Spatially Explicit Bioenergetic Analysis of Habitat Quality for Age-0 Atlantic Salmon

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Abstract.—Spatial and temporal variation in growth conditions for young juveniles may determine the ultimate success of salmonid populations. To assess this aspect of habitat quality, we developed a spatially explicit bioenergetics model to predict age-0 Atlantic salmon *Salmo salar* growth rate potential (GRP) in rearing streams of the Connecticut River, from the time of stocking in the spring, to the end of the summer. During the first month after stocking, there appears to be a paucity of suitable habitat. Most available habitat is predicted to result in low foraging success of small fish and to be energetically stressful because of the combination of high spring discharge and low water temperature. Although less than 14% of available habitat was predicted to support positive growth in the spring, 47% of the fish we observed occupied microhabitats predicted to yield positive growth, indicating the importance of habitat selection. In contrast, from mid-June to August, 67% of available habitat was predicted to yield positive growth, and 92% of all fish occupied positive growth microhabitats. Consistent with these results, sites with higher salmon GRP in the early season, but not in the mid- or late season, had higher final salmon densities by the end of August. Hydroclimatic regimes characteristic of more southerly rearing streams in the Connecticut River basin were predicted from our model to cause a potential shift from early-season to late-season habitat-related growth constraints along this environmental gradient. This work demonstrates the value of applying a bioenergetics approach to issues related to conservation of Atlantic salmon and provides a framework for future research on early life history energetic determinants of habitat quality.

Differences among streams in the availability of habitats with favorable growth conditions may translate into spatial variation in performance of stream fish populations. For juvenile salmonids, increased growth confers fitness advantages with respect to foraging and competitive ability (Kennedy and Strange 1986; Hill and Grossman 1993), overwinter survival (Orciari et al. 1988), and age to first reproduction (Holtby 1988). Environmental constraints on growth may be particularly important for juvenile salmonids in the first few months after they begin exogenous feeding. For instance, high levels of mortality experienced by age-0 brown trout *Salmo trutta* 2 to 9 weeks after emer-

gence appear to determine year-class strength and have been hypothesized to result from limited availability of appropriate feeding locations (Elliott 1989; Armstrong 1997). Previous work on age-0 Atlantic salmon *Salmo salar* in parts of the Connecticut River basin suggests that environmental constraints on feeding may be very strong during this early life history period. Nislow et al. (1999), using a foraging rate–based habitat suitability model, found that age-0 salmon strongly preferred microhabitats predicted to yield maximum consumption rates. Moreover, stream reaches with the highest proportion of microhabitats favorable for foraging in the first month after stocking had the highest age-0 salmon densities by the end of summer. These results suggest that capture success of early fry is limited relative to late-season fry and point to the ability of fry to forage as a key determinant of their survival and persistence during their first spring and summer. However, there are factors other than availability of prime foraging locations that could produce different spatial and temporal patterns of energetic limitation. For example, Keeley and Grant (1997) found that prey availability decreased in the

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months following Atlantic salmon emergence because of lower prey delivery rates and prey size. Lower prey availability, combined with increased metabolic demands of larger fish foraging at warmer summer temperatures, could favor late-season, as opposed to early-season, growth limitation as the primary determinant of first-year survival. Understanding these energetic constraints on habitat suitability for juvenile salmonids in any system requires a framework capable of determining how prey availability, temperature, and capture success interact to produce spatial and temporal variation in salmon growth conditions.

Spatially explicit bioenergetics models, which incorporate the spatial distribution of fish, their prey, and the physical conditions that affect foraging and growth, are valuable for investigating the underlying basis for seasonal and spatial differences in habitat suitability. For stream salmonids, energetics models have been used to address aspects of microhabitat selection (Fausch 1984; Hughes and Dill 1990; Hill and Grossman 1993), effects of temperature and food abundance on rainbow trout growth in a lake outlet river (Filbert and Hawkins 1995), and interspecific competition (Clark and Rose 1997). However, a spatially explicit bioenergetics approach has not been used previously to directly measure habitat quality for stream salmonids. Moreover, a model parameterized for juvenile Atlantic salmon has not been published yet would be very useful for a wide range of applications, including assessment of habitat quality.

In this study, we weighed seasonal and site variation in growth potential as measures of habitat quality for juvenile Atlantic salmon currently being re-introduced to former rearing tributaries of the Connecticut River basin, northeast USA. We added a number of key components (e.g., empirical measures of seasonal changes in temperature and prey availability) to our foraging rate-based habitat suitability model and built a new submodel translating consumption into potential salmon growth to construct a spatially explicit bioenergetics model (Brandt et al. 1992) for age-0 Atlantic salmon. Our objective was to predict when stream locations (potential or actual feeding territories) were likely to yield positive growth rates for age-0 salmon. The model was used to test whether (1) growth potential changed significantly over the course of the spring and summer, (2) final salmon densities were greater in stream sites with a greater proportion of habitats predicted to provide positive growth, and (3) seasonal patterns of growth con-

ditions changed significantly along a major hydroclimatic (North to South) gradient in the Connecticut River basin. Elasticity analyses were used to determine which model attributes had the strongest influence on the predictions, and we compared our model predictions to observed rates of foraging and growth in several streams.

Atlantic salmon in the Connecticut River basin are ideal for examining the link between habitat availability and growth potential. All fry originate from a common genetic stock, so that differences in growth and production across habitats can be ascribed to environmental effects (Taylor 1991). Fry are stocked just prior to the onset of exogenous feeding at approximately the same time of year (across both sites and years), so the first spring and summer is their first significant environmental challenge. Spatial patterns in growth and survival therefore result from site-specific conditions experienced during this period, rather than differences in incubation or hatching conditions. Low stocking densities (< 0.6 individuals/m^2) and low population densities of other salmonid species (McMenemy 1995) in these sites make it unlikely that competition or predation (although we have no information on the impact of avian or mammalian predators) significantly affects the relationship between habitat suitability and age-0 performance. Finally, the Connecticut River basin, the largest river in New England, at the southern edge of the worldwide distribution of the species, spans a wide range of climatic, hydrologic, and biotic conditions, making it ideal for investigating environmental influences on juvenile growth potential.

Methods

In this section, we describe (1) the bioenergetics model, (2) the field data used as inputs to the model, and (3) our hypotheses and model applications.

