Mechanistic Linkage of Hydrologic Regime to Summer Growth of Age-0 Atlantic Salmon

K. H. Nislow*

*U.S. Department of Agriculture, Forest Service,
Northeastern Research Station, University of Massachusetts,
Amherst, Massachusetts 01003, USA*

A. J. Sepulveda and C. L. Folt

*Department of Biological Sciences, Dartmouth College,
Hanover, New Hampshire 03755, USA*

Abstract.—Significant reductions in juvenile stream salmonid growth have been observed in association with low summer flow, but underlying mechanisms are poorly understood and predictive power is limited. We conducted a stage-specific analysis of the relationship between summer flow and the growth of age-0 Atlantic salmon *Salmo salar* in two rearing sites in the upper Connecticut River basin, New Hampshire. We contrasted effects of variation in foraging habitat availability and temperature on individual age-0 Atlantic salmon mass during one high-flow year and two low-flow years and from high- and low-flow sites within years. Overall age-0 Atlantic salmon mass was positively correlated with the availability of model-predicted favorable foraging locations and negatively correlated with density during the summer. Individual Atlantic salmon mass and the proportion of temperature-predicted maximum mass were lowest during the two low-flow years and were lower in upstream than in downstream sections. Between-year variation in growth was not closely associated with temperature model predictions. However, some of the difference between upstream and downstream sections appeared to be associated with lower summer temperatures in the upstream section. Our case study provides a framework for combining empirical and modeling approaches to quantify the potential impact of hydrologic change on fish growth and for linking variation in stream discharge to juvenile Atlantic salmon performance across time and space.

Variation in hydrologic regime (the magnitude, timing, and variability of streamflow) impacts the growth, survival, and population viability of stream fishes. Natural hydrologic regimes are undergoing extensive modification (Benke 1990; Richter et al. 1996; Poff et al. 1997). Therefore, to effectively restore and conserve native fish stocks, we must understand the influence of hydrological change on fish performance. Conclusions of studies regarding the influence of hydrologic variation on salmonid growth often conflict. For instance, low-flow years have been found to have both positive and negative effects on growth and survival (Elliott et al. 1997; Deegan et al. 1999; Good et al. 2001; Arndt et al. 2002). Similarly, effects of flow differ between subyearling versus yearling salmonids in empirical observations (Deegan et al. 1999; McKinney et al. 2001; Arndt et al. 2002) and predictions from habitat models (Nislow et al. 2000).

Streamflow affects foraging and growth in a complex manner. Reduced streamflow decreases total habitat area, increases effective conspecific density, and decreases delivery rates of drifting invertebrate prey (Nislow et al. 1998), potentially decreasing foraging and growth. However, reduced streamflow can also increase prey capture and detection rates (Hill and Grossman 1993; Nislow et al. 1999), and decrease swimming and station-holding costs (Fausch 1984; Hughes and Dill 1990), potentially increasing growth. Further complicating the interpretation of these patterns is that variations in hydrologic and thermal regimes are often linked and exert strong, nonlinear controls on maximum growth rates (Elliott and Hurley 1997; Jonsson et al. 2001).

In this study, we test for effects of spatial and temporal variation in hydrologic regime on summer growth of age-0 Atlantic salmon *Salmo salar*. We link streamflow with growth variation by use of a mechanistic, foraging-based model that is stage-specific for age-0 Atlantic salmon parr in the mid- to late summer (July to early September) (Nislow et al. 1999). We also include effects of variation in temperature via a recent, temperature-based growth model developed for juvenile salmon

(Jonsson et al. 2001). Other studies link low flow to poor growth, but without mechanistically distinguishing among factors (food, temperature, density) or effects that are stage-specific (different responses for different stages). Application of general, stage-specific, mechanistic models increases our capacity to link flow variation to growth variation in other studies, and provides a framework for evaluating the relative contribution of several processes driving growth during the critical summer period.

Methods

Overall Approach

We tested for effects of natural spatial and temporal variation in summer flow regime on the growth of age-0 Atlantic salmon in Mink Brook, New Hampshire. This stream is part of ongoing efforts to restore Atlantic salmon to the Connecticut River watershed. Our prior work in nearby streams suggests that the growth potential for age-0 Atlantic salmon is greatest during the summer (Nislow et al. 2000) in this region. However, summer flow regimes vary greatly, both spatially and annually (Magilligan and Graber 1996). Hence, growth rates are also likely to vary significantly with the magnitude of summer flow. We focused on two sources of variation in summer streamflow: (1) differences between years, and (2) differences between longitudinal stream positions (upper versus lower reaches). We sampled physical microhabitat and temperature conditions, fish growth, and abundance, and modeled growth rates in the two sections during two summers. We then compared the growth of age-0 fish approximately 115 d after stocking to the predicted maximum growth based on a foraging-based habitat model (Nislow et al. 2000) and a temperature-based growth model (Jonsson et al. 2001). Individual age-0 Atlantic salmon mass and the proportion of maximum predicted mass were used to analyze the spatial and temporal effects of flow regime on age-0 fish growth.

