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HABITAT-MEDIATED FORAGING LIMITATIONS DRIVE SURVIVAL BOTTLENECKS FOR JUVENILE SALMON

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Abstract. Realistic population models and effective conservation strategies require a thorough understanding of mechanisms driving stage-specific mortality. Mortality bottlenecks for many species occur in the juvenile stage and are thought to result from limitation on food or foraging habitat during a “critical period” for growth and survival. Without a way to account for maternal effects or to measure integrated consumption rates in the field, it has been virtually impossible to test these relationships directly. Hence uncertainties about mechanisms underlying such bottlenecks remain. In this study we randomize maternal effects across sites and apply a new method for measuring consumption integrated over weeks to months to test the hypothesis that food limitation drives early-season juvenile mortality bottlenecks in Atlantic salmon (*Salmo salar*). Using natural signatures of geologically derived cesium (¹³³Cs), we estimated consumption rates of >400 fry stocked into six streams. Two to four weeks after stocking, consumption was extremely low across sites (0.005 g·g⁻¹·d⁻¹) and was predicted to be below maintenance rations (i.e., yielding negative energy balances) for the majority of individuals from five of six sites. However, consumption during this time was positively correlated with growth rates and survival (measured at the end of the growing season). In contrast, consumption rates increased in mid- (0.030 g·g⁻¹·d⁻¹) and late (0.035 g·g⁻¹·d⁻¹) seasons, but juvenile survival and consumption were not correlated, and correlations between growth and consumption were weak. These findings are consistent with predictions of a habitat-based bioenergetic model constructed using the actual stream positions of the individual fish in the present study, which indicates that habitat-based models capture important environmental determinants of juvenile growth and survival. Hence, by combining approaches, reducing maternal effects and controlling initial conditions, we offer a general framework for linking foraging with juvenile survival and present the first direct consumption-based evidence for the early season bottleneck hypothesis.

Key words: bioenergetics; cesium; consumption; critical period; fish; food limitation; foraging; growth; juvenile Atlantic salmon; population; *Salmo salar*; survival bottleneck.

INTRODUCTION

Transition from maternally derived (endogenous) to independently derived (exogenous) energy sources is a ubiquitous phenomenon across species that has important consequences for survival and population dynamics. This transition, and the period immediately following it, are frequently marked by high mortality (Roff 1992, Gosselin and Qian 1997) due to starvation (Elliott 1989) or size- or condition-dependent vulnerability to predators and pathogens (Hare and Cowen 1997, Armstrong and Nislow 2006). Variation in survival within and across populations often depends on individual condition after completing the transition (Searcy and Sponaugle 2001, Zabel and Achord 2004), which may be determined by the extent to which favorable environmental conditions match juvenile

requirements during the so-called “critical period” following birth (Underwood and Fairweather 1989, Cushing 1990). However, juveniles are subject to strong maternal effects (Einum and Fleming 2000) that can obscure the link between habitat and performance in early life history. Given the importance of such critical periods to survival, population dynamics, life histories, and ultimately conservation of many species, developing an approach to distinguish these effects would be particularly valuable.

These issues are particularly relevant for the many species with complex life cycles, where adults produce large numbers of small, vulnerable juveniles that are exposed to potentially harsh environmental conditions. Salmonids (trout and salmon) provide an excellent example of such taxa. Even with relatively long life spans (2–10 years) (Fleming 1998), a large portion of their total mortality occurs during the first few weeks after fry emerge when they deplete yolk reserves and begin exogenous feeding (Elliott et al. 1989, Armstrong 1997, Einum and Fleming 2000). Prior studies have

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addressed population consequences (Elliott 1990, Armstrong 1997, Achord et al. 2003) of bottlenecks in this critical period, but none distinguish among factors driving this mortality.

Several lines of evidence support the hypothesis that early-season food and habitat availability force environmentally driven population bottlenecks and site-specific density dependence in salmonids (Elliott 1990, Einum and Nislow 2005). Environmental conditions following emergence that are exacerbated by intraspecific competition for suitable foraging sites (Elliott 1989) are believed to result in greater survival of competitively dominant individuals (Einum and Fleming 2000, Nislow et al. 2004a). However, inferences from previous studies have been limited by a lack of decisive information regarding consumption during the critical period. Extensive review of studies in marine fish populations offers only limited evidence for effects of abundance and timing of food resources on juvenile fish survival (Leggett and DeBlois 1994). Hence, relating environmental conditions to larval or juvenile mortality in salmonids is limited because it has not been feasible to sample organisms through the key transitions and simultaneously measure environmental as well as maternal effects. Similar constraints apply to many populations where juvenile mortality occurs over short time frames and environmental conditions vary greatly in space and time.

To circumvent these limitations, bioenergetic models are used to explore causal relationships between consumption, growth, and survival (Boisclair and Sirois 1993, Brandt and Hartman 1993). Nislow et al. (1999, 2000) developed a habitat-based bioenergetics model for juvenile Atlantic salmon. It predicted that foraging conditions could influence among-site differences in fry survival throughout the first growing season but that these effects would be greatest in the initial weeks following stocking and independent feeding. As in most prior studies, direct and independent measurements of consumption rates integrated over time were not possible. However, in 2004, Kennedy et al. demonstrated that tissue signatures of geologically derived stable cesium (^{133}Cs) could be used to measure integrated in situ consumption rates. Extending from well-established radioisotope approaches (Forseth et al. 1992, Rowan and Rasmussen 1994, Ugedal et al. 1997), they parameterized a model of Cs uptake and turnover in salmon fry to measure consumption rates integrated over various time intervals during the first growing season. The ^{133}Cs approach thus provides a promising method for examining independent relationships between consumption and growth or survival that is applicable for many species.

Our overarching goal is to test the general hypothesis that consumption limits growth and establishes an early-season survival bottleneck for age-0 Atlantic salmon. In this study, we use the ^{133}Cs method to determine consumption by 400+ age-0 fry from six streams in

southern Vermont, USA, and combine habitat-specific information with direct measures of consumption for the first time. We significantly reduce confounding maternal effects across sites because all individuals in our study are produced in a single environment (Nislow et al. 1999), grown under controlled conditions, and then randomly released across sites. We control for differences in initial densities, allowing effects of environmental patterns on growth and survival following hatching to be independently examined. We then test five general predictions that were generated previously from the habitat-based foraging and bioenergetic model, which was built from information for habitat availability and use for these same individuals (Nislow et al. 1999). The model predictions we test are (1) mass-specific consumption rates are lowest in the early season due to constraints on small fish foraging in swiftly flowing streams, (2) fish in streams with the greatest amount of suitable foraging habitat in the early season have the highest mean consumption rates, (3) consumption and growth are positively correlated except in sites where habitat conditions required high energy expenditure, (4) sites with highest consumption and growth during the early season have the highest survival of salmon parr (young salmon actively feeding in freshwater) at the end of the growing season, and (5) consumption rates in the mid-to-late season have little effect on survival because foraging habitat is no longer limiting.