Bioenergetics Model

Our model uses input data on environmental factors (e.g., water temperature, prey availability, current speed) to estimate the growth rate potential (GRP, see Brandt et al. 1992) for juvenile salmon within microhabitats and stream reaches. A microhabitat is a discrete area less than 1 m^2 (Kalleberg 1958; Grant and Kramer 1990; Nislow et al. 1998) that is occupied by or available to a single individual for use as a feeding territory. We use GRP as an indicator of habitat quality at both microhabitat and stream reach scales. Microhabitats providing high growth rate potential are more like-

TABLE 1.—Equations and parameter values used in the foraging submodel of the age-0 Atlantic salmon bioenergetics model.

Parameter	Units	Equation or value	Derivation
Consumption (C)	Prey·d^{-1}	$= P \cdot S \cdot T$	
Prey supply rate (P)	Prey·d^{-1}	$= D \cdot A \cdot V$	
Prey density (D)	Prey·(m^3)$^{-1}$	Early $= 7.85$	Folt and Parrish (1994)
		Mid $= 23.33$	
		Late $= 15.17$	
Proportion of appropriate-sized prey (A)		Early $= 0.8$	Folt and Parrish (1994)
		Mid $= 0.5$	
		Late $= 0.4$	
Volume flux (V)	m^3·d^{-1}	$= TW \cdot Z \cdot CV$	
Territory width (TW)	m	Early $= 0.1$	Kalleberg (1958); Grant and Kramer (1990)
		Mid $= 0.25$	
		Late $= 0.3$	
Water depth (Z)	m	Individual measurements	Nislow et al. (1999)
Current velocity (CV)	m·s^{-1}	Individual measurements	Nislow et al. (1999)
Capture success (S)		$= SI + SC(CV)$	
Capture success coefficient (SC)		Early $= -3.2$	Nislow et al. (1999)
		Mid $= -2.17$	
		Late $= -1.12$	
Capture success intercept (SI)		Early $= 0.83$	Nislow et al. (1999)
		Mid $= 0.93$	
		Late $= 1.0$	
Time spent at feeding station (T)	h	12 h/d	Nislow et al. (1998)

ly to be suitable for individual salmon, and stream reaches with a large proportion of suitable microhabitats should support greater salmon abundance.

In this study, we estimated the GRP of age-0 salmon throughout the first summer (i.e., from the time of stocking in May through the end of August). In late August, feeding rates generally decrease (Metcalfe et al. 1986), and salmon spend more time hiding in shelters (Rimmer et al. 1985; Gries et al. 1997). To assess seasonal differences in GRP within this time period, we divided the age-0 spring–summer into three discrete periods of similar duration: early season (May 7–June 10), midseason (June 11–July 14), and late season (July 15–August 29). We did not distinguish between upper modal group and lower modal group individuals (Metcalfe et al. 1986), as age-0 salmon in these streams do not exhibit a bimodal size distribution (K. H. Nislow, unpublished data).

Growth rate potential predictions were generated separately for two types of microhabitats: ''used'' (locations where we actually observed individual fish) and ''available'' (randomly assigned locations on the stream bottom selected to characterize this reach as a whole) (Manly et al. 1993). This distinction is critical. The GRP in used microhabitats provide an estimate of the potential growth and habitat suitability for the survivors—the fish that were able to persist—up to the point that they were observed. In contrast, the GRP in available microhabitats provides an estimate of the

overall suitability of a reach for salmon. High available GRP indicates a high probability that fish will find energetically favorable microhabitat and persist within specific reaches.

Model overview.—The model is divided into (1) a foraging submodel, which converts prey into potential consumption (C; number of prey consumed · d^{-1}) and (2) a growth submodel, which converts C into potential growth rate (G; g · g^{-1} · d^{-1}). Where available, we used our own site- and species-specific input parameters obtained for juvenile salmon in New England, then supplemented this information with published studies on Atlantic salmon or closely related species (Tables 1–2).

Foraging submodel.—The foraging submodel for age-0 salmon (Table 2) predicted potential consumption (C) as:

$$C = P \cdot CS \cdot T \qquad (1)$$

where P is prey supply rate, CS is detection and capture success of the predator, and T is total time spent on the feeding territory. In our model, fish remain on their territories continually through the daylight hours and intercept prey items of appropriate size flowing past them. Prey supply rate is a function of prey density, the proportion of appropriate-sized prey, and the volume flux of water through the individual territory. Volume flux is determined by current velocity, water depth, and territory width (related to fish body size in the

TABLE 2.—Equations and parameter values used in the growth submodel of the age-0 Atlantic salmon bioenergetics model.

Parameter	Units	Equation or values	Derivation
Growth (G)	$g^{-1} \cdot g^{-1} \cdot d$	$= EAG \cdot SED^{-1} \cdot SWT$	
Energy available for growth (EAG)	J	$= EI - (W + R)$	
Energy intake (EI)	$J \cdot d^{-1}$	$= C \cdot PWT \cdot PED$	
Prey dry weight (PWT)	g	$1.35 \cdot 10^{-4}$	Folt and Parrish (1994)
Prey energy density (PED)	$J \cdot g^{-1}$	4,800	Cummins and Wuychek (1971)
Salmon energy density (SED)	$J \cdot g^{-1}$	9,800	Gardiner and Geddes (1980)
Salmon dry weight (SWT)	g	Early = 0.4	
		Mid = 1.2	
		Late = 3.0	
Waste losses (W)	$J \cdot d^{-1}$	$= EG + EXC$	
Egestion (EG)	$J \cdot d^{-1}$	$= 0.15 \cdot EI$	Hill and Grossman (1993)
Excretion (EXC)	$J \cdot d^{-1}$	$= 0.10 \cdot EI$	Hill and Grossman (1993)
Respiration (R)	$J \cdot d^{-1}$	$= M + SDA$	
Metabolism (M)	$J \cdot d^{-1}$	$= M_r + M_a$	
Activity metabolism (M_a)	$J \cdot d^{-1}$	$= (T \cdot 24^{-1}) \cdot M_r$	
Resting metabolism (M_r)	$J \cdot d^{-1}$	Early = 24	Hill and Grossman (1993)
		Mid = 65	
		Late = 80	
Specific dynamic action	$J \cdot d^{-1}$	$0.15 \cdot EI$	Hewett and Johnson (1992)

three seasons as in Grant and Kramer 1990). Capture success (the proportion of appropriate-sized prey passing through the territory that are successfully captured and ingested) is a function of fish body size (increases success), water temperature (increases success), and current velocity within the feeding territory (decreases success). Current speed/capture success relationships (slope and *y*-intercept) were available for early-season fish (30 mm standard length, SL) experiencing mean water temperatures of 12°C and for late-season fish (75 mm SL) experiencing mean water temperatures of 18°C (Nislow et al. 1999). Because capture success has been shown to increase monotonically over this fish size and water temperature ranges (Hill and Grossman 1993), midseason current speed–capture success relationships were modeled as intermediate between early- and late-season values.

