Food and foraging behavior in relation to microhabitat use and survival of age-0 Atlantic salmon

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Abstract: We examined, using underwater snorkeling observations and field experiments, the influence of food availability on foraging behavior, habitat use, and survival of age-0 Atlantic salmon (*Salmo salar*) during the critical first-summer growth period. While most feeding attempts were directed at drifting invertebrate prey, we found a higher rate of benthic feeding forays than previously reported for salmon. Greater food abundance was associated with higher feeding foray rates, more time allocated to foraging, occupancy of higher microhabitat velocities, and greater first-year survival between two study streams. Experimental drift reduction reduced drift foray rates and triggered a change in behavior to increased benthic feeding. In contrast, within a single stream, greater predicted invertebrate drift in high-velocity microhabitats (1 m^2) was unrelated to either microhabitat occupancy or drift foray rates of age-0 salmon. We suggest that, in some situations, salmonid foraging is related more directly to overall prey density than to the availability of high-velocity, high drift rate microhabitats. Differences in resource tracking (increased foraging, growth, or survival with increased food abundance) at different scales, along with the use of alternative predation modes, underscore the importance of considering behavior when linking food resources to growth and survival of stream salmonids.

Résumé : Nous avons fait des observations sous-marines par plongée avec masque et tube et des expériences sur le terrain pour étudier l'influence de l'abondance de la nourriture sur la recherche de nourriture, l'occupation de l'habitat et la survie du saumon atlantique (*Salmo salar*) d'âge 0 durant la première période estivale de croissance, une étape déterminante pour cette espèce. Presque toutes les recherches de nourriture ont visé des invertébrés en dérive, mais nous avons constaté que la recherche en zone benthique était plus importante que ce dont on avait antérieurement fait état à propos du saumon. Nous avons comparé deux cours d'eau et constaté que l'abondance supérieure de la nourriture était associée à une recherche de nourriture plus intense, à une période de recherche plus longue, à l'occupation accrue des microhabitats à courant plus fort et à une meilleure survie durant la première année. La réduction expérimentale de la dérive a entraîné une baisse des recherches d'organismes en dérive et déclenché un changement de comportement, les saumons se nourrissant davantage d'organismes benthiques. Par contre, dans l'un des cours d'eau, l'abondance accrue des invertébrés en dérive que nous avons prévue dans les microhabitats à courant fort (1 m^2) s'est révélée sans lien avec l'occupation des microhabitats et avec l'intensité de la recherche d'organismes en dérive par le saumon d'âge 0. Nous pensons que dans certaines situations la recherche de nourriture chez les salmonidés est plus directement liée à la densité générale des proies qu'à l'abondance des microhabitats à fort courant et à forte densité d'organismes en dérive. Les différences de recherche de nourriture (l'augmentation de l'intensité de la recherche, de la croissance ou de la survie avec l'abondance accrue de nourriture) observées à diverses échelles, de même que le recours à d'autres modes de prédation, montrent combien il est important de considérer le comportement lorsqu'on étudie la relation entre l'abondance de nourriture, la croissance et la survie des salmonidés dans les cours d'eau.
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Introduction

Predicting survival and growth of salmonid juveniles in different rearing environments is a long-standing goal of fisheries research and management. Growth and survival are quite variable in the field (e.g., Bjornn and Reiser 1991; Bley and Moring 1988), and several studies suggest that underlying variation in invertebrate biomass, production, or drift rate causes some of this variation (Bjornn and Chapman 1968; Cada et al. 1987; Richardson 1993; Filbert and Hawkins 1995). Yet, despite its potential importance, very few studies directly link food availability to foraging behavior or incorporate food availability in models of habitat suitability (Fausch et al. 1988).

The relationship between food availability and stream salmonid foraging, growth, and survival remains unclear for several reasons. First, physical habitat features have been the focus of most studies of habitat suitability or rearing capacity of salmonid streams (Fausch et al. 1988). This focus downplays the potential importance of food and the fundamental interaction between food and other habitat attributes that may determine overall habitat quality. For example, one common physical habitat measure, current velocity, affects potential prey encounter rates (Bjornn and Chapman 1968; Smith and Li 1983; Hill and Grossman 1993) for juvenile salmonids, as well as abilities to detect and capture prey items (Hughes and

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Table 1. Summary of physical habitat characteristics and Atlantic salmon survival (May–August) in Hancock (low-survival) and West Branch (high-survival) study sites (survival data from Newbrough et al. 1995).

	Hancock Branch	West Branch
Gradient (%)	1	1.5
Width (m)	11.2	10.7
Depth (m)	18.3	20.1
Velocity (cm·s^{-1})*	25 (7.2)	27 (6.0)
Substrate size (cm)	15	17
Streamside land use	Field, forest	Field, forest
Salmon survival (%)*	14 (5.6)	61 (18.7)
n (years)	7	4

*Values are mean with SE given in parentheses.

Dill 1990; Hill and Grossman 1993) and maintain position against the force of the current (Fausch 1984). Second, most prior studies (Cada et al. 1987; Stradmeyer and Thorpe 1987; Erkinaro and Niemala 1995; Filbert and Hawkins 1995) have been based on correlative analyses between food abundance (usually estimated indirectly or measured sporadically) and performance (generally standing stock density or, within a stream, microhabitat use), which are unable to differentiate clearly effects of food from effects of physical habitat. These studies rarely have attempted to relate differences in food abundance to direct use by salmonids via diet analysis or observations of foraging behavior.

Finally, the behavioral strategies of foragers may strongly influence the relationship between food abundance and food consumption rates (Stephens and Krebs 1986). Foraging theory predicts that for sit-and-wait predators (such as drift-feeding salmonids), which are unlikely to affect prey abundance within their foraging area, consumption rates should be closely correlated with prey abundance. However, changes in prey abundance may cause predators to switch to alternative prey resources, or adjust the time or area in which they spend foraging, without changing foraging rates. As salmonids may alter their foraging behavior in response to changes in either habitat or food abundance (Grant and Noakes 1987; McLaughlin and Grant 1994), directly linking availability to use is crucial in understanding effects of food on foraging, growth, and survival.

Our study examines the relationship between food availability, foraging, habitat use, and first-summer survival of age-0 Atlantic salmon (*Salmo salar*). First, we compare food abundance and salmon foraging behavior between two streams that differ largely with respect to first-year salmon survival. We use these data to examine the prediction that overall foraging activity (e.g., percentage of time spent feeding and feeding rates) will be greatest in the site with higher food abundance and higher survival. Second, we measure behavioral responses of salmon to a field manipulation of drifting invertebrates in several streams. We separate food abundance from other physical habitat characteristics and test whether a decrease in drift abundance results in a decrease in drift feeding forays and an increase in benthic feeding forays. Third, we examine the relationship between food, habitat selection, and foraging behavior at different microhabitats within each study stream. We derive an empirical relationship between invertebrate density and current velocity in situ and test whether

salmon select for microhabitats within each stream where current velocities are likely to produce the greatest food abundance. We also test whether overall foraging activity (e.g., percentage of time spent feeding, feeding foray rates) is greatest in high current velocity, high food abundance microhabitats. This is the first study to assess simultaneously the relation of food to both habitat selection and foraging behavior for salmon occupying different positions within a stream and is unique in its combination of measures of food abundance with foraging behavior and experimental manipulations in situ.

