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[Article]

Survival and Growth Responses of Juvenile Salmonines Stocked in Eastern Lake Ontario Tributaries

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Abstract.—To evaluate the species-specific and stream-specific suitability of juvenile salmonine habitat in the southern Lake Ontario watershed, we studied the effects of multiple environmental gradients on the first-summer apparent survival and growth of various combinations of Atlantic salmon *Salmo salar*, rainbow trout *Oncorhynchus mykiss*, and coho salmon *O. kisutch* stocked in tributaries. Costocking of either *Oncorhynchus* species had no detectable effect on the apparent survival or change in cohort biomass of Atlantic salmon, but their growth rates were reduced slightly when they were stocked with rainbow trout. Generally, Atlantic salmon outperformed their putative competitors. Summer temperatures were near the physiological optimum for Atlantic salmon but may have limited the success of rainbow trout and especially coho salmon. Total salmonine biomass was maximized at sites in which only Atlantic salmon were planted. Apparent survival and biomass elaboration of Atlantic salmon varied inversely with stream size, temperature, and the abundance of wild salmonines and piscivores, whereas growth rate responded positively to moderate increases in summer temperature, agricultural development, and nutrient enrichment. These regional and species-specific differences in stocked salmonine success may, in part, be explained by variations in temperature, geomorphology, and anthropogenic influences. We recommend that the feasibility of restoring Atlantic salmon continues to be evaluated, especially in those tributaries considered to be of marginal quality for other salmonines.

Landlocked Atlantic salmon *Salmo salar* were abundant historically in the Lake Ontario watershed, where juveniles occupied nursery habitat in tributaries of Lake Ontario and the Finger Lakes (Webster 1982). Atlantic salmon were extirpated from the watershed in the 1890s because of ecosystem changes resulting from anthropogenic activities such as deforestation, damming of rivers, industrial and agricultural pollution, and exotic species invasion (Webster 1982; Ketola et al. 2000). Since that time, populations of exotic brown trout *S. trutta*, steelhead *Oncorhynchus mykiss* (anadromous rainbow trout), coho salmon *O. kisutch*, and Chinook salmon *O. tshawytscha* have become naturalized in portions of the historical range of the Atlantic salmon (Fausch 1998; Crawford 2001) and may be affecting survival, growth, behavior, and reproduction of Atlantic salmon (Heland et al. 1997; Jones and Stanfield 1993; Scott et al. 2003, 2005; Coghlan and Ringler 2005b). Evaluating survival, growth, and habitat suitability for several salmonine species on a site-specific basis would be useful in predicting the outcomes of Atlantic salmon restoration efforts and assessing the likelihood of competition with naturalized salmonines (e.g., Johnson and Wedge 1999).

In a study of 15 New York tributaries to Lake Ontario accessible to migratory salmonines, Wildridge (1990) classified streams according to wild salmonine production capacity and identified variation in natural production corresponding to physiographic region. Because abundance values were point estimates from 1 year, Wildridge (1990) could not determine conclusively if low densities of wild juveniles in certain streams were due to poor habitat quality, some unidentified factor, or were simply low points in highly variable cycles of juvenile recruitment (e.g., Milner et al. 2003). Alternately, longer-term data sets exist on wild salmonine production in high-quality tributaries to Lake Ontario in New York (Trout Brook, Orwell Brook, and Little Sandy Creek; McKenna and Johnson 2005) and Ontario (Bowlby and Roff 1986; Stoneman and Jones 2000). In addition, survival and growth of stocked Atlantic salmon have been estimated in several north-shore Lake Ontario tributaries (McCrimmon 1954; Jones and Stanfield 1993; Stan-

