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FAVORABLE FORAGING LOCATIONS FOR YOUNG ATLANTIC SALMON: APPLICATION TO HABITAT AND POPULATION RESTORATION

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Abstract. Declines in the populations of salmonid fishes have generated major interest in conservation and restoration of wild populations and river habitats. We used a foraging-based model, combined with field observations and surveys, to predict individual habitat use, and to assess the effects of stream habitat conditions and management practices on the potential for reestablishing Atlantic salmon, *Salmo salar.* Using a model based on a simple trade-off between increasing prey encounter rate and decreasing salmon capture success with increasing stream current velocity, we predicted favorable foraging locations for salmon in their first (age-0) spring and summer. We tested, in six streams, whether (1) salmon preferred locations (=microhabitats) that were predicted to yield high consumption rates, (2) salmon growth and survival was greater in streams with a greater proportion of preferred, profitable, microhabitats, and (3) stream habitat remediation (introduction of large in-stream structures such as large woody debris) increased the availability of microhabitats found to be preferred by salmon, and energetically profitable.

Salmon early in their first season (May–June) were predicted to obtain the highest consumption rates (within 10% of maximum) in microhabitats with a narrow range of relatively slow current velocities (0.08–0.18 m/s). In contrast, later in the season (July–August) fish were predicted to obtain highest consumption rates over a wide range of fast current velocities (0.21–0.57 m/s). Salmon in both the early and late seasons showed strong preferences (use in proportion to availability) for microhabitat in velocity categories predicted to provide high consumption. Streams with the greatest proportion of preferred early-season, but not late-season, microhabitats retained a higher proportion of salmon as measured at the end of the first summer. Stream habitat remediation increased the amount of preferred early-season microhabitat and did not negatively affect invertebrate prey abundance, or the amount of preferred late-season microhabitats. Thus, the availability of favorable foraging areas for juveniles significantly improves the retention of salmon during the critical first summer, and stream remediation provides better foraging habitat during this important period. Our results are encouraging for broader application to identify sites that show promise for salmon reintroduction, and to help guide restoration of particular sites to provide suitable habitat.

Key words: aquatic invertebrates; foraging-based habitat models, habitat preference; Salmo salar; salmon restoration; stream habitat; stream restoration; Vermont, USA.

INTRODUCTION

The Atlantic salmon (*Salmo salar*), like many other fishes in the family Salmonidae, has been eliminated from much of its former range, and dramatically reduced in abundance where it is still found. Atlantic salmon originally occurred throughout the North Atlantic region (Mills 1991). In New England, human activities eliminated the species from all but several small drainages in northern Maine (Moffitt et al. 1982) more than 150 yr ago. Like other salmonids, the Atlantic salmon is an important economic and cultural resource (Mills 1991), and may play a key role in stream and river ecosystems (Power 1990, Schuldt and Hershey 1995, Bilby et al. 1996). As a consequence,

salmonid decline has generated public interest in conservation and restoration of wild populations and river habitats (Allendorf et al. 1997).

Atlantic salmon restoration has been underway in New England for 20 years. In the Connecticut River basin, hatchery-reared fry are stocked into former natal tributaries (U.S. Atlantic Salmon Assessment Committee 1996), where they spend 1–3 yr before migrating to the ocean. Overall growth during the stream territorial phase is thought to affect success during migration and while at sea (Bjornn and Reiser 1991). However, major changes in physical and biological conditions over the last century (Moore et al. 1997) make it difficult to determine which streams are suitable for restoration. Rearing streams in the Connecticut River basin monitored over the past 10 yr (McMenemy 1995) differ greatly in first-year retention of salmon (from

≤20% to ≥60%; Newbrough et al. 1994). Understanding the causes of this variation should help with the identification of sites that show promise for salmon reintroduction, and guide restoration of particular sites to provide suitable habitat.

Most attempts to predict salmonid production rely on empirical correlations between fish abundance and physical habitat variables (Bovee 1986, Fausch et al. 1988). Yet, correlation-based models generally perform poorly when applied to streams other than those for which they were developed (Fausch et al. 1988, Bourgeois et al. 1996). These models are not based on the mechanisms by which habitat change affects individual performance, which may explain why their predictions fail. They also focus almost exclusively on physical habitat characteristics, which may not be the most important determinants of fish production; numerous studies show that biotic factors such as prey availability (Cada et al. 1987, Filbert and Hawkins 1995, Poff and Huryn 1998) strongly influence salmonid distribution and abundance.

An alternative to using correlation-based models is to construct models based on mechanisms relating particular habitat features to fish preference, growth, and survival. Foraging-based models have been developed for a number of drift-feeding stream fish species (Fausch 1984, Hughes and Dill 1990, Hughes 1992, Hill and Grossman 1993, Baker and Coon 1997). In these models, prey encounter rates increase, while capture success decreases and energy costs increase, with increasing microhabitat current velocity. Maximum energy gain is predicted at intermediate velocities, and fish are expected to preferentially occupy these microhabitats. Baker and Coon (1997) found that optimal habitat predicted by correlation-based and foraging-based models differed significantly for juvenile brook trout (*Salvelinus fontinalis*), and they argued that the foraging-based model provided a more accurate representation of habitat quality. Hughes (1998) also used a foraging-based model to successfully explain changes in fish size along a longitudinal stream gradient as a function of habitat, streamflow, and food availability.

If foraging models are robust across a range of situations, their simplicity makes them attractive for application to pressing issues in habitat management and conservation. For example, many stream-improvement projects seek to increase fish production by restoring large woody debris and other large structural elements to stream channels. While successful in some cases (Hunt 1976, Hunt 1988, Moore and Gregory 1988, Riley and Fausch 1995), Kellerhals and Miles (1996) found less than half of the 99 restoration projects they reviewed met biological goals. The shortcomings of these projects may arise from a failure to approach the question mechanistically. The presence of large structure tends to decrease current speed (Riley and Fausch 1995), which foraging models predict affects fish energy gain and performance. However, the precise ef-

fects on fish performance depend on specific relationships between fish size or life-stage, and actual current speeds and prey abundance, so each system and fish stage must be evaluated individually. Structure additions may also affect invertebrate prey communities, but the overall direction of such effects is not well established; addition of large structure has increased, decreased, or had no effect on different types of invertebrates (Molles 1982, Burgess and Bider 1984, Wallace et al. 1995). Applying foraging-based models to predict the effects of stream-structure addition on salmonid performance requires measuring impacts on both physical habitat and invertebrate communities (Coutant 1996).

Our goal was to take a multi-stream, multi-period approach to test the general applicability of foraging models to assess habitat quality, and to evaluate their potential value for management and conservation of Atlantic salmon. First, we developed a simple, foraging-based, microhabitat selection model parameterized for juvenile Atlantic salmon (age-0), and tested whether it accurately predicted habitat use and preference of salmon in six important rearing tributaries with known differences in first-year retention (i.e., survival plus immigration [Elliott 1985]). Second, we tested whether reaches with a greater proportion of suitable habitat retained a higher proportion of the salmon originally stocked there, and had higher per capita growth rates, over their first summer. Third, we tested whether ongoing stream-restoration practices successfully increased availability of preferred foraging locations (i.e., produced good habitat), and therefore were likely to improve overall fish performance.