Methods

We studied age-0 Atlantic salmon in several central Vermont rearing streams in the Connecticut River drainage, which has not supported natural salmon reproduction in the 100+ years since construction of major hydroelectric dams on the river's mainstem (Stolte 1982). Salmon are stocked as first-feeding fry at ≈20–25 mm total length in May (McMenemy 1994) at a density of 30/100 m², and reach ≈75 mm by the end of August. Spring through summer survival of age-0 salmon varies among tributaries from <15% to >80%, averaged over several stocking seasons (Newbrough et al. 1995). Salmon in these streams are stocked at approximately the same size and time, come from the same broodstock, and are reared under the same hatchery conditions. Thus, site-specific differences in foraging, growth, and survival result from site characteristics rather than genetic or maternal differences.

Food and foraging in a high- versus a low-survival stream
We sampled invertebrates and conducted behavioral observations of age-0 salmon in summer 1993 in two physically similar tributaries of the White River, Vermont, U.S.A. (Table 1), that differ primarily with respect to age-0 salmon survival. Both tributaries are medium-gradient, fourth-order streams, with an average width of 11 m during the summer. Riparian land use is a mixture of agricultural, residential, and forest. Fish communities at the two sites consist of naturalized populations of rainbow trout (*Onchorhynchus mykiss*) and brown trout (*Salmo trutta*); native brook char (*Salvelinus fontinalis*), blacknose dace (*Rhinichthys atratulatus*), longnose dace (*Rhinichthys cataractae*), and slimy sculpin (*Cottus cognatus*); and stocked Atlantic salmon. Study sites consisted of a single 200-m section of each stream that also is used as an index site by state and federal agencies in their assessment of juvenile Atlantic salmon survival. Average first-summer survival of Atlantic salmon since the initiation of stocking unfed fry in the West Branch site (hereafter the high-survival site) for the years 1990–1992 was 62% and for 1993 was 80%. Survival at the Hancock Branch site (hereafter the low-survival site) averaged 18% from 1988 to 1992 (Table 1; Newbrough et al. 1995). Survival is defined as age-0 density determined from electrofishing censuses conducted in late August, expressed as a percent of initial stocking density and determined jointly by rates of mortality, immigration, and emigration.

Snorkeling observations were made at three different times (termed "sampling periods" from June to August, 1993. Each sampling period lasted for three or four consecutive days within no more than a 6-day period and consisted of observations of 20–27 different fish at each site, for a total of 146 individuals. This design was necessary to provide a sufficient sample size (i.e., we could not observe enough fish in a single day) and enabled us to avoid sampling during high water or storms, yet ensured that all fish were observed at roughly the same time during the season and under similar environmental conditions. Sampling periods at each site were spaced at 3- to 4-week intervals.

On each day of sampling, observations were made within three time intervals, early (08:30–10:30), middle (11:30–13:30), and late

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(14:30–16:30) day, which enabled us to test for differences in foraging behavior at different times of day. We chose these times because our preliminary surveys indicated that fish were largely inactive before 08:00 and after 17:00. Fish were selected for observation using a protocol that randomized diver entry points and search directions to ensure that observations were made on a random sample of individuals and to minimize the possibility of repeated observations of the same fish, assuming that different fish occupied different locations in the stream, similar to procedures used by DeGraaf and Bain (1986). Each age-0 salmon was observed for 5–20 consecutive minutes. During the observation period, we recorded two types of behavioral data: (*i*) all occurrences of feeding forays and (*ii*) the primary behavior observed in a 5-s intervals taken once every minute (categories described below). Following the observation period, the diver marked the salmon focal point (the point on the substrate on or over which the individual fish was most frequently observed (DeGraaf and Bain 1986)) using an anchored float.

A number of behaviors, including feeding forays (drift or benthic), station holding, aggression, and seeking cover were recorded, but only feeding behaviors are discussed here. A drift feeding foray is a directed movement upward the water column, followed by a return to the original position or another frequently used station. During a drift feeding foray, the fish's mouth does not make contact with the substrate. A benthic foray is a directed movement downward toward the benthos followed by a return to the original position or another frequently used station. The fish's mouth does contact the substrate in a benthic foray. We were unable to determine whether a food item was actually ingested during a foray; however, we could easily distinguish between behaviors obviously directed at food items and other more unfocused behaviors. For this reason, we record feeding behaviors as feeding-foray rates, rather than feeding rates, a designation used in several previous studies (McLaughlin and Grant 1994; Keeley and Grant 1995).

Results are reported as drift or benthic feeding foray rates (number of forays per minute). We also recorded total forays (drift + benthic forays), and the relative proportion of drift and benthic forays per individual fish, represented as

$$(1) \qquad RP = \frac{D}{D + B}$$

where RP is the relative proportion of drift forays, D is the total drift forays, and B is the total benthic forays.

We constructed time budgets for each fish by compiling the primary behaviors observed during the final 5 s of each complete minute of the observation period (e.g., in a 20-min observation period, there would be 20 behavioral observations recorded). When two different types of behavior were recorded during the 5-s subinterval, each was given half as much weight in the calculation of the time budgets.

To compare foray rates, RP values, and percent time spent foraging between sites and seasons, we conducted separate *t*-tests, with site and season as grouping variables. RP values and time spent foraging parameters were arcsine-transformed prior to analysis. Where we observed no time-of-day differences, fish observations were pooled for site and season comparisons.

To assess food abundance, we collected two drift and two benthic invertebrate samples at the conclusion of each behavioral sampling period. Samples were taken along lateral transects placed at randomly selected distances along the 200-m study reach. We used 0.3×0.3 m drift nets (125-µm mesh size) to obtain drift samples, and a Surber net of the same dimensions and mesh size for benthic samples. Samples were preserved in 75% ethanol. Invertebrates were sorted and identified to lowest feasible taxonomic level (generally to genus level, subfamily level for larval Chironomidae). We used invertebrate density as our measure of prey availability for age-0 Atlantic salmon. Analysis of a large invertebrate database (150 samples) collected from six salmon streams within the same river systems as our study sites found no significant differences in invertebrate size distributions between

different stream sites (ANOVA, $F_{[20,73]} = 0.63$, $p = 0.87$). Given similar size distributions, invertebrate density should represent adequately between-site differences in both prey number and prey biomass. Densities of both overall invertebrates and selected taxa are reported as number of individuals per square metre for benthos and, by dividing the total number of invertebrates by the volumetric discharge through the drift net, the number of individuals per cubic metre for drift.

Drift and benthic invertebrate densities from the high- and low-survival sites were compared with *t*-tests using sample means (pooled over two samples/season, collected on the same day at the end of the behavioral sampling period) for each season (early, middle, and late) as replicates. We compared total invertebrate densities and the densities of chironomid larvae and baetid mayfly nymphs, taxa which are particularly important in age-0 salmon diets (Folt and Parrish 1994; Allen 1940).