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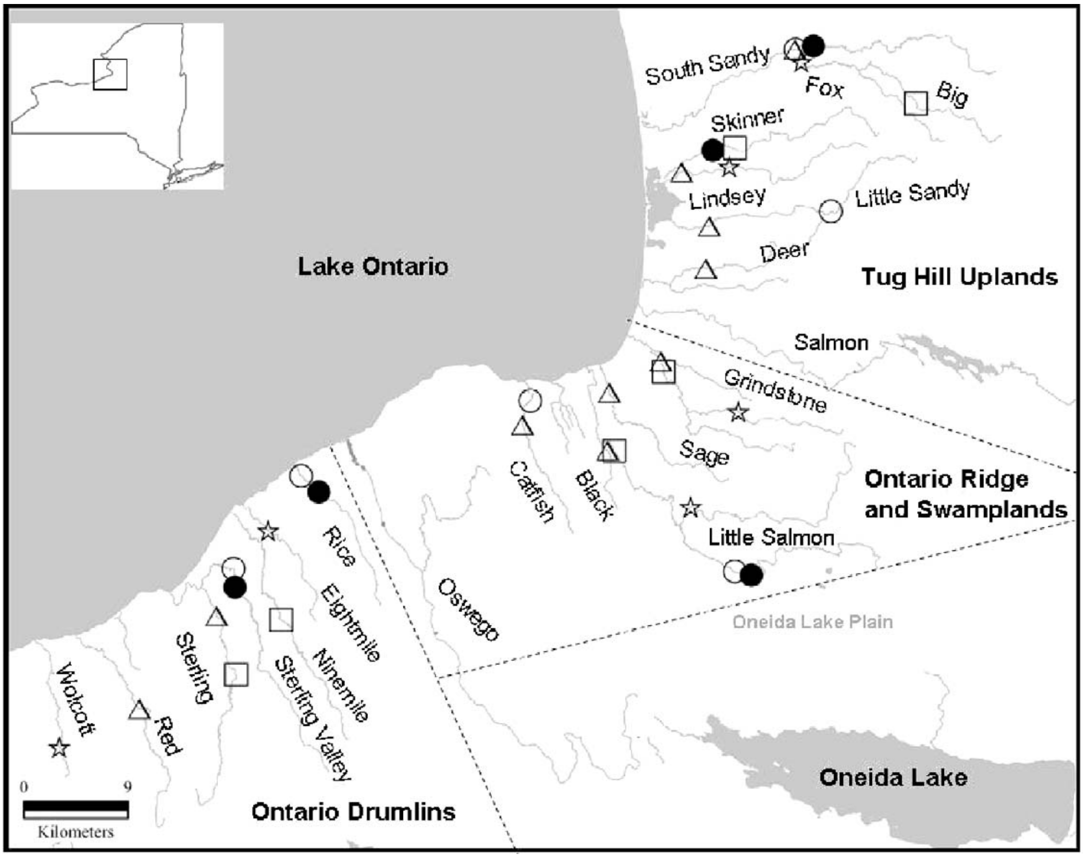

FIGURE 1.—Locations of tributaries draining the eastern and southern shores of Lake Ontario where the survival and growth of stocked juvenile salmonines were studied. Stocking treatments included Atlantic salmon only (triangles), coho salmon only (open circles), rainbow trout only (squares), Atlantic and coho salmon (filled circles), and Atlantic salmon and rainbow trout (stars). The dashed lines separate physiographic regions but do not represent watershed boundaries.

field and Jones 2003). However, estimates of survival and growth of stocked salmonines across a wide range of south-shore Lake Ontario tributaries are lacking. Given the importance of stocked salmonines to the Lake Ontario fishery (Jones et al. 1993), the absence of data from many potentially productive tributaries in New York, and a management interest in Atlantic salmon restoration, we conducted a study with these objectives: (1) to test for the effects of stocking regime on the survival and growth of stocked Atlantic salmon, rainbow trout, and coho salmon in south-shore Lake Ontario tributaries; (2) to build explanatory models of Atlantic salmon survival and growth responses using biotic, thermal, microhabitat, and landscape features; and (3) to identify site-specific limiting or enhancing features of salmonine production capacity and make recommendations regarding the suitability of streams within each of three physiographic regions.

Methods

Study area.—The tributaries flowing directly into Lake Ontario along its southeastern and eastern shore originate in three physiographic regions of New York State (Wildridge 1990; originally described by Cressey 1966): (1) the Tug Hill Uplands, (2) the Ontario Ridge and Swamplands, and (3) the Ontario Drumlins (Figure 1). The Tug Hill Uplands region (also known as Tug Hill Plateau) is heavily forested with localized areas of agriculture and minimal urbanization. The Ontario Ridge and Swamplands region contains a mixture of forests, agriculture, and some urbanization, and soils are generally poorly drained. The Ontario Drumlins region contains deep, calcareous, and well-drained soils, extensive agricultural development, and relatively sparse forests (Table 1). Distinct gradients exist in stream physical habitat, temperature, water quality, and fish and macroinvertebrate assemblages and are oriented in a northeast-to-southwest direction, corre-

TABLE 1.—Selected geographic and climatological variables for three physiographic regions of New York State. Thermal data are from NOAA (2001), snowfall data from Muller (1966), approximate elevation ranges from U.S. Geological Survey 7.5' maps, land-use data from M. J. Connerton (unpublished), and soil data from Cline (1955).