Establishing differences in summer flow between the study years, and the relationship of observed flows to the overall range of expected summer flows, was essential to our approach. However, the long-term U.S. Geological Survey (USGS) stream discharge gauge at Mink Brook was discontinued the year prior to the study (1998). As July and August mean daily flows measured at the nearby Ayers Brook gauge were closely correlated to Mink Brook flows ($R = 0.735$, $P < 0.0001$), we

used Ayers Brook discharge data to compare overall summer flow magnitudes across study years, and to place these years in the context of expected flows based on a 26-year period of record.

Site Description

We surveyed habitat characteristics and sampled fish populations in the upper and lower reaches of Mink Brook, a third-order tributary of the Connecticut River watershed, in May–September of 1999, 2000, and 2001 (Figure 1). Mink Brook originates in the foothills of the Appalachian Mountains near the town of Hanover, New Hampshire, drains an area of 11.91 km^2, and flows 10 km to its confluence with the Connecticut River. The average stream gradient is 0.0046 m/km, and the basin is about 90% forested and 10% agricultural and residential land. Canopy cover is relatively high, and the stream is dominated by cobble-sized substrate throughout its length. Fish assemblages differ substantially between the upper and lower reaches of Mink Brook. Stocked Atlantic salmon and native brook trout *Salvelinus fontinalis* dominate the upper reaches. In the lower section, these two species are joined by coolwater species, including blacknose dace *Rhinichthys atratulus*, longnose dace *Rhinichthys cataractae*, creek chub *Semotilus atromaculatus*, fallfish *Semotilus corporalis*, and white sucker *Castostomus commersoni*, along with brown bullhead *Ameiurus nebulosus*, bluegill *Lepomis macrochirus*, and largemouth bass *Micropterus salmoides*. Invertebrate assemblages are similar between the upper and lower sections, and are dominated by the aquatic insect orders Diptera, Trichoptera, Plecoptera, and Ephemeroptera.

Study Design

We sampled two, 410-m-long sampling sections, one located in upper Mink Brook (UMB) and the other in lower Mink Brook (LMB). Study sections were representative of general physical habitat conditions, and consisted largely of suitable Atlantic salmon rearing habitat, defined as relatively shallow (0–0.5 m) habitat dominated by cobble–boulder substrate (McMenemy 1995). Each site was partitioned into three, 70-m-long plots, separated by 100-m intervals. The UMB and LMB were separated by about 8 km of stream length, and a waterfall impassable to juvenile fishes made it highly unlikely that fish were able to move between sections. In 1999, we only sampled age-0 fish, and did not record temperature or microhabitat characteristics.
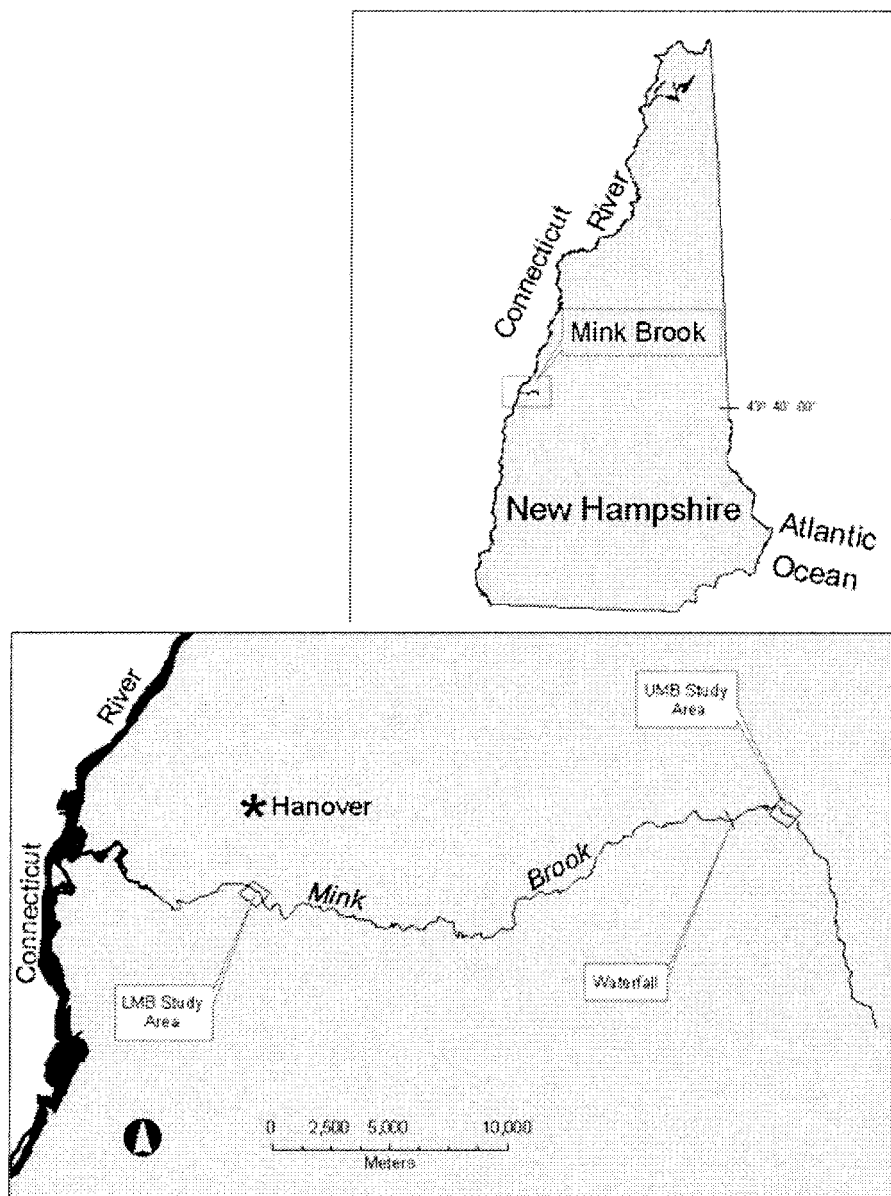
FIGURE 1.—Map of Mink Brook, New Hampshire, showing the locations of study areas from which Atlantic salmon and habitat measurements were collected (UMB = Upper Mink Brook; LMB = Lower Mink Brook).