At high levels of prey supply and capture success, satiation will prevent continued increase in daily consumption rates. To include this aspect of salmon behavior in the model, we constrained foraging rate to 3.5 items · min⁻¹ (maximum rate observed in prior feeding studies; Nislow et al. 1998) and limited daily ration (g · d⁻¹) to 13% of fish body weight (Hayward and Weiland 1998), which is the highest maximum daily ration obtained from three separate studies of salmonids (Elliott and Persson 1978; Rand et al. 1993; Hayward and Weiland 1998). Predicted daily ration rarely exceeded maximum daily ration for any site or season.

Growth submodel.—The growth submodel pre-dicted daily relative growth rate (G; $g \cdot g^{-1} \cdot d^{-1}$) following the basic equation; of Winberg (1956), which partitions the ingested energy (EI; $J \cdot d^{-1}$) contained in consumed prey (C) to waste products (W), respiration (R), or energy available for growth (EAG). This energy is then converted into G (positive or negative) in proportion to salmon energy density (SED; $J \cdot g^{-1}$) divided by mean salmon weight (SWT) to derive growth:

$$G = EAG \cdot SED^{-1} \cdot SWT^{-1} \qquad (2)$$

$$EAG = EI - (W + R) \qquad (3)$$

Respiration (R) consists of specific dynamic action (SDA; a constant in our model) plus metabolism (M). We modeled metabolism ($J \cdot d^{-1}$) as the sum of resting metabolism (M_r) and activity metabolism (M_a). To determine M_r, we used Facey and Grossman's (1990) relationship between swimming speed and metabolic rate in age-0 rainbow trout *Oncorhynchus mykiss* to extrapolate metabolic rate at zero swimming speed (as per Huuskonen and Karjalainen 1998). To determine M_a, we assumed that age-0 Atlantic salmon act as sit-and-wait foragers, waiting at station to intercept drifting prey. Activity metabolism for sit-and-wait foragers can be adequately represented as a constant multiple of resting metabolism, with a multiplier of 1.0 (Hewett and Johnson 1992), such that $M_a = M_r$. Given $M_a > 0$ only during the active daylight hours, M can be estimated as

$$M = M_r + M_a \qquad (4)$$

$$M_a = (T \cdot 24^{-1}) \cdot M_r \qquad (5)$$

where T (hours) is the total time spent foraging (as in equation 1). Metabolism is the only parameter in our growth model that differs among seasons, increasing from May through August as a function of increasing water temperature and fish size.

Model output.—We generated two separate estimates of habitat quality with respect to growth rate potential. Our first measure is the spatially explicit growth rate potential (SGRP; g · g^{-1} · d^{-1}),

$$SGRP = (G) \cdot N^{-1}, \qquad (6)$$

where N is the total number of microhabitats (separately for used and available microhabitats) measured in the study site. From the habitat perspective, SGRP estimates the potential for a section of stream to gain (via positive growth or immigration of salmon to energetically favorable microhabitats within the study site) or lose (via negative growth or emigration from energetically unfavorable microhabitats within the study site) salmon biomass. From the fish perspective, SGRP is the GRP expected from a randomly encountered microhabitat. Our second measure is the proportion of positive growth microhabitats (PGRP),

$$PGRP = N_{(G>0)} \cdot N^{-1}, \qquad (7)$$

where $N_{(G>0)}$ = the number of positive-growth microhabitats. From the habitat perspective, this dimensionless measure gives the proportion of a study site fulfilling the minimum criteria of positive growth. From the fish perspective, it is the probability that a randomly encountered habitat will be predicted to yield positive growth.

Field Measurements

Growth rate predictions were generated using data from repeatedly sampled index sites in six study streams in the northern Connecticut River basin in central and southern Vermont (Nislow et al. 1999). Index sites were about 100 m long and 5–8 m wide. These streams were selected to span the wide range of variation in age-0 proportional retention (= number of individuals sampled by late August/number of individuals stocked into the reach in May) that occurs in this part of the basin. Proportional retention includes both in situ survival and net immigration into the study section. Retention estimates are made using multiple-pass

electrofishing censuses conducted annually in the index sites by Vermont Department of Fish and Wildlife personnel (McMenemy 1995); relative differences in proportional retention between streams have been consistent over the last 10 years (Nislow et al. 1999).

Our goal in the field study was to obtain an unbiased sample of both used and available microhabitats. To characterize available microhabitats, we measured current speed and water depth in point locations at 1-m intervals along four randomly assigned transects traversing the stream within the index sites (details in Nislow et al. 1999). Used microhabitats were characterized by locating and measuring current speed and depth at the positions held by 5 to 10 randomly located individual age-0 salmon on each sampling day. Located fish were removed from the stream (via dip netting) for gut content analysis, eliminating the possibility of resampling fish; the number of fish removed over the course of the entire study never exceeded 10% of the fish originally stocked into the section. In order to characterize habitat use and availability throughout each period, each site was sampled every 7 to 9 d from mid-June through August 1991 (mid- and late-season period), and from early May through mid-June 1992 (early-season period). We collected habitat measurements at 650 locations along random transects and at 301 age-0 salmon positions over all sites and all three seasons.

To characterize prey availability and use, we collected three to eight, 15-min invertebrate drift samples during each sampling day and analyzed the gut contents of all fish (Folt and Parrish 1994). From gut contents analysis, we determined minimum and maximum prey sizes used during each time period. The number of prey items in drift samples that fell within this size range divided by the total number of prey items was used to estimate the proportion of appropriate-sized prey. In addition, we calculated stream discharge at each of the four transects within each index site and measured water temperature with a continuously recording thermograph (May–August) placed within the main channel of each stream.

Model Applications

H1: Growth rate potential and the availability of microhabitats yielding positive growth differ significantly among seasons.—We tested this hypothesis using two-way analysis of variance (ANOVA), with state (used versus available) and season (early, mid-, and late) as categorical variables and

TABLE 3.—List of model parameters used in elasticity analysis of the age-0 Atlantic salmon bioenergetics model. See Tables 1 and 2 for abbreviations; GRP = growth rate potential.

Parameter	Type	Effect of increase in parameter value	Effect on GRP	Similar parameters
Capture success coefficient (SC)	Capture success parameters (CS)	Decreases negative effect of current speed on capture success (CS)	Increase	SI
Proportion of appropriate-sized prey (A)	Prey numerical parameters (PN)	Increases consumed energy (C)	Increase	D, TW, T, PWT, PET
Resting metabolism (M_r)	Metabolic parameters (M)	Decreases energy available for growth (EAG)	Decrease	EG, EXC, SDA, M_r
Salmon energy density (SED)	Energy density parameters (SED)	Determines conversion of EAG into fish biomass	GRP > 0; decrease GRP < 0; increase	None

SGRP or PGRP as dependent variables. For all tests, the unit of replication was the study site (*n* = 6; Table 1). Tukey tests were used to test pairwise differences between means.