	Physiographic region		
Variable	Tug Hill Uplands	Ontario Ridge and Swamplands	Ontario Drumlins
Mean temperature (°C; Jan 2001)	−5 to −3.8	−3.2 to −1.2	−1.8 to −0.3
Mean temperature (°C; Jul 2001)	19.2–21.2	20.1–21.6	20.3–21.7
Mean annual snowfall (cm)	330–460	260–350	200–260
Elevation range (m)	140–550	110–160	100–150
Forest cover (%)	58.6	45.1	30.6
Agriculture (%)	2.3	2.5	10.7
Urban development (%)	1.7	2.2	3.1
Dominant soil associations	Worth–Empeyville–Westbury, Sodus–Ira	Sodus–Ira, Fulton–Toledo	Ontario, Sodus–Ira

sponding to the three physiographic regions (Coghlan 2004. Many tributaries contain barriers impassable to fish migration and experience municipal or agricultural water diversions during the summer.

Field studies.—In May 2003, we selected 34 study sites on 15 tributaries, including at least 10 sites within each physiographic region (Figure 1), to encompass a variety of points located along various environmental gradients.We selected sites based on past studies (i.e., Wildridge 1990; Coghlan 2004), present accessibility, and observation of seemingly suitable habitat for juvenile salmonines (e.g., coarse substrate, juxtaposition of moderate-velocity and low-velocity microhabitats, riparian vegetation present, and maximum summer temperatures <27°C). Sites that appeared completely unsuitable for juvenile salmonines were deliberately excluded (e.g., beaver impoundments with summer temperatures >30°C) to focus our efforts. Site lengths ranged from 50 to 125 m, and mean wetted widths at time of site selection ranged from 4 to 16 m. We assigned one of five stocking treatment*s* to each site: Atlantic salmon only, rainbow trout only, coho salmon only, Atlantic salmon with rainbow trout, and Atlantic salmon with coho salmon; each physiographic region contained at least two sites receiving each stocking treatment. At 1–2 weeks before stocking, we surveyed for wild juvenile salmonines in all sites that were accessible to migratory adults from Lake Ontario (i.e., reaches below impassable barriers) and noted the presence and relative abundance of spawning adults, redds, or emergent fry. Temperature monitors were placed at each site to record hourly stream temperatures (nearest 0.1°C) during the study period (Figure 2a). We obtained the landlocked Lake Mephremagog strain of Atlantic salmon (mean mass, 0.22 g) from the Ed Weed Fish Culture Station (Grand Isle, Vermont) and rainbow trout (0.45 g) and coho salmon (2.1 g) from the Salmon River Hatchery (Altmar, New York). Although body size varied considerably among the three species, this interspecific variation was a result of normal hatchery production schedules in the region and thus would be typical in most stocking events. Between 21 May and 29 May 2003, salmonines were scatter-stocked in sites to approximate a total density of 1.0 fish/m^2; at sites stocked with two species, density of each species approximated 0.5 fish/m^2. We based our stocking densities upon work by Murphy (2003) and Millard (2005), who found little evidence of density-dependent survival and growth in Atlantic salmon stocked at these and higher densities in cold streams of the northeastern Tug Hill Plateau. In streams where wild salmonine production has been identified previously, typical late-summer densities of wild age-0 salmonines range from 0.05 to 1.03 fish/m^2 (Tug Hill), 0.01–0.54 fish/m^2 (Ontario Ridge and Swamplands), and 0.02–0.46 fish/m^2 (Ontario Drumlins) (Johnson and Ringler 1980; Wildridge 1990; Coghlan 2004).