METHODS AND RESULTS

After a brief introduction to the study system, we provide the methods and results for the development of the habitat-selection model. This is followed by the methods and results for a field test of the model's predictions of habitat preference. Finally, we present the methods and results for two applications of the model, which test whether habitat quality as predicted by the model is (1) a good predictor of salmon growth and retention in situ, and (2) enhanced by specific habitat manipulations (large-structure addition).

Study system

In the Connecticut River basin (USA), hatchery spawning of returning adult salmon provides the source of eggs and fry for the restoration program. Unfed fry are stocked into 2nd–5th order tributaries in the spring, just after they have absorbed their yolk sacs and are ready to begin feeding. Stocking densities are ~30 fish per 100 m² of rearing habitat, (shallow habitat dominated by coarse gravel, cobble, and small-boulder substratum (J. McMenemy, *personal communication*). Most rearing streams consist of this general habitat type (Newbrough et al. 1994, McMenemy 1995). Fry av-

TABLE 1. General characteristics of study sites (from habitat surveys, S. Roy, *personal communication*, and Newbrough et al. [1994]). The sites were on 3rd- and 4th-order streams in the White River and West River drainages of Vermont, USA.

Site		Age-0 salmon retention	Stream					
Type	Name		Order	Gradient (%)	Width (m)	Structures added	pH	Temp. (°C)
Index	Flood	0.31	3	NA	8	···	NA	15.4
	Marlboro	0.51	3	1.43	7	···	7.2	14.6
	Utley	0.54	3	1.2	6	···	7.3	15.4
	BG	0.38	3	1.35	7	···	7.4	14.7
	Hancock	0.16	4	1.2	10	···	7.0	15.1
	Tweed	0.12	3	1.25	8	···	7.2	14.1
Manipulation	Greendale	NA	3	NA	6	1991	NA	NA
	Tabor	NA	2	NA	4	1989	NA	NA
	West Branch	NA	4	1.5	11	1988	NA	NA
	Brandon	NA	3	1.5	8	1990	NA	NA

Notes: Index sites, maintained by the Vermont Department of Fish and Wildlife, were used to test microhabitat preferences and habitat vs. growth/survival correlations. Manipulation sites were used to test the effects of large-structure addition on foraging microhabitats. NA = not available.

erage 20–25 mm standard length (SL) when stocked (McMenemy 1995), and reach 70–85 mm SL by August.

The consistent, repeatable differences in age-0 salmon retention (=number of individuals sampled in August/number of individuals stocked into the reach in May) across stocking sites was a major motivation for our study. Six study streams were selected to span this wide range of variation, with retention in these streams ranging from <15% to >50% averaged over 4–7 yr of annual censuses (Table 1).

Habitat-selection model

Methods.—Our foraging model predicts the consumption rate by drift-feeding salmon (G; prey/s), as the product of prey encounter rate (P; prey/s), and the proportion of prey detected and captured (C) (Fig. 1a):

$$G = P \times C. \tag{1}$$

For drift-feeding fishes, P is determined by the density of drifting prey (D; no. prey/m^3), the area of the feeding territory perpendicular to streamflow (A, in square meters), and the current velocity (V; m/s) in the feeding territory:

$$P = D \times A \times V. \tag{2}$$

In natural streams with turbulent flow, rapid mixing tends to homogenize drift densities among locations (Everest and Chapman 1972, Hart et al. 1991). When territory area is constant for a given fish size (Grant and Kramer 1990) supply rate can then be simply expressed by regressing P on V, yielding

$$P = a \times V \tag{3}$$

where a is the slope of the line representing a statistical summary of $D \times A$, with origin set at zero, as zero flow equals zero prey supply. Capture success (C), the percentage of prey items encountered that are detected and captured by the forager is modeled as a negative

linear function of current velocity for a given size of fish foraging at a given temperature:

$$C = -b \times V + c \tag{4}$$

We used a linear function as the simplest description of the negative effect of increasing current velocity on capture success, in the absence of a theoretical mechanism specifying a particular function for this relationship (also see *Results,* below, and Fig. 2a).

The relationship between predicted rate of prey intake (G) and current velocity (V) results in a single humped (Fig. 1b) velocity–consumption curve. Consumption rates are predicted to peak at intermediate current velocities, which salmon should then preferentially select.

Our model has the simplifying assumption that energy costs do not significantly influence microhabitat selection. Both Hughes and Dill (1990) (Arctic grayling, *Thymallus arcticus*) and Hill and Grossman (1993) (rainbow trout, *Onchorhynchus mykiss,* and rosyside dace, *Clinostomus funduloides*) include energy costs of maintaining station against the current in their models. We omit these costs for three reasons. First, Atlantic salmon generally do not swim actively to maintain station. Instead, they place their large, wing-like pectoral fins against the substrate to hold station without active swimming (Kalleberg 1958, Arnold et al. 1991, Keeley and Grant 1995). Arnold et al. (1991) found that the current velocity required to initiate active swimming to maintain station for Atlantic salmon was considerably higher (~50 cm/s) than the near-bed velocities we observed for salmon holding station during our study (Newbrough et al. 1994). Second, extensive behavioral observations of juveniles in our study streams indicate that most of their time was spent resting on the substrate without swimming while waiting for drifting prey (Nislow et al. 1998). Longnose dace (*Rhinichthys cataractae*), which also use their pectoral fins to maintain station, showed little or no
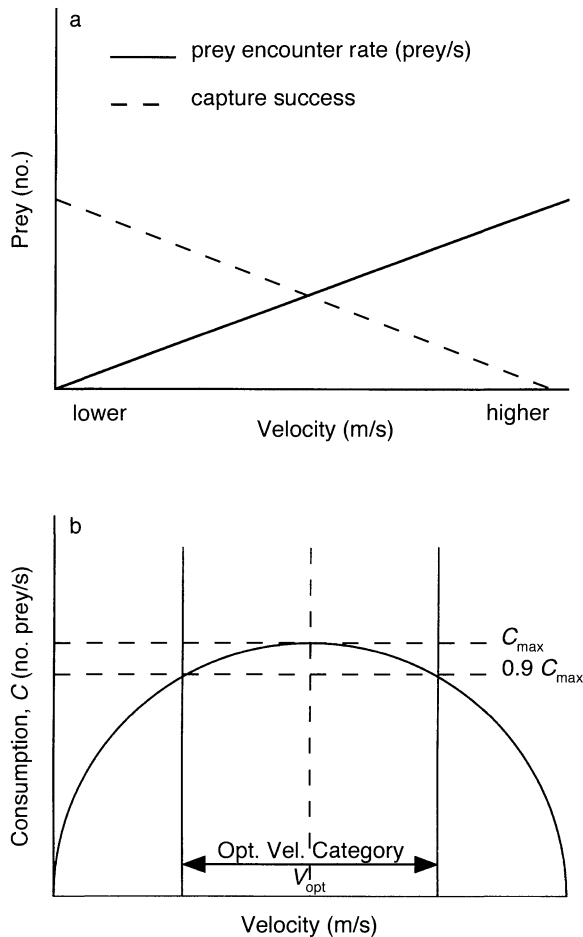
FIG. 1. Theoretical relationship between current velocity within a foraging territory and (a) capture success (prey captured/prey encountered) and prey encounter rate (prey/time), and (b) predicted consumption (number of prey consumed/time) for a drift-feeding fish. The optimal-velocity category for a velocity–consumption curve is here defined arbitrarily by velocities yielding within 10% ($0.9 \times C_{max}$) of the predicted maximum consumption rate, C_{max}. The optimal velocity category is the range shown by the arrows between the two solid vertical lines; V_{opt}, the velocity yielding maximum consumption rate, is shown by the vertical dashed line. The designation scheme is adapted from Hill and Grossman (1993).

increase in metabolic rate with increasing velocity in a laboratory flume (Facey and Grossman 1990). Finally, even for actively swimming species such as rosyside dace and rainbow trout, Hill and Grossman (1993) found that increased metabolic costs of station-holding as a function of current velocity were far outweighed by current-velocity effects on capture success. As a consequence, their model predictions were essentially unaffected by omitting these costs.

