tagged fish	1,2,3,4,5
	2 Sept.	Habitat use measurements	1,2,3,4,5
	3 Sept.	Habitat availability measurements	1,2,3,4,5
	4 Sept.	Drift samples	1,2,3,4,5
	21-30 Sept.	Electrofishing of tagged fish and measurement of fork length and mass	1,2,3,4,5

Table 2. Modified Wentworth scale of substrate particle sizes and coinciding codes used for the analyses (adapted from DeGraaf and Bain 1986).

Substrate	Particle size diameter (mm)	Code
Plant detritus or clay	clay < 0.004	1
Sand or silt	0.004-2	2
Gravel	2-16	3
Pebble	16-64	4
Cobble	64-250	5
Boulder	>250	6
Bedrock		7

Table 3. Seasonal variation in the habitat available for young-of-the-year Atlantic salmon during the summer of 1999 in Catamaran Brook, New Brunswick.

Variable	Early^a	Middle^b	Late^c	ANOVAR
	$\bar{x} (\bar{x} - S.E.; \bar{x} + S.E.)$	$\bar{x} (\bar{x} - S.E.; \bar{x} + S.E.)$	$\bar{x} (\bar{x} - S.E.; \bar{x} + S.E.)$	F Value
Current velocity bottom (cm·s ⁻¹)	1.20 (1.06-1.36)	1.42 (1.25-1.61)	1.03 (0.91-1.17)	13.06*
Current velocity nose (cm·s ⁻¹) ^e	1.38 (1.22-1.57)	2.14 (1.90-2.41)	1.14 (1.00-1.30)	39.31*
Current velocity mean (cm·s ⁻¹)	1.98 (1.75-2.24)	3.20 (2.84-3.60)	1.66 (1.45-1.89)	66.28*
Water column depth (cm)	15.10 (14.13-16.14)	15.24 (14.22-16.33)	14.59 (13.65-15.60)	49.88*
Substrate size ^f	4.42 (4.33-4.52)	—	—	—
Cover ^g	0.26, 0.37, 0.37^h	—	—	—

Note: *Repeated measures ANOVA; P<0.001, df = 2,376.

^a July 2 & 24, 1999.

^b Aug. 21-22, 1999.

^c Sept.3, 1999.

^d Mean and standard error, back transformed from log₁₀.

- e Current velocity taken at the mean distance of the fish's "nose" above the substrate, while holding position in the water column at a particular site and time (range: 2.03-6.70 cm).
- f Modified Wentworth scale of particle size diameter (1 = plant detritus or <0.004 mm, 2 = 0.004-1.9 mm, 3 = 2-16 mm, 4 = 16-64 mm, 5 = 64-256 mm, 6 = >256 mm)
- g Degree of overhead cover from aerial predators (0 = no cover, 1 = partial cover, 2 = complete cover)
- h % frequency of cover available for each category (0, 1, 2)

Table 4. Seasonal variation in the habitat used by young-of-the-year Atlantic salmon during the summer of 1999 in Catamaran

Brook, New Brunswick.

Variable	Early^a \bar{x} (\bar{x} - S.E.; \bar{x} + S.E.) ^d	Middle^b \bar{x} (\bar{x} - S.E.; \bar{x} + S.E.)	Late^c \bar{x} (\bar{x} - S.E.; \bar{x} + S.E.)	ANOVAR F Value df
Current velocity bottom (cm·s ⁻¹)	2.57 (2.34-2.82)	4.14 (3.73-4.59)	2.17 (1.92-2.45)	5.26** 4,264
Current velocity nose (cm·s ⁻¹) ^e	3.75 (3.47-4.04)	5.86 (5.41-6.87)	3.33 (3.03-3.66)	7.08** 4,248
Current velocity mean (cm·s ⁻¹)	5.98 (5.59-6.40)	10.92 (10.28-11.60)	5.93 (5.55-6.33)	11.40** 4,264
Water column depth (cm)	24.66 (23.93-25.41)	29.79 (28.97-30.62)	27.93 (27.10-28.77)	4.91** 4,264
Substrate size ^f	4.57 (4.51-4.63)	4.63 (4.57-4.68)	4.68 (4.62-4.74)	1.41 4,264
Cover ^g	0.19, 0.35, 0.47 ^h	0.31, 0.28, 0.42	0.18, 0.23, 0.59	-----

Note: Repeated measures ANOVA: * P ≤ 0.05, ** P ≤ 0.001

^a July 6-28, 1999.

^b Aug. 10-20, 1999.

^c Aug.30-Sept.2, 1999.

^d Mean and standard error, back transformed from log₁₀.

- ° Current velocity taken at the distance of each fish's "nose" above the substrate, while holding position in the water column at a particular site and time.
- † Modified Wentworth scale of particle size diameter (1 = plant detritus or < 0.004 mm, 2 = 0.004-1.9 mm, 3 = 2-16 mm, 4 = 16-64 mm, 5 = 64-256 mm, 6 = > 256 mm)
- ‡ Cover from aerial predators (0 = no cover, 1 = partial cover, 2 = complete cover)
- h % frequency of cover used by fish for each category (0, 1, 2)

Table 5. Summer habitat use and preference of young-of-the-year Atlantic salmon according to previous studies.

Habitat Use		Habitat Preference		References
\bar{x} CVM ^a	\bar{x} WD ^b	\bar{x} CVM ^a	\bar{x} WD ^b	
7.61	27.46	8-32	22-36	This study
34.93	34.90	9-45	17-45	DeGraaf & Bain 1986
29.29	34.29	0-50	16-46	Morantz et al. 1987

^aCurrent velocity taken at the mean of the water column (cm·s⁻¹)

^bWater depth (cm)

Figure 1. Map of the location, size and respective position of each study site (1-5) in Catamaran Brook, New Brunswick. Also shown is the direction of the current through the sites (arrow). The area between sites 3 and 4 was too shallow for snorkeling (i.e. < 10 cm) and hence, was not included in the study area.