H2: Sites with higher growth rate potential retain a higher proportion of salmon throughout the spring/summer.—We used correlation analysis to test the relationship between age-0 salmon retention and growth rate potential (SGRP and PGRP) in the six study streams. Growth rate potential was correlated with retention estimates (1) for the study years (1991 to mid- and late-season; 1992 to early-season) and (2) that were averaged over 5 years, in order to correlate habitat quality to general patterns of retention among study sites.

H3: Changes in environmental determinants of growth rate significantly affect seasonal patterns of age-0 salmon growth rate potential.—We constructed a simulated scenario to test the effects of larger scale spatial variation on Atlantic salmon GRP. Three major environmental gradients in the Connecticut River basin (north to south, high altitude to low altitude, inland to coastal), correspond to predictable decreases in the relative magnitude of stream discharge (Magilligan and Graber 1995) and to predictable increases in spring and summer water temperatures. We hereafter refer to this condition of decreased spring discharge and increased spring–summer water temperatures as ''southern'' conditions; model predictions derived from our field study streams represent ''northern'' conditions.

In southern-condition model runs, early-season fish experience the reduced current speeds, warmer temperatures, reduced prey sizes, and increased prey densities (due to predicted earlier aquatic insect emergence) characteristic of midseason northern conditions. Increased water temperatures will (1) decrease the slope of the capture success/current speed relationship so that fish are better able to detect and capture prey at high current speeds and (2) increase metabolic rates. Mid- and late-season fish experience no change in flow or prey conditions under southern conditions but do experience increased stream temperatures. In the absence of habitat use information under southern conditions, we compared northern and southern GRP scenarios for available habitats only, using paired *t*-tests for each of the three seasons.

Elasticity analysis.—Individual parameter perturbations (Heppell and Crowder 1996; Sabo et al. 1996) were used to test the effect of selected parameters on model predictions. For these analyses, we divided the model into four classes of parameters: two (capture success and prey availability) that turn prey into consumed energy and two (metabolism and salmon energy density) that determine how this consumed energy is turned into fish biomass. We then chose a single parameter whose effect was representative of all the members of its class (Table 3) to use in the elasticity analyses. Analyses involved changing the value of a selected parameter by 60% while holding all other input parameters equal (Heppell and Crowder 1996). The effect of these decreased and increased values on GRP (i.e., elasticity) was expressed as

$$\mathrm{EL} = E_i \cdot \bullet E_{\max}^{-1}, \qquad (8)$$

where EL is elasticity, E_i is the magnitude of change in the output caused by a change in the *i*th input parameter, and $\bullet E_{\max}$ is the magnitude of change caused by the most influential parameter in the model. Separate elasticity analyses were run for used and available microhabitats in each of the three seasons.

Comparisons to empirical foraging and growth rates.—Model predictions were primarily intended as a measure of habitat quality; however, we were also interested in how model-predicted consump-

tion and GRP compared to actual measures of foraging and growth. To this aim, we compared model-predicted foraging rate and SGRP generated from used habitats to observed foraging and growth in several study sites. For foraging, we generated independent foraging rate predictions for two additional study sites where fish foraging attempt rates were observed during mid- and late season (Nislow et al. 1998). For growth, we used site-specific growth curves averaged over the six index sites in 1991 and 1992 to provide growth increments for each of the three time periods and compared them to model-predicted SGRP for used habitats.

Results

Hypothesis Tests

Hypothesis 1.—Salmon growth rate potential differed significantly among seasons. In available habitats, both SGRP (ANOVA; $f_{[2,18]} = 7.721$, $P < 0.01$) (Figure 1a) and PGRP (ANOVA; $f_{[2,18]} = 5.675$, $P < 0.05$) (Figure 1b) were significantly lower in the early season (Tukey test; $P < 0.005$) than in either the mid or late season, which did not differ from one another. Early season SGRP in available microhabitats was negative (-0.032 ± 0.006 SE), and fewer than 14% of these microhabitats were predicted to yield positive growth rates. In contrast, available SGRP during the mid and late seasons was positive, as the majority of available microhabitats were predicted to yield positive growth rates (PGRP = 0.57 ± 0.05 mid season; PGRP = 0.61 ± 0.032 late season).

Microhabitats where fish were found had higher growth rate potential than available habitats (ANOVA; $f_{[1,18]} = 7.845$, $P < 0.005$) (Figure 1). Fish were significantly less likely to occur in negative- or zero-growth microhabitats than predicted by chance, indicating selection for positive-growth microhabitats (early $\chi^2_{[1,370]} = 53.04$; mid $\chi^2_{[1,590]} = 20.19$; late $\chi^2_{[1,548]} = 40.52$; $P < 0.005$ for all comparisons). SGRP (ANOVA; $f_{[2,18]} = 4.20$, $P < 0.05$) and PGRP (ANOVA; $f_{[2,18]} = 40.52$, $P < 0.005$) in used habitats also differed significantly among seasons. Early season used SGRP and PGRP were significantly lower than mid- or late-season predictions, as about 90% of mid- and late-season fish occupied microhabitats predicted to yield positive growth, whereas slightly less than 50% of early season fish occupied positive growth microhabitats.

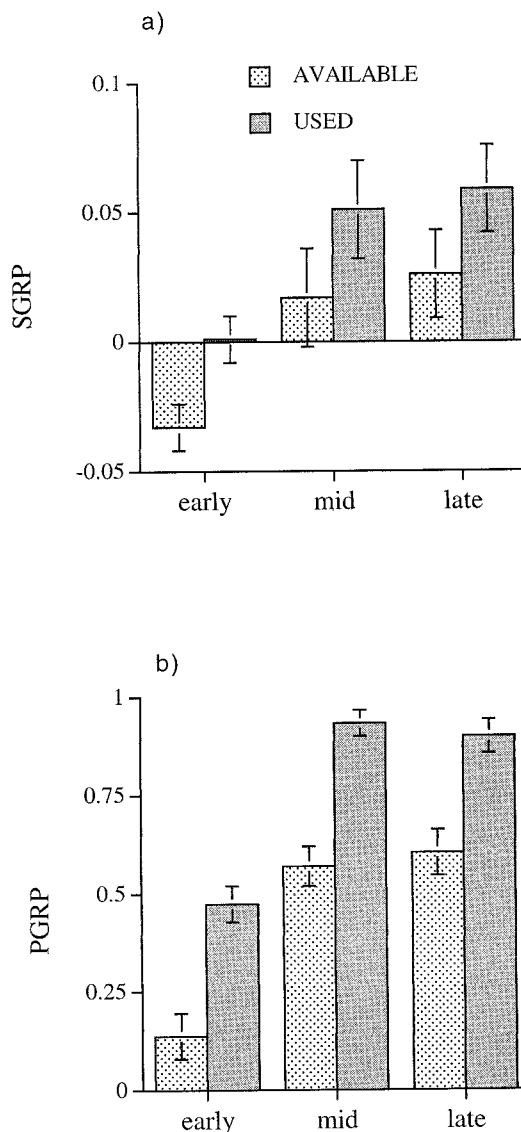Differences between seasons and between used versus available microhabitats are also apparent