Atlantic salmon fry stocked in the study streams were incubated under identical conditions at the U.S. Fish and Wildlife Service's White River National Fish Hatchery, Bethel, Vermont. These fish were the offspring of domestic broodstock originally derived from adults returning to the Connecticut River. Because broodstock were randomly selected and eggs were mixed together during incubation, our premise is that differences in growth

of age-0 fish between sites resulted from habitat conditions and food availability rather than systematic genetic or maternal differences. Mean initial fry size (0.2–0.22 g; 20–22 mm total length) varied little (<10%) from plot to plot and year to year. Following standard practices for Atlantic salmon restoration streams in the Connecticut River basin (McMenemy 1995), we scatter-stocked unfed fish fry at a density of 50 fry per 100 m^2 of

rearing habitat throughout the entire stream during the first week of May in 1999, 2000, and 2001.

Growth and abundance of age-0 Atlantic salmon.—Age-0 Atlantic salmon growth and abundance were estimated from three-pass electrofishing censuses conducted approximately 115 d after stocking (early September of each year) in 1999, 2000, and 2001. We restricted immigration and emigration from plots during electrofishing passes by use of blocking nets, and waited 0.5 h between passes. All salmonids (brook trout and Atlantic salmon) were anesthetized with clove oil, identified, weighed (wet mass to the nearest 0.01 g), and then returned to the stream.

Foraging-based habitat model.—The availability of foraging locations favorable for growth has been shown to be a primary determinant of habitat quality for age-0 Atlantic salmon (Folt et al. 1998; Nislow et al. 2000). To measure this aspect of habitat quality across our sites, we applied the foraging-based habitat model developed by Nislow et al. (1999, 2000) to field data collected in Mink Brook in 2000 and 2001. The basic unit of this model is the microhabitat, an idealized area roughly equal to the size of an age-0 Atlantic salmon feeding territory (approximately 1 m^2) during the summer (Grant et al. 1998).

Within a potential territory, microhabitat foraging quality (MFQ; prey captured per unit time) is modeled as:

$$MFQ = P \times C, \qquad (1)$$

where P is the prey encounter rate and C is capture success (the proportion of appropriate prey encountered that are predicted to be successfully captured). This relationship is primarily determined by current speed within the potential territory or microhabitat. P (prey encountered per unit time) is determined by the volume flux (V; volume per unit time, jointly determined by current speed, territory width, and water depth) of water through the microhabitat, the invertebrate drift density (D; number of prey per unit volume), and the proportion of prey of a size appropriate for consumption by age-0 fish (S; dimensionless).