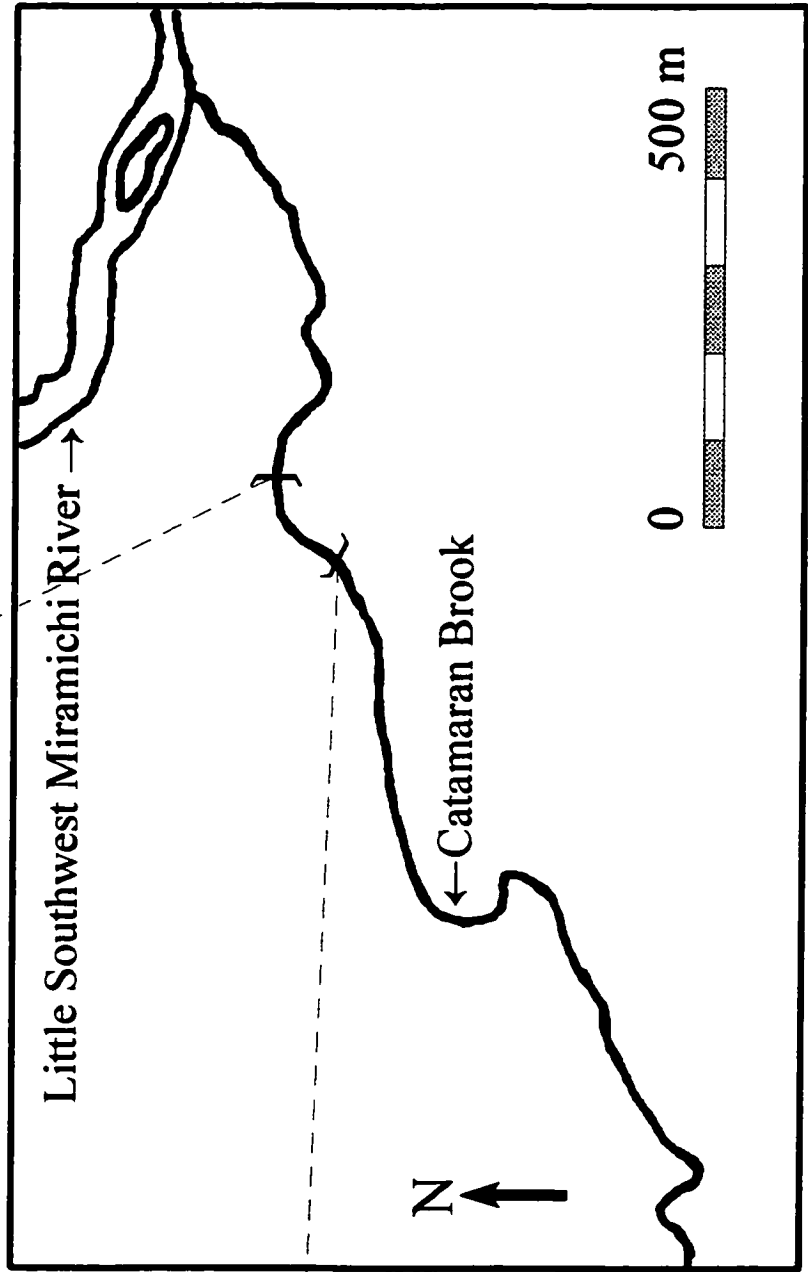
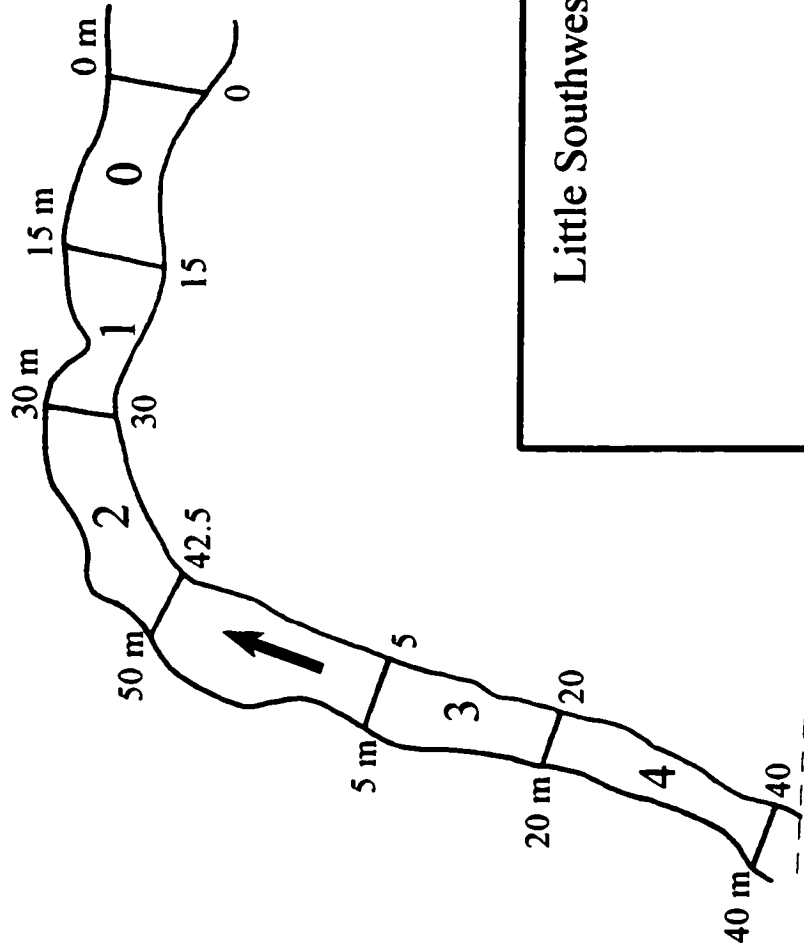


Figure 2. Eight possible locations of fluorescent elastomer paint on the left and right side of young-of-the-year Atlantic salmon (1 = tip of the left operculum, 2 = tip of the right operculum, 3 = base of the first ray in the dorsal fin, 4 = base of the last ray in the dorsal fin, 5 = caudal peduncle close to the dorsal junction between the caudal peduncle and the caudal fin, 6 = caudal peduncle close to the ventral junction between the caudal peduncle and the caudal fin, 7 = base of the last ray of the left pectoral fin, 8 = base of the last ray of the right pectoral fin).

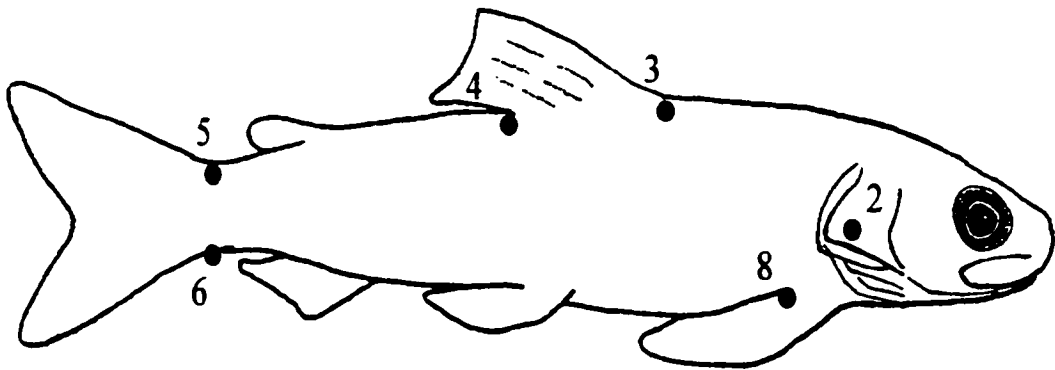
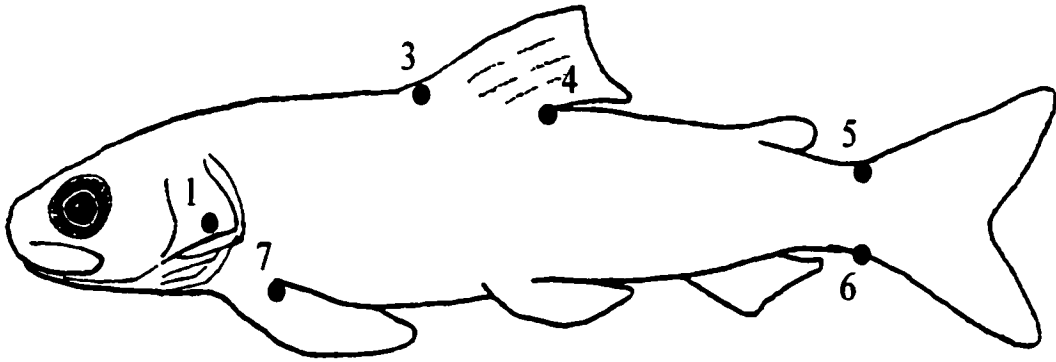


Figure 3. Frequency distribution of the mean current velocity of the water column used by and available for young-of-the-year Atlantic salmon, in (a) early (2-28 July), (b) middle (10-22 Aug.) and (c) late summer (30 Aug.-3 Sept.) of 1999. Hatched bars indicate current velocities used by young-of-the-year salmon, while solid bars indicate current velocities available for fish in the study sites. Asterisks represent current velocity categories where single degree-of-freedom chi-square tests were significant (i.e. use was significantly different from availability). Horizontal lines show which categories were grouped together for the chi-square tests.