We visited each site between 16 July and 8 August 2003 and sampled physical habitat, water chemistry, and the fish and benthic macroinvertebrate communities. Before collecting fish, we chose two sampling points within each site randomly. At each point, we selected a sampling reach (10–21 m long) that seemed to encompass a distinct "habitat unit" as described by Wildridge (1990). Because most of our sites did not contain classic riffle–pool sequences, the sampled reaches are best described as predominately riffle habitat interspersed with areas of deeper pocket waters, and demarcated by obvious features such as chutes and channel restrictions. Maximum depths in these reaches did not exceed 1.0 m. Based upon known summer habitat preferences of age-0 Atlantic salmon and rainbow trout (e.g., DeGraaf and Bain 1986; Johnson and Kucera 1985; Hearn and Kynard 1986; Morantz et al. 1987; Beland et al. 2004), all of our sampled reaches appeared to offer at least some suitable habitat. Because of the potential for species-specific habitat segregation (i.e., coho salmon prefer relatively slow and deep microhabitats; Hartman 1965), whenever possible we deliberately included slower and deeper

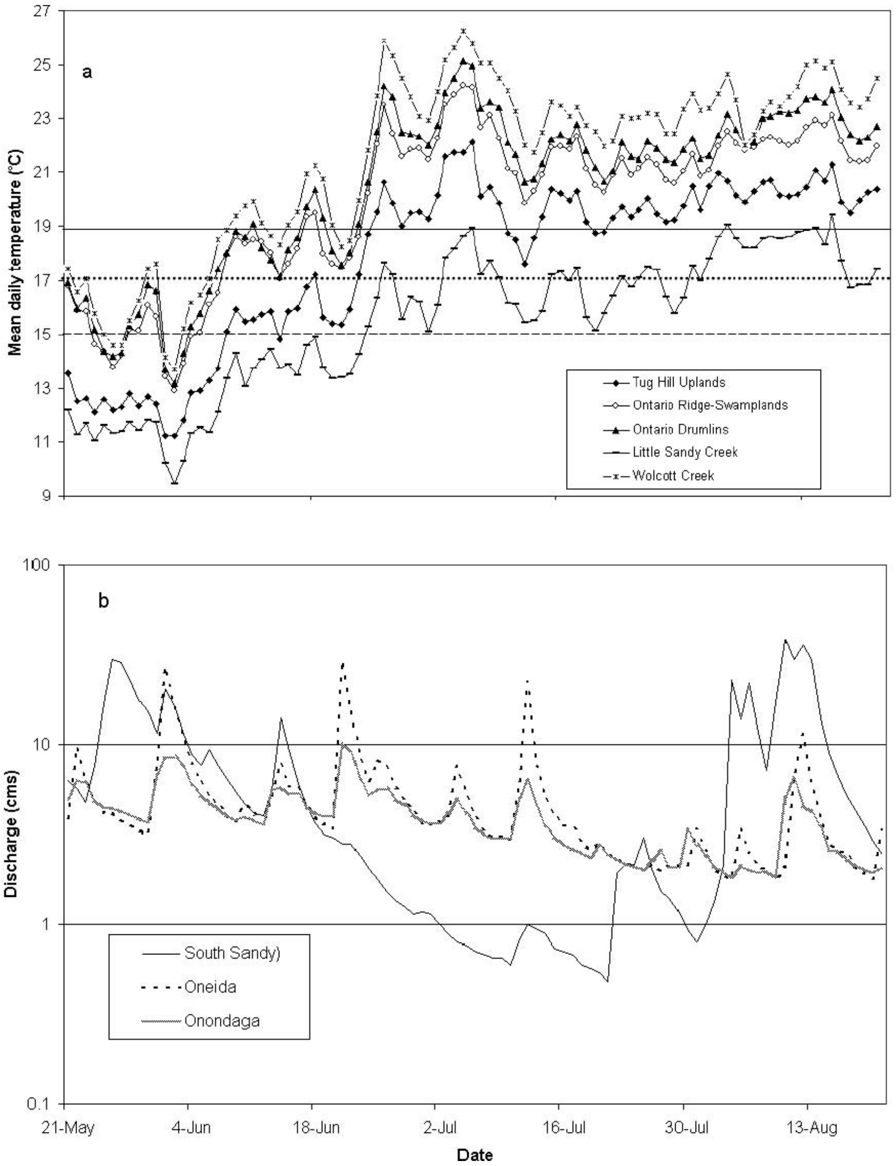

FIGURE 2.—(**a**) Mean daily temperatures of tributaries draining the eastern and southern shores of Lake Ontario, May–August 2003, and (**b**) and the discharge (m^3/s) of three other nearby creeks. Temperatures were averaged over all study sites within each physiographic region; the data from the warmest (Wolcott Creek) and coolest (Little Sandy Creek) sites are included to illustrate the degree of thermal variation across sites. The horizontal lines indicate the optimum temperatures for the growth of Atlantic salmon, rainbow trout, and coho salmon. Mean daily streamflows were obtained from U.S. Geological Survey (USGS) gauging stations for streams representative of the Tug Hill Uplands (South Sandy Creek [USGS reference 4250750]), Ontario Ridge and Swamplands (Oneida Creek [4243500]), and Ontario Drumlins physiographic regions (Onondaga Creek [4240010]).

habitats in our sampled reaches at sites stocked with coho salmon. At the few sites containing distinct riffle–pool sequences, we chose reaches that included one complete sequence.

We isolated each reach with 4-mm-mesh seines and conducted a two-pass depletion sampling (Seber and LeCren 1967) with backpack electrofishers. Wetted sampling areas ranged from 78 m^2 to 280 m^2 and encompassed between 15% and 52% of the original stocking areas. All fish were identified to species and measured for total length (TL; mm) and wet mass (0.1 g). If no stocked salmonines were collected in either reach, we conducted exploratory sampling in likely habitats within 25 m downstream of the site's