METHODS

Study system

Our study took place in six third-order streams in the White and West River watersheds, two major watersheds of the Connecticut River in central and southern Vermont, USA (Appendix A). For the past 35 years, juvenile Atlantic salmon have been stocked into dozens of watersheds in the Connecticut River basin in an effort to restore salmon to their historic range (McMenemy 1995). Salmon are stocked as unfed fry in the late spring, just after they have absorbed their yolk sacs and are ready to begin exogenous feeding. The timing of stocking coincides both developmentally and historically with fry emergence times for Atlantic salmon in this region. Stocking densities are $\sim 30\text{--}50$ fry/100 m² of rearing habitat. Rearing habitat, defined as relatively shallow (0–0.5 m) habitat dominated by cobble–boulder habitat, occupies the majority of the stream area in these sites (McMenemy 1995).

All six streams have similar temperature profiles, hydrographs, and water chemistry (Nislow et al. 1999). Stream gradients range from 1.2% to 1.4%, widths range from 6 to 10 m, and mean temperatures throughout the growing season are all between 14.5° and 15.5°C (Nislow et al. 1999). Each stream contains a long-term census site ($\sim 200\text{--}400$ m reach) in which data on growth and survival of salmon have been collected annually every fall for the past 20 years (McMenemy 1995). For this study, snorkelers collected salmon (age-0) using dipnets

from 100-m study reaches adjacent to the long-term census sites in 1991 and 1992. Fish were collected every 7–9 days (described in Nislow 1999, 2000) and grouped into three periods: early season (0–6 weeks post stocking), middle season (6–10 weeks post stocking), and late season (10–15 weeks post stocking). In 1991, fish were sampled beginning two weeks after stocking until the end of August. In 1992, fish were sampled immediately after stocking in early May until the middle of June (all grouped as early season samples). Stomachs were removed for gut content analysis; fish were stored on ice and immediately frozen (–20°C) in the laboratory.

Cs-based consumption rates

Integrative consumption rates of juvenile Atlantic salmon were estimated using a kinetic model that describes the turnover and accumulation of a nonessential, metabolically inert trace element in tissues (Kennedy et al. 2004). The model was originally developed for estimating consumption rates with fluxes of radiocesium (^{137}Cs) and is based upon mass balances for growth and metal body burdens (Forseth et al. 1992, Rowan and Rasmussen 1996, Tucker and Rasmussen 1999). Fish take in Cs via their diet. Dissolved concentrations are very low and uptake through gills and body surfaces is negligible (King 1964, Hewett and Jefferies 1978). Cs is not respired and its elimination from fish can be described by a relatively simple first-order equation (Rowan and Rasmussen 1995). Hence, the accumulation of Cs in fish tissues over a given time interval is in direct proportion to the quantity of food eaten.

The radiocesium method has been used extensively to quantify the consumption rates of many freshwater fish species (Kolehmainen 1974, Forseth and Jonsson 1994, Rowan and Rasmussen 1996, Ugedal et al. 1997) and has been compared favorably with estimates for consumption based on other methods (Forseth et al. 1992). Our approach is novel in that we use fluxes of geologically derived stable ^{133}Cs , which allows us to estimate individual consumption rates of very small (0.2 g, 28 mm) fish. The full development, parameterization, and sensitivity analysis of the stable Cs model is described in Kennedy et al. (2004). Briefly, Cs body burdens (Q) change as a function of dietary uptake, fish growth, and excretory losses. Combining the mass balance equations for Cs gains and losses over time ($Q_t - Q_0$) and solving the equation for mass-specific consumption rates gives

$$C = \frac{(Q_t - Q_0 e^{-Et})(G + E)}{\alpha(^{133}\text{Cs}_{\text{food}})w_0(e^{Gt} - e^{-Et})} \quad (1)$$

where C is the specific consumption rate ($\text{g wet food} \cdot [\text{g wet fish}]^{-1} \cdot \text{d}^{-1}$), α is the assimilation efficiency of ^{133}Cs from food (0 to 1), $^{133}\text{Cs}_{\text{food}}$ is the concentration of Cs in food (ng/g), w_0 is the initial body mass (in grams), G is

the specific growth rate ($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$), and E is the elimination rate of ^{133}Cs ($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$).

Parameter values used in the model are described in Kennedy et al. (2004). We calculated the mean Cs concentration in salmon diets (7.783 ng/g) by (1) measuring the concentration of Cs in six families that constitute the majority of invertebrate prey for age-0 salmon and (2) weighting each taxon-specific Cs concentration by its relative representation in fish gut contents (Nislow et al. 1999, Kennedy et al. 2004). To estimate assimilation efficiency, we tracked the Cs concentrations of invertebrate prey as a meal passed from benthos to the foreguts and hindguts of >100 age-0 salmon. We standardized the uptake of Cs through the digestive tract by comparing concentrations with the concentration of an unassimilable marker, acid-insoluble ash (Tucker and Rasmussen 1999). The proportion of Cs assimilated is

$$\alpha = 1 - \frac{(\text{AIA}_{\text{fg}})(^{133}\text{Cs}_{\text{hg}})}{(\text{AIA}_{\text{hg}})(^{133}\text{Cs}_{\text{fg}})} \quad (2)$$

where AIA is the proportion of stomach wet mass composed of acid-insoluble ash and ^{133}Cs is the concentration of Cs in both foregut (fg) and hindgut (hg) (Kennedy et al. 2004).

Using the equation from Rowan and Rasmussen (1995), we calculate a single component elimination rate (E) for each salmon at steady state with respect to Cs in the environment as

$$\ln E = -6.583 - 0.111(\ln W) + 0.093T \quad (3)$$

where W is fish wet mass (in grams) and T is the interval mean temperature (°C). There were no significant differences across sites for measured parameters, so means were taken from sites and applied to fish from all six streams (Kennedy et al. 2004). There are no biological reasons to expect quantitative differences among parameters for different streams or individuals because the study sites are all located in similar headwater streams with similar invertebrate assemblages, prey phenology, thermal regimes, chemical patterns, and low suspended clay loads.