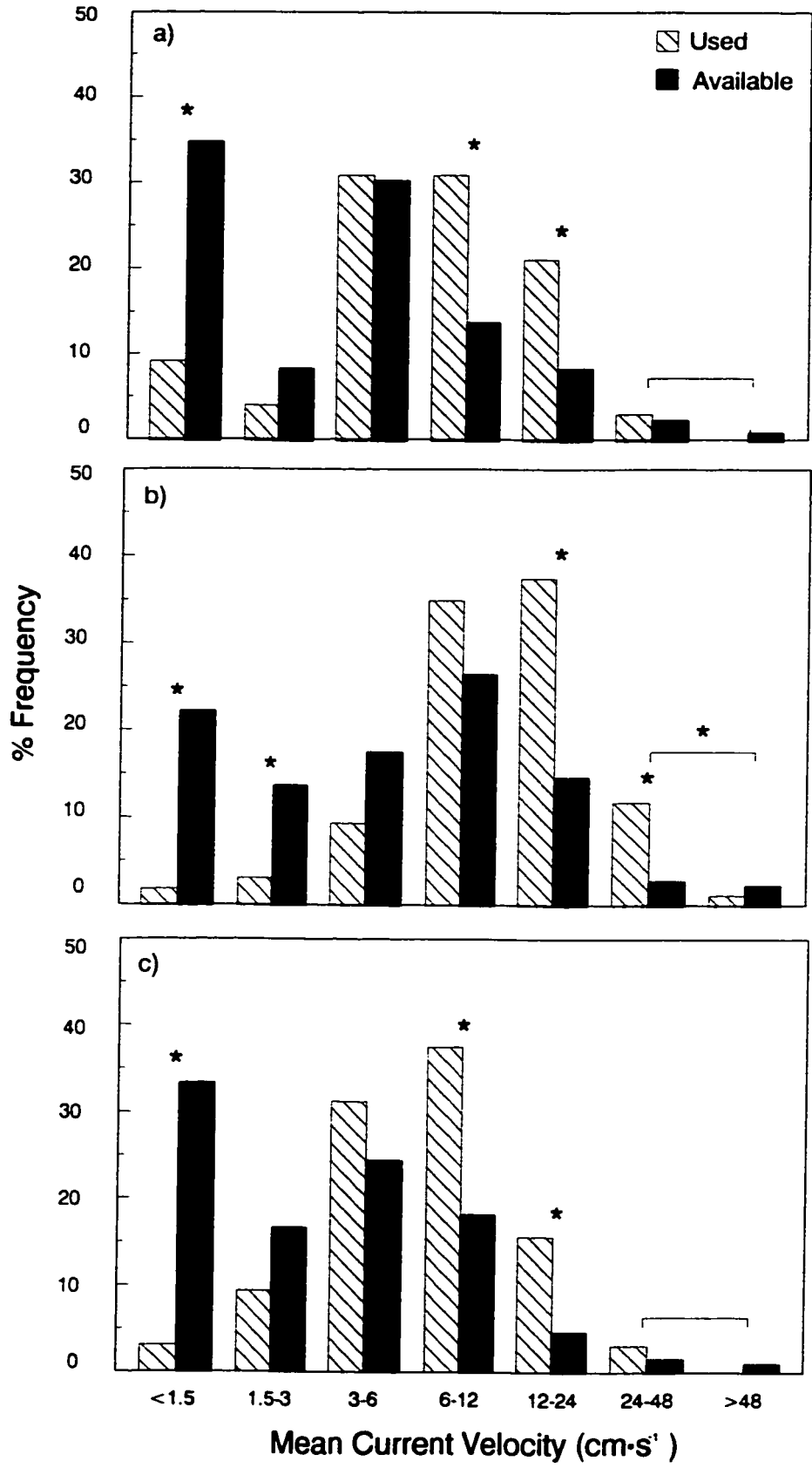


Figure 4. Frequency distribution of the water column depths used by and available for young-of-the-year Atlantic salmon, in (a) early (2-28 July), (b) middle (10-22 Aug.) and (c) late summer (30 Aug.-3 Sept.) of 1999. Hatched bars indicate water depths used by young-of-the-year salmon, while solid bars indicate the water depths available for fish in the study sites. Asterisk's represent current velocity categories where single degree-of-freedom chi-squares were significant (i.e. use was significantly different from availability). Horizontal lines show which categories were grouped together for the chi-square tests.

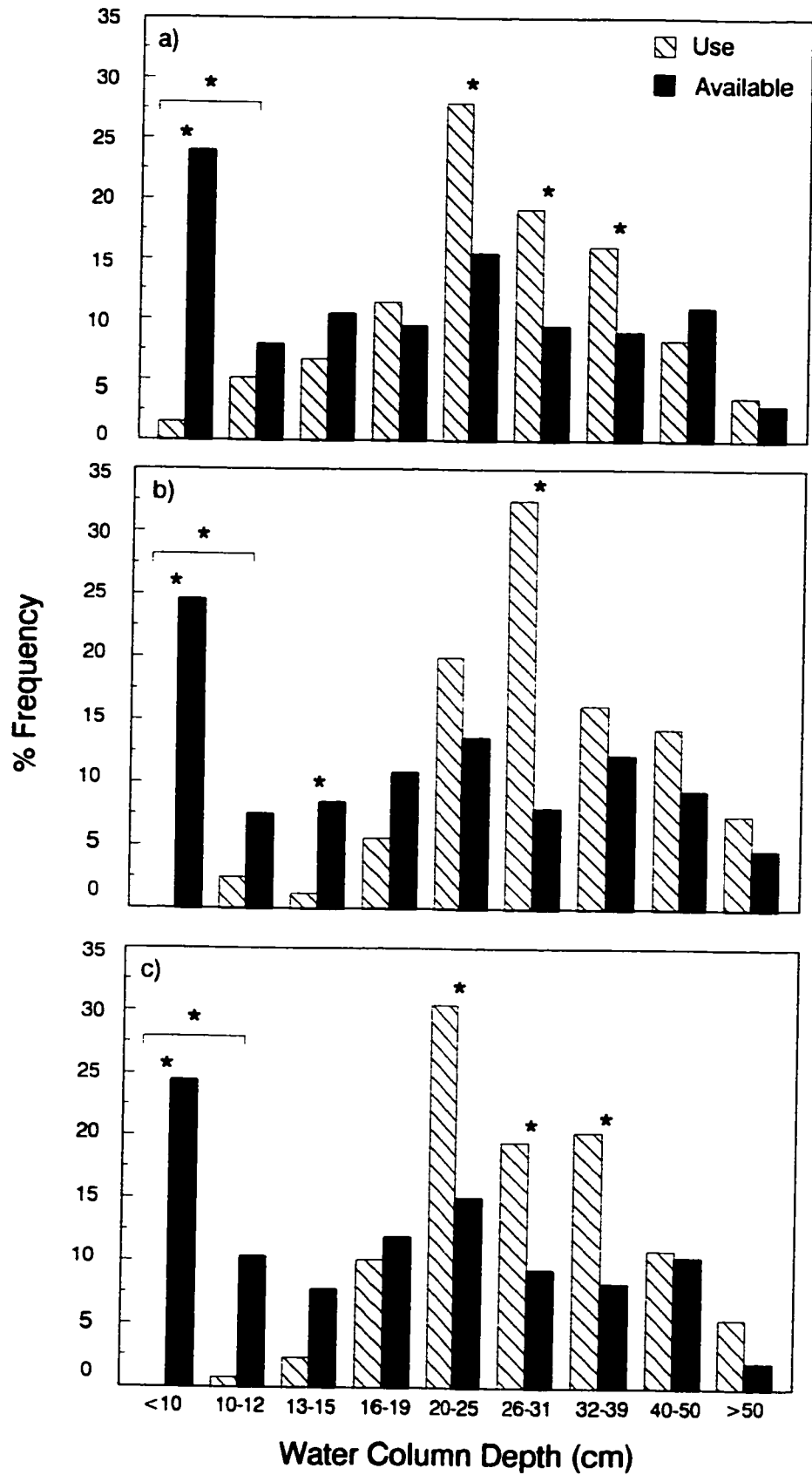


Figure 5. Frequency distribution of (a) substrate sizes (1 = plant detritus and particles < 0.004 mm, 2 = sand or silt, 3 = gravel, 4 = pebble, 5 = cobble, 6 = boulder), and (b) degree of overhead cover (0 = no cover, 1 = partial cover, 2 = complete cover) used by and available for young-of-the-year Atlantic salmon in the summer of 1999. Hatched bars indicate the substrate or cover used by young-of-the-year salmon, while solid bars indicate the substrate or cover available for fish in the study sites. Asterisk's represent categories where single degree-of-freedom chi-squares were significant (i.e. use was significantly different from availability). Horizontal lines show which categories were grouped together for the chi-square tests.