FIGURE 1.—Average ($\pm$ SE) growth rate potential (SGRP) ($g \cdot g^{-1} \cdot d^{-1}$) of age-0 Atlantic salmon **(a)** and proportion of habitats predicted to yield positive growth (PGRP) **(b)** averaged across six index streams for three seasons. ''Used'' refers to microhabitats occupied by salmon; ''available'' refers to microhabitats measured along randomly placed sampling transects. Differences between seasons (early < mid = late) are significant for both SGRP and PGRP; used microhabitats had significantly greater SGRP and PGRP than available habitats across the three seasons.

from a direct comparison of frequency distributions of salmon GRP (Figure 2). Between early and mid-season and between used and available microhabitats, means are distinctly shifted to high-
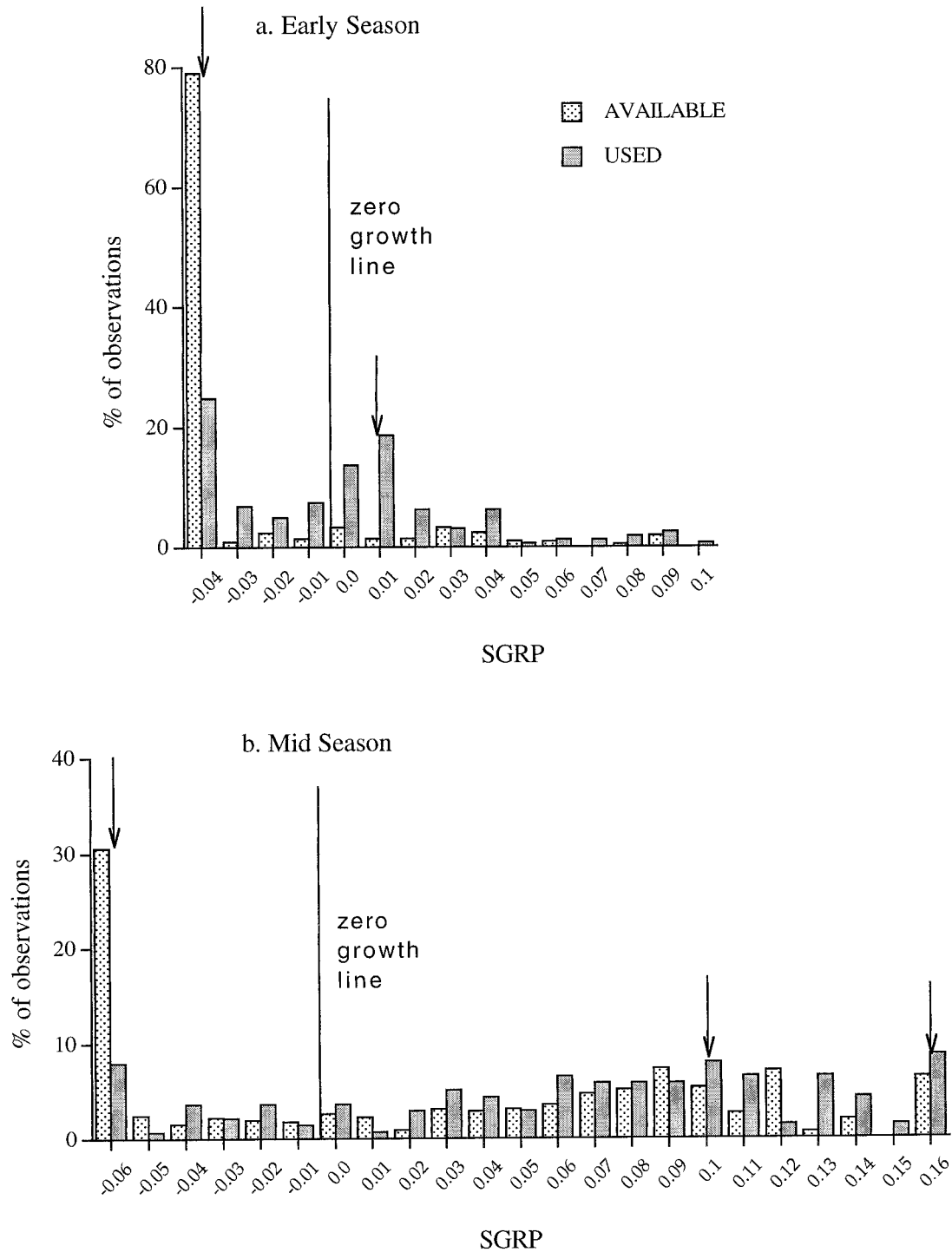
FIGURE 2.—Frequency distribution of salmon growth rate potential ($g \cdot g^{-1} \cdot d^{-1}$) in (a) early and (b) mid-season in available (light bars) and used (dark bars) microhabitats for all six study sites combined. Arrows indicate modes in frequency distributions discussed in the Results section of the text.
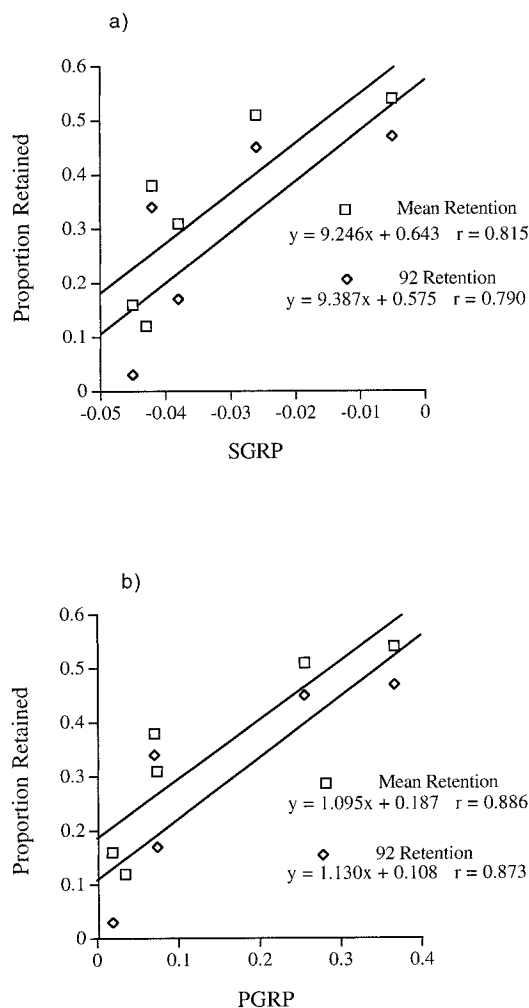
FIGURE 3.—Correlations between proportional retention of age-0 Atlantic salmon (= number of fish censused at the end of August/number of fish stocked) and **(a)** growth rate potential (SGRP) $(g \cdot g^{-1} \cdot d^{-1})$ and **(b)** proportion of habitats yielding positive growth (PGRP), with each index site $(n = 6)$ depicted as a single point in the graph. Correlations between 5-year mean retention estimates and 1992-only estimates are shown on the same axes. All correlations are significant $(P < 0.05)$.