Concentrations of Cs were measured on whole fish with stomachs removed. Fish were stored frozen until prepared for metal analysis, at which time they were rinsed three times with distilled and deionized water and placed into clean Teflon beakers. Fish were dried at 60°C, weighed, and digested in a microwave oven using double-distilled concentrated HNO_3 (Seastar Chemicals, Seattle, Washington, USA) in class-100, ultraclean laboratory conditions. Elements were analyzed using a Finnigan Element high-resolution inductively coupled plasma mass spectrometer (Fisher, Waltham, Massachusetts, USA) with relative detection limits of ~ 0.1 ng Cs/kg. National Institute of Standards and Technology (NIST) 1643d SRM standard was analyzed with each sample batch and yielded 100% (98–102% max/min)

recovery for Rb and K, with a relative standard deviation of 2.4%. The Cs concentration of 11 replicates of a laboratory standard (Cs = 0.0251 $\mu\text{g}/\text{kg}$) over the course of all analyses was $0.0251 \pm 0.0004 \mu\text{g}/\text{kg}$ (mean \pm SD). Duplicate analyses of Cs in fish samples were always within 2.5% of the mean value. We estimate that the overall precision and accuracy of the method was in the range of 2–2.5%.

Initial concentrations of Cs in salmon were measured in hatchery fry from three different stocking dates in May 1998. Hatchery fish were similarly sized and had similar Cs concentrations (mass $0.196 \pm 0.02 \text{ g}$, mean \pm SD; Cs concentration $1.291 \pm 0.120 \text{ ng}\cdot\text{g}^{-1}$ wet mass, mean \pm SD). Given the low variance in initial conditions, we could confidently apply a single value for Cs body burdens of stocked salmon fry.

If large changes in consumption rate are occurring over relatively short time scales, the consumption estimate could be biased by the initial conditions and interval length chosen. To test how these parameters (initial conditions and interval length) influenced our measurements of consumption, we calculated consumption in the late season in two different ways. First, consumption was estimated on late-season fish using the entire growing season as the time interval. Next, late season consumption rates were estimated using changes in Cs body burdens and mass between the final two sampling periods, which provides a measurement of consumption over the last 5–6 weeks. In the first scenario, initial conditions were based upon the size and Cs concentration of hatchery fry at the time of stocking (as in the case with all other fish). In this case, the interval length was equal to the entire growing season (>10 weeks). In the second scenario, initial conditions were based upon mean mass and Cs concentrations from fish that were sampled in early to mid-July. Therefore, late season consumption rates for fish in this case were based upon the changes in Cs body burden between the final sampling period and mean condition of individuals from the same site ~40 days earlier.

Some consumption estimates during the early season (2–4 weeks) were negative. Negative consumption rates (NCRs) are a unique property of this mass balance approach that other methods of estimating consumption cannot approximate. NCRs indicate that there was a net decrease in the body burden of Cs between stocking and sampling ($Q_t < Q_0$). A more negative consumption estimate therefore implies a greater degree of starvation. A decrease in net Cs body burden during a time interval can be explained through biological processes such as the direct elimination of Cs without replacement (Eq. 4) and/or tissue loss as a result of catabolism. Net Cs losses through elimination may be expected when fish undergo periods of starvation. Any attempt to eradicate negative values in the model would inflate consumption rates to unrealistically high values for some individuals. Therefore, we included the actual negative values for

consumption in our analyses. Estimated consumption rates were compared with maximum daily consumption rates and maintenance rations (consumption required to meet metabolic demands with no growth). Maximum and maintenance rations ($\approx 0.01 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) were derived from previous models developed for Atlantic salmon (Tucker and Rasmussen 1999, Forseth et al. 2001) and were based upon the size and thermal experience of individuals.

Habitat-based bioenergetic model

In this study we test several predictions that arise directly from a published, foraging-based, spatially explicit bioenergetic model that predicts consumption and growth of juvenile Atlantic salmon in our six study sites (Nislow et al. 1999, 2000). For an individual salmon occupying a feeding territory, consumption rate ($\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) is described by

$$C = P \times CS \times T \quad (4)$$

where P is prey supply rate (determined by drifting prey density, current velocity, and territory size), CS is detection and capture success of the predator (determined by current velocity, fish body size, and temperature), and T is total time spent on the feeding territory. Model parameters were obtained from (1) field data for seasonal prey availability at each site, (2) flow conditions measured within individual salmon territories (hereafter referred to as “used” sites) and at randomly selected point locations along transects (hereafter referred to as “available” sites), (3) laboratory experiments and foraging observations (Nislow et al. 1998), and (4) literature values (Hill and Grossman 1993). Season-specific terms for territory size were estimated using the sizes of fish during different seasons and published values for the allometric relationship between territory area and fish size (Grant et al. 1998). Fish analyzed here for Cs were a random subset ($\geq 50\%$) of the fish that were used in the formulation and testing of the original bioenergetic model.

Growth and survival

To measure growth and survival over the first growing season we compared sizes and densities of parr at the end of the season to fish at initial conditions (Fig. 1). Initial sizes of stocked Atlantic salmon fry vary little (<10%) from site to site and year to year. Fry were ~25 mm standard length ($24.8 \pm 1.0 \text{ mm}$; mean \pm SD) and weighed $\sim 0.20 \pm 0.027 \text{ g}$; mean \pm SD) when they were stocked. Final masses of age-0 fish were measured in the field to the nearest 0.1 g. Daily growth rates were determined using the standard equation: specific growth rate = $\ln(W_t/W_{t=0})/t_{\text{days}}$. Growth efficiency (%) represents the fraction of consumption that is allocated to growth. We calculated growth efficiency on late-season individuals as the mass gain over the entire growing season divided by cumulative consumption summed over the same period.