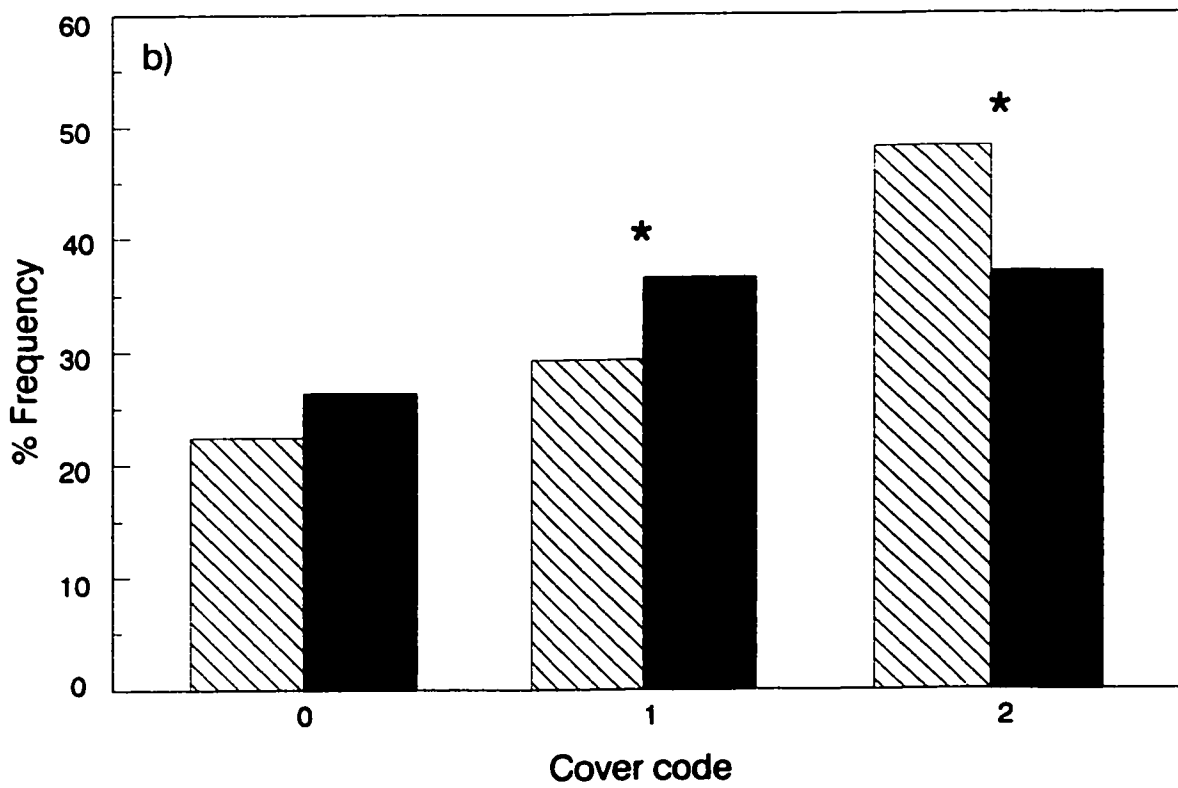
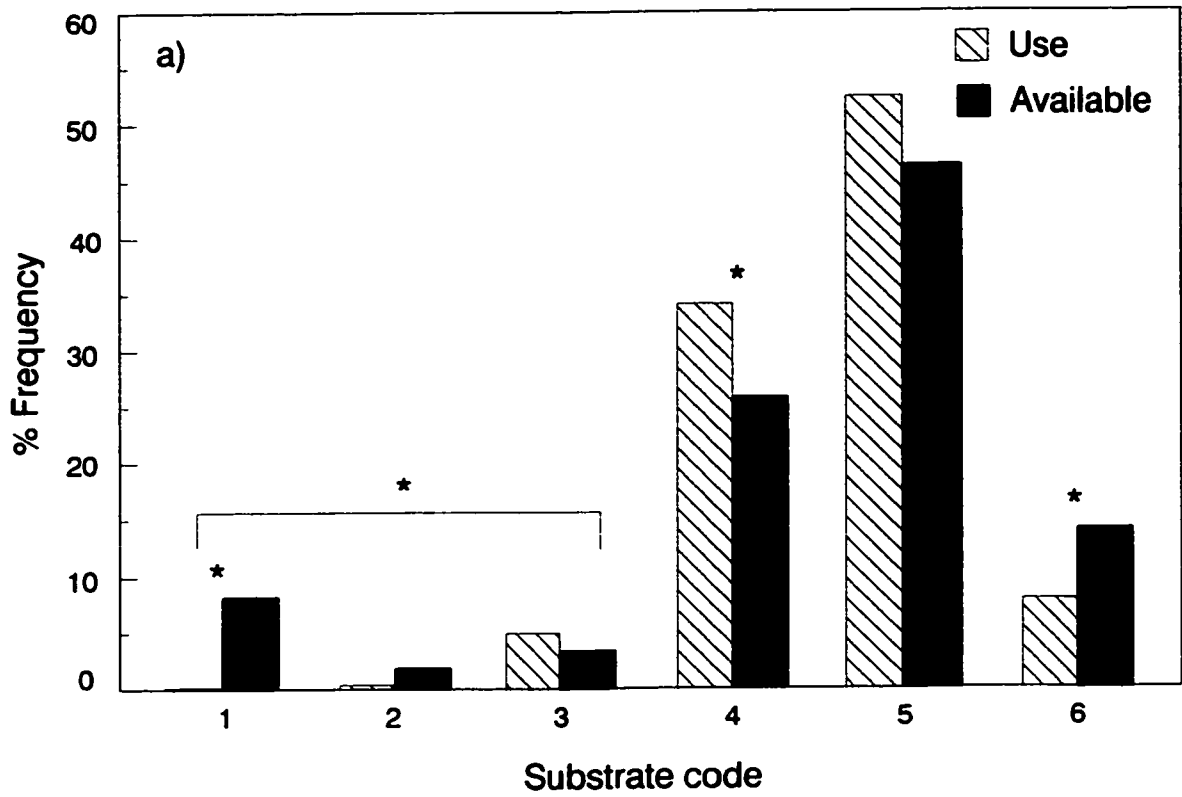
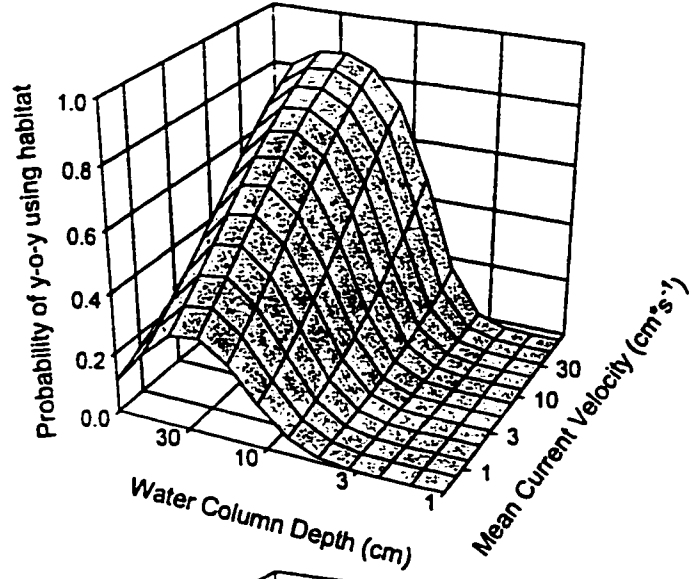
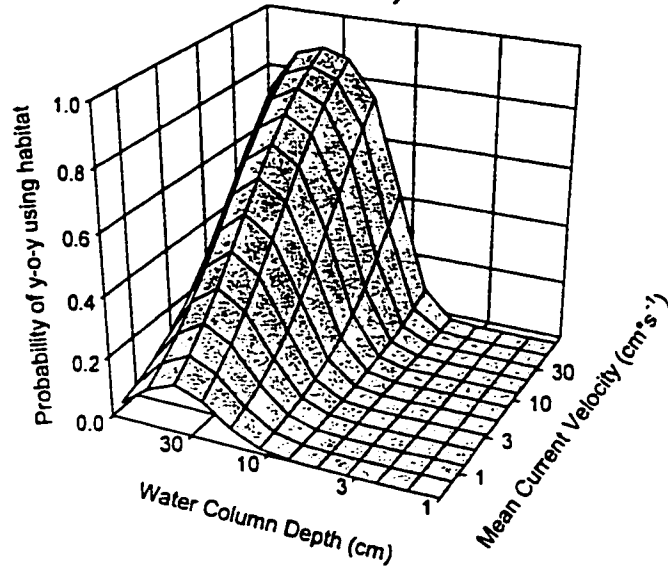


Figure 6. Multivariate logistic regression model relating the probability of young-of-the-year Atlantic salmon using a habitat to the mean current velocity of the water column and water column depth, in (a) early (2-28 July), (b) middle (10-22 Aug.) and (c) late summer (30 Aug.-3 Spt.) of 1999. The probability of y-o-y using a habitat was best described in early summer by: $\ln(p/1-p) = 1.28 \log_{10} \text{current velocity (m}\cdot\text{s}^{-1}) + 17.82 \log_{10} \text{water depth (cm)} - 6.10 \log_{10} \text{water depth}^2 \text{ (cm}^2) - 10.85$ ($\chi^2 = 89.94$, $n = 393$, $df = 3$, $P \ll 0.001$); mid-summer by: $\ln(p/1-p) = 1.77 \log_{10} \text{current velocity (m}\cdot\text{s}^{-1}) + 28.73 \log_{10} \text{water depth (cm)} - 9.15 \log_{10} \text{water depth}^2 \text{ (cm}^2) - 20.17$ ($\chi^2 = 126.60$, $n = 371$, $df = 3$, $P \ll 0.001$); and late summer by: $\ln(p/1-p) = 1.79 \log_{10} \text{current velocity (m}\cdot\text{s}^{-1}) + 40.64 \log_{10} \text{water depth (cm)} - 13.30 \log_{10} \text{water depth}^2 \text{ (cm}^2) - 28.14$ ($\chi^2 = 115.27$, $n = 320$, $df = 3$, $P \ll 0.001$).