$$P = V \times D \times S. \qquad (2)$$

In the absence of microhabitat-specific invertebrate drift data, we modeled drift density (D) as a constant across plots. S (the proportion of prey appropriate for Atlantic salmon foraging) was set at 0.4, a value taken from previous studies across multiple rearing streams (Nislow et al. 2000). Cap-

ture success (C) is modeled as a negative linear function of microhabitat current speed, with the slope of this relationship determining how quickly capture success declines with increasing current speed. For small fish, capture success declines rapidly with increasing current speed (based on previous laboratory studies; Nislow et al. 1999). In contrast, current speed has a much smaller effect on larger, stronger fish. Early-season fish have their highest MFQs at a narrow range of relatively low current speeds, while late-season fish have their highest MFQs at a relatively wide range of faster current speeds (Nislow et al. 1999). Given the fact that, in these streams, most age-0 Atlantic salmon growth occurs in the summer, when streamflows tend to be low (Nislow et al. 2000), we therefore predicted that growth would increase with increasing stream velocity and stream discharge during the summer.

To estimate the expected MFQ for age-0 fish in 2000 and 2001, we used the protocol established by Nislow et al. (1999). At multiple times (three sampling bouts per year) throughout the summer study period (July and August), we collected microhabitat measurements at 1-m intervals along bank-to-bank transects established at 10-m longitudinal intervals in each study plot. Each point was used to characterize a microhabitat. We then calculated MFQ (using equation 1) for each microhabitat based on current speed and depth, as well as the volume flux through the microhabitat (mean microhabitat discharge [MMD]), and we used the mean of all MFQs within each plot to estimate the expected MFQ for the study plot as a whole. This plotwide MFQ was our estimate of the extent to which a plot provided favorable foraging habitat for age-0 Atlantic salmon in a given time period.

Temperature model.—Temperature can have pronounced effects on the growth of age-0 Atlantic salmon and may be significantly correlated with flow regime. To account for the effects of between-site and between-year differences in temperature, we modeled the expected maximum growth rates in 2000 and 2001 for each site based on a temperature model, and compared these growth rates to observed growth. The 24-h mean daily temperature (°C) for each site was calculated for each day from the date of stocking to the date of electrofishing in each year. The temperature data were collected hourly with Onset Boxcar temperature data loggers placed in the highest plot of the upstream site and the lowest plot of the downstream site.

The maximum mass of age-0 Atlantic salmon expected at temperature T when all other factors are optimal (unlimited rations, no density dependence) was calculated by use of the Ratkowsky functional growth model, adapted for Atlantic salmon by Jonsson et al. (2001). Average daily temperatures were employed in the model to predict an expected mass (M_t in grams) for age-0 Atlantic salmon at time t (115 d) as,

$$M_t = M_0^b + \{b \times [t \times d(T - T_L)$$
$$\times (1 - e^{g(T-T^u)})]/100\}^{1/b}. \quad (3)$$

Values for the model's five parameters (Jonsson et al. 2001) include the lower ($T_L = 6.0°C$, SE = 0.3°C) and upper ($T_U = 24.5°C$, SE = 0.2°C) critical temperatures for growth, the coefficients governing the allometric relationship ($b = 0.31$) between growth rate and fish mass, d (0.530, SE = 0.043) and g (0.208, SE = 0.032), which determined the temperature for maximal intake and the maximal growth rate of a 1-g, age-0 Atlantic salmon at the optimal temperature. Successful application of the original model to both southern and northern populations of age-0 Atlantic salmon in Europe suggests that it has wide geographical applicability (Forseth, personal communication). We attributed the difference between realized mass (measured in the field collections) from the expected mass (as modeled) to site-specific habitat effects other than site-specific temperature effects, and expressed this difference as the proportion of predicted mass.

Data analysis.—Atlantic salmon in our study system varied only slightly in their mass at stocking (1999 data: SD = 0.018 g, $N = 80$), and increased in mass by at least an order of magnitude in their first 3–4 months after stocking (from < 0.2 g to > 2 g). Hence, we used individual mass at capture as our measure of Atlantic salmon growth. We used two-way analysis of variance (ANOVA) to determine the effect of site and year on mean age-0 fish mass, total biomass (sum of individual mass within a plot), density, MFQ, and MMD. We used regression analysis to assess the relationships between mean age-0 fish mass and MMD, and MFQ and MMD. All variables were transformed with arcsine transformations (percentage data) or natural logarithms (Atlantic salmon mass data) to satisfy assumptions of ANOVA and regression models. In all analyses, plot means ($n = 3$ per site per year) were the unit of replication.

TABLE 1.—July and August streamflow in 1999, 2000, and 2001 recorded at the U.S. Geological Survey long-term gauging station in Ayers Brook, New Hampshire. Flow quartiles were calculated from a 26-year period of record (1975–2001).