Drift manipulation

To test for effects of drifting prey abundance on foraging behavior of age-0 salmon, the density of drifting prey was experimentally reduced, while leaving benthic availability unchanged. The foray rates of individual fish were measured prior, during, and following the experimental reduction in drift densities. Manipulations were performed at three separate sites on third- or fourth-order tributaries of the West and White rivers. Two sites were on the West Branch of the White River (separated by 500 m), one of which was in our high-survival study site. We could not perform a manipulation at the low-survival (Hancock Branch) study site, as we were unable to locate stream sections with sufficiently high densities of age-0 salmon. The third site was on the Marlboro Branch of the West River. All experiments were performed between 08:30 and 12:00 within a 3-week period in August 1994.

Drift nets (125 µm mesh size; 30×30 cm wide) were placed across the stream in an array that maximized the removal of suspended material, including drifting invertebrates, from the water. A small portion of the total discharge always escaped the straining nets, and we could not remove drifting prey derived from areas directly adjacent to the foraging fish, downstream of the straining nets. To estimate the effect of the manipulations on drift density, we sampled drift before and during net placement using two drift nets placed at the downstream limit of the observation area (10 m downstream). To eliminate the effects of disturbance on our behavioral observations, these tests were conducted several days prior to the experiments but at the same time of day and under the same weather and flow conditions as the experiments. Drift density was reduced by approximately 60% downstream of the blocking nets ($p < 0.05$, $n = 3$, paired *t*-test).

Behavioral observations were made by divers using protocols detailed in the previous section. For each experiment, one or two divers randomly selected individual fish found within 1–10 m downstream of the blocking nets. After a brief acclimation period, fish were observed for 5 min, and we recorded all drift and benthic feeding forays. Following the initial observations, drift nets were inserted upstream of the observation area. We allowed 10 min following drift net placement to account for passage of any material disrupted by net placement activities, then randomly chose a new set of fish to observe while the nets were in place. Following these observations, we removed the drift nets and repeated the procedure with new fish to obtain after-treatment observations. Five to nine different fish were observed at each site during each observation period (prior, during, and after manipulation).

Differences in foraging behavior associated with drift exclusion were tested using a randomized block design, with site as a block and treatment (before-treatment control, after-treatment control, and treatment) as a main effect. To avoid pseudoreplication (artificial inflation of sample size caused by considering individual fish, and not experimental units, as replicates) we used mean foray rates for all fish in a given experimental and treatment group to make comparisons.

Effect of current velocity on food, foraging behavior, and microhabitat use

We tested whether fish occupied microhabitats where food was most abundant and whether foray rates were correlated with food abundance across microhabitats within a stream. We used measurements of current velocity in stream microhabitats (area 1 m^2) to determine the extent to which microhabitat velocity could serve as a surrogate for prey availability. We then tested for differences in predicted prey availability in occupied versus unoccupied microhabitats, and correlated prey availability to observed salmon feeding foray rates and percent time spent foraging.

To determine the relationship between microhabitat velocity and invertebrate abundance, we conducted a detailed study in 1992 at the high survival site (West Branch). Twelve drift and 20 benthic samples were taken at randomly assigned locations in late June and another 10 benthic and 10 drift samples were taken in mid-August. Current velocity measurements at each invertebrate sampling location were made with a Swoffer 2100^{TM} flow meter equipped with a 2-cm diameter propeller, at three depths (near-bed (within 2–3 cm of the stream bottom), middle (~0.6 of depth), and surface (just below the water surface)). The relationship between microhabitat velocity and invertebrate abundance was tested using correlation analysis, with water-column velocity (mean of pooled surface and middle velocities) as the independent variable and invertebrate abundance as the dependent variable. We used water-column, as opposed to near-bed, velocity in our analyses because of the fact that the majority of salmon drift feeding forays took place in the water column. All three velocity measures were strongly correlated (near-bed vs. middle: $R^2 = 0.68$, $p < 0.001$; near-bed vs. surface: $R^2 = 0.577$, $p < 0.001$; middle versus surface: $R^2 = 0.825$, $p < 0.001$).

To test for the effect of current velocity on habitat occupancy, we compared average velocities between microhabitats occupied and unoccupied by salmon at three sites. Comparisons were made once at each site, on a date between the middle- and late-season behavioral observation sampling periods. These measurements were taken separately from the behavioral observations. For each site, using the procedure developed in the behavioral study, we located 10–12 fish. For each fish, to represent the occupied microhabitat or salmon territory, we measured current velocity at 0, 25, and 50 cm from the fish focal point, aligned with the prevailing direction of flow, in four horizontal directions (directly in front, directly to the rear, to the right, and to the left) and at the three depths defined previously. After each fish was located, we randomly selected adjacent microhabitats 2 m from the occupied sites that were unoccupied by station-holding salmonids. A microhabitat was designated as unoccupied if no fish were observed there following 5 min of observation. If unoccupied, a center point, corresponding to a potential salmon focal point, was determined and microhabitat parameters were measured. Comparisons of occupied versus unoccupied sites were performed in three streams: the high- and low-survival sites, and a third stream, Greendale Brook, a third-order tributary of the West River, Vermont. At each site, we measured an equivalent number of occupied and unoccupied microhabitats. We used t-tests to compare mean velocities (mean of pooled surface- and middle-flow velocities) in occupied versus unoccupied microhabitats for each of the three streams. In addition, we compared variability among occupied versus unoccupied microhabitats using t-tests of mean coefficient of variation (CV) in velocity ($n = 3$ sites).

To correlate food availability with salmon foraging behavior, we measured current velocities within microhabitats occupied by a subset of the age-0 salmon observed in the behavioral study. We took velocity measurements (using the same array of locations around the fish focal point as described previously) on the first three fish observed in the early morning and the first three fish observed in the midday sampling bouts at each site, in all three seasons of the behavioral study. For each fish, we used the mean of combined mid-flow and surface current speeds as a surrogate for drift rate through the occupied microhabitat.

We used these microhabitat velocity and foray data to test (*i*) whether salmon occupied different microhabitat velocities in the high- versus low-survival site, (*ii*) whether salmon occupied different microhabitat velocities in different seasons, and (*iii*) whether foraging activity was correlated with microhabitat velocity. We tested for mean differences in occupied current speeds between sites and seasons using t-tests and differences in frequency distributions using Kolmogorov–Smirnov (K–S) two-sample tests with water column velocity as the dependent variable and site and season as grouping variables. We tested the relationship between foraging behavior (as foray rates and time spent foraging) and microhabitat velocity within each stream using regression, with microhabitat velocity (maximum, mean within a 25-cm radius of the salmon position, and mean within a 50-cm radius) as the independent variable and feeding foray rate as the dependent variable.

Results

Differences in invertebrate abundance between the two sites

Drift ($t_{[4]} = 2.932$, $p = 0.043$) and benthic ($t_{[4]} = 3.320$, $p = 0.029$) invertebrate densities were significantly greater at the West Branch (high-survival) than the Hancock Branch (low-survival) site (Fig. 1). The abundances of mayflies in the family Baetidae and midges in the subfamily Orthocladiinae, which are the invertebrate taxa most commonly encountered in the diet of age-0 salmon in these streams (Folt and Parrish 1994), were greater in the high-survival site, but differences were not significant.

Effect of site and season on foraging behavior

Over both study sites and all seasons, salmon spent 13 ± 1% (mean ± SE) of their time engaged in drift forays, at a rate of 1.5·min^{-1}, and 10 ± 0.9% of their time engaged in benthic forays, at a rate of 0.9·min^{-1}. We found no significant differences in foray rates or percent time spent foraging between early, mid-day, and late-afternoon time intervals (Table 2), allowing data from all time intervals to be pooled to test for differences between sites and seasons.