a)



b)



c)

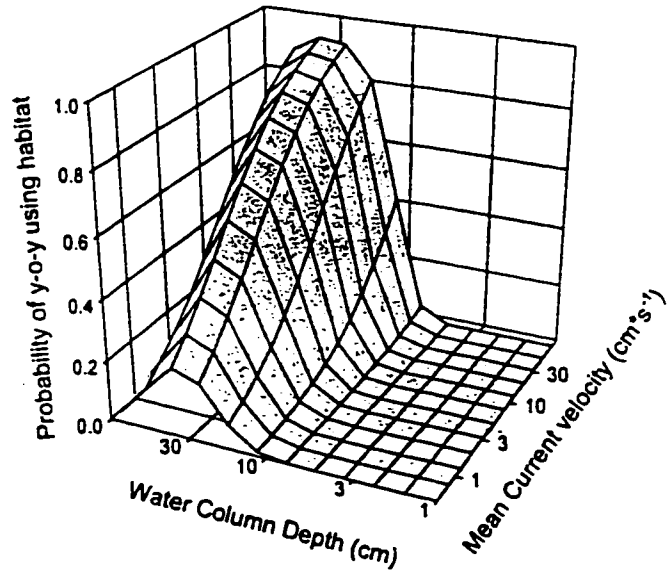


Figure 7. Relationship between predicted food abundance and probability of using a habitat for young-of-the-year Atlantic salmon, in (a) early (6-23 July), (b) middle (10-20 August) and (c) late summer (30 Aug.-2 Sept.) of 1999. The model used to predict food abundance was: \log_{10} Number of organisms * 20 minutes⁻¹ = 1.38 \log_{10} current velocity (m·s⁻¹) - 0.0083 Julian date - 0.94 water depth (cm) + 5.48 ($r^2 = 0.96$, $n = 25$, $P \ll 0.001$). Food abundance was then expressed as the number of organisms flowing, at one time, through the width of a drift net (15.2 cm) prorated to the height of the water column experienced by each fish.

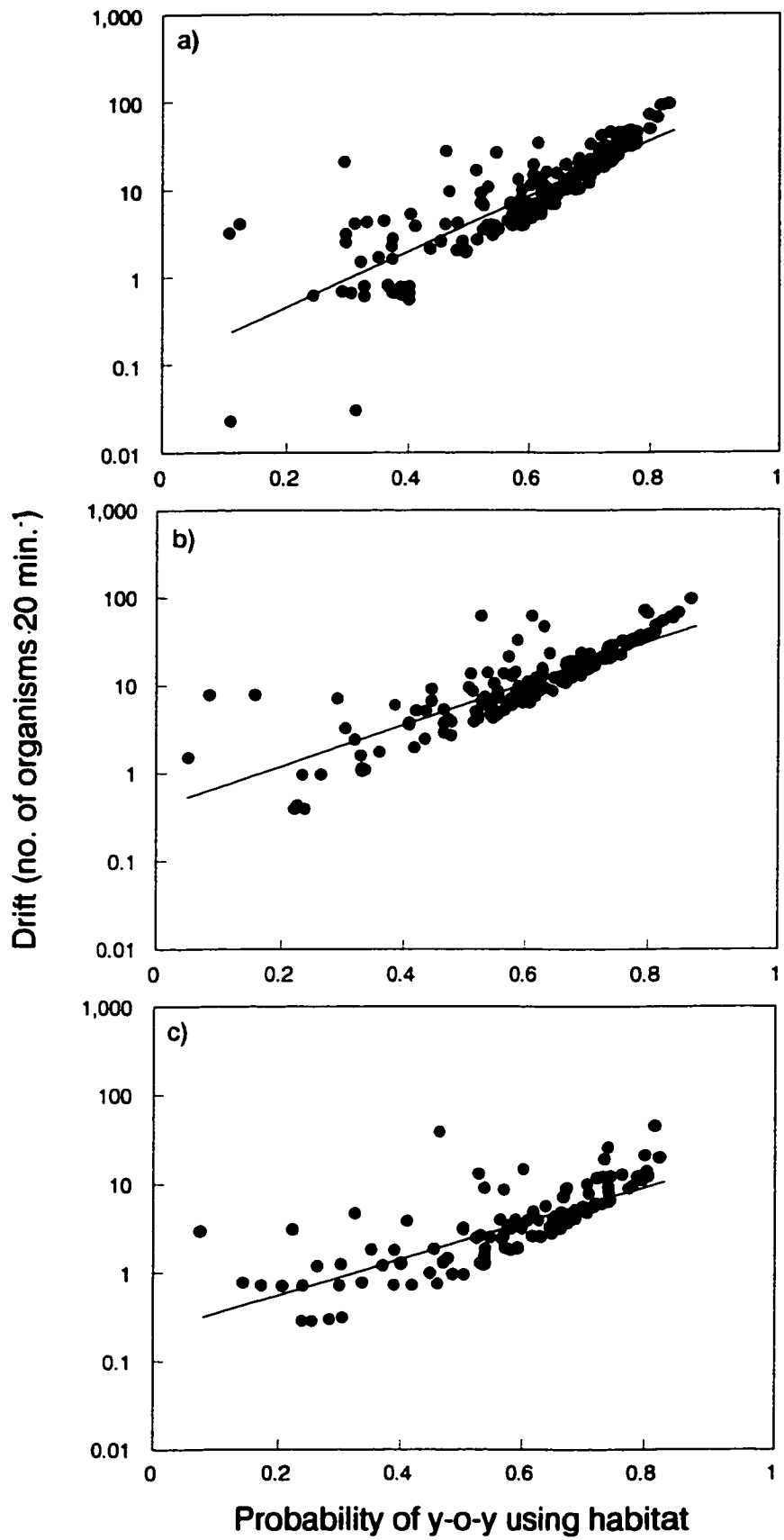


Figure 8. Relationship between foraging rate and mean current velocity of the water column in relation to the degree of overhead cover (solid circles, squares and triangles indicate no cover, partial cover, and complete cover, respectively) for 43 young-of-the-year Atlantic salmon in late summer (26-27 Aug.) of 1999. Dashed line: Log_{10} foraging rate ($\text{attempts}\cdot\text{min}^{-1}$) = $0.302 * \text{Log}_{10}$ mean current velocity ($\text{m}\cdot\text{s}^{-1}$) + 0.64, solid line: Log_{10} foraging rate ($\text{attempts}\cdot\text{min}^{-1}$) = $0.302 * \text{Log}_{10}$ mean current velocity ($\text{m}\cdot\text{s}^{-1}$) + 0.84, dotted line: Log_{10} foraging rate ($\text{attempts}\cdot\text{min}^{-1}$) = $0.302 * \text{Log}_{10}$ mean current velocity ($\text{m}\cdot\text{s}^{-1}$) + 0.76 ($r = 0.37$, $n = 43$, $p_{\text{current}} < 0.005$, $p_{\text{cover}} < 0.05$).