TABLE 4.—Correlation coefficients (R) for relationships between model-predicted growth rate potential (GRP) and proportional retention (averaged over five census years) of age-0 Atlantic salmon; $N = 6$ for all correlations. Significant correlations indicated with an asterisk; SGRP = spatially explicit GRP; PGRP = positive GRP.

	Season	R
SGRP	Early	0.815*
	Mid	0.229
	Late	−0.218
PGRP	Early	0.886*
	Mid	−0.437
	Late	−0.115

er GRP. In the midseason, the GRP frequency distribution has three distinct modes: (1) GRP predicted for maximum consumption rates, (2) GRP predicted for zero consumption rates, generally the result of zero predicted prey flux at very low current speeds, and (3) the central tendency of the remaining observations (Figure 2b). In the early season, however, the GRP distribution was bimodal. The dominant mode in the early season was at GRP predicted from zero consumption, with the

second mode representing the mean of the remaining, nonzero consumption microhabitats and essentially no microhabitats predicted to yield maximum consumption (Figure 2a). In contrast to the mid-season, where zero consumption was in most cases the result of low prey flux at very low current speeds, zero consumption in the early season was generally the result of low capture success at high current speeds. The second mode of the early season distribution was the central tendency of the remaining microhabitats.

Hypothesis 2.—Study sites yielding higher SGRP and PGRP in the early season, when GRP in available habitats was negative, had higher retention rates of age-0 salmon over the study period (May–August) (Figure 3). These relationships were statistically significant when either 1992 retention data (year of the study) or average spring–summer retention over a 5-year period were used. Underlying this correlation, in the two sites with the highest proportional retention of age-0 salmon, more than 25% of the available microhabitats were predicted to yield positive growth, compared to less than 10% of available microhabitats in the sites with the lowest proportional retention. In contrast, we found no significant correlation between retention rates and mid- or late-season GRP (Table 4) when SGRP was positive in all sites.

Hypothesis 3.—Seasonal patterns of age-0 salmon growth potential differed significantly between northern and southern conditions (Figure 4). SGRP summed over the full growing season was similar between northern $(0.063 \pm 0.03 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1})$ and southern $(0.079 \pm 0.06 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1})$ conditions, and mid-season predictions were essentially unchanged (SGRP $n = 6$, $t = -1.19$, $P > 0.2$; PGRP $n = 6$, $t = -1.66$, $P > 0.15$). However, southern early-season SGRP $(0.027 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1})$ was significantly greater than northern SGRP $(-0.033 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1})$, and PGRP was three times as great
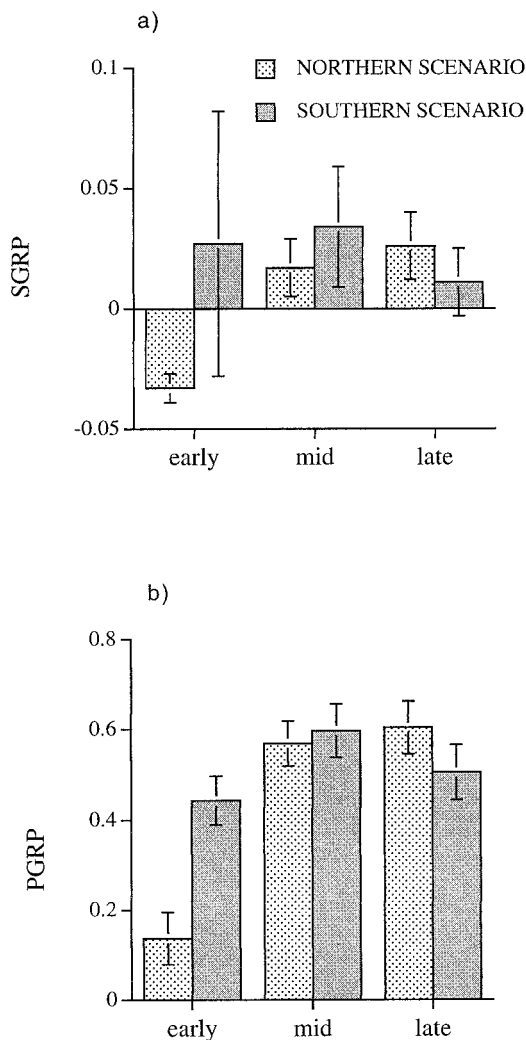
a)

b)

FIGURE 4.—Average ($\pm$SE) growth rate potential (SGRP) ($g \cdot g^{-1} \cdot d^{-1}$) of age-0 Atlantic salmon **(a)** and proportion of habitats predicted to yield positive growth (PGRP) **(b)** for available habitats under northern versus southern habitat conditions. The northern-condition scenario is identical to Figure 1; the southern-condition scenario generates growth rate potential, averaged across the six study streams, predicted to occur under southerly hydroclimatic conditions (see text for details). Southern SGRP and PGRP predictions were significantly higher than northern predictions in the late season; there were no significant differences in mid-season predictions. Differences between seasons are significant for both SGRP and PGRP under northern conditions but are not significant under southern conditions.