Feeding activity of age-0 salmon was generally greater at the high-survival, high-food site (Figs. 2 and 3). Drift (early: $t_{[50]} = 2.872$, $p = 0.006$; middle: $t_{[41]} = 2.622$, $p = 0.012$) and total (early: $t_{[50]} = 2.777$, $p = 0.008$; middle: $t_{[41]} = 2.418$, $p = 0.02$) foray rates and total percent time spent foraging (early: $t_{[50]} = 3.018$, $p = 0.004$; middle: $t_{[41]} = 2.11$, $p = 0.041$), were significantly greater at the high-survival site during the early and middle season sampling periods. Benthic foray rates were greater at the high-survival site during the late-season period ($t_{[49]} = 2.635$, $p = 0.011$) but did not differ between sites during the earlier periods. Salmon spent significantly more time feeding on drift in the high-survival site during the early season ($t_{[50]} = 2.102$, $p = 0.041$), but sites did not differ with respect to this parameter in the middle or late season. Time spent on benthic and total forays and the relative proportion of drift versus benthic forays (RP) did not differ between sites in any season.

Benthic foray rates were significantly greater in midseason than early season ($t_{[93]} = 3.071$, $p = 0.003$) or late-season ($t_{[92]} = 3.014$, $p = 0.003$) sampling periods. Reflecting these high midseason benthic foray rates, the relative proportion of

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Fig. 1. Mean drift and benthic invertebrate densities at the West Branch (high-survival) and the Hancock Branch (low-survival) study sites. Depicted densities are the pooled averages of two samples per season for early-, middle-, and late-season sampling periods. Densities are significantly greater for both total drift and benthos (*t*-test, $p < 0.05$, $n = 3$) at the West Branch (high-survival) site. Error bars are 1 SE.
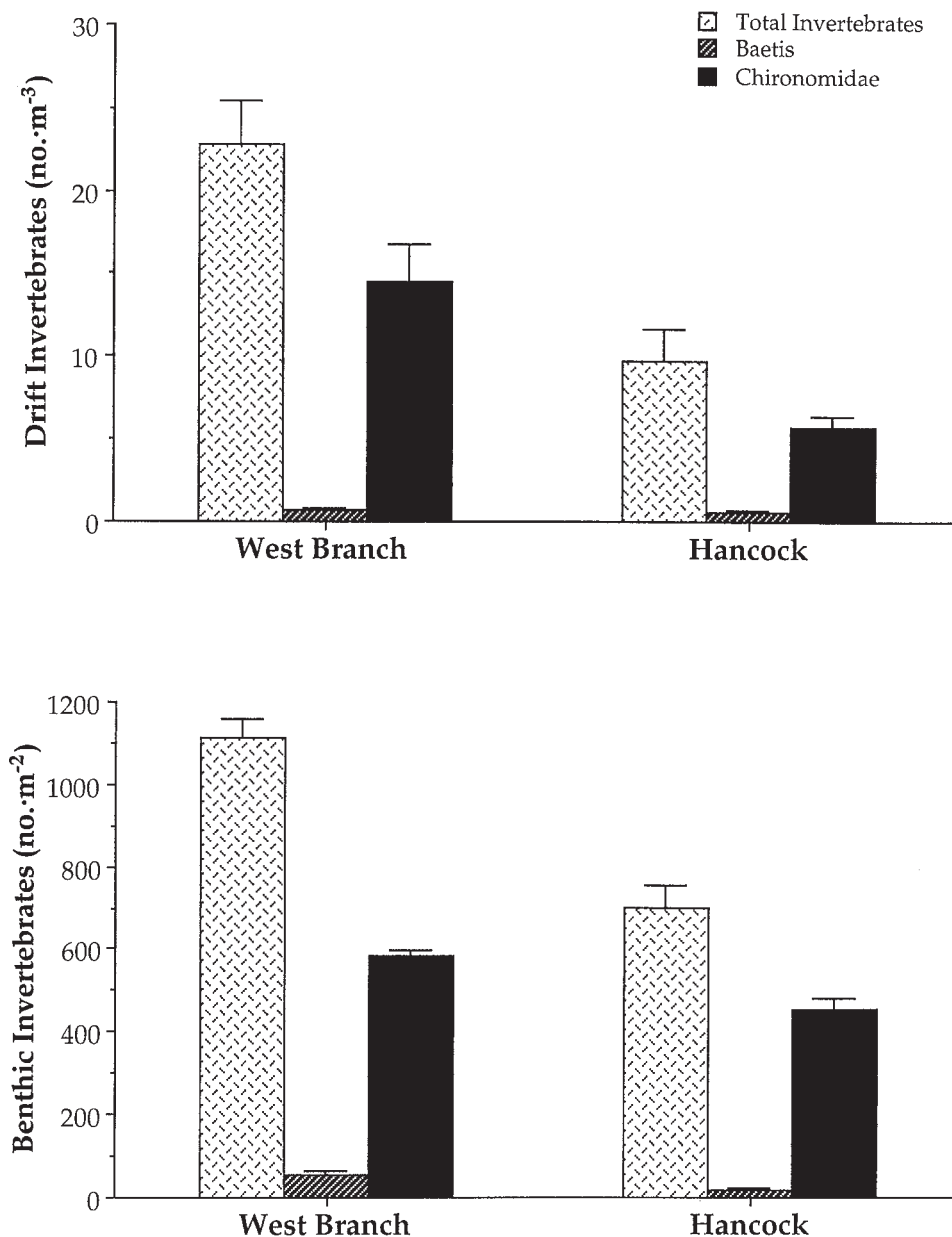

Table 2. Age-0 salmon foray rates (forays·min^{-1}).

Forays	Early	Middle	Late	*F*	*P*
Drift	1.54 (0.118)	1.69 (0.105)	1.33 (0.115)	2.668	0.073
Benthic	0.82 (0.093)	1.07 (0.083)	1.07 (0.091)	2.612	0.077
Total	2.36 (0.150)	2.76 (0.134)	2.41 (0.147)	2.456	0.09

Note: Values for foray rates are mean, with SE given in parentheses, at three time intervals (early, 08:30–10:30; middle, 11:00–13:00; late, 14:30–16:30). Differences between time intervals tested with ANOVA (df = 2, 128); observations are pooled over site and season.

drift forays (RP), was lower in the middle- versus late-season sampling period ($t_{[92]} = -2.185$, $p = 0.033$). Total foray rates were greater in the midseason than the early season but did not

differ between middle and late season or between early and late season. There were no differences between season in drift-foray rates and no seasonal differences in time spent on drift, benthic, or total forays.