Following Hughes and Dill (1990) and Hill and Grossman (1993), we did not include the energy costs of burst swimming associated with feeding forays as a function of velocity. We justify this based on Godin and Rangeley (1989), who presented direct evidence
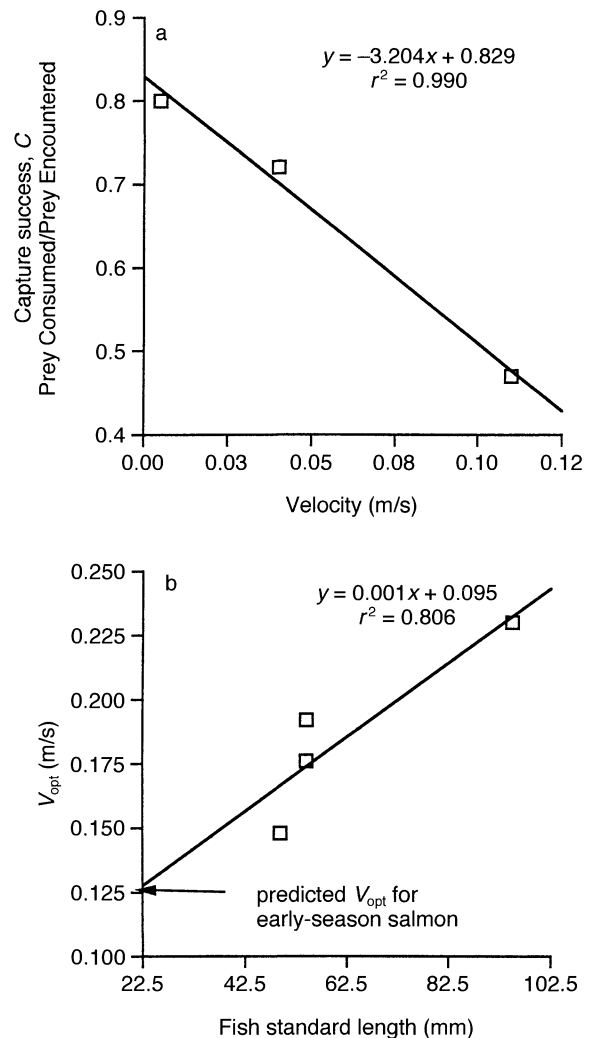

FIG. 2. (a) Capture success (prey consumed/prey encountered) in relation to current velocity for early-season age-0 Atlantic salmon, derived from laboratory feeding trials (see *Methods and results: Habitat selection model* for details). (b) Relationship between the optimal stream velocity, V_{opt}, and fish body-size data from Hill and Grossman (1993) for two size classes of rainbow trout and two size classes of rosyside dace, foraging at 10°C. The y intercept gives the predicted optimal velocity (0.0127 m/s) for a 22.5-mm fish, the average size of early-season age-0 salmon.

that the energy costs of burst-swimming forays made by juvenile Atlantic salmon to capture drifting prey did not vary with increased velocity. Also, Hughes and Dill (1990) indicated that for salmonids in general, burst-swimming costs should be a minor fraction of standard-activity metabolism.

The first key model parameter was the effect of current velocity on prey-capture success (Table 2). For early season salmon (20–25 mm SL), we determined this relationship with laboratory feeding trials. Trials were conducted in recirculating, 19-L aquaria, outfitted with baffles to maintain a unidirectional flow of water.

TABLE 2. Foraging-model parameters for linear equations relating capture success (C) and prey encounter rate (P) to current velocity (V).

Parameter	Season	Slope	Intercept	Derivation
Capture success	Early	−3.2	0.82	Laboratory experiments
	Late	−1.18	0.99	Hill and Grossman (1993)
Prey encounter rate	Early	7.85	0	Invertebrate drift samples
	Late	13.8	0	Invertebrate drift samples

As prey we used late-instar mayfly nymphs of the genus *Baetis,* an important component of juvenile salmon diets (Folt and Parrish 1994). Trials were run on 10 individual fish at each of three velocity levels, for a total sample of 30 fish. Each fish was used only once during the trials. Experiments were initiated after fish had been feeding on live prey for 1 wk. In each trial, fish were presented eight prey items, introduced consecutively, and capture success was calculated as the proportion of these eight prey items consumed. Trials were held at a constant 10°C, approximate ambient field temperature in our study streams during mid- to late May (Newbrough et al. 1994).

For late-season fish, we fit a linear relationship to the capture-success values obtained by Hill and Grossman (1993) for rainbow trout (45–65 mm total length) foraging at 15°C. This is the size range of late-season age-0 salmon, at the approximate July and August water temperatures in our sites (Newbrough et al. 1994). In using values borrowed from another species, we assume that while rainbow trout and Atlantic salmon may differ with respect to station-holding behavior, they show similar drift-foraging techniques (Nislow et al. 1998), and should have similar velocity–capture-success relationships. Supporting this assumption, Hill and Grossman (1993) found that velocity–capture-success relationships were primarily a function of fish size, and did not differ between the two fish species in their study.

The second key parameter was the relationship between current speed and prey encounter rate, P. We used drift densities from the six study streams obtained by Folt and Parrish (1994) to calculate P. Because changes in drift density (equivalent to the slope of the velocity–drift-rate relationship) were not significantly different among streams (Folt and Parrish 1994), we used the average drift density across streams in all streams in each season (Table 2).

Results.—Predicted optimal-velocity ranges were considerably different for early- vs. late-season fish, resulting from the large differences in velocity–capture-success relationships between seasons. For early-season fish, from our laboratory data on capture success (Fig. 2a), we obtained a predicted optimal velocity of 0.128 m/s, with velocities between 0.08 and 0.18 m/s yielding within 10% of the maximum predicted consumption rate (Fig. 3a). Because our laboratory trials were limited both with respect to sample size, and ve-

locity range, we used data from Hill and Grossman (1993) to corroborate our early-season parameterization. We regressed optimal current speed (at early-season temperatures) vs. fish size for four Hill and Grossman (1993) experiments, involving 45–125 mm rainbow trout and rosyside dace. We then extended this line and used it to predict optimal current speed for early-season age-0 salmon. The predicted optimal velocity (0.127 m/s) derived from this regression was within 1% of V_{opt} obtained from our laboratory trials (Fig. 2b). From the early-season velocity–consumption curve, we delineated four velocity categories (Fig. 3a). The use of four categories provided categories of equivalent velocity range, which encompassed >99% of velocities used by early-season fish.

For late-season fish, due to the reduced effects of velocity on foraging success, our model predicted foraging gain within 10% of maximum consumption at velocities between 0.21 and 0.57 m/s. Because of the wide range of velocities yielding optimal foraging gain, we divided the total velocity range into just two categories (Fig. 3b), equivalent in velocity range and encompassing >90% of total available velocities. Late-season fish were predicted to prefer the high-current-speed optimal category (category 2; 0.21–0.57 m/s) over the low-current-speed category (category 1; 0.01–0.21 m/s).