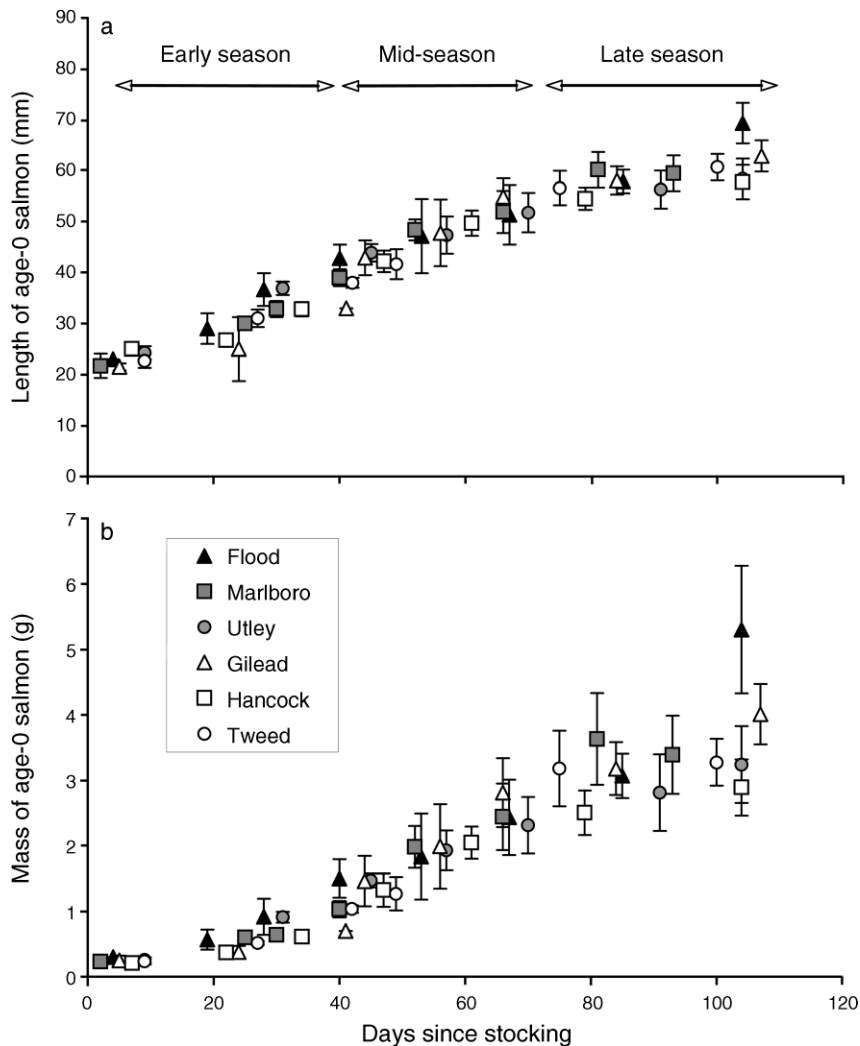


FIG. 1. Means and standard deviations for (a) length (in millimeters) and (b) mass (in grams) of age-0 Atlantic salmon. Each point represents the mean of 8–10 individuals from each of the six study sites throughout the growing season in 1991. Open symbols are from the White River drainage, and gray and black symbols are from the West River drainage. Classifications of season (early [0–6 weeks], mid [6–10 weeks], and late [10–14 weeks]), are delineated. Habitat variables for every individual were incorporated into the bioenergetic model. Realized consumption, using cesium (^{137}Cs) mass balance, was measured on only about half of all individuals. These were chosen to control for ages within specific seasons.

Survival estimates were obtained from multiple-pass electrofishing censuses conducted annually in late August to September at established monitoring sites (McMenemy 1995). Survival estimates were proportional to density at the end of the summer, as all streams were stocked at the same density. Survival was assumed to be equal to *retention* over the growing season, as immigration and emigration were not measured directly. In related studies from a subset of our sites, otolith microchemistry of genetically marked fish suggested that very few fish (<5%) are long-distance immigrants and that at least 50% of fish in study reaches were stocked there at the beginning of the experiment (Kennedy et al. 2000, 2005). Moreover, when fish move during the growing season, these movements appear to be of fish

sampling their environment (Kennedy et al. 2002), in which case the abundance and condition of individuals in a site generally reflects local habitat conditions during that time. To assess the effects of consumption on survival, we used site-specific survival estimates for the specific years in which consumption estimates were made in addition to the mean site survival across 5–6 years. The choice of which survival estimate to use did not change our results, as survival rates in 1991 and 1992 were similar to the means across years. Survival generally followed a similar pattern of ranking across sites from year to year (McMenemy 1995). In addition to using the mean consumption estimates, we also calculated the proportion of individuals within each site that were predicted to achieve at least 50% of

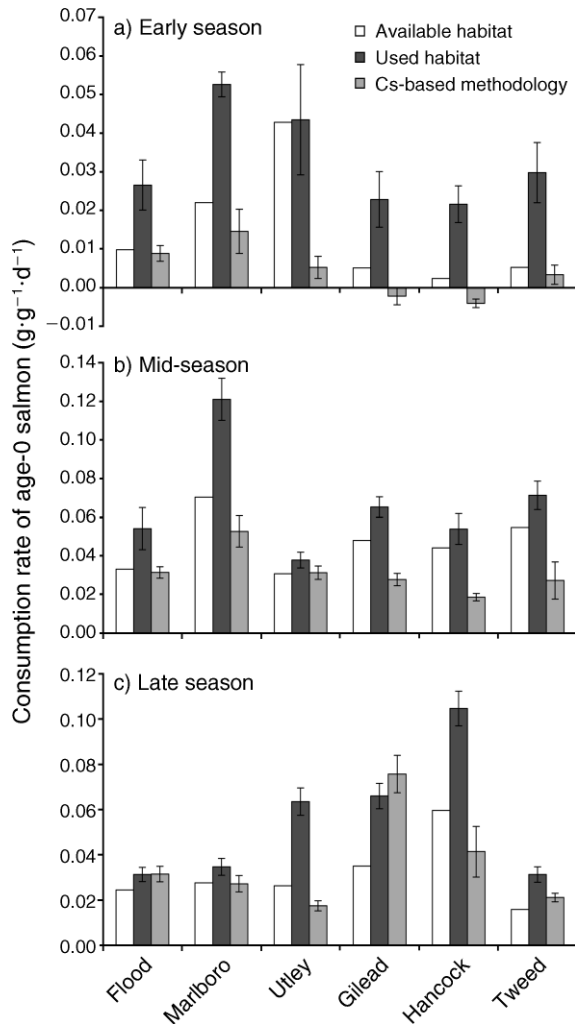


FIG. 2. Consumption rates (mean \pm SE) of age-0 salmon predicted by the bioenergetic model and measured using Cs mass balance (light gray bars) for (a) early, (b) mid-, and (c) late seasons. Within figures, different bars represent (1) consumption rates predicted from average available habitat (open bars), which are measured at random sites of similar dimension to age-0 salmonid territories in the stream, (2) consumption rates predicted for individuals occupying known territories that were used as foraging stations for fish prior to collection (used habitat; dark gray bars), and (3) consumption rates determined using the calculations of Cs mass balance (Cs methodology, light gray bars).

maintenance consumption as a predictor of survival across sites.