lower boundary. After collecting fish in each reach, we established 6–10 transects across each sampling reach at regular intervals and measured wetted width at each transect. At 10 discrete points along each transect we measured depth and velocity and characterized substrate composition according to White and Brynildson (1967). We measured pH, total dissolved solids (TDS; mg/L), conductivity (COND; μs/cm), and dissolved oxygen (DO; mg/L) at the upstream boundary of each site. Finally, using kick-screens in the thalweg riffle at the upstream boundary of the site, we collected approximately 200 benthic macroinvertebrates for preservation in 70% ethanol; later we identified all benthic macroinvertebrates to genus, except those in the family Chironomidae.

Because Atlantic salmon no longer reproduce in New York's Lake Ontario tributaries, we were certain that all of the Atlantic salmon caught were from our stocking. At sites where both stocked and wild *Oncorhynchus* could be present, we retained age-0 rainbow trout and coho salmon and froze them for future identification. Several weeks later, we removed sagittal otoliths from all frozen salmonines and polished the otoliths in the sagittal plane to reveal early growth increments. Using otoliths from known wild individuals (from sites in which that species was not stocked) and known stocked individuals (from sites upstream of impassable barriers in which wild populations are absent; authors' unpublished data) as references, we distinguished between stocked and wild fish according to criteria described by Brothers (1990). Only three sites yielded both stocked and wild rainbow trout, and none yielded both stocked and wild coho salmon.

Preliminary data analysis.—We estimated population size (*N*; Seber and LeCren 1967), population density (N/m^2), and standing biomass (*B*; $\mathrm{g/m}^2$) of all fish species within sampled reaches, and data from both reaches within each site were pooled to yield site means (Coghlan and Ringler 2004). For stocked salmonines, we divided estimated density by initial (stocking) density to yield apparent survival (SURV; e.g., Elliott 1994; apparent survival is similar to Nislow's et al. (2000) "proportional retention"). Because different stocking treatments contained different initial biomasses of stocked salmonines, we calculated the proportional change in biomass (ΔB) from time of stocking as $(B_2 - B_1)/B_1$, where B_1 is the initial estimate and B_2 the final estimate. Mean instantaneous growth rate (G_{inst}) was calculated according to Ricker (1968). For each species–site combination, SURV, *B*, ΔB, and G_{inst} were considered thereafter as response variables. Because stocked coho salmon were collected at only one site, we omitted coho salmon from further analyses.