Year	Month	Mean discharge (m^3/s)	Quartile (%)
1999	Jul	0.269	0–25
	Aug	0.152	0–25
2000	Jul	1.045	75–100
	Aug	0.646	50–75
2001	Jul	0.289	0–25
	Aug	0.081	0–25

Results

Spatial and Temporal Patterns in Streamflow and Stream Habitat

Streamflow differed markedly among years. Based on the nearby Ayers Brook long-term USGS gaging station, summer flows were lower than normal (generally in the 0–25% range of recorded monthly flows) in 1999 and 2001, whereas summer flows in 2000 were significantly greater than normal (75–100% range of recorded flows) (Table 1). Correspondingly, total stream area (m^2) was significantly greater in LMB than in UMB ($F_{1,12} = 19.55$, $P < 0.0005$) and in 2000 than in 2001 ($F_{1,12} = 6.32$, $P < 0.05$) (Table 2), with a marginally significant year × stream interaction ($F_{3,12} = 3.31$, $P = 0.10$) as the increase in stream area in 2000 (as compared with 2001) was substantially greater in UMB (4.5 versus 2.7 m^2) than in LMB (5.7 versus 5.4 m^2). Daily stream temperatures varied considerably within years, but only slightly between years and sections (Figure 2). Within sites, temperatures were slightly lower in 2000 than in 2001, and LMB was slightly warmer than UMB in both years (Table 2).

Spatial and Temporal Patterns in Age-0 Atlantic Salmon Growth and Abundance

A total of 1,305 age-0 Atlantic salmon were captured, weighed, and measured. Mean Atlantic salmon mass at the end of the summer varied substantially among study plots, ranging from less than 1.5 g to over 6 g per study plot. Density also varied considerably, ranging from 0.03 to 0.65 individuals/m^2 per study plot, encompassing much of the range of late-summer age-0 Atlantic salmon densities observed throughout the Connecticut River basin (Connecticut River Atlantic Salmon Commission, unpublished data). Atlantic salmon density was significantly greater in UMB and in 2001 ($F_{1,12} = 11.0616$, $P = 0.0104$; $F_{1,12} =$

TABLE 2.—Means ($\pm$SE) of summer habitat measurements for Mink Brook, New Hampshire ($N = 3$ plots/section). Abbreviations are as follows: MMD = mean microhabitat discharge (m^3/s); MFQ = microhabitat foraging quality (see explanation in text); UMB = upper Mink Brook study section; and LMB = lower Mink Brook study section.

Year	Section	Mean area (m^2)	Mean daily temperature and range	MMD	MFQ
2000	UMB	316.4 (16.8)	15.8 11.3–18.0	2.04×10^{-3}	0.247 (0.023)
	LMB	398.1 (28.9)	17.0 12.6–19.7	3.11×10^{-3}	0.381 (0.061)
2001	UMB	180.4 (21.5)	16.2 12.3–21.0	3.20×10^{-4}	0.043 (0.02)
	LMB	376.3 (48.6)	18.0 13.7–24.0	9.90×10^{-4}	0.127 (0.026)

79.9246, $P < 0.0001$), with no significant year $\times$ section interaction.

Relationship between Growth and Habitat

Age-0 Atlantic salmon grew best under the highest summer discharge conditions. In 2000, the high-flow year, fish achieved twice the average mass (5.7 g) than in 1999 (2.2 g) or 2001 (2.7 g), the low-flow years ($F_{2,12} = 129.451$, $P < 0.0001$), which were not significantly different from one another (Bonferroni multiple comparisons test; $P < 0.10$). In addition, mean age-0 fish mass was approximately 40% greater in LMB (4.1 g) than in UMB (2.97 g) plots across all three study years ($F_{1,12} = 32.657$, $P < 0.0001$). Although differ-

ences between sections appeared to be lower in the high-flow year, the year $\times$ section interaction term was not significant ($F_{2,12} = 2.29$, $P > 0.15$). Corresponding to these differences in Atlantic salmon mass and to overall differences in summer flow regime (Table 1), MMD (discharge within individual microhabitats) was also significantly greater in LMB than in UMB ($F_{1,12} = 6.74$, $P < 0.05$) and in 2000 than in 2001 ($F_{1,12} = 20.90$, $P < 0.005$) (Table 2).