Statistical analyses

We used a combination of ANOVA and Student *t* tests (SAS Institute 2000) to test for variation in consumption rates, growth, and growth efficiency across the six study sites and the three collection periods (seasons). Sites and seasons were treated as fixed effects. A Tukey-Kramer multiple comparison test was applied when significant differences in treatment effects were

found (Tukey 1953, Kramer 1956). We tested for homogeneity of variances using a Levene's test (Levene 1960). In some cases, unequal variances violated the assumption of an ANOVA. This was only a problem when comparing consumption rates across seasons because consumption rates in the early season were generally lower and more variable. No transformation corrected for this problem. Significant differences in variances across treatments were an ecologically meaningful outcome for which we were explicitly testing, and therefore we continued with ANOVA in some cases even though treatment variances were unequal. When variances were significantly different, we conducted additional nonparametric tests to compare the significance of statistical results, and we used a Welch ANOVA to test for treatment effects despite unequal variances (Welch 1951). Model II regression analyses tested for the dependence of growth and survival on consumption rates. When trends in the relationship between consumption and survival were suggestive of a relationship, but were insignificant due to low sample size ($n = 6$), we used the nonparametric, one-tailed Jonckheere-Terpstra test (Jonckheere 1954) to determine whether the consumption distribution increased in groups with increasing survival rank. Spearman rank-order correlation coefficients were calculated on ranked comparisons of the two independent ways of estimating consumption.

RESULTS

Cs-based consumption rates

Both site and season affected mass-specific consumption rates (hereafter, consumption rates; for site, $F_{5,226} = 4.53$, $P < 0.001$; for season, $F_{2,226} = 40.47$, $P < 0.001$; Appendix B). The largest differences among fish from different sites were during the early period (2–4 weeks after stocking), when the absolute difference in mean consumption rates between sites with highest and lowest consumption was 130%. Fish in Marlboro Brook had the highest mean consumption rates, consuming 1.5% of their body mass ($0.015 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$). Fish from Gilead Brook and Hancock Branch had negative consumption rates ($-0.002 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ and $-0.004 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$, respectively), with the average fish starving at two weeks post stocking (Fig. 2a). In the late season, differences among sites were significant but less pronounced (Fig. 2c), with a significant interaction between site and season ($F_{10,226} = 6.60$, $P < 0.001$; Appendix B).

Consumption rates also differed by season (Fig. 2), and were 250–800% higher in the mid- than early season. Overall, mean consumption rate increased from $0.005 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ (i.e., 0.5% per day) in the early season to $0.030 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ (i.e., 3.0% per day) in the mid-season ($n = 187$, $t = 7.59$, $P < 0.0001$). Within sites, mean consumption rates in the mid-season ranged from $0.019 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ to $0.053 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ and were consistently higher than consumption rates in the early season at all six sites (Table 1). Sites with the highest early-season consumption rates had the highest mid-season rates, and sites

TABLE 1. Consumption rates (mean \pm SE) of mid-Atlantic salmon on invertebrate prey in tributaries of the Connecticut River in southern Vermont, USA, during the early and mid-seasons.

Site	Consumption rate ($\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$)				<i>t</i>	<i>P</i>
	Early season (2–4 weeks)	Mid-season (6–10 weeks)	No. fish			
Flood	0.008 \pm 0.002	0.032 \pm 0.003	16		6.63	<0.0001
Marlboro	0.015 \pm 0.006	0.053 \pm 0.008	29		3.00	<0.005
Utley	0.005 \pm 0.003	0.032 \pm 0.003	40		4.22	<0.0001
Gilead	-0.002 \pm 0.002	0.028 \pm 0.003	30		6.36	<0.0001
Hancock	-0.004 \pm 0.001	0.019 \pm 0.002	47		5.79	<0.0001
Tweed	0.003 \pm 0.002	0.028 \pm 0.010	25		2.02	0.055

Note: Statistics are based upon results from a standard *t* test for differences in consumption rates.

with the lowest early-season consumption rates had the lowest mid-season rates. Again, fish from Marlboro Brook consumed significantly more during this period than fish from any other sites (Fig. 2).

By the late season (10–14 weeks after stocking), differences in consumption across sites were eliminated, with one exception. Consumption rates in Gilead Brook were 2–3 times higher than all other sites (Tukey-Kramer, $P < 0.05$). Fish in Hancock Branch, which had consistently low consumption rates during the early and mid-seasons, had relatively high consumption rates during this period. Thus, the two sites with negative values for early-season consumption had, on average, the highest consumption rates in the late season (Fig. 2).

The length of the time interval used to estimate late-season consumption rates did not influence our measurements of consumption in any sites (Table 2). There were no significant differences between late-season consumption rates measured either as consumption over

the last 3–6 weeks or over the entire summer ($P > 0.05$ for all sites).

Relationship between Cs-based consumption and growth rates

Growth rates increased with increasing consumption during the early season. When sites were pooled, age-specific mass and growth rates were positively correlated with consumption rates ($n = 57$, $F_{1,56} = 16.85$, $P < 0.0001$; Fig. 3). However, within sites, there was no significant relationship between consumption rates and growth. Among sites, only Gilead Brook fish had significantly lower early-season growth (Tukey-Kramer, $P < 0.05$).

During the late season, there was no relationship between consumption and growth when individuals from all sites were pooled. However, a positive relationship between consumption and growth during the late season was significant in three of the six sites (Marlboro Brook, $n = 15$, $F_{1,13} = 54.17$, $P < 0.0001$;

TABLE 2. Comparison of late-season consumption rates based upon two alternative interval lengths per site for calculations.

Site, interval length (days)	Consumption rate, mean \pm SD ($\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$)	Growth rate, mean \pm SD (% per day)	Growth efficiency, mean \pm SD (%)
Flood			
45	0.022 \pm 0.009		
85	0.032 ^a \pm 0.010	3.2 ^{a,b} \pm 0.13	37.1 ^{b,c} \pm 8.4
Marlboro			
53	0.021 \pm 0.011		
93	0.027 ^a \pm 0.011	3.0 ^{a,c} \pm 0.13	41.8 ^a \pm 15.1
Utley			
46	0.008 \pm 0.007		
91	0.017 ^a \pm 0.007	2.9 ^c \pm 0.24	64.3 ^a \pm 25.4
Gilead			
40	0.070 \pm 0.026		
84	0.076 ^b \pm 0.025	3.3 ^b \pm 0.15	16.2 ^c \pm 5.1
Hancock			
32	0.041 \pm 0.040		
79	0.042 ^a \pm 0.035	3.2 ^{a,b} \pm 0.18	43.8 ^{a,b} \pm 23.3
Tweed			
26	0.020 \pm 0.009		
75	0.021 ^a \pm 0.006	3.6 ^d \pm 0.15	62.3 ^a \pm 17.0

Notes: In the shorter interval at each site, the means from mid-season individuals were used for initial conditions, and consumption was measured integratively only for the last 4–7 weeks of the growing season. In the longer interval at each site, consumption was averaged over the entire growing season, and hatchery fry were used as initial conditions. There were no significant differences between the consumption rates for any site using either approach. Growth efficiencies, the ratio between total growth and total consumption, were measured for the entire study period. With columns, sites that share a common superscript letter were not significantly different ($P < 0.05$).