From the fish community data, we calculated the species richness, Shannon–Wiener species diversity, and density and biomass of wild salmonines; the density and biomass of piscivores (defined here as salmonines and cyprinids >150 mm TL and centrarchids and yellow perch *Perca flavescens* >100 mm TL); and total fish density and biomass. From the benthic macroinvertebrate assemblage data we calculated taxa (genera) richness; Shannon–Wiener diversity (genera); the percentages of Ephemeroptera, Plecoptera, Trichoptera, Diptera, and noninsects (mostly crustaceans); and a generic biotic index (GBI; Coghlan and Ringler 2005a, as adapted from Hilsenhoff 1982), where GBI indicates the relative degree of organic and agricultural pollution. The GBI is strongly correlated with COND, TDS, and agricultural development (Pearson's product-moment correlation coefficients, >0.80), and increasing values of GBI indicate reduced water quality due to anthropogenic perturbation. Means of site width, depth, velocity, percent cover of each substrate category, and daily temperature were calculated, along with weekly maximum temperatures, weekly minimum temperatures, thermal coefficients of variation (100·SD/mean), and number of days with water temperatures greater than 25°C. From digital elevation and land-cover maps, we calculated landscape-level attributes at each site, including elevation, slope, and percent land use in each subcatchment devoted to agriculture, forest, and urban–suburban development. Daily stream discharge data were available from U.S. Geological Survey (USGS) gauging stations for only one stream in our study (South Sandy Creek), and logistical constraints prevented us from monitoring discharge at regular intervals. Therefore, we present USGS data from nearby streams merely to illustrate representative flow regimes across the three regions (Figure 2b).

All variables were tested for normality, and necessary transformations were made before analysis (Zar 1974). From each of the two data sets described above (i.e., abiotic and biotic variables), we used principal components analysis to extract a smaller number of explanatory variables to better summarize environmental gradients encountered across streams. For further consideration and analyses, we retained only those principal components with eigenvalues greater than those derived from a broken-stick model (McCune and Grace 2002). We examined Pearson's product-moment correlation coefficients between the original variables and each principal component (PC) score to make inferences regarding the position of each site in gradient space.

Stocking treatment and species comparisons.—First, we conducted separate two-way analyses of variance on the SURV, B, and ΔB of stocked salmonines, considering species (Atlantic salmon versus rainbow trout) and stocking treatment (stocked with or without a heterospecific) as the main effects. We did not include coho salmon in this analysis because of their extremely low apparent survival. Where significant effects were found, we conducted post hoc, Bonferroni-adjusted mean separation tests (MSTs). Because of species-specific differences in initial body size, interspecific comparisons of G_{inst} would have little meaning, so we conducted one-way ANOVAs on the effect of stocking treatment on G_{inst}, separately for each species. Finally, to determine the relative success of each stocking treatment in contributing to overall salmonine SURV, B, and ΔB, we conducted one-way ANOVAs with stocking treatment as the main effect. Calculating a mean salmonine growth rate here would be of little value, so again, we omitted G_{inst}.

Multiple regression models.—Due to restrictions in sample sizes, we limited regression analyses to stocked Atlantic salmon. Using stocking treatment (stocked alone, with rainbow trout, or with coho salmon) as a dummy variable, we conducted bivariate regressions of each Atlantic salmon response variable (SURV, B, ΔB, and G_{inst}) with each PC axis score. No significant effect due to stocking treatment was found (all $p > 0.10$), so thereafter we pooled data from all stocking treatments. Bivariate plots were also inspected visually for any potential nonlinear relations; none were obvious. Next, we conducted multiple linear regressions of each response variable with PC scores generated from biotic and abiotic data sets via stepwise selection, where thresholds of $P = 0.10$ were used for a variable to enter or leave each model. We also conducted regressions using all possible combinations of independent variables and evaluated competing models using Akaike's information criterion (AIC) and the criteria suggested by Shaw (2003). Principal components analyses were conducted with PC-ORD version 4.10 (McCune and Mefford 1999), and all other statistical procedures were conducted with SAS 9.0 (SAS 2003).