($\sim$44%) as predicted under northern conditions ($\sim$14%) ($n = 6$, $t = -3.974$, $P < 0.05$). Conversely, southern SGRP in the late season was $\sim$50% lower than northern SGRP ($n = 6$, $t = 14.979$, $P < 0.001$), and PGRP was reduced from more than 60% to about 50% of available habitat. As a result, in contrast to northern conditions, there was no significant seasonal effect on either SGRP (ANOVA; $f_{[2,15]} = 1.779$, $P > 0.2$) or PGRP (ANOVA; $f_{[2,15]} = 0.103$, $P > 0.9$) under the southern conditions.

Model Evaluation

Elasticity analysis.—The influence of model parameters GRP predictions differed between seasons. For early-season fish, changes in the velocity–capture success coefficient had the greatest overall effect on model output (Figure 5). A 60% increase in this parameter, resulting in a shallower negative slope of the current speed/capture success relationship, increased SGRP for available microhabitats in the early season by a factor of two and caused a qualitative change from net negative to net positive SGRP. No other parameter increased SGRP for early season available microhabitats by more than a factor of 0.82, and none caused a qualitative change. Because capture success was predicted to be zero or near zero in the majority of early season available habitats, the proportion of prey appropriate for consumption had the least influence on model predictions. However, the effect of this parameter increased in the mid-season, and by the late season, the effects of prey and metabolism both outweighed the effects of capture success parameters on GRP.

Model predictions versus empirical observations.—Model-predicted consumption rates accurately reflected the differences in foraging rates between two sites and were within one standard error of observed foraging rates within each site (Figure 6a). The seasonal pattern of SGRP predictions was consistent with empirical observations of lowest relative growth rates in the early season (Figure 6b). However, SGRP was lower and more variable than observed growth rates for the early and mid-season period and was higher than observed growth rates in the late season.

Discussion

In this, the first development and application of a spatially explicit bioenergetics model for age-0 Atlantic salmon, we found that seasonal and spatial differences in growth rate potential (GRP) emerged as vital determinants of habitat quality.
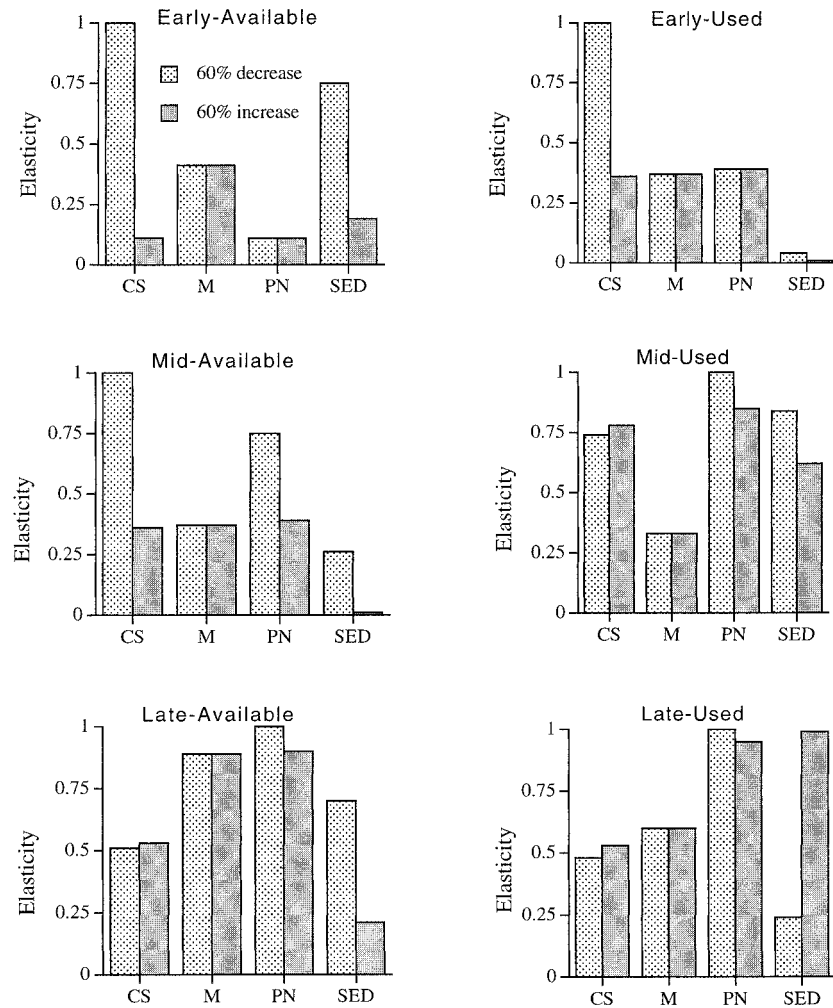
FIGURE 5.—Elasticity analysis of four major parameter types (CS = capture success, M = metabolism, PN = prey numerical parameters, SED = salmon energy density; see Table 3) for the age-0 Atlantic salmon bioenergetics model. Elasticity values (see equation 8 in text) give the proportional magnitude of effects on SGRP of 60% changes in parameter values. Values range from 0 (no effect on model output) to 1 (strongest effect on model predictions) within each season (early, mid, late) and state (used, available) combination; each combination is represented by a single graph in the figure.

As predicted (H1), salmon growth rate potential was significantly lower in the early season period (first month after stocking) than during the mid- and late-season periods. Early season negatives (low capture success, low prey densities) outweighed early season positives (low metabolic costs, large prey sizes), resulting in a relative paucity of energetically suitable microhabitats. In contrast, mid- and late-season positives (high capture success, high prey densities) outweighed late-season negatives (high metabolic rates, low prey fluxes, small prey sizes), producing an abundance of mi-