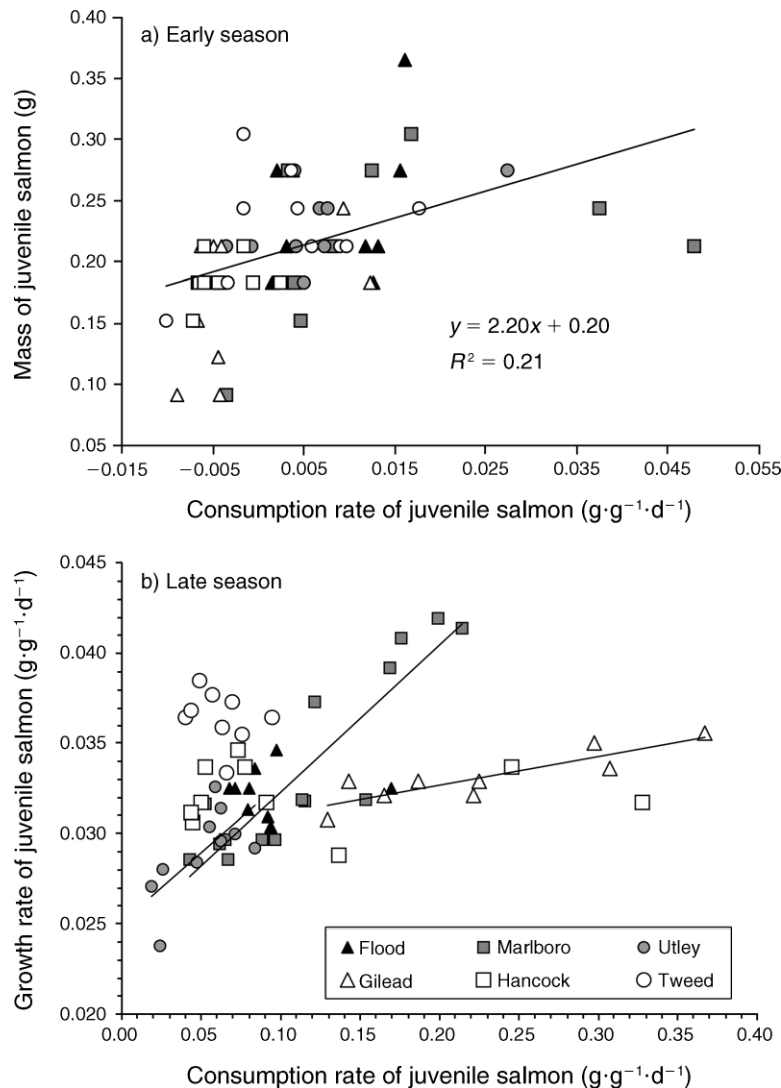


FIG. 3. Relationship between mass-specific consumption ($\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) and growth ($\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) for (a) early-season (expressed as size [in grams] with 0.196 g as the starting condition) and (b) late-season (expressed as growth [$\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$]) age-0 Atlantic salmon. Only regressions from significant relationships are plotted ($P < 0.05$). The regression line for the early season is calculated with individuals from all sites pooled. The three regression lines for the late-season individuals are from Marlboro, Utley, and Gilead. None of the site-specific relationships during the early season was significant, nor was the overall relationship between consumption and growth in the late season.

Utley Brook, $n = 10$, $F_{1,8} = 6.92$, $P < 0.05$; Gilead, $n = 9$, $F_{1,7} = 22.20$, $P < 0.005$; Fig. 3). There were also significant differences in growth rates across sites ($n = 56$, $F_{5,50} = 21.15$, $P < 0.0001$; Table 2). The site with the highest mean growth rates (Tweed Branch) had consistently low consumption rates throughout the study.

Growth efficiencies were also significantly different among sites ($n = 56$, $F_{5,50} = 9.35$, $P < 0.0001$; Table 2). Because of relatively small differences in growth rates among sites throughout the season (with the exception of Tweed), growth efficiencies were strongly influenced by differences in consumption rates. Fish from sites that had relatively low late-season consumption (e.g., Utley Brook and Tweed) had the highest growth efficiency and

those from the site with the highest consumption during this time had low growth efficiency.

Comparing Cs-based consumption rates with predictions from the bioenergetic model

Rank comparisons.—Our Cs-based estimates of integrated consumption supported many of the key predictions of the bioenergetic model that had been previously applied to these populations. For example, the bioenergetic model predicted lower consumption in the early season and greater but similar consumption during the mid- and late seasons. The Cs-based consumption estimates clearly supported both of these season-specific model predictions.

The two methods produced similar relative rankings for consumption rates of fish across sites and seasons (Fig. 4). In the early season, the highest consumption was predicted in the three sites that had the highest measured consumption, and the lowest consumption was predicted for fish from the two sites that had no net positive consumption (Fig. 2; Spearman's $r_s = 0.829$, two-tailed $P = 0.042$). In the mid-season, juvenile salmon from all sites were predicted to have similar consumption, with the exception of Marlboro Branch, wherein individuals were predicted to consume approximately twice as much those from the other streams. In agreement, measured rates of consumption did not differ across sites in the mid-season, with the exception of significantly higher consumption in Marlboro Branch. Age-0 salmon in Marlboro consumed a mean $0.052 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$, compared to $0.027 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$, the mean consumption rate of individuals from the other five sites. In the late season, fish from three sites were predicted from the bioenergetics model to have significantly higher consumption than the others. Fish from two of these three sites (Gilead and Hancock Branch) had significantly higher measured consumption than the others. Both approaches showed the same seasonal trends, with fish from the two sites with the lowest predicted and measured consumption rates in the early season having the greatest consumption in the late season.

Cs-based and model-based consumption rates.—Although not necessarily designed for this purpose, the success of the bioenergetic model at predicting actual consumption rates of salmon depended upon the season to which it was applied. Measured consumption rates were generally lower than those predicted by the bioenergetic model (Fig. 2). However, these differences were greatest during the early season, when the model predicted that the average fish across all sites consumed more than $0.03 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ (Fig. 2). In comparison, fish in Marlboro Brook, where rates were the highest of the six sites, had a mean measured consumption of only about half that amount ($0.015 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$). Moreover, many individuals at this time appeared to have no detectable consumption or growth.