Greater Atlantic salmon mass was also associated with a greater availability of favorable foraging microhabitats. Corresponding to differences in Atlantic salmon mass between years and sites, MFQ was significantly greater in LMB versus
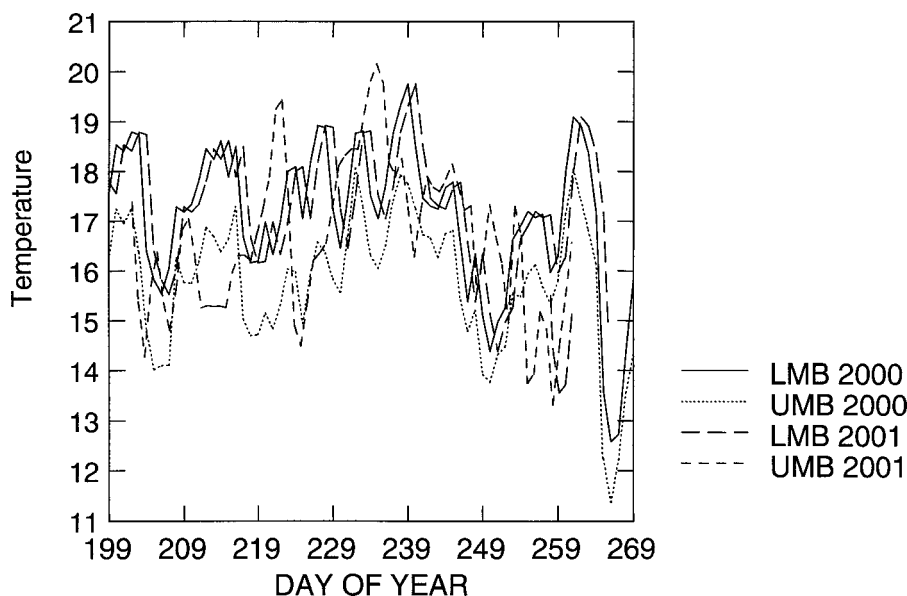

FIGURE 2.—Daily stream summer temperatures in Mink Brook study sections in 2000 and 2001 (UMB = Upper Mink Brook; LMB = Lower Mink Brook). Daily temperatures are averages of readings taken at 15-min intervals by temperature loggers placed at the upstream and downstream ends of the study sections.
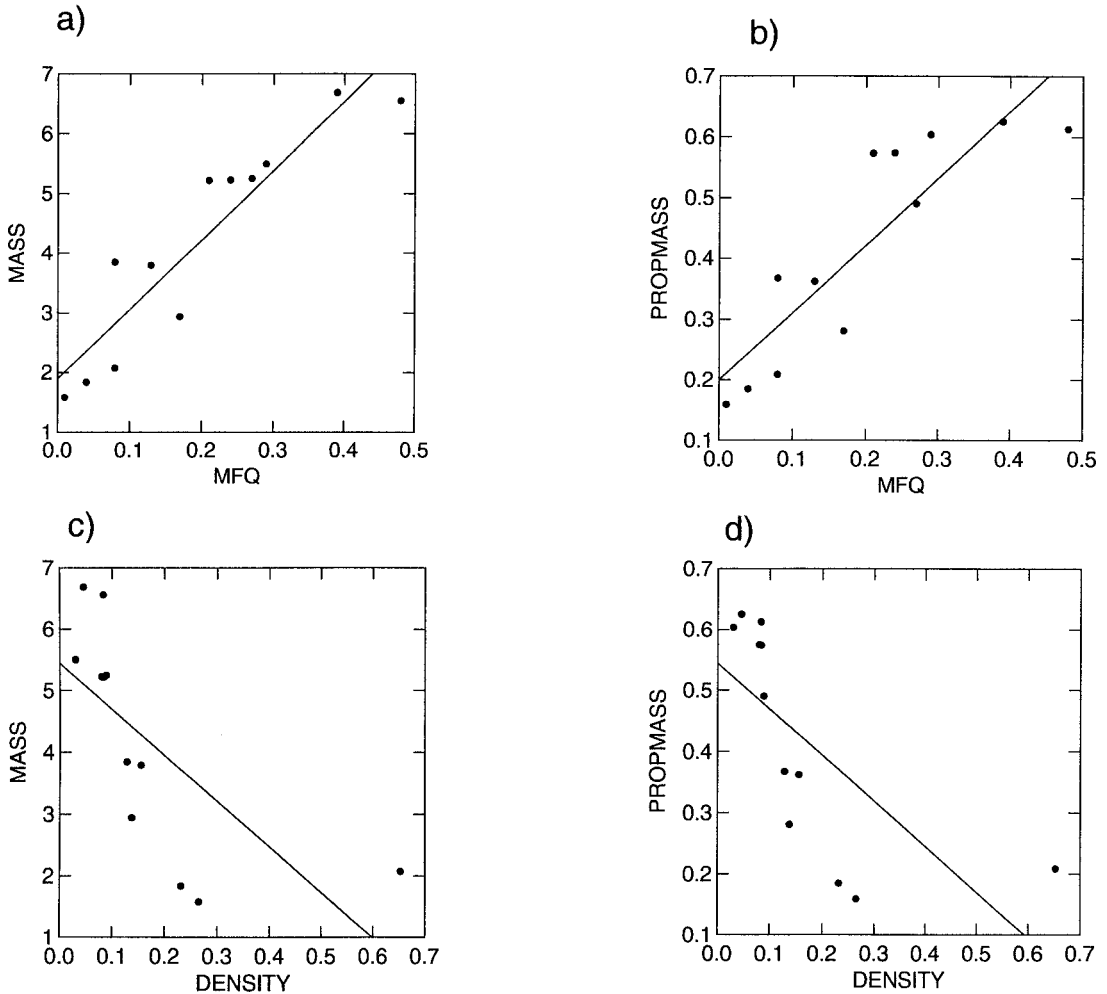
FIGURE 3.—Microhabitat foraging quality (MFQ) and age-0 salmon density (number/m²) versus mean age-0 salmon mass (g) and the proportion of maximum predicted mass that was actually achieved (PROPMASS) 115 d after stocking. All relationships are significant (see text for summary statistics) ($N = 12$ for all graphs).