Results

Apparent Survival, Biomass, and Growth Summary

The apparent survival of Atlantic salmon ranged from 0.01 to 0.66; parr were recovered from all 22 sites stocked. The absolute numbers of Atlantic salmon recovered from each site ranged from 1 to 45. Standing biomass ranged from 0.03 to 1.08 g/m^2, ΔB ranged from −0.75 to 6.1 (13 of 22 sites yielded a net gain in biomass), and G_{inst} ranged from 0.029 to 0.048 (Figure 3). The apparent survival of stocked rainbow trout ranged from 0 to 0.54. Individuals were recovered from 11 of 12 sites, and the absolute numbers ranged from 0 to 12. The standing biomass of stocked rainbow trout ranged from 0 to 0.98 g/m^2, ΔB ranged from −1 to 1.49 (5 of 12 sites yielded a net gain in biomass), and G_{inst} ranged from 0.01 to 0.035. Stocked coho salmon were recovered from one site only ($N = 6$); apparent survival was 0.16, the proportional change in biomass was −0.33, and G_{inst} was 0.02. With respect to apparent survival and standing biomass, there were no statistically significant effects of species (Atlantic salmon versus rainbow trout) or stocking regime (with or without heterospecifics; $0.11 < \text{all } P < 0.95$); however, Atlantic salmon stocked alone were nominally the most successful. With respect to the proportional change in biomass, Atlantic salmon were more successful than rainbow trout overall ($F_{3,24} = 6.53$, $P = 0.017$), but stocking regime was not significant ($F_{3,24} = 0.01$, $P = 0.95$). Atlantic salmon exhibited higher growth rates when stocked alone than when stocked with rainbow trout ($F_{1,15} = 8.15$, $P = 0.013$), but this stocking effect was not significant for rainbow trout ($F_{1,11} = 0.59$, $P = 0.54$). At sites in which Atlantic salmon and rainbow trout were stocked together, total salmonine biomass ranged from 0.03 to 1.1 g/m^2, which was intermediate to the biomass for each species stocked separately but not significantly different from that of either species stocked alone ($F_{2,19} = 0.38$, $P = 0.69$). The proportional change in biomass of both species stocked together ranged from −0.95 to 2.32, which was intermediate to the values for each species stocked separately but not statistically significant ($F_{2,19} = 1.69$, $P = 0.21$).

Principal Components Analysis and Regression Models

For the abiotic habitat variables, the first three principal components accounted for about 60% (34.7, 14.6, and 10.1%, respectively) of the total variance in the original data set. PC1 was correlated most positively with elevation, slope, percent forested land, thermal variation, and percent gravel and most negatively with percent agricultural and urban development, mean temperature, minimum temperature, maximum temperature, and water chemistry measures (pH, TDS, and conductivity; Table 2; Figure 4a). Thus, PC1 implied a transition from upland, forested, cool but thermally variable, and nutrient-poor sites to lowland, developed, warm but thermally stable, and nutrient-rich sites. PC2 was correlated most positively with temperature and measures of stream size (width, depth, and velocity) and most negatively with pH. Thus, PC2 implied a gradient from small, shallow, slow-flowing, cool streams to large, deep, fast-flowing,