Model test: microhabitat selection

Methods.—We collected field data on microhabitat use and availability from six 3rd- and 4th-order streams in the White and West River drainages, two major tributaries of the Connecticut River in central and southern Vermont (USA) (Table 1). In each stream, we established a single 40-m study plot within a Vermont Department of Fish and Wildlife index site, where salmonid populations are censused annually. We divided each plot into four 10-m sections, and used a random-number table to select a single (bank-to-bank) transect location within each section. To characterize available habitat, we measured current speed at 1-m intervals along the four transects within the study plot. At each interval, we measured current speed at three depths (adjacent to the substrate [=near bed], at mid-water-column depth, and just below the water surface) using a Swoffer 2100 flow meter (Swoffer Instruments, Inc., Seattle, Washington, USA) equipped with a 2-cm-diameter propeller. Study streams did not exhibit regular riffle/pool structure, and corresponded closely to the

a) Early season

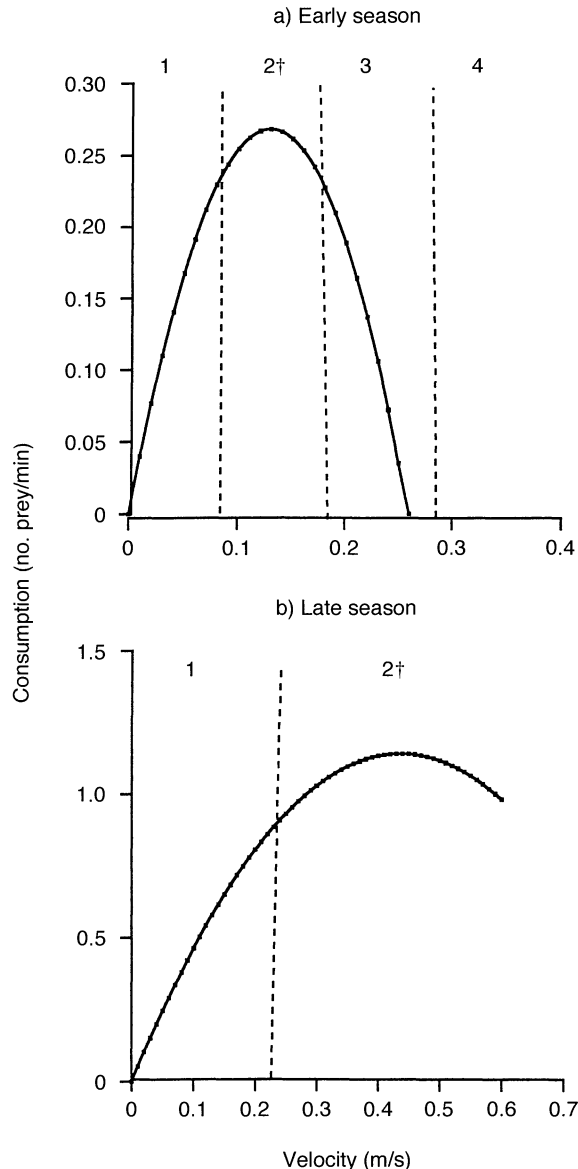b) Late season

Velocity (m/s)

FIG. 3. Predicted consumption curves (consumption as a function of velocity) and designated velocity categories for (a) early-season and (b) late-season age-0 Atlantic salmon. Vertical dashed lines separate the numbered velocity categories; the "†" indicates the optimal velocity category (velocities yielding within 10% of maximum consumption rate) for each season.

"complex" designation of Hankin and Reeves (1988); hence, we did not stratify transect locations with respect to these macrohabitat types.

To characterize habitat occupied by salmon, on each sampling day we located and marked the positions held by up to 10 age-0 salmon using a systematic snorkel search of the stream directly adjacent to the physical-habitat study plot. As located fish were removed from the stream via dip-netting, there was no possibility of resampling fish; in all study sites the number of fish

removed over the course of sampling did not exceed ~10% of the number of fish stocked. At each fish position, we measured current speed at nine points within a 1-m² area, which we chose to represent an individual salmon territory. Each site was sampled every 7–9 da from mid-June through August 1991, and from early May through mid-June 1992. Over all sites and both seasons we collected current speed measurements at 650 locations along random transects, and at 301 age-0 salmon territories.

We used the categorical approach of Hill and Grossman (1993) to test whether fish preferentially occupied velocity categories that were predicted to yield high consumption rates. Because the major determinants of foraging gain across microhabitats were expected to be similar across streams, we used the same velocity–capture-success curve and categorization scheme, within a season, across all study streams. Even if drift density did differ among streams (contrary to Folt and Parrish [1994]), this would affect how much food fish are predicted to gain, but not where they are predicted to forage (see *Habitat-selection model*, above). Apart from current velocity, other factors that have been shown to affect capture success (e.g., water temperature, Hill and Grossman 1993, and turbidity, Barrett et al. 1992) were largely similar among our study streams (Newbrough et al. 1994), and fish originated from a common genetic stock.

Model tests were based on determining whether age-0 salmon occupied and selected the predicted optimal velocity categories. Age-0 Atlantic salmon hold exclusive feeding territories during the spring and summer. As a result, microhabitat preference should be manifest in terms of occupancy or vacancy (e.g., ideal despotic distribution), as opposed to differential density within a microhabitat (e.g., ideal free distribution [Fretwell and Lucas 1970]), particularly at the relatively low stocking densities used in these rearing streams (McMenemy 1995). We used field measurements of occupied and available free-stream current speeds (average of mid-depth and surface measurements), as opposed to near-bed current speeds where salmon rested on the substrate, to test model predictions. Our observations of behavior indicated that the majority of drift-feeding forays were directed upward from the station-holding position on the substrate into the water column, with relatively little drift-feeding in near-bed flows. For each stream we determined whether salmon showed greater use and preference of the optimal velocity category. Microhabitat preference, for each velocity category, in each study stream, was calculated using Chesson's α (Chesson 1983), as

$$\alpha_i = (R_i/N_i) \bigg/ \sum_{j=1}^{k} (R_j/N_j) \qquad (5)$$

where R = the number of times salmon were observed using a particular velocity category, N = number of