UMB ($F_{1,12} = 8.422$, $P < 0.05$) and in 2000 versus 2001 ($F_{1,12} = 37.07$, $P < 0.0001$). Across all study plots, MFQ was a strong predictor of fish mass ($F_{1,12} = 58.7$, $R^2 = 0.85$, $P < 0.0001$; Figure 3). In addition to the positive relationship between MFQ and mass, mass was significantly and negatively related to age-0 fish density across sections and years ($F_{1,12} = 9.43$, $R^2 = 0.49$, $P < 0.05$; Figure 3).

In contrast, overall growth differences between sites and seasons were not explained by differences in temperature regime. Mean summer temperatures in 2000 and 2001 (15–18°C) were close to or slightly below optimal levels for age-0 fish growth, but observed mass (1.7–6.1 g) was substantially lower than predicted by the temperature

model (>9 g) (Table 3). Temperature was a poor predictor of age-0 fish growth over the course of the study. Temperatures were generally closer to optimal conditions in 2001 than in 2000, whereas mass was significantly greater in 2000. As a result of limited variation in temperature-predicted maximum mass across sites and years, the proportion of predicted maximum mass was strongly correlated with realized mass (Pearson's correlation coefficient = 0.98). Consequently, results for the proportion of predicted mass were similar to those obtained for realized mass (Table 3), with significant year ($F_{1,12} = 138.4$, $P < 0.0001$) and section ($F_{1,12} = 7.15$, $P < 0.05$) effects, and a significant overall relationship between MFQ and the proportion of predicted mass (Figure 3). However, in

TABLE 3.—Means (±SE) of fish density and mass measurements for Mink Brook, New Hampshire ($N = 3$ plots per section). Temperature-predicted mass was calculated with the Ratkowsky functional growth model (Jonsson et al. 2001). The abbreviation UMB stands for upper Mink Brook, the abbreviation LMB for lower Mink Brook.

Year	Section	Density (number/m^3)	Mass (g)	Predicted maximum mass (g)	Proportion of maximum mass
1999	UMB		1.73 (0.14)		
	LMB		2.56 (0.05)		
2000	UMB	0.082 (0.002)	5.26 (0.09)	9.77	0.538 (0.01)
	LMB	0.045 (0.014)	6.16 (0.46)	10.61	0.576 (0.04)
2001	UMB	0.384 (0.135)	1.82 (0.38)	10.71	0.184 (0.01)
	LMB	0.141 (0.008)	3.52 (0.14)	11.82	0.337 (0.28)

contrast to realized mass, there was also a significant year $\times$ section interaction ($F_{1,12} = 8.72$, $P < 0.05$) in proportion of predicted mass, indicating that some of the differences in growth may be associated with lower summer temperatures at the upper study site.

Discussion

Our goals were to quantify effects of hydrologic change on juvenile Atlantic salmon growth and to interpret these effects mechanistically. To do so, we contrasted relationships among foraging habitat availability, temperature, and fish growth and survival measured in the field to predictions derived from mechanistic, stage-specific models linking habitat and temperature to growth and performance. Age-0 fish mass varied substantially among sites and years in Mink Brook, spanning a range of variation equaling that found across seven rearing streams in the nearby Green Mountain National Forest (Roy, unpublished data). Atlantic salmon mass was lowest during the low-discharge summer of 2000 and was positively correlated with availability of model-predicted favorable foraging locations. In contrast, variation in growth was not closely associated with temperature model predictions. Hence, we conclude that spatial and temporal differences in age-0 fish mass in Mink Brook are likely attributable to differences in the availability of high-quality habitat. Our results are consistent with Weatherly et al. (1991), who found that deviations from maximum temperature-predicted growth rates for brown trout *Salmo trutta* in upland Wales were greatest during drought years. However, our use of a foraging-based model in combination with a temperature model enabled us to provide a mechanistic explanation for growth variation associated with summer hydrologic regime.