In all seasons and sites, sites occupied by salmon (used microhabitats) were predicted to have higher consumption than the mean value for randomly selected sites in the stream (available habitats) based upon a bioenergetic model (Nislow et al. 1999). From these data it was inferred that fish select the most energetically advantageous sites. During the early season, the differences between modeled consumption in used and available habitats were greatest, with used habitats predicted to be up to 10 times more profitable for consumption than average available habitat (Fig. 2). However, our estimates of consumption during the early season are much closer to the predictions for available habitat than for the used habitats; estimated consumption was indistinguishable from the predictions for mean available consumption in three of the six sites.

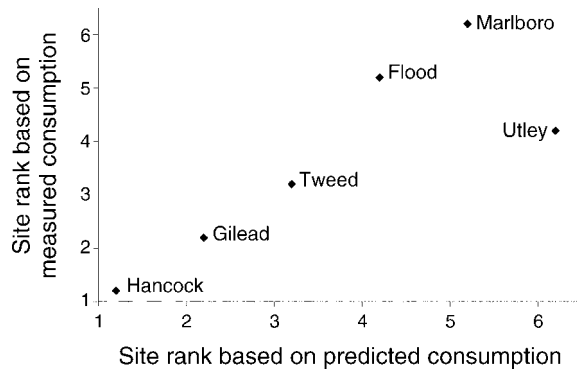


FIG. 4. Comparison of site rankings for mass-specific consumption estimates in the early season based upon the predicted consumption rate from a habitat-based bioenergetic model (x-axis) and the measured consumption using the mass balance of Cs (y-axis) ($r_s = 0.829$, two-tailed $P = 0.042$). Site rankings in both cases are from lowest to highest mass-specific consumption rates.

In mid-season, estimated consumption rates were also very close to the predictions for consumption based on average conditions, and lower than the consumption rates predicted for the used habitats. However, by the late season, the bioenergetic model predicted very similar consumption rates to our estimates. During this time, rates predicted by the bioenergetic model for used habitat overlapped with Cs estimates in four out of six sites. This is also the time during which predictions for foraging gain in used habitats were most similar to those from average stream conditions.

Cs-based consumption and site-specific survival.—Consumption rates in the early season explained 40% of the variation in survival of age-0 salmon calculated using either mean survival within six study sites over five years or survival in individual years (mean survival, $n = 6$, $P = 0.18$, $r^2 = 0.40$ [Fig. 5]; 1991–1992 survival, $n = 6$, $P = 0.19$, $r^2 = 0.39$). The slope was positive for increased age-0 salmon survival (May–August) with increased early-season consumption; however, the regression analysis was not significant due to low sample sizes. A Jonckheere-Terpstra test, which considered the distribution of consumption rates within sites, supported a positive relationship between survival and consumption rates in the early season (JT statistic = 422, one-tailed $P = 0.014$). Survival patterns across sites were similarly explained by the percentage of the population that exceeded maintenance ration during the early season (between 0% and 55%). Moreover, a similar trend exists for the relationship between consumption rates in the mid-season and survival to the end of the growing season. The relationship between early-season consumption and survival was stronger than the same relationship for the late season. In contrast, late-season consumption rates had no effect on survival (JT statistic = 676, one-tailed $P = 0.37$), regardless of whether survival was averaged across multiple years or considered exclusively for 1991, when late-season fish were

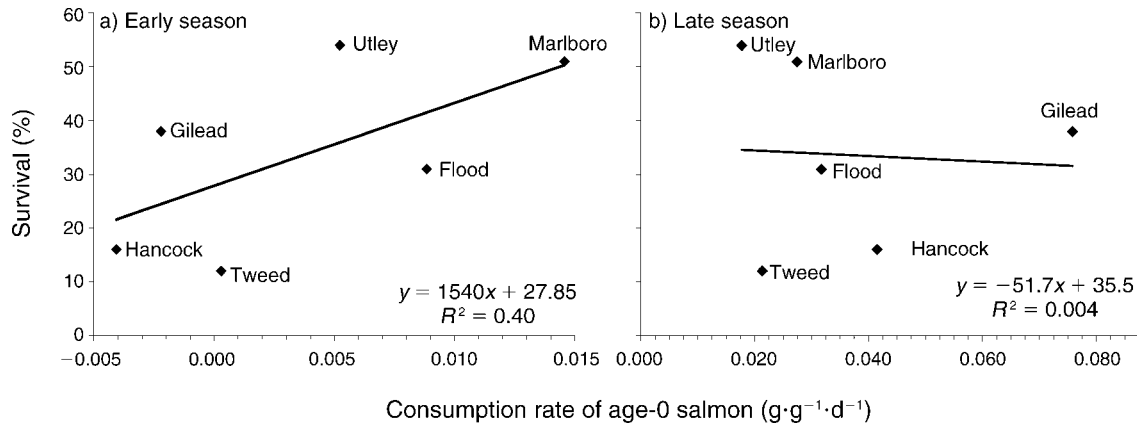


FIG. 5. Relationship between survival (survival of individuals to the end of the summer averaged over five growing seasons) and consumption rates of age-0 Atlantic salmon during (a) the early season (0–6 weeks after stocking; Jonckheere-Terpstra test statistic [JT] = 422, one-tailed $P = 0.014$) and (b) the late season (10–14 weeks after stocking; JT = 676, one-tailed $P = 0.37$).

collected (mean survival, $n = 6$, $P = 0.91$, $r^2 = 0.004$ (Fig. 5); 1991–1992 survival, $n = 6$, $P = 0.54$, $r^2 = 0.10$).

DISCUSSION

By combining habitat-based energetic models with state-of-the-art stable isotope techniques, we demonstrated that juvenile Atlantic salmon experience energetic limitation mediated through habitat availability during a critical period of their life cycle. Energetic constraints on juvenile survival are thought to be important in the population dynamics and habitat requirements of a wide range of species (Nislow and King 2006). However, the difficulty of accurately measuring the effects of key drivers (such as habitat) on key mechanisms (such as consumption) over brief but critical time periods has prevented direct tests. Because first-feeding salmon fry face many of the same environmental challenges as other juveniles transitioning from dependence on maternally provided resources and habitats, we expect that this approach will be generally applicable across a range of taxa. For example, the use of dense shrub cover by post-fledging juvenile songbirds has been suggested to result from either increased prey availability or from decreased metabolic expenditure (King et al. 2006), but direct observations in these habitats are difficult. The approach we present in this study may well be capable of resolving these alternative explanations.