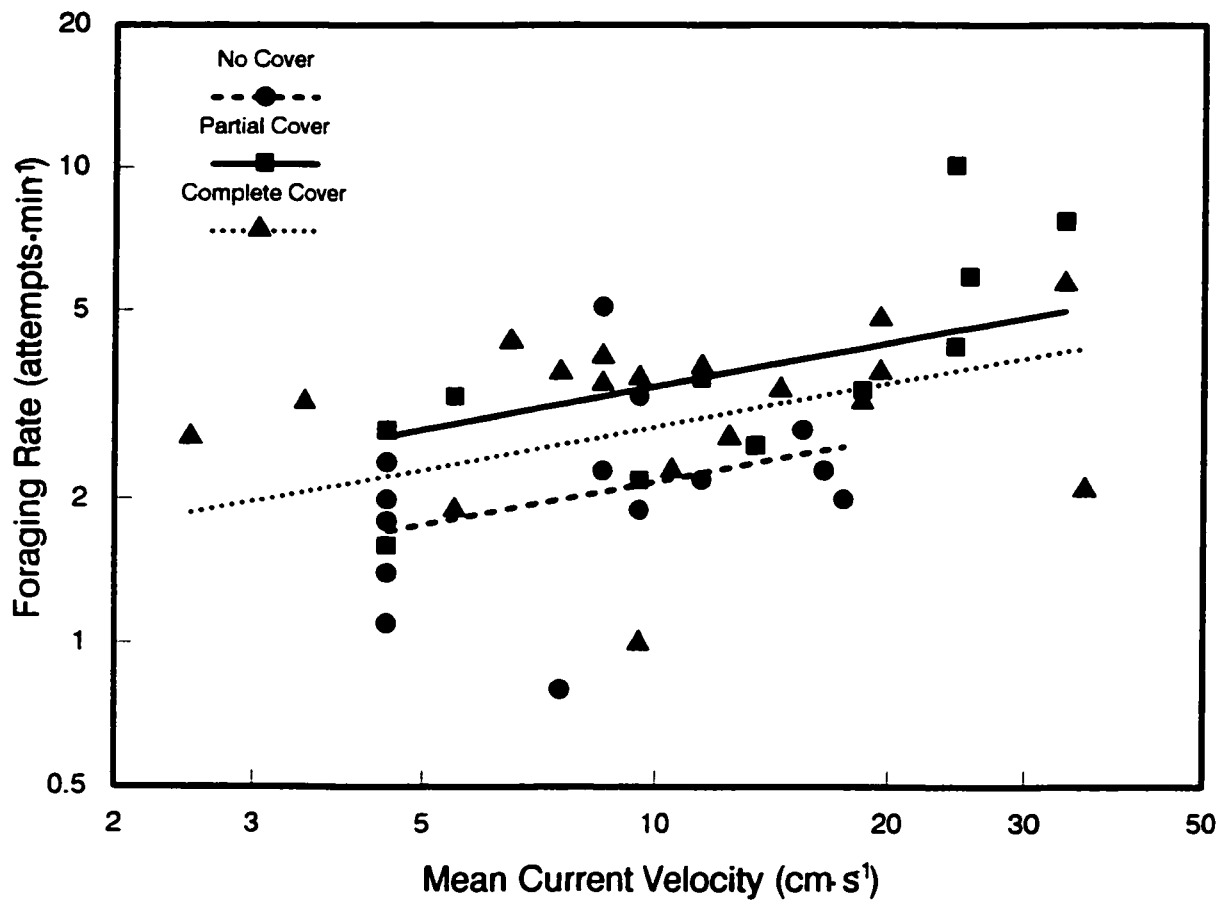


Figure 9. Relationship between foraging rate (measured in late summer (26-27 Aug. 1999, n = 43) and probability of using a habitat in late summer (average probability between middle and late summer) for 43 young-of-the-year Atlantic salmon, in 1999. Solid line: Log_{10} foraging rate (attempts·min.⁻¹) = 0.646* average probability of y-o-y using a habitat (between middle and late summer) + 0.056.

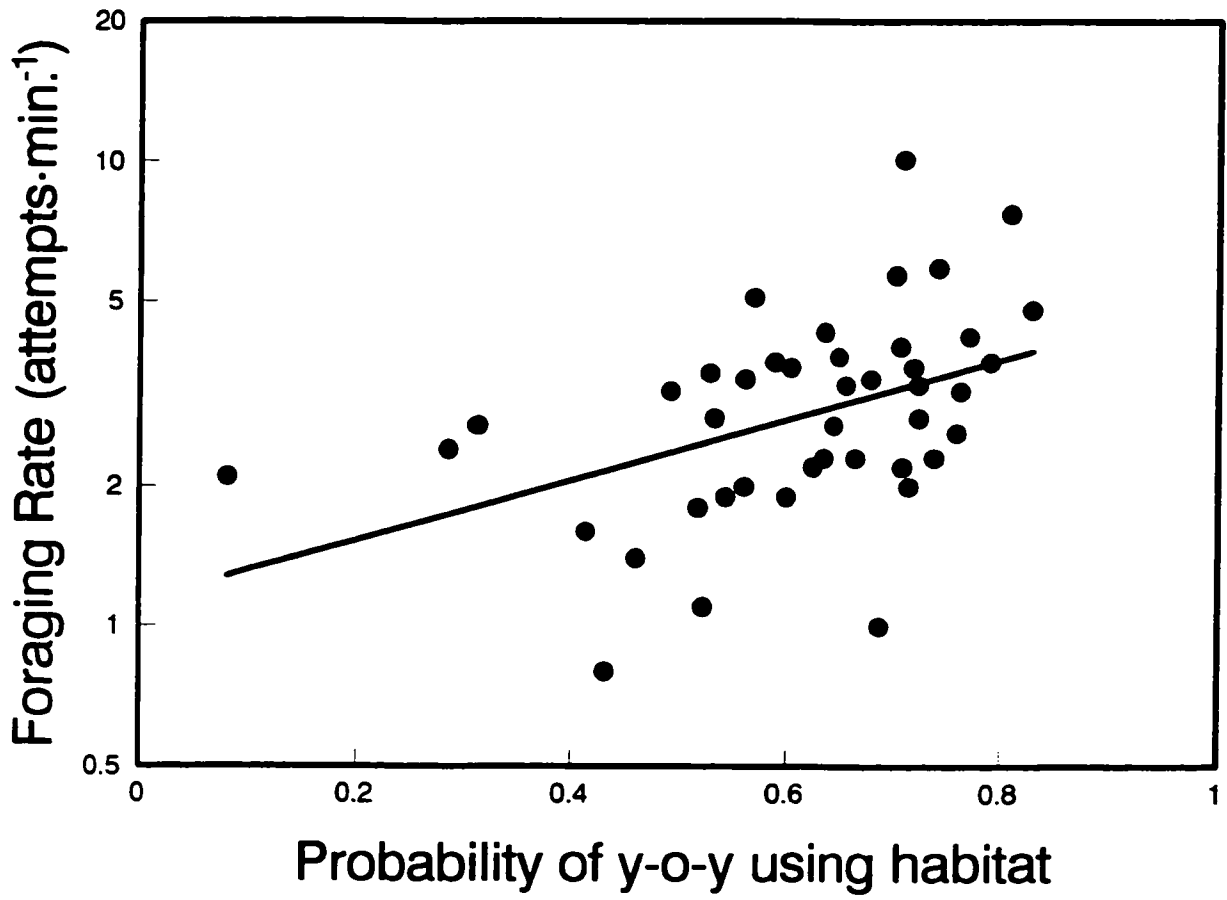


Figure 10. Relationship between fork length and Julian date for 216 young-of-the-year Atlantic salmon throughout the summer (6 July-30 Sept.) of 1999. This relationship is best described by a quadratic regression (dashed line): fork length (mm) = $-0.0016 \text{ Julian date}^2 + 0.909 \text{ Julian date} - 72.23$; $r^2 = 0.78$, $n = 477$, $P \ll 0.001$). The solid line shows the intersection of a linear regression of fork length versus date prior to Julian day = 241 (fork length (mm) = $0.24 \text{ Julian date} - 2.0056$; $r^2 = 0.67$, $n = 362$, $P \ll 0.001$) and the average fork length of fish captured by electrofishing between days 264 and 273 ($\bar{x} = 57.1 \text{ mm}$).