FIG. 4. Comparisons (means and 1 SE) of three test criteria for stream-velocity categories, over the six study streams in each season. The criteria include (1) preference (Chesson's α ["alpha"]), (2) proportion of total fish observed, and (3) proportion of total available habitat among velocity categories for (a) early season and (b) late season age-0 salmon. Category 2 denotes the optimal velocity category in both seasons. N = total number of velocity measurements: available, early season $N = 251$; used, early season $N = 142$; available, late season $N = 399$; used, late season $N = 149$.
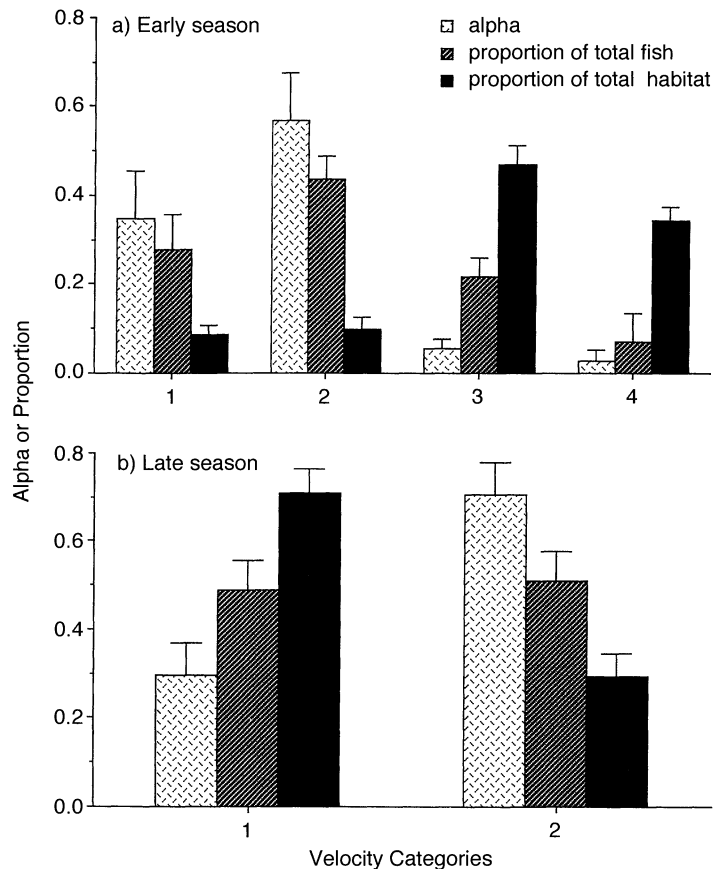
times the category was observed along random transects, i = velocity category, j = first velocity category, and k = number of velocity categories. $\alpha > 1/k$ indicates positive selection (use in greater proportion than expected on the basis of availability).

To test overall model performance, we first established three separate test criteria. We predicted that, for the optimal velocity category, fish would demonstrate (1) positive preference ($\alpha > 1/k$), (2) highest preference ($\alpha > \alpha$ for all other categories), and (3) highest frequency of use (more fish using the optimal category than any other category). The "highest preference" criterion was included because fish may show positive preference for the optimal category, but even higher preference for another category (when $k > 2$). The "frequency of use" criterion was included due to the sensitivity of α to "rare" categories; we wanted to ensure that high alphas involved not just rarity but also actual use. We then assessed the probability, for each of the criteria, of observing a given number of model "successes" (i.e., the number of streams in which concordance was demonstrated) compared to the number of successes expected by chance alone. We used a binomial test (Zar 1984) to calculate this probability across the six study streams, for each season. In order to conclude statistical significance at the 0.05 level for

each hypothesis, five of the six study streams needed to fulfill the hypothesis criteria (positive preference, highest preference, greatest proportion of individuals).

Results.—Early-season fish consistently preferred slow-velocity categories, which were consistently avoided by late-season fish (Fig. 4). Differences in preferences between the two seasons resulted from differences in both microhabitat use and availability. In the early season, the majority of available microhabitats had fast current speeds (>0.18 m/s; Categories 3 and 4), while most of the fish occupied slow currents (<0.18 m/s; Categories 1 and 2) (Fig. 4a). This situation was reversed in the late season; the majority of available microhabitats had slow current speeds (<0.21 m/s; category 1), while half of the fish were found occupying fast-current-speed microhabitats (>0.21 m/s; Category 2) (Fig. 4b).

Age-0 salmon microhabitat preferences upheld model predictions (Table 3). Predicted optimal velocity categories were both strongly preferred and frequently used. Early-season fish exhibited positive preference, strongest preference, and highest occupancy for the optimal category; this category was most preferred, with highest occupancy, in five of the six study streams ($P < 0.05$). Positive mean preferences in the early season

TABLE 3. Number of streams (out of six total streams) in which a microhabitat velocity category was preferred ($\alpha >$ 1/total number of velocity categories), was most preferred (highest α values), or contained the highest percentage of age-0 salmon, in early- and late-season sampling periods. Significant binomial tests ($P < 0.05$; Zar 1984) are indicated in boldface type.

Season†	Velocity category (m/s)	Preferred	Most preferred	Most indi- viduals
Early	1 (0.01–0.08)	3	1	1
	2‡ (0.08–0.18)	**5**	**5**	**5**
	3 (0.18–0.28)	0	0	0
	4 (0.28–0.38)	0	0	0
Late	1 (0.01–0.21)	1	1	2
	2‡ (0.21–0.57)	**5**	**5**	4

† Early season = May through mid-June; late season = mid-July through August.
‡ Optimal velocity category.

were also observed for category 1 (0.01–0.08 m/s). For late-season fish, significant binomial tests indicated highest preference (5/6 streams), but not highest occupancy (4/6 streams), of the predicted optimal category (0.21–0.57 m/s).

Model application: effects of habitat on growth and retention

Methods.—We used correlation analysis to test whether streams with a greater proportion of microhabitats preferred by age-0 salmon ($\alpha > 1/k$), and with a greater proportion of microhabitats predicted to yield within 10% of maximum consumption rates, would have higher per capita growth and higher retention rates. Retention estimates were obtained from multiple-pass electrofishing censuses conducted annually in 100-m index sites by Vermont Department of Fish and Wildlife personnel (McMenemy 1995). The proportion of preferred and optimal microhabitats (from habitat surveys—see *Model test: Microhabitat selection,* above) was correlated with (1) age-0 May–August retention estimates averaged over 4–7 yr (Newbrough et al. 1994) and (2) 1991 and 1992 retention, the years for which microhabitat data were collected. For growth, we used growth data obtained from fish collections conducted every 1 wk in conjunction with the 1991 and 1992 habitat-use study. Correlations were made separately for early-season and late-season fish.

Results.—Results of correlation analyses provided partial support for our predictions. Both mean ($n = 6$ sites, $P < 0.05$) and 1992 ($n = 6$ sites, $P < 0.01$) spring–summer retention (May–August) was positively correlated with preferred microhabitat availability (categories 1 plus 2; 0.01–0.018 m/s) for early-season fish

(Table 4). Retention was also positively correlated with early-season optimal-category availability, but due to the presence of one outlier, relationships were not significant (Table 4). In contrast, there was no significant relationship between either mean or 1991 retention and availability of the preferred/optimal category for late-season fish (category 2; 0.021–0.057 m/s). We found no relationship between per capita growth and preferred microhabitat availability for either early- or late-season fish (Table 4).

Model application: effect of large-structure addition on microhabitat quality

Methods.—We tested whether habitat restoration via the introduction of large structures improves foraging habitat for age-0 Atlantic salmon. We addressed three aspects of habitat quality that we predicted would be altered by large-structure addition: (1) the availability of preferred and optimal microhabitat current velocities, (2) the abundance of invertebrate prey, and (3) the availability of preferred microhabitat depths.

The study was conducted in four streams where large structures (large woody debris, boulder clusters) had been added to ~150-m-long stream reaches as a part of stream habitat improvement projects (Table 1) 1–3 yr prior to the initiation of our study, using standard USDA Forest Service techniques (S. Roy, *personal communication*). Project locations on each stream were, as far as possible, selected to be representative of the rearing stream as a whole (S. Roy, *personal communication*). At each stream we designated an 80-m study plot (hereafter referred to as a "manipulation plot") within a reach where large structures (large woody debris, boulder dams, and boulder clusters) had been added, and an adjacent 80-m study plot, 20-m upstream of the manipulation plot, where no manipulation had occurred (hereafter referred to as a "reference plot"). Sites were sampled and surveyed twice during the spring and summer of 1992 and 1993. In all cases, physical habitat and invertebrate data for each reference–manipulation pair were collected on the same day.