Effect of manipulation on foraging

There was a decline in drift foray rates and an increase in benthic foray rates of age-0 salmon with experimental drift reduction (Fig. 4). Drift foray rates were lower during the manipulation (while invertebrate drift density was reduced) than either before- or after-treatment rates ($f_{[2,9]} = 32.05$, $p = 0.003$). Before- and after-treatment rates did not differ. In contrast, benthic foray rates increased during experimental drift

Fig. 2. Mean drift, benthic, and total foray rates (forays·min^{-1}) of age-0 Atlantic salmon at the West Branch (high-survival) and Hancock Branch (low-survival) study sites over the early-, middle-, and late-season sampling periods ($n = 146$ fish). Significant differences between sites are indicated by an asterisk; solid bars connect significantly different seasons. Error bars are 1 SE.
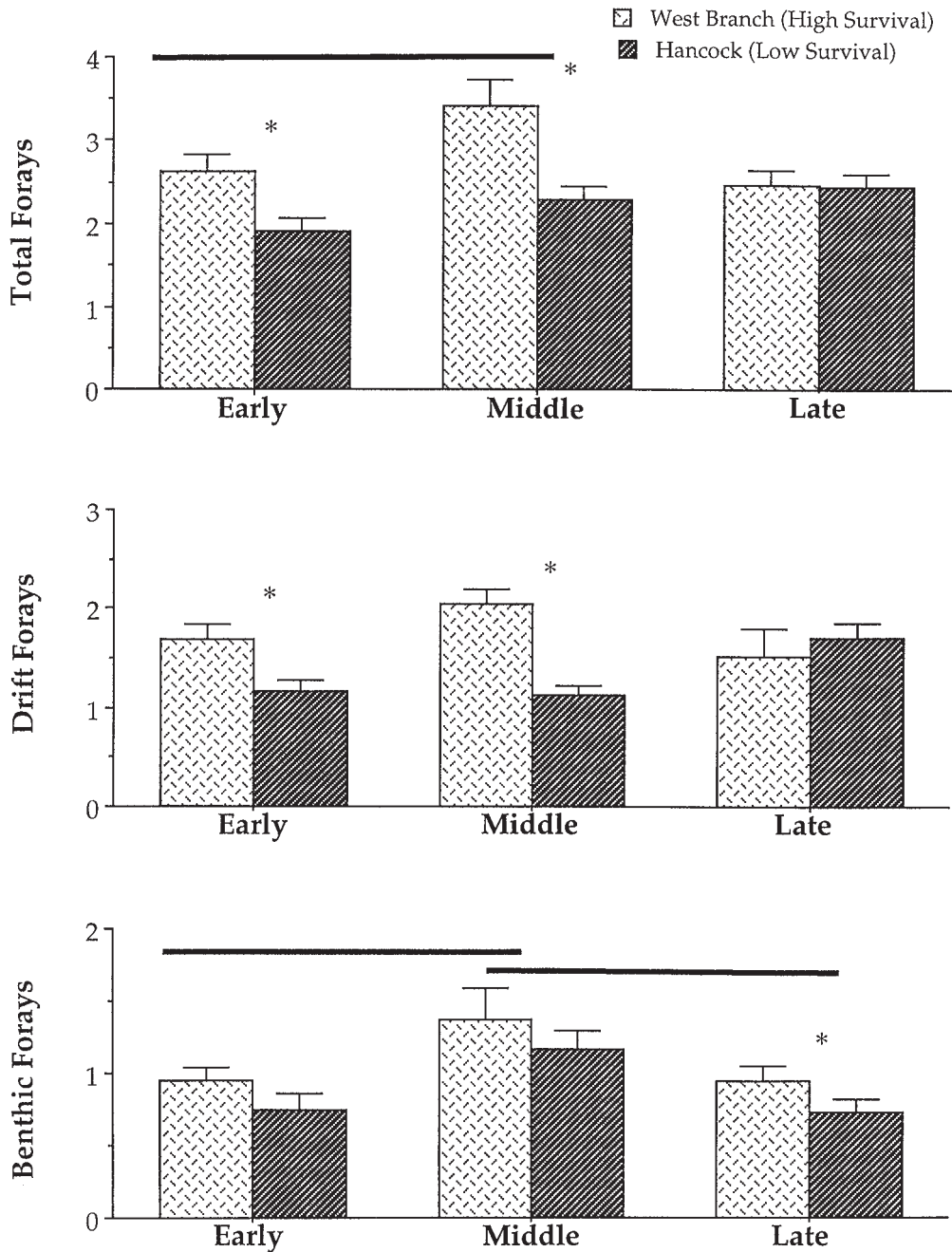
exclusion ($f_{[2,9]} = 10.94$, $p = 0.024$). Drift reduction significantly reduced total foray rates ($f_{[2,9]} = 24.851$, $p = 0.006$). There was a significant site effect on drift foray rate ($f_{[2,9]} = 7.07$, $p = 0.002$) but not on benthic foray rate.

Effect of current speed on food abundance, microhabitat preference, and foraging behavior

In the detailed invertebrate study, conducted at the high-survival site, invertebrate drift rate increased linearly with microhabitat velocity (average of middle and near-surface velocities; Fig. 5a), whereas benthic abundance showed no significant relationship with velocity (Fig. 5b). Results were similar (strong linear relationship between velocity and drift; no relationship between velocity and benthos) for both early season and late-season sampling periods.

In all study sites, salmon occupied moderate- to high-velocity, coarse substrate, riffle–run habitats, although many individuals were found near the tail end of plunge pools in relatively deep water. In the habitat occupancy study, we found no significant differences in mean middle or surface microhabitat velocities between occupied versus unoccupied microhabitats (Table 3) within each of the three streams, nor were