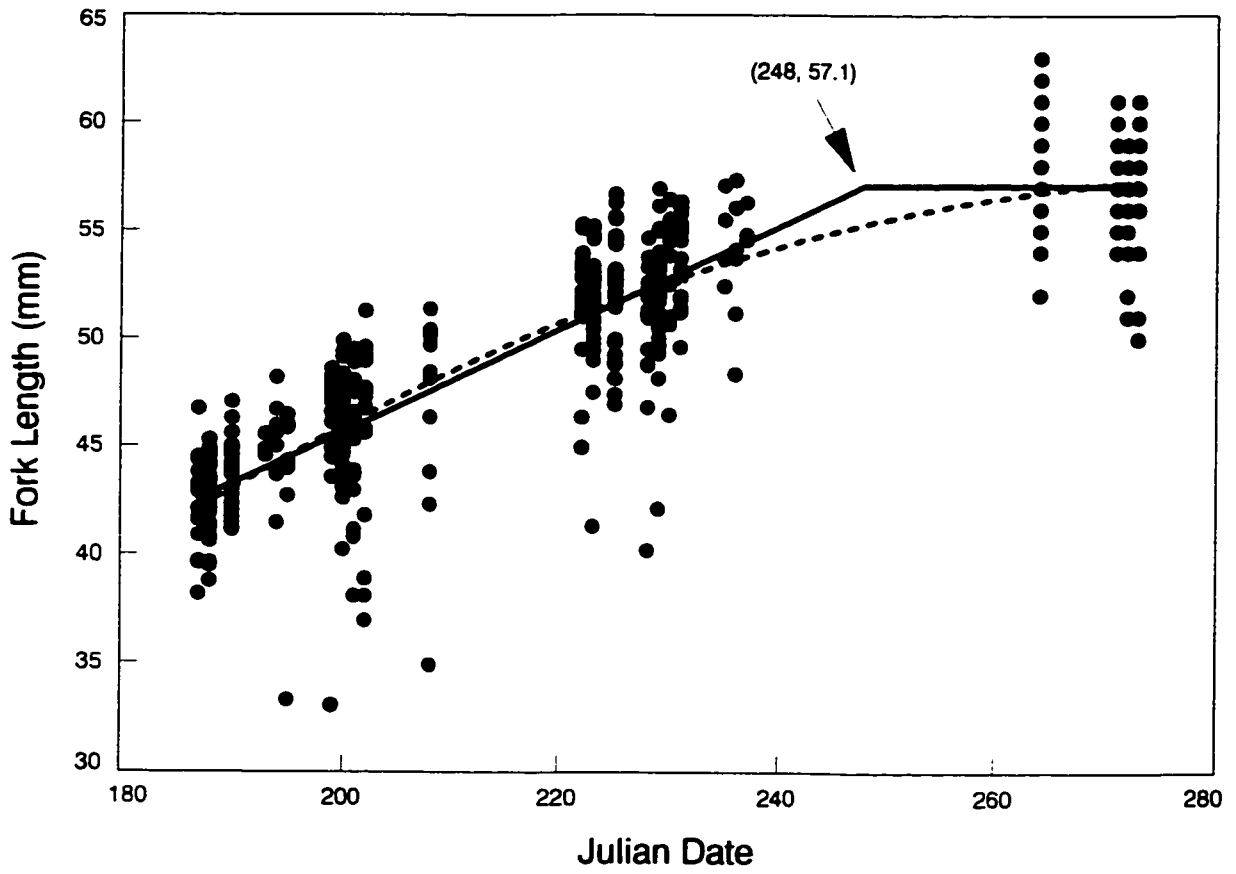


Figure 11. Relationship between growth rate and initial fork length for individually tagged young-of-the-year Atlantic salmon, in (a) early (6 July-19 Aug.) and (b) late summer (10 Aug.-30 Sept.) of 1999. The relationship for early summer is best expressed by: early growth rate = $0.00064 \text{ initial fork length}^2 - 0.065 \text{ initial fork length} + 1.88$ ($r^2 = 0.33$, $n = 137$, $P \ll 0.001$), while late summer is best expressed by: late growth rate = $0.0013 \text{ initial fork length}^2 - 0.14 \text{ initial fork length} + 4.088$ ($r^2 = 0.40$, $n = 107$, $P \ll 0.001$). Solid circles indicate individual fish and the solid triangle indicates an outlier.