Microhabitat and invertebrate data were not available in either reference or manipulation reaches prior to large-structure addition in the four study sites. Three lines of evidence suggest that observed differences between reference and manipulation reaches resulted from large-structure addition, rather than simply reflecting pre-existing differences among plots. First, USDA Forest Service habitat survey data indicate that general habitat characteristics in these reference vs. manipulation plots were similar prior to large-structure addition (S. Roy, *personal communication*). Second, an extensive survey of a 19-km unmanipulated section of one of our study streams (West Branch of the White River) revealed no significant differences between 38 adjacent 100-m reaches (each reach separated by 450 m) in velocity, depth, or substrate (C. L. Folt, *unpub-*

TABLE 4. Effects of habitat on age-0 Atlantic salmon growth and retention: Multiple coefficients of determination between proportion preferred or optimal habitat vs. retention or growth.

Fish season	Habitat category†	Coefficients of determination, R^2‡		
		1991	1992	4–7 yr mean
Retention				
Early	Preferred	⋯	0.883* (+)	0.722* (+)
	Optimal	⋯	0.393 (+)	0.440 (+)
			0.777* (+)	0.821* (+)
			(outlier removed)	(outlier removed)
Late	Preferred/optimal	0.162 (−)	⋯	0.335 (−)
Growth				
Early	Preferred	⋯	0.18 (+)	NA
	Optimal	⋯	0.011 (−)	NA
Late	Preferred/optimal	0.236 (+)	NA	NA

Notes: Correlations were performed between retention estimates in the year in which the habitat study was conducted (1991 for late season, 1992 for early season) and mean retention averaged over a 4–7 yr period. Growth correlations are from 1991 and 1992 only. In the optimal category vs. retention analyses, one site had no observations in the optimal category and was a major outlier; results of correlations both with and without this outlier are presented.

* $P < 0.05$.

† For late-season fish, the optimal category is equal to the preferred category.

‡ (+) = positive, (−) = negative; NA = not available.

lished data). Third, at one site, in a preliminary survey prior to large-structure addition, we found that the manipulation reach had significantly higher current speeds and shallower depths than observed after large structures had been added; these effects were similar in both magnitude and direction to differences we subsequently observed between manipulation and reference plots (see *Results,* below).

We measured microhabitat conditions in reference and manipulated reaches using a similar, but more extensive, physical habitat sampling protocol than that used to test the microhabitat selection model. On each sampling date, we measured physical habitat along four lateral (bank-to-bank) and four longitudinal (parallel to bank) sampling transects within the 80-m manipulation and reference plots. Each plot was divided into four 20-m sections, and a random-number table was used to select a single lateral transect location. We then located a longitudinal transect to originate at a randomly selected distance along the lateral transect and continue upstream for a distance of 5 m. At 1-m intervals along the transects we measured both near-bed and water-column stream velocity, depth, cover (instream and overhead), substrate size, and substrate embeddedness (Heggenes and Saltveit 1990).

We sampled drift and benthic invertebrates at randomly selected locations along microhabitat survey transects. Two drift and two benthic samples were collected per lateral transect, for a total of eight samples of each type on each study plot, per sampling date, between 0900 and 1000. Benthic samples were collected by removing invertebrates from substrates within in a given sample area (0.33 m²) to a depth of 3 cm, then straining the contents through a 100-μm mesh net. Drift samples were collected using standard 0.3-m²

drift nets (100-μm mesh size) set for 15 min per sample. All samples were preserved in 70% ethanol and later sorted and identified, usually to the genus level.

We compared the abundance of total drift and total benthic invertebrates, and also the abundance of invertebrate taxa important in age-0 salmon diets. Results of a previous study of food use by >350 age-0 salmon in these watersheds (Folt and Parrish 1994) were used to determine invertebrate taxa important in salmonid diets. Invertebrates were included in our important-taxa category based on both frequency of occurrence in the diet and proportional use relative to availability in the drift (Chesson's α). Important taxa were those that occurred in >50% of salmon guts, regardless of preference, or those that were positively selected by salmon, and occurred in ≥24% of guts. Seven taxa met these criteria and were included in the important-taxa category (Table 5). We did not measure invertebrate length or biomass. Preliminary studies found no significant differences in sizes of individual taxa, or in the size structure of entire assemblages, between reference vs. manipulation reaches (K. H. Nislow, *unpublished data*), indicating that abundance was an appropriate measure to assess prey availability.

To test for the effect of plot (reference vs. manipulation) on invertebrate parameters (total abundance, and abundance of important prey taxa) we used a multilevel block-design ANOVA, with site and season (early vs. late season) as blocks, plot (reference vs. manipulation) as a treatment effect, and site × date and plot × date as interaction terms. Blocking served to reduce the effect of variation among sites and seasons on reference vs. manipulation reach comparisons. We used mean values of all samples collected on a sampling date for invertebrate parameters in statistical tests.

TABLE 5. Invertebrate taxa important in age-0 Atlantic salmon diets, based on selection intensity and frequency of use (proportions of fish guts containing specific taxa) (based on C. L. Folt and D. L. Parrish, *unpublished data*).

Taxon	Selection intensity†	Proportion of fish guts‡
Chironomidae	−0.21	0.87
Simuliidae	0.54	0.26
Baetidae	1.48	0.81
Ephemerellidae	0.52	0.34
Heptageniidae	1.45	0.29
Hydropsychidae	0.78	0.24
Hydropotilidae	1.56	0.46

† Selection intensity represents the mean (over the entire 1991 season) Chesson's α for the taxon, standardized to $\alpha = 0$ for no selection (opportunistic feeding). Values > 0 indicate positive selection; values < 0 indicate negative selection.

‡ The proportion of fish having members of the taxon in their guts.

Effects of large-structure addition on microhabitat quality were tested using physical habitat data collected from manipulation and reference plots, along with habitat-preference estimates and model predictions obtained from the independent set of six streams described previously (see *Model test: Microhabitat selection*). In our analysis, quality of a potential microhabitat falling into a given category of velocities was proportional to preference for that category as measured in the microhabitat-use study. We derived an overall microhabitat quality index with respect to velocity (MQI$_{vel}$) for each study plot as:

$$\text{MQI}_{\text{vel}} = \sum (N_i \cdot \alpha_c)/N \qquad (6)$$

where N = total number of current-velocity observations, N_i = number of observations in velocity category i, and $\alpha_c = \alpha$ for microhabitat category I. $(N_i \cdot \alpha_c)/N$ is the proportion of observations in a velocity category, weighted by fish preference (Chesson's α) for that category. MQI$_{vel}$ for a study plot is the sum, over all velocity categories, of these weighted proportions; study plots with high MQI$_{vel}$ values have a high proportion of preferred microhabitats.

There is no mathematical model to predict microhabitat depth preferences for age-0 salmon. Instead, we used a correlational approach and calculated salmon depth preferences based on field observations of use and availability for the 1991 and 1992 data. We calculated fish preferences for four depth categories in both the early and late season (Table 6), then derived

MQI$_{depth}$ values using the procedure outlined above, and compared MQI$_{depth}$ values between reference and manipulation plots. Differences in mean microhabitat velocity and depth were evaluated using a multilevel block design, blocking by site and date, with mean values for each study plot measured in each sampling period as replicates. To compare velocity and depth MQIs between reference and manipulation plots, we performed separate analyses for each season (due to changes in preference with season) using one-way ANOVA, with site as a block and plot (manipulation vs. reference) as a main effect. We used paired t tests to compare optimal-velocity observations for each season.