crohabitat predicted to yield positive growth. In spite of substantial seasonal variation in other energetic parameters, environmental constraints on foraging likely produce a period of limited energy availability for age-0 salmon in the first month after stocking. These results reinforce and expand beyond the findings of our previous work (Nislow et al. 1999). Furthermore, the seasonal patterns in prey and environmental conditions found in the study streams are characteristic of many northern temperate streams (Poff and Huryn 1998), suggesting that similar seasonal patterns of growth
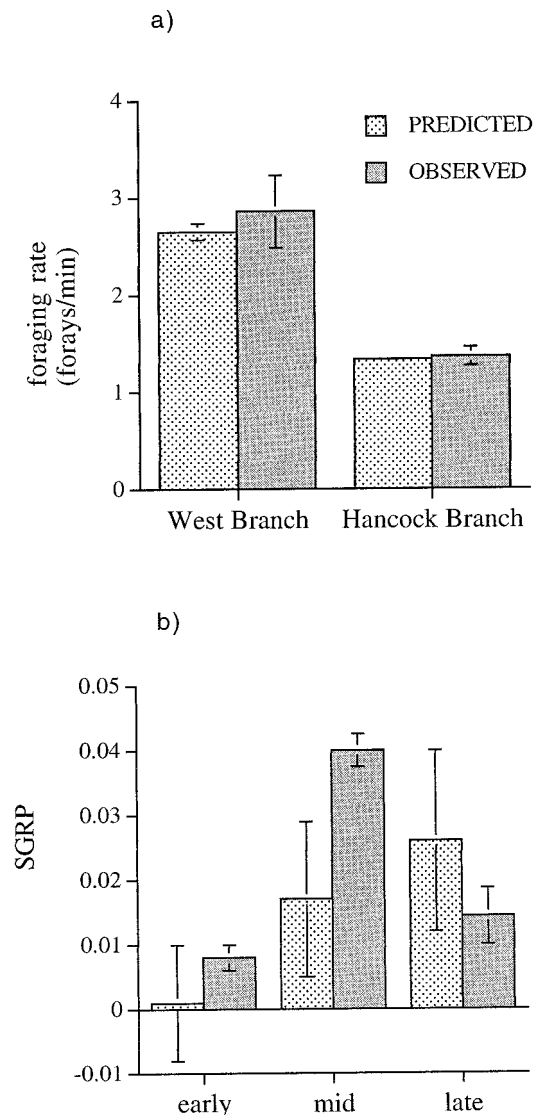
a)

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FIGURE 6.—(a) Observed versus model-predicted average (± SE) foraging rates for late-season fish in two study streams. Predicted values based on microhabitat conditions in feeding territories used by the same fish on which foraging observations were made. $N = 33$ individual fish for West Branch, $N = 35$ individual fish for Hancock Branch. (b) Observed versus model-predicted average (± SE) growth rates $(g \cdot g^{-1} \cdot d^{-1})$ in three seasons. Growth rates are derived from 1991 and 1992 growth curves averaged over six index streams (Folt and Parrish 1994).

rate potential may occur across a broad geographical range. Energetic constraints may be significant therefore to many populations, potentially contributing to the major postemergence mortality observed for stream salmonids (Elliott 1989), in-

cluding Atlantic salmon (Einum and Fleming, in press).

Reinforcing our model predictions, age-0 Atlantic salmon distribution and abundance were positively associated with growth rate potential at two spatial scales (supporting H2). First, in all three seasons, salmon selectively occupied microhabitats within stream sections that were predicted to yield positive growth rates. This finding is consistent with previous studies of Atlantic salmon (Nislow et al. 1999) and other drift-feeding stream fishes (Fausch 1984; Hughes and Dill 1990; Hill and Grossman 1993). Moreover, our early season results underscore the importance of habitat selection in allowing fish to maintain positive energy budgets under energetically unfavorable conditions. Second, differences in proportional retention among stream reaches were associated with differences in growth rate potential. Study sections with higher growth rate potential during the early season, but not in the mid- or late season, had higher final densities and higher proportional retention of age-0 Atlantic salmon during the first summer. Greater availability of positive-growth microhabitats, at the time when growth rate potential was predicted to be most limited, thus appears to be an important determinant of habitat suitability.

Whereas model predictions point to early season energetic limitation in our northern study streams, this mechanistic, energetics-based approach also allowed us to predict the conditions under which contrary seasonal patterns of growth limitation may prevail (H3). Under our modeled southern conditions, higher temperatures and reduced current speeds would increase the capture success of early season fish, which is the factor predicted to be most limiting to their growth. Under southern conditions in the late season, the positive effect of temperature on capture success is outweighed by temperature-associated increases in metabolic costs. The cumulative result of these two effects is that growth rate potential is predicted to be similar across seasons under southern conditions. Taking regional differences into account in management strategies may prove essential to salmon restoration in the Connecticut River basin, as well as in other large river systems where environmental determinants of growth change significantly over large spatial scales. More generally, the ability to fully assess how these types of environmental gradients influence energetic habitat quality is a major strength of a bioenergetics modeling approach and an important extension from simpler, foraging-

based habitat suitability models (Nislow et al. 1999).

Our goal was to use growth rate potential as an indicator of habitat quality, rather than to provide precise quantitative estimates of growth rate for Atlantic salmon. However, comparing model predictions to empirical patterns of foraging and growth is useful and instructive. Correspondence between growth rate potential and measured foraging and growth can increase confidence in GRP as an indicator of habitat quality. Alternatively, discrepancies between predictions and measurements can reveal knowledge gaps or suggest alternative modeling strategies. Our model predictions corresponded well to empirical measures in two ways. Foraging rate estimates were quite close to observations in two streams, if we assume that most of the foraging attempts observed led to successful consumption (as found by Biro et al. 1996). The model also correctly predicted the increase in relative growth rates observed in the mid- and late season compared to the early season (Figure 6).

There were several important differences between GRP and observed growth rates, however. First, early-season GRP was lower and more variable than empirical growth. Interestingly, this particular discrepancy is precisely what we expect if fish that lose weight or grow slowly are more likely to die or emigrate. It also occurs during the season with the most limited growth rate potential, when selective mortality and emigration of poorly performing individuals should be greatest. Second, midseason GRP was lower than observed growth. One potential explanation is that during the midseason period, fish direct a significant portion of their foraging attempts at benthic prey, in addition to feeding on drift (Nislow et al. 1998). The availability and use of benthic prey was not considered in our model and may partially account for the difference between predicted and observed growth during the midseason. Third, late-season predictions were higher than observed growth. This difference may be explained by the reduced feeding motivation (Metcalfe et al. 1986) and increased shelter-seeking behavior (Gries et al. 1997) as the summer progresses, which would cause actual growth to be lower than growth potential in the late season. In general, further development of species- and stage-specific bioenergetic model parameters should help close the gap between predictions and observations and increase confidence in model results.

Our study provides evidence that energetic limitation influences stream habitat quality for salmon in their first spring and summer. Our long-term goal is to determine whether differences in age-0 retention rates between sites, associated with differences in growth rate potential, translate into population consequences beyond the first spring and summer of the life cycle. However, this extension is presently inhibited by methodological constraints on tracking out-migrating and returning individuals to their natal streams (Kennedy et al. 1997), by the lack of data on density dependence of later life history stages (e.g., overwintering, migration), and by the paucity of information on demographics of marine survival (Friedland 1998). Nevertheless, understanding the determinants of habitat quality during early life history is a key step toward this larger aim. As such, we view this work as an instructive case study and as a framework for future research on early life history energetic determinants of the distribution and abundance of salmonid fishes.

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