Foraging-based models for salmonids (Hughes and Dill 1990; Hill and Grossman 1993; Baker and Coon 1997; Nislow et al. 1999) have successfully predicted microhabitat use and survival in many streams. We found that discharge affects individual growth and performance in addition to habitat choice, drift rate, and capture success. Incorporating the stage-specific temperature model into our evaluation was also very useful because we determined that variation in temperature across these sites was a poor predictor of growth variation. A major reason for the lack of a strong temperature effect on growth variation in our study is probably due to the relatively minor temperature differences between years and sites. Summer temperatures only ranged from about 16.5°C to 18°C, close to predicted optimum temperatures for Atlantic salmon growth. This significantly improved our ability to attribute measured differences in growth to differences in flow regime. Temperature clearly sets an upper limit to growth (Elliott and Hurley 1997; Jonsson et al. 2001), but temperature is most likely to drive growth variation over scales where differences are large, such as between basins or across regions (Folt et al. 1998). Though insignificant as an overall predictor of Atlantic salmon mass variation, slight temperature differences may explain some of the difference in size between upper and lower study sections. We observed a significant year $\times$ section interaction when expressing mass as a proportion of temperature-predicted values, but no significant interaction for actual mass. This suggests that some of the differences in growth between sections may be associated with lower-than-optimal summer temperatures in the upper study section (Table 2).

In addition to positive associations between predicted favorable foraging locations and Atlantic salmon mass, mass was negatively associated with density (Figure 3). Density-dependent growth of stream-dwelling salmonids, including Atlantic salmon, has been observed in a number of previous

studies (Bohlin et al. 1994; Vollestad et al. 2002). Therefore, it is likely that the reduced growth we observed in low-discharge sections and years was a function of both decreased habitat quality (lower MFQ) and increased demand due to high fish densities. We also cannot rule out the possibility of other density-dependent effects driving these differences. However, given low predation rates apart from the period immediately after stocking (Henderson and Letcher 2003), low rates of both intra- and interspecific aggression (Nislow et al. 1998), and little evidence of parasitism in these systems, our explanation appears to be the most likely scenario.

Our study may have important implications for smolt production and Atlantic salmon restoration in the region. It appears likely that, during periods or in places of low discharge, overall smolt production will decline due to the production of small fish. Small fish are less successful at overwintering (Metcalfe 1998) and often require an additional year of freshwater growth (if they survive) before emigrating (Marschall et al. 1998). The small size of fish from the UMB study section suggests constraints on the ability of headwater streams in this region to serve as Atlantic salmon nursery areas. While age-0 fish appeared to have high survival in the UMB section, growth was strongly limited in the two low-flow years. These results suggest that the upper reaches of small streams may be suitable for Atlantic salmon rearing only under particular conditions of summer streamflow.

Our results also suggest that anthropogenic changes in summer flow regimes may substantially alter smolt production by altering juvenile size. Many rearing streams in this region are associated with small-scale impoundments (O'Leary, personal communication). These structures, especially when associated with municipal water supplies, can divert a significant fraction of streamflow during periods of high water demand in the summer. A great deal of attention has been focused on the establishment of instream flow criteria for stream fishes, with increasing calls for linking fish population dynamics directly to changes in streamflow (Van Winkle et al. 1998). However, instream flow assessments still rely heavily on frequency of use as an indicator of habitat suitability (LeClerc et al. 1996). Without mechanistic links to growth, particularly in species such as Atlantic salmon, for which size thresholds are closely linked to life history strategy and recruitment dynamics (Metcalfe 1998), these approaches will be limited in their scope and predictive power. In addition to the effects of flow regulation, increased summer temperatures and evapotranspiration rates associated with global climate change in the New England region (Moore et al. 1997) may also reduce growth and production of juvenile salmon. Our study provides the framework for quantifying the potential impact of these changes by directly linking streamflow to salmon growth. Our conclusions, however, are limited by the temporal and spatial scale of the study, and our inability to follow the growth of individuals. Future studies that encompass multiple high- and low-flow years and sites, and that track individuals, will greatly enhance our understanding of the links between flow regime and fish growth.

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