Results.—Manipulation plots had higher total benthic densities ($F_{1,6} = 8.75$, $P = 0.025$) than reference plots (Fig. 5a). However, for the seven taxa important in salmon diets, we found no differences between manipulation and reference plots (Fig. 5b and c). There were no differences in invertebrate drift density between manipulation and reference plots for either total density, or for any particular taxonomic categories (Fig. 5a).

Large-structure addition significantly affected depth and current velocity. Microhabitats in manipulation plots were deeper ($F_{1,6} = 7.631$, $P < 0.05$), and had slower current velocities ($F_{1,6} = 32.825$, $P < 0.005$), than reference plots (Fig. 6a). Other habitat parameters (stream width, substrate size, overhead cover) did not differ between plots.

Large-structure addition resulted in significantly higher microhabitat quality (Fig. 6b). For early-season fish, MQI$_{vel}$ was ~45% higher in manipulation plots ($F_{1,3} = 28.165$, $P = 0.031$), which had ~40% more model-predicted optimal-velocity microhabitats (paired t test, $n = 4$ sites, $t = 2.481$, $P < 0.10$). For late-season fish, MQI$_{dep}$ was ~20% higher in manipulation plots ($F_{1,3} = 19.33$, $P = 0.022$). Early-season fish did not show strong preferences for any depth categories, and greater depths in manipulation reaches did not affect microhabitat quality in this period. Similarly, a smaller effect of manipulation on current velocity in the late season, along with broader current-velocity preferences, resulted in no significant effect on MQI$_{vel}$ for late-season fish. Availability of optimal-velocity categories was substantially lower in manipulation plots for late-season

TABLE 6. Mean preference (Chesson's α) values (1 SE in parentheses) of age-0 Atlantic salmon for depth categories over six study streams. Alpha values greater than 0.25 (1 divided by 4 categories) indicate positive selection of the category.

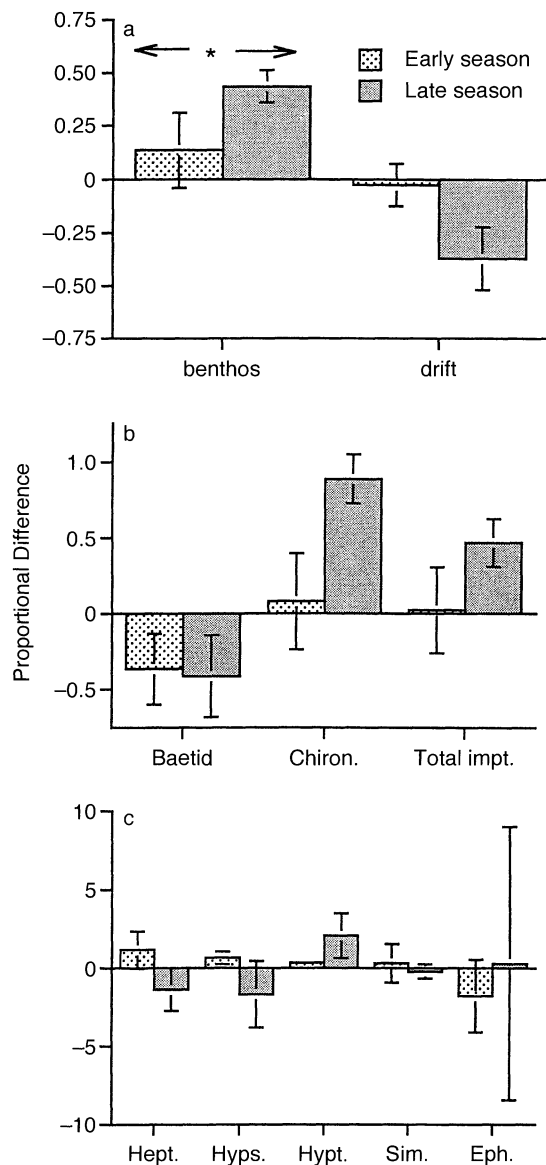| Fish season	Categories			
	1 (0–10 cm)	2 (10–20 cm)	3 (20–30 cm)	4 (30–40 cm)
Early	0.18 (0.068)	0.369 (0.06)	0.235 (0.056)	0.216 (0.073)
Late	0.039 (0.018)	0.428 (0.141)	0.319 (0.112)	0.214 (0.171)

FIG. 5. Proportional difference ([manipulation − reference]/[average across both manipulation and reference plots]) in (a) total benthic invertebrate density (no./0.33 m²) and drift-invertebrate density (no./m³), and in (b and c) benthic invertebrate taxa important in age-0 salmon diets. Histogram bars above zero indicate manipulation reaches (large structures added) had higher values than reference reaches. Asterisks indicate pairs of bars that are significantly different (P < 0.05). N = 16 sampling bouts for all comparisons. Baetid = Baetidae, Chiron. = Chironomidae, Hept. = Heptageniidae, Hyps. = Hydropsychidae, Hypt. = Hydroptilidae, Sim. = Simuliidae, Eph. = Ephemerellidae, Total impt. = sum over all important taxa.

fish, but high variance among sites resulted in no significant difference.

DISCUSSION

Application of a simple, foraging-based model successfully addressed key questions concerning Atlantic
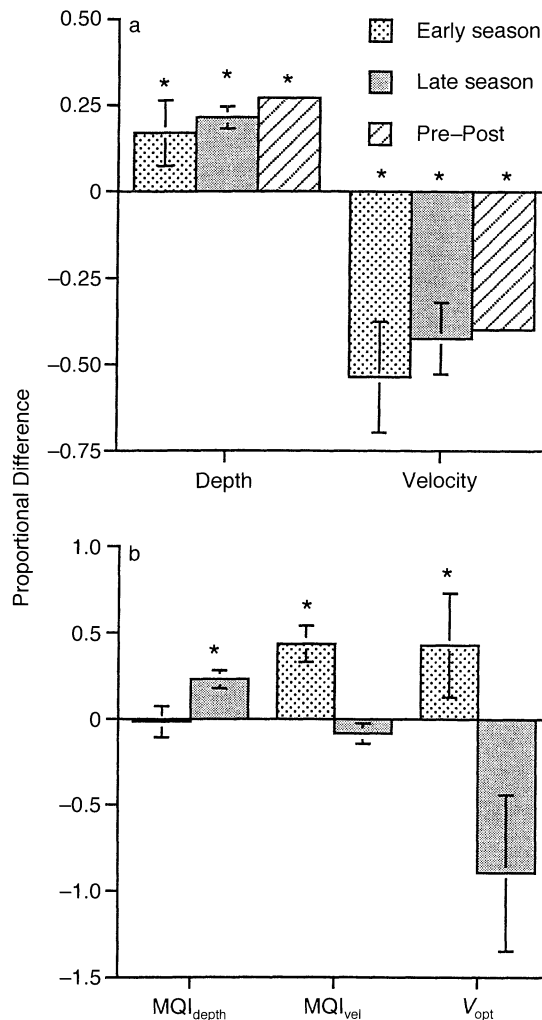
FIG. 6. Stream depth and velocity effects from the addition of large physical structures (large woody debris, boulder clusters). (a) Proportional difference in microhabitat velocity and depth between reference and manipulation plots (where data are standardized across each pair of manipulation and reference plots). Early- and late-season bars are the mean differences between four manipulation vs. reference plots; pre–post bars are the proportional differences in velocity and depth before and after large-structure addition to one study plot (Greendale Brook). (b) Proportional difference in microhabitat quality indices (MQI) for depth and velocity, and in optimal-velocity category availability in four manipulation vs. reference plots. Bars above the zero-difference line indicate that manipulation reaches (large-structures added) had higher values that reference reaches. Aterisks indicate bars significantly different from zero difference (P < 0.05). N = 16 sampling bouts for all comparisons.

salmon habitat. Across multiple rearing streams, age-0 salmon strongly preferred microhabitats that, based on current speed, were predicted to maximize consumption. Streams with a greater proportion of preferred microhabitats retained more salmon, and adding large structures increased the proportion of these preferred locations. This study demonstrates that simple forag-

TABLE 7. Stream fish species for which foraging-based habitat models have been developed and tested.