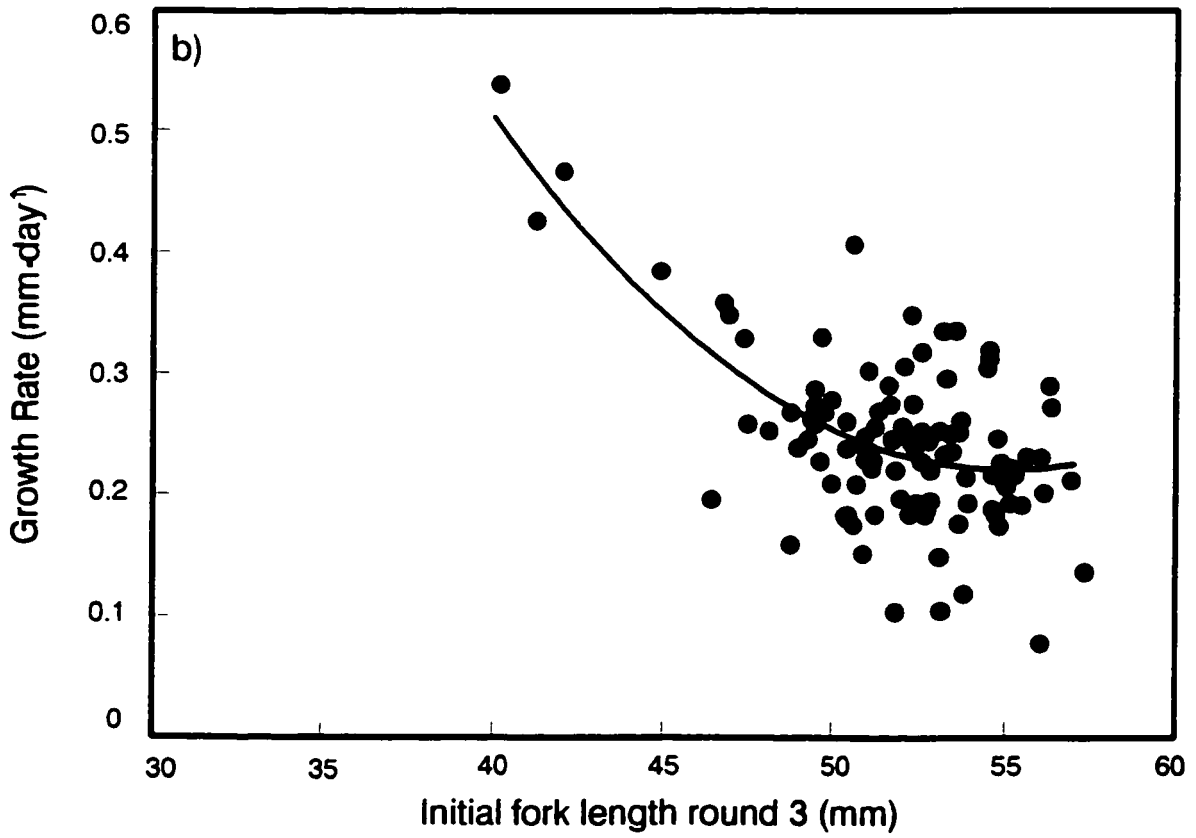
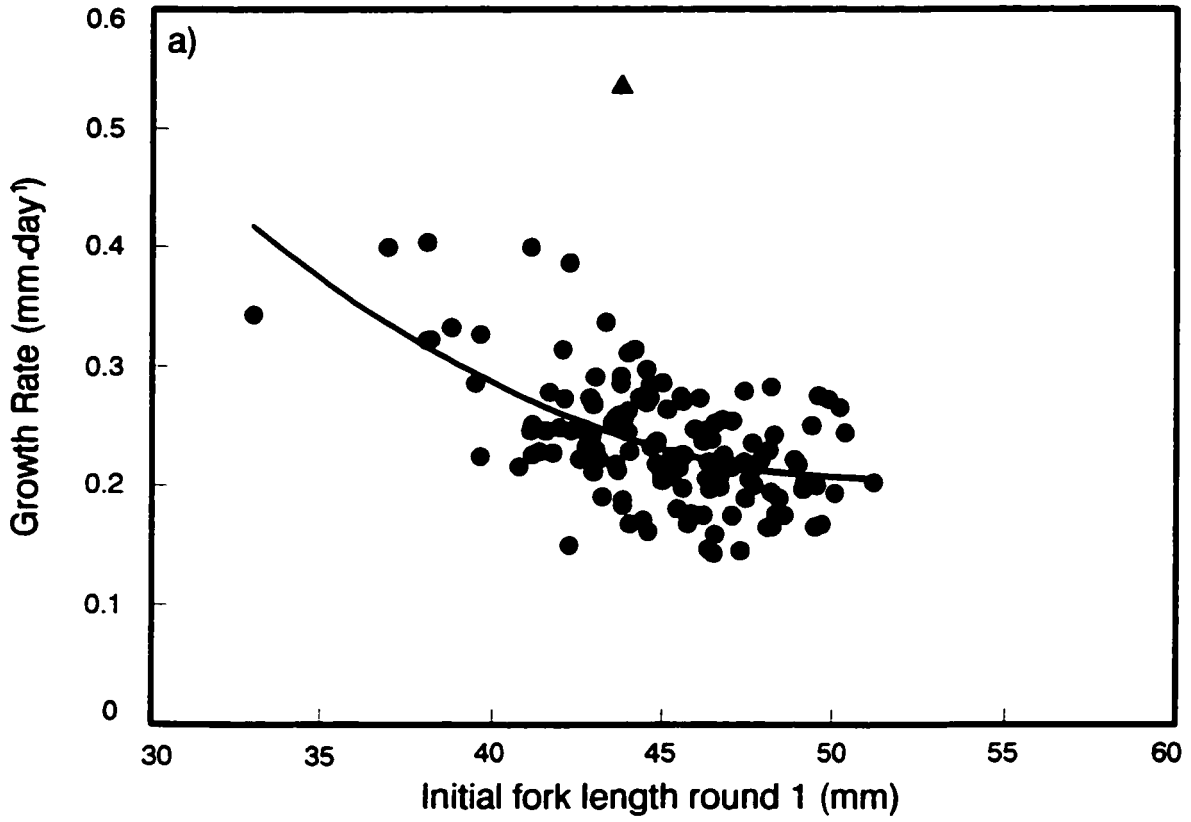
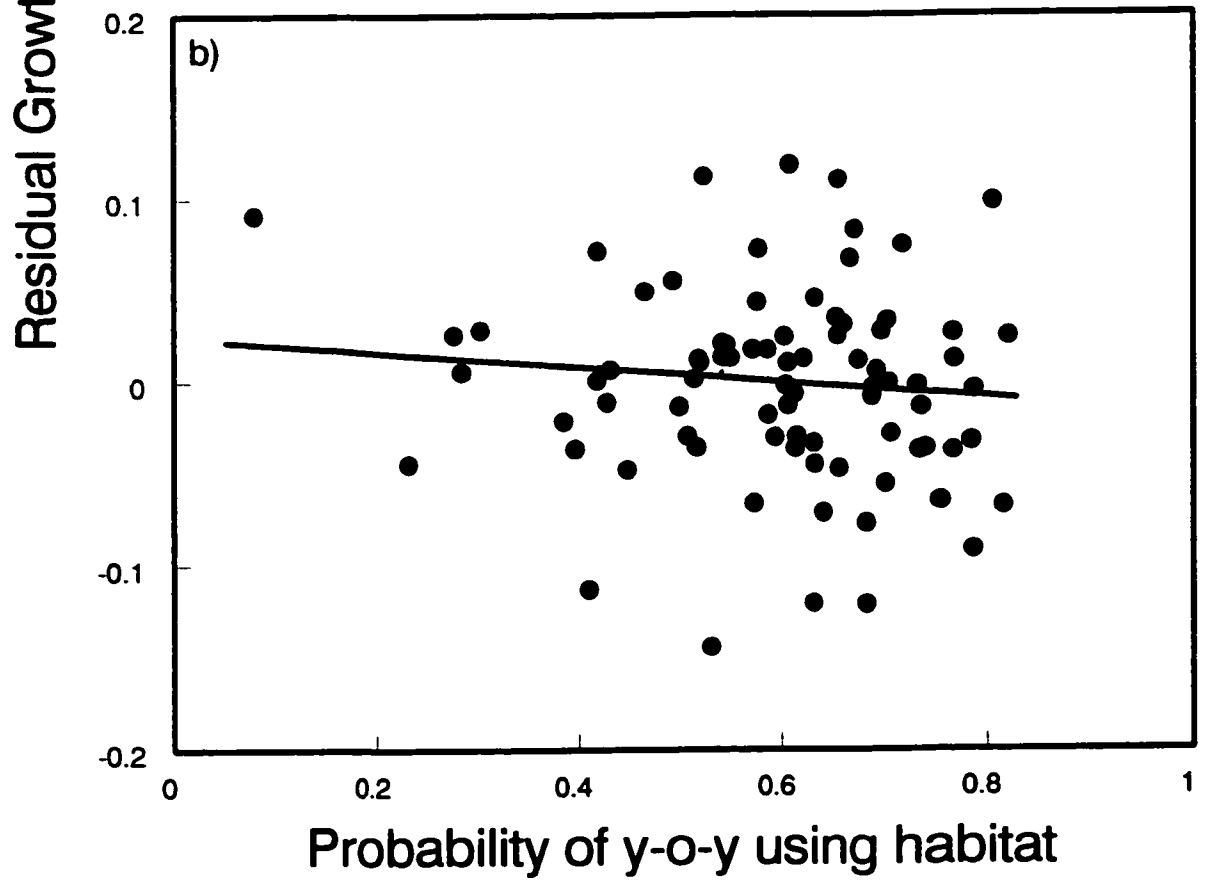
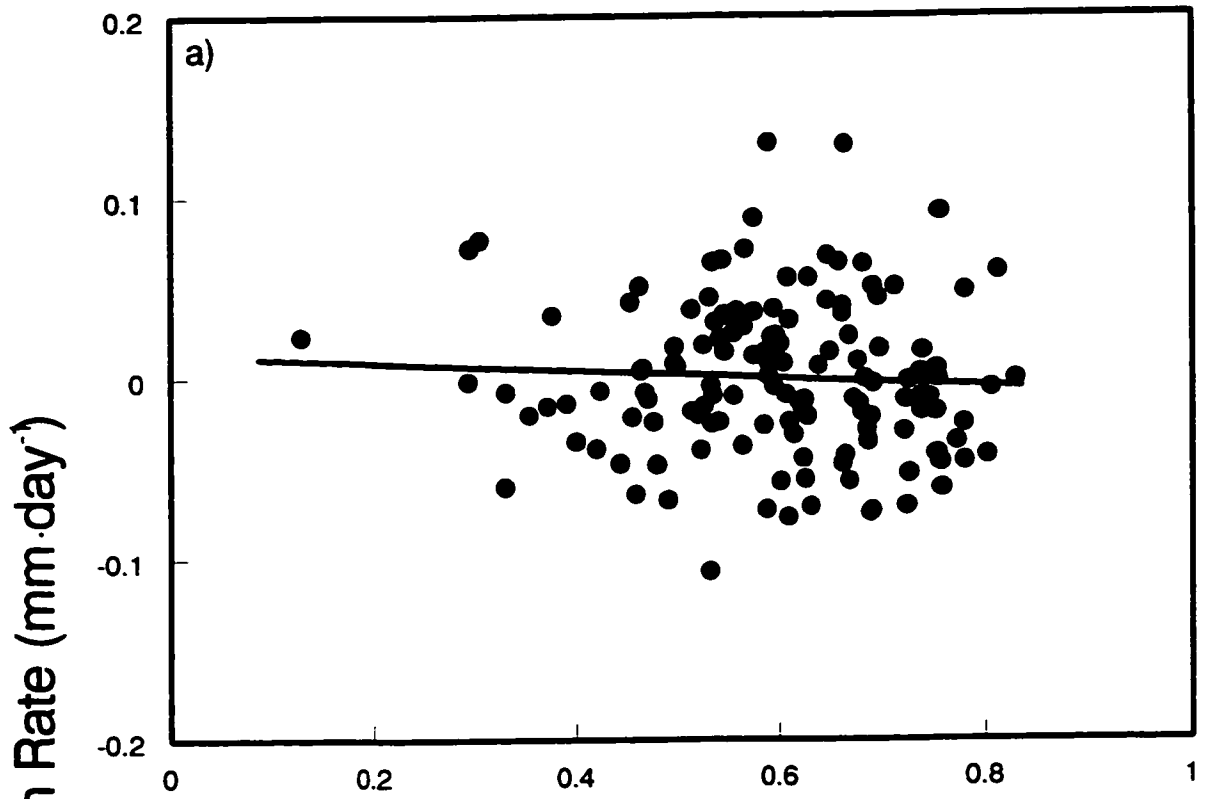


Figure 12. Relationship between residual growth rate and average probability of using a habitat and for young-of-the-year Atlantic salmon, in (a) early (July 6-19 Aug., n = 137) and (b) late summer (10 Aug.-30 Sept., n = 81) of 1999. The average of the probability of y-o-y using a habitat between early and middle summer was compared to early growth rate, whereas the average of the probability of y-o-y using a habitat between middle and late summer was compared to late growth rate.



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