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Fig. 3. Mean drift, benthic, and total proportion of time spent foraging (time spent foraging/total time) of age-0 Atlantic salmon at the West Branch (high-survival) and Hancock Branch (low-survival) study sites over the early-, middle-, and late-season sampling periods ($n = 146$ fish). Significant differences between sites are indicated by an asterisk; solid bars connect significantly different seasons. Error bars are 1 SE.
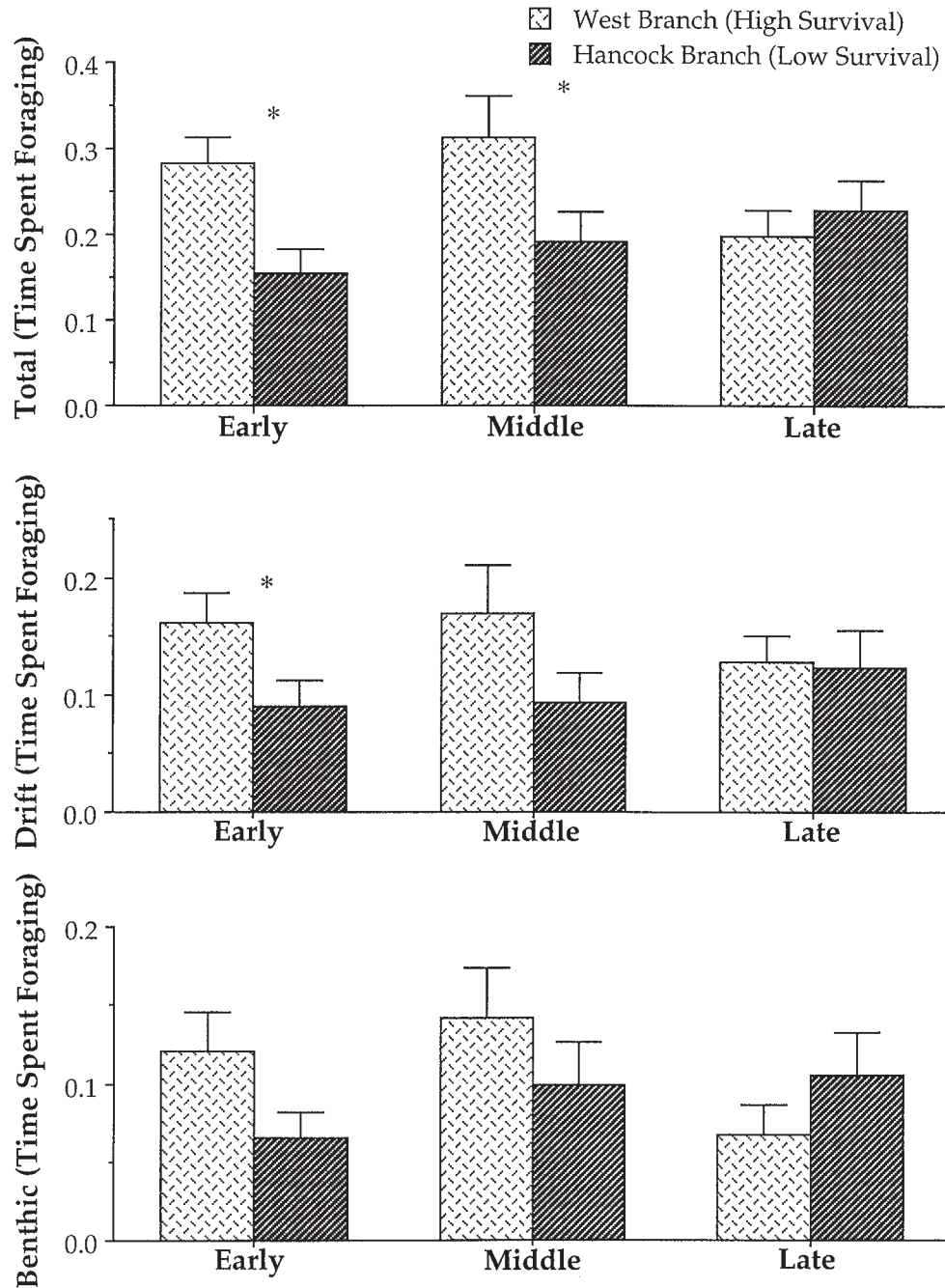
there any significant differences in near-bed velocities. There were no differences in either occupied or unoccupied microhabitats between the West Branch (high-survival) and Hancock Branch (low-survival) study sites, whereas both sites differed in both occupied and unoccupied microhabitats from the Greendale Brook study site. We observed greater variability (higher CV) with respect to mean microhabitat velocity among unoccupied microhabitats than among occupied microhabitats ($t_{[2]} = 4.137, p = 0.05$). In contrast to the habitat occupancy study, in the behavioral study, fish at the high-survival site occupied significantly higher velocity microhabitats than

those observed at the low-survival site (Fig. 5; $t_{[80]} = 3.134$, $p = 0.003$; K–S test, $p = 0.010$).

We found no relationship between drift feeding and current velocity in occupied microhabitats (Table 4). Drift foray rates were uncorrelated with either maximum or mean current velocity in both the low-survival (maximum flows: $n = 42$, $R^2 = 0.088, p = 0.056$; mean flows: $R^2 = 0.036, p = 0.226$) and the high-survival (maximum flows: $n = 40$, $R^2 = 0.001, p = 0.836$; mean flows: $R^2 = 0.013, p = 0.492$) streams. Similarly, proportion of time spent on drift foraging showed no significant relationship with current velocity.

Fig. 4. Effect of drift manipulation on mean drift and benthic foray rates (forays·min^{-1}) for age-0 Atlantic salmon. Drift foray rates were significantly lower ($f_{[2,9]} = 32.05$, $p = 0.003$) and benthic rates were significantly higher ($f_{[2,9]} = 10.94$, $p = 0.024$) when blocking nets were in place (During) than either before net placement (Before) or after net removal (After). Error bars are 1 SE.
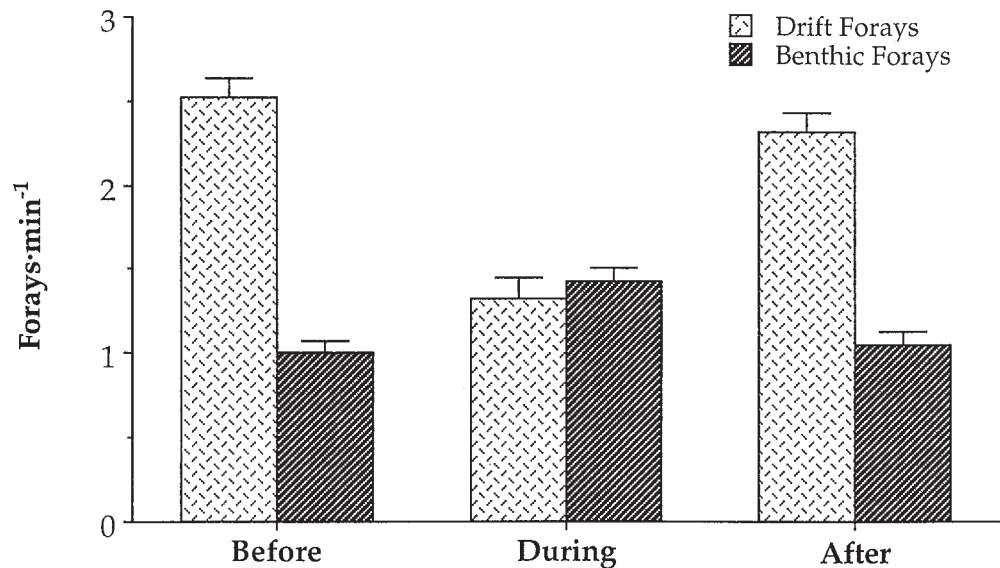

Table 3. Comparison of microhabitat current speeds (cm·s^{-1}; mean of combined surface and mid-depth velocity measurements within a 50-cm radius of an individual salmon or of an unoccupied focal point) in occupied and unoccupied microhabitats in three study streams.

	Occupied				Unoccupied			
	n	Mean (SE)	Range	CV	n	Mean (SE)	Range	CV
West Branch	11	33.5 (3.3)	20.9–46.4	27.9	11	33.2 (3.3)	5.1–53.5	46.4
Hancock Branch	10	41.5 (3.5)	28.2–51.3	19.4	9	32.1 (3.9)	10.7–52.0	48.6
Greendale	11	12.5 (3.3)	3.9–23.8	52.1	9	12.5 (3.7)	2.4–25.3	64.7

Note: Study streams were sampled once during August 1993. Mean current speeds were not significantly different between occupied and unoccupied microhabitats. Coefficients of variation (CV) were significantly different between occupied and unoccupied microhabitats ($t_{[2]} = 4.137$, $p = 0.05$).

Discussion

This is the first study to link explicitly food, foraging, and survival in juvenile Atlantic salmon and to support this link with a field manipulation of food availability. Juvenile salmon exhibited resource tracking (i.e., greater foraging rates and higher spring–summer survival with higher resource levels (Hart and Fonseca 1995)) between two streams, which differed largely with respect to food abundance. Greater overall food abundance (2.5 times greater) was associated with higher foray rates (26% greater) and more time spent foraging (36%) by salmon at the high-survival site in the early and middle season. The positive relationship between food abundance and foraging behavior was further supported by the strong reduction observed in salmon drift foray rates (1.5 times lower) when drifting prey abundance was experimentally reduced.