Species	Study	Age class	Study type
Onchorhynchus mykiss (rainbow trout)	Smith and Li (1983)	Juveniles	Field
	Hill and Grossman (1993)	Juveniles	Field
O. kisutch (coho salmon)	Fausch (1984)	Juveniles	Laboratory
Salmo trutta (brown trout)	Fausch (1984)	Juveniles	Laboratory
	Fausch and White (1981)	Juveniles	Field
S. salar (Atlantic salmon)	Nislow et al. (present study)	Juveniles	Field
Salvelinus fontinalis (brook charr)	Fausch (1984)	Juveniles	Field
	Baker and Coon (1997)	Juveniles	Field
Thymallus arcticus (Arctic grayling)	Hughes and Dill (1990)	Juveniles	Field
	Hughes (1992)	Adults	Field
Clinostomus funduloides (rosyside dace)	Hill and Grossman (1993)	Adults and juveniles	Field

ing-based models can accurately predict microhabitat use, link availability of preferred habitats to salmonid population performance, and provide a mechanism by which commonly used stream-restoration techniques should enhance juvenile-salmonid growth and survival.

Foraging-based models have now been used to predict microhabitat preferences for a fairly diverse array of stream fishes (Table 7). This broad application indicates that the relationship among velocity, drift rate, and capture success is an important general mechanism by which drift-feeding stream fishes choose habitats. In addition to generality across species, we found that for juvenile Atlantic salmon, both model predictions and observed habitat preferences were consistent across rearing streams. Incorporating biological mechanisms involved in microhabitat choice appears to increase the generality of habitat models (Fausch et al. 1988).

Both early- and late-season age-0 salmon selected microhabitats predicted to yield high consumption rates. However, while salmon retention was significantly greater in streams with more early-season preferred habitat, we found no correlation between retention and late-season preferred habitat. This difference may result from several important seasonal changes in the characteristics of age-0 fish, and concurrent changes in stream conditions. Compared to early-season fish, late-season fish were predicted to have high foraging gain over a broad range of microhabitat velocities. Consequently, small, among-stream differences in late-season microhabitat availability would have less effect on late-season fish, as long as availabilities shifted within their broad optimal category. In addition, changes in the foraging behavior of late-season fish may reduce the influence of late-season microhabitat availability on age-0 performance. Several studies suggest that age-0 Atlantic salmon change their general orientation from maximizing energy gain in the early season towards minimizing both predation risk and energy expenditure late in the summer. Evidence of this change in strategy includes declines in feeding motivation (Metcalfe et al. 1986), decreased overall activity, and increased shelter seeking (Rimmer et al. 1984) towards the end of the summer. In our study, we found that late-season fish showed strong preferences for deep microhabitats, further suggesting that shelter may be more important than foraging gain during this period.

Most significantly, strong effects of preferred habitat for early-season fish on overall age-0 performance may be due to the potentially strong influence of the post-emergent (=early-season) life-history stage on survival and recruitment. Bley and Moring (1988) report greater variation in post-emergent survival of age-0 salmon than was observed for later age classes. Elliott (1985) suggested that the ability of newly emerged brown trout (Salmo trutta) to locate an appropriate feeding territory was a major determinant of first-year survival, and total year-class strength, proposing that newly hatched (or newly stocked) fish either quickly find suitable microhabitats, or leave the system (via mortality or emigration). Streams with a higher percentage of good microhabitats would then retain more fish, leading to higher calculated survival rates. Individual growth rates across streams, however, would be similar for those individuals that managed to find good microhabitats during the critical post-emergent period. Our observation of no significant relationship between habitat and growth, but a significant relationship between early-season habitat and survival, is consistent with this explanation. Targeting rearing streams that provide preferred early-season microhabitats, and improving early-season habitat in low-performance streams, should therefore improve production of age-0 salmon. However, effects of improved first-year success on the overall goal of salmon restoration will depend critically on the interaction between early life-history processes and potential population bottlenecks later in the salmon life cycle.

Addition of large instream structures fulfilled the objective of improving early-season habitat for age-0 Atlantic salmon. Adding physical structure to streams should therefore aid Atlantic salmon restoration efforts. For stream salmonids in general, directly relating large-structure effects to habitat preferences, food use, and potential energy gain represents an important step towards establishing a mechanistic link between stream habitat manipulation and juvenile performance. While this effect has been previously proposed as a mechanism of enhancement for young juveniles, we are unaware of other studies that directly relate large-structure addition to specific microhabitat preferences and predicted energy gain.

To adequately interpret the effect of instream structure for age-0 salmon, we needed to consider both prey and physical habitat. Manipulation reaches had a higher proportion of microhabitat velocities preferred by early-season fish, with no significant effect on preferred velocities in the late-season period. Large-structure addition therefore appears to improve foraging habitat. This conclusion, however, requires that large-structure addition has no major negative effect on either invertebrate prey or on other physical habitat attributes influenced by habitat manipulation. We found that instream structure may have marginally increased total invertebrate abundance, and found no evidence of any negative effect. Similarly, large-structure addition increased the availability of preferred microhabitat depths for late-season fish. The physical effects of large-structure addition (increased depth, decreased current speed) we observed are consistent with results of previous studies dealing with both the natural occurrence (Anderson and Sedell 1979, Maser et al. 1988) and artificial addition (Riley and Fausch 1995) of large structures. Generality of both physical effects, and of velocity–capture success relationships suggest that increased foraging gain may serve as a potential general mechanism for enhancement of juvenile stream-fish growth and survival via large-structure addition.

Early-season habitat limitation, and associated effectiveness of stream remediation, is particularly relevant to stream conditions in the New England (USA) region. In these streams, sustained high discharges associated with both snowmelt runoff and low evapotranspiration rates occur in the spring (Magilligan and Graber 1995). As salmonids begin to emerge (or, in our case, are stocked) and feed in the spring, they are likely to be exposed to high flows and low temperatures, which strongly reduce capture success for small fish (Hill and Grossman 1993). Streams that maintain greater proportions of preferred low-velocity microhabitats during this period may therefore experience reduced mortality of early-season fish, and overall increases in first-year survival. In contrast, in some salmonid streams of the Pacific coast of North America (Power 1990), winter precipitation falls largely as rain. In these systems, high spring discharges and conse-

quent early-season limitation may be less important than summer droughts or other factors in limiting first-year salmonid growth and survival. Understanding specific mechanisms therefore helps to determine the conditions under which habitat should be limiting, and whether restoration of both habitats and population is likely to be either required, or effective.

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