The significance of variation in consumption for larval and juvenile organisms depends upon the relationships between maternal provisioning, the onset and ontogeny of feeding, and the accessibility of foraging opportunities. Our study design minimizes the impacts of maternal and ontogenetic differences across sites and controls for initial densities, enabling us to focus directly on habitat and foraging factors. Our application of a novel method to estimate individual consumption rates in combination with a spatially explicit habitat-based bioenergetic model allowed us

for the first time to link spatial and temporal variation in habitat conditions, the foraging ecology of individuals, and the underlying mechanism for a survival bottleneck. Directly measuring consumption rates using Cs isotopes in wild populations generally extends the reliability and utility of bioenergetic models. Consumption rates have been a major source of uncertainty in these models and are generally estimated from growth (which is straightforward to measure; Ney 1993) involving various assumptions concerning metabolic rates and assimilation efficiency. These metabolic parameters themselves are difficult to accurately measure in the wild, particularly for small, cryptic species and life history stages. Given that bioenergetic models are increasingly used for applications spanning physiological, population, and ecosystem ecology, refinements in parameter estimation are crucial.

As predicted by a habitat-based bioenergetic model, consumption rates of juvenile salmon were critically low during the first few weeks after the onset of independent feeding, with >50% of all individuals having estimated consumption rates insufficient to meet metabolic demands. Further, among-site variation in consumption at this stage was positively correlated with growth and with age-0 survival. Our results provide direct support for foraging habitat limitation as a mechanism underlying early mortality in stream salmonids. As suggested by Elliott (1989), it appears that the majority of salmon fry failed to adequately establish independent feeding during the early critical period. While energetic limitations frequently interact with other factors, such as predation risk and local competitive interactions (Werner and Hall 1988, De Leaniz et al. 2000, Henderson and Letcher 2003, Einum and Nislow 2005), our results indicate that fish are likely to suffer direct starvation mortality during the early critical period. Laboratory experiments performed on hatchery-born Atlantic salmon fry at ambient stream temperatures suggest that they can survive for up to three weeks after absorbing their

yolk sac in the absence of exogenous feeding (Letcher and Terrick 2001). The timing of our sampling of early season fry (2–4 weeks) coincides with the interval during which critically low rations would begin to result in mortality. We observed no among-site differences in predator density that could account for differences in growth or survival (Nislow et al. 1999), and other studies conducted in the region have found no relationship between overyearling trout and age-0 salmon (Raffenberg 1998).

In strong contrast to the early season, but also in accord with model predictions, consumption rates increased markedly in the mid- and late season. By 6–10 weeks after stocking, the consumption rates of nearly all individuals exceeded maintenance rations and were frequently close to predicted maximum consumption. Consumption rates during these later periods were unrelated to age-0 survival. Growth was also unrelated to consumption in the mid and late seasons. As a majority of these fish were at or near maximum consumption rates, it makes sense that most of the variation in growth was likely associated with factors other than consumption, such as intrinsic or environmentally associated variation in metabolic rates. Previous studies have demonstrated that fish using different life-history strategies have different standard metabolic rates that begin to be manifest after the early critical period (reviewed in Metcalfe 1998). Juvenile Atlantic salmon appear to have a high capacity for compensatory growth (Nicieza and Metcalfe 1997), which may also tend to decouple growth from consumption. We observed some evidence of compensatory feeding in this study, as sites with the highest late-season consumption (Gilead and Hancock Branch) were the sites that had the lowest mid-season consumption and a majority of starving individuals in the early season.

Understanding mechanisms underlying early mortality is an important component of predicting population responses to environmental change. While high consumption rates later in the age-0 spring and summer may be the result of a number of factors, including reduced density following early mortality (Elliott 1989; but see Grant et al. [1998] for an opposing view), our study suggests that environmental conditions are likely to play a key role in regulating the population. In the habitat-based bioenergetic model, the decreased current speeds and increased stream temperatures experienced later in the growing season were predicted to increase the availability of microhabitats yielding high consumption rates. The generality of this pattern of flow and temperature regime in many salmonid streams in the north temperate region (Poff and Huryn 1998) suggests that high consumption, growth, and survival of age-0 salmonids following an early critical period should be common. However, changes in temperature and hydrologic conditions, resulting from either small-scale (dams, diversions, habitat change) or large-scale (climate change) change could significantly affect these patterns.

As an example, it appears that very low flow during mid- and late-season periods was associated with significant reductions in age-0 salmon growth, which was accurately predicted by a foraging-based habitat model (Nislow et al. 2004b).

Aquatic landscapes are complex, heterogeneous environments in which population dynamics are often influenced by connectivity among subpopulations (Schlosser 1991, Fausch et al. 2002). We were constrained by our inability to follow individuals, as is the case for many studies of early life cycle stages, and we could not directly quantify immigration and emigration rates during the course of this study. Therefore, we do not know the impact that movements have on our survival estimates. We would be concerned if movements could result in biasing our survival estimates, however several lines of evidence suggest that this was not the case. Our collective studies over the past decade show that dispersal over long distances is rare (Kennedy et al. 2000, 2002, 2005). Otolith microchemistry of genetically marked fish suggest that very few fish are long distance (i.e., 8–16 river km) immigrants and that at least 50% of fish within short reaches were stocked there at the beginning of the experiment (Kennedy et al. 2002). Trends in consumption rates would suggest that immigrating into a high-survival site after the survival bottleneck comes at the expense of foraging opportunity; consumption is lowest in the high survival sites. Based upon the density-dependent consumption trends in the late season, one would expect that, if immigration and emigration were important prior to our survival estimates, their net effect would be to moderate the survival differences that we consistently measure.

In general, consumption rates estimated using the Cs-based method corresponded well to consumption predicted by the habitat-based bioenergetic model. In addition to the general pattern of low early-season and high mid- and late-season consumption, the model accurately predicted consumption site ranks in all three sampling periods. This correspondence suggests that the model captures important environmental determinants of juvenile growth and survival. However, some discrepancies between modeled and estimated consumption were apparent. For example, estimated consumption rates during the early season were more similar to model predictions based on available microhabitats than they were to predictions based on used microhabitats. This discrepancy might be due to the fact that consumption estimates for early-season fish are integrated for the entire period from stocking to sampling, while model predictions for used habitats are based only on habitats occupied at the time when fish were collected. If fish had “sampled” available habitats until finding a suitable location, we might expect consumption rates to more closely correspond to available, as opposed to used, habitat predictions. Both model concordance and model discrepancies (by targeting knowledge gaps and suggesting alternative model

structures) can be used to increase our understanding of the energetic determinants of habitat suitability. Further, these results demonstrate that the stable cesium method can be effectively used to evaluate consumption rates in conjunction with bioenergetic models strengthening the link between environment, energetics, and growth and survival.

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APPENDIX A

Map of six study sites in central and southern Vermont, USA (*Ecological Archives* E089-141-A1).

APPENDIX B

Results from ANOVA of consumption rates for six sites and three seasons (*Ecological Archives* E089-141-A2).