In our behavioral study, salmon at the low-survival site occupied a greater proportion of low-velocity microhabitats than at the high-survival site (Fig. 6) despite similar available microhabitat velocities (Table 1). Discrepancy between the habitat occupancy study, which found no difference in occupied velocities between sites, and the behavioral study are likely due to differences in the time periods over which the two studies were conducted. Lower current speeds at occupied microhabitats alone would predict lower food availabilities and

lower foraging rates for salmon at the low-survival site, even if overall prey abundances had been similar between sites. However, we found that foray rates were uncorrelated with current velocity within either of the two sites, suggesting that differences in microhabitat velocity alone were not the cause of these differences in foray rates. Instead, greater drift and benthic densities in the high-survival site appear to have resulted in greater food availability and generally greater foraging activity over the entire range of occupied microhabitats within the two streams.

These results have implications for the growth and survival of age-0 salmon in shallow second- to fourth-order rearing streams. From other studies, we know that prey densities and physical habitat conditions in our two sites characterize known variation in central Vermont salmon rearing streams (Folt and Parrish 1994). Hence, food availability across this region, may be a good predictor of overall age-0 salmon foraging success in situ. Further, based on the association between food, foraging, and salmon survival found in these two physically and geographically similar streams, we infer that food availability and foraging behavior of age-0 Atlantic salmon are likely to play an important role in explaining differential first-summer survival among similar rearing sites.

However, our ability to link food abundance to survival is strongly limited by lack of replication of high- and low-

Fig. 5. Effect of microhabitat velocity ($m \cdot s^{-1}$, mean of combined surface and mid-depth velocities) on (*a*) drift (no.$\cdot min^{-1}$) and (*b*) benthic invertebrate abundance (no.$\cdot area^{-1}$) at the West Branch (high-survival) study site for the early-season intensive invertebrate study, July 1, 1992. The regression of drift rate versus velocity is significant ($p < 0.001$, $n = 10$), and there is no significant regression of benthic density versus velocity ($n = 16$).
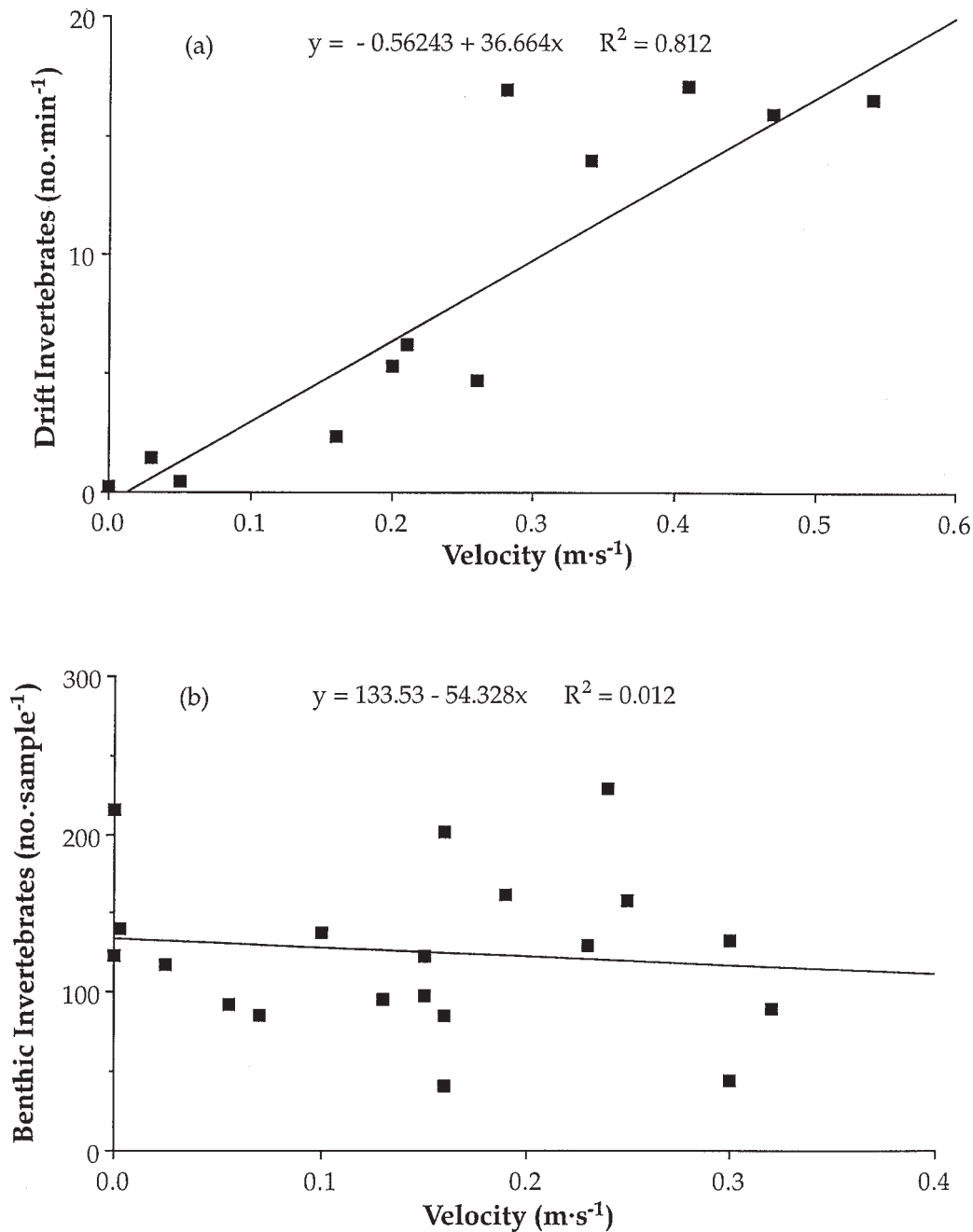
survival sites. A complete test of the effect of food and foraging on survival would require a large-scale manipulation of food availability at multiple, independent sites. A less severe limitation is that we and others (e.g., McLaughlin and Grant (1994) and Keeley and Grant (1995)) cannot distinguish successful from unsuccessful feeding attempts while conducting SCUBA or snorkeling observations in situ. We therefore cannot be certain that the significantly greater level of foraging activity we observed in the high-survival site necessarily resulted in greater consumption and energy gain.

In contrast to the resource tracking observed between streams (higher average feeding rates found with higher average food abundance), neither microhabitat occupancy nor foraging rates within streams were influenced by differences in drift abundance among microhabitats. This lack of correlation may be expected for several reasons. First, both habitat choice and foraging activity may appear uncorrelated with microhabitat velocity within sites if salmon occupy a relatively narrow range of microhabitat velocities in any specific location, or if the range of available velocities is low. Second, fish may not

Fig. 6. Frequency distributions of mean combined surface and mid-depth velocities within a 50-cm radius of salmon positions in the West Branch (high-survival) and Hancock Branch (low-survival) study sites. Observations are pooled over early-, middle-, and late-season sampling periods. Distributions (K–S test, $p = 0.01$) and means ($t_{[80]} = 3.134$, $p = 0.003$) were significantly different between sites.
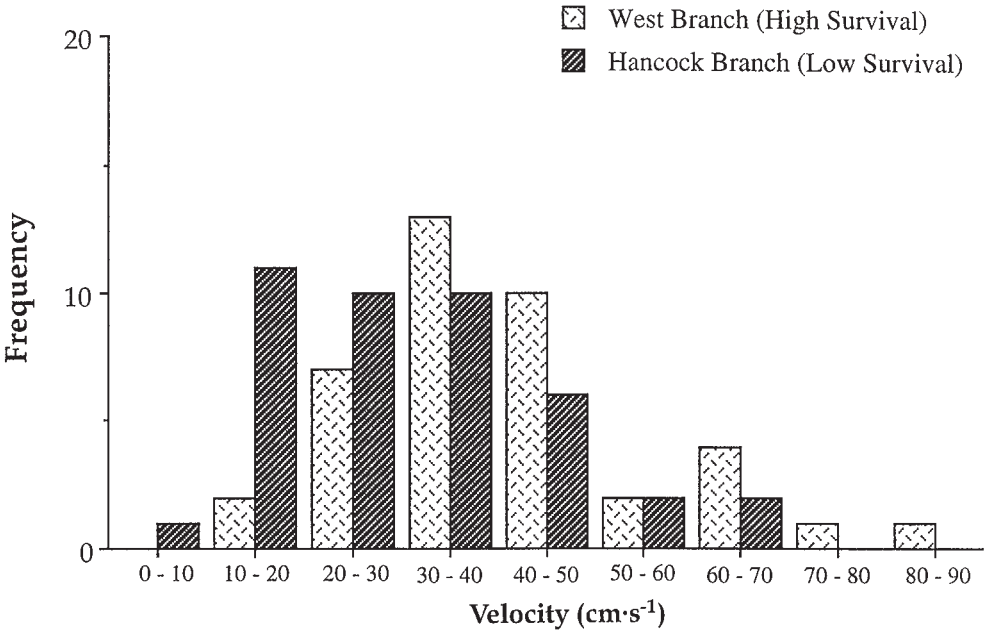

Table 4. Effects of microhabitat current speed (combined surface- and middle-depth velocities ($cm \cdot s^{-1}$)) on age-0 salmon foray rates and time spent foraging.

		Mean[a]			Mean (25 cm)[b]			Maximum[c]		
		R^2	t	p	R^2	t	p	R^2	t	p
West Branch	Foray rate	0.007	0.5	0.62	0.013	0.69	0.49	0.001	0.21	0.83
($n = 40$)	Time spent foraging	0.035	1.181	0.245	0.045	1.331	0.191	0.017	0.80	0.427
Hancock Branch	Foray rate	0.078	1.84	0.073	0.036	1.231	0.226	0.088	1.967	0.056
($n = 42$)	Time spent foraging	0.003	0.362	0.719	0.001	–0.234	0.82	0.056	1.545	0.13

[a]Mean velocity within a 50-cm radius of a forager.
[b]Mean velocity within a 25-cm radius.
[c]Maximum velocity within a 50-cm radius.

differentially occupy the highest velocity, highest prey abundance sites if they choose microhabitats largely on the basis of other parameters (e.g., depth, substrate, or the availability of cover from predators). Third, fish may actually avoid the highest velocity microhabitats in spite of high drift rates because high current speed can have negative effects on feeding efficiency (e.g., decreased prey detection and capture success (Hill and Grossman 1993, Hughes and Dill 1990)) and can carry high energetic costs of swimming (Fausch 1984).

Our results provide some support for the first and third of these mechanisms. While there were no significant differences in mean occupied and unoccupied microhabitat velocities in three streams, salmon consistently selected a narrower range of velocities than available (mechanism 1) (Table 5). Fish selected against lower microhabitat velocities in all three sites (mechanism 1) and against high microhabitat velocities (mechanism 3) in two of three sites. Consistent with these findings, in a study of six Vermont rearing streams, Newbrough et al. (1994) found no clear relationship between microhabitat velocity and gut contents of age-0 Atlantic salmon. Similarly, McLaughlin and Grant (1994) found no difference in dry

weights of total prey consumed by newly emerged brook char occupying high- versus low-velocity microhabitats. With respect to microhabitat use, previous studies have yielded equivocal results. Some studies have found that juvenile salmon preferentially use the highest available microhabitat current speeds (with the highest drift rates) (Wankowski and Thorpe 1979; Bagliniere and Arribe-Moutounet 1985), while others have found no preference for high current speed locations (DeGraaf and Bain 1986; Heggenes and Saltveit 1990; Newbrough et al. 1994).

Our combination of approaches revealed three other aspects of age-0 salmonid foraging behavior that previously have not been addressed. First, we found that juvenile Atlantic salmon spent considerably more time engaged in benthic foraging than has been estimated in previous studies (Stradmeyer and Thorpe 1987; Keeley and Grant 1995). The results of the field manipulation further underscore the potential importance of benthic feeding to this species. Age-0 Atlantic salmon increased their rate of benthic forays when drift availability was reduced, indicating they may compensate, in part, for reduced drift availability by foraging on benthic prey.

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Second, we found less variation in foraging behavior over the season than may have been expected, given the change in growth and body size of juvenile salmonids that occurs during the critical first summer. Overall differences in foray rates between sites and in the relative allocation of effort between benthic and drifting prey were similar during all three sampling periods. The main reason we may have found little variation is that our first observations were taken on 28 June. These individuals were stocked 6–8 weeks earlier and already had undergone considerable growth and acclimation to the stream environment. It is likely that observations early in the first season may reveal greater differences in behaviors. However, high stream discharge that characterizes these streams in the spring combined with smaller fish make this a difficult season to observe fish in situ.

Third, we observed that drift and total foray rates were greater at the high- versus low-survival site in the early and middle-season sampling periods but appeared to converge in the late season (Figs. 2–3). Previous studies (Metcalfe et al. 1986) indicate that foraging behavior of Atlantic salmon toward the end of the summer may show considerable intrapopulation variation. They found that feeding motivation of juvenile salmon (the probability of detection, attack, and capture of prey items) in a laboratory study declined towards the end of the summer, regardless of food availability, for those fish that did not migrate to the sea the following spring. In Connecticut River tributary streams, few first-year fish migrate (McMenemy 1994), and convergence of foray rates between sites in the late season may then be expected if feeding motivation is sufficiently decreased.

Overall, our results argue for the importance of food resource availability in consideration of salmonid habitat suitability. Existing models, which do not explicitly consider food resources, would be unable to predict survival differences between our study streams. In addition, the link between foraging and food availability suggests that observations of foraging behavior may provide an assessment of resource levels that is more relevant and easier to quantify than traditional invertebrate sampling. Our results also indicate that, in some situations, differences in overall prey density between streams or stream reaches may be more directly related to salmonid survival than differences in the availability of high current speed, high drift rate microhabitats within streams. The potential effect of microhabitat velocity on capture success and the use of alternative predation modes further underscore the importance of individual behavior in linking resources to growth and survival of stream salmonids.

Acknowledgments

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