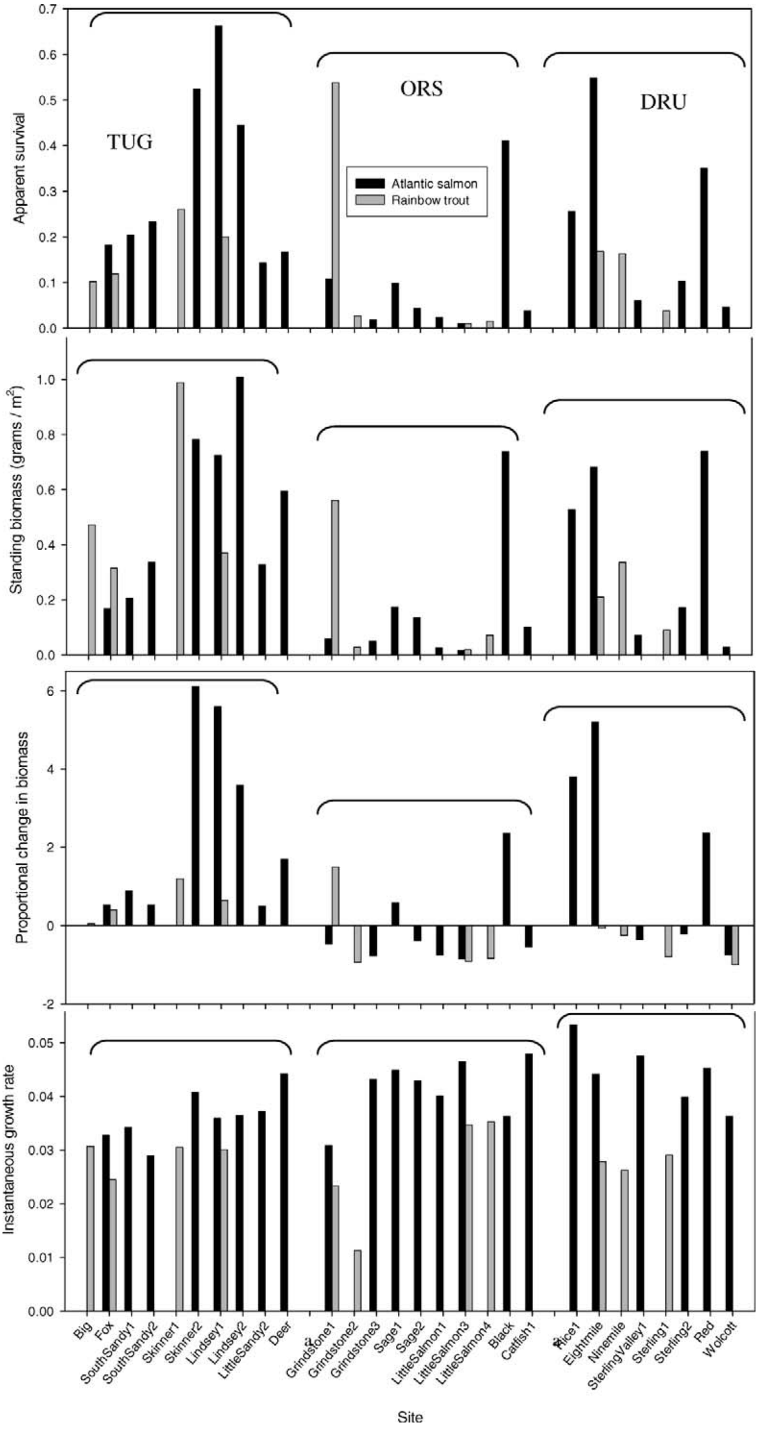

FIGURE 3.—Survival, standing biomass, proportional change in biomass, and instantaneous growth rates of Atlantic salmon and rainbow trout stocked in study streams. The names of the physiographic regions comprising the study area are abbreviated as follows: TUG = Tug Hill Uplands, ORS = Ontario Ridge and Swamplands, and DRU = Ontario Drumlins.

TABLE 2.—Pearson's product-moment correlation coefficients between habitat variables and habitat principal components (PCs) for streams draining the eastern and southern shores of Lake Ontario. Correlation coefficients greater than 0.5 are shown in bold italics.

Variable	PC1	PC2	PC3
Percent urban development	***−0.69***	−0.36	***0.51***
Percent agricultural development	***−0.70***	−0.35	−0.16
Percent forest	***0.91***	0.22	0.15
Elevation	***0.66***	0.31	***−0.54***
Stream channel slope	0.34	0.15	−0.25
Week 1 temperature			
Mean	***−0.82***	0.47	−0.11
Minimum	***−0.82***	0.47	0.01
Maximum	***−0.64***	0.39	−0.38
Mean CV[a]	0.42	−0.22	−0.33
Week 7 temperature			
Mean	***−0.87***	0.32	−0.10
Minimum	***−0.87***	0.39	0.06
Maximum	−0.45	−0.01	−0.36
Mean CV[a]	***0.57***	−0.47	−0.18
Number of days > 25°C	***−0.81***	0.41	−0.22
Mean width	−0.03	***0.61***	0.06
Mean depth	−0.03	***0.68***	0.04
Mean velocity	0.23	***0.52***	0.02
Mean percent boulder	−0.27	0.37	***−0.62***
Mean percent cobble	−0.10	−0.27	0.24
Mean percent gravel	***0.51***	−0.45	0.09
Mean percent sand	−0.23	0.33	***0.54***
Mean percent silt	−0.14	0.03	0.08
Mean percent bedrock	−0.01	0.10	−0.43
Mean percent woody material	−0.36	0.43	0.28
pH	−0.42	***−0.60***	−0.44
Conductivity	***−0.79***	−0.41	−0.13
Total dissolved solids	***−0.76***	−0.43	−0.11

[a] CV = coefficient of variation, computed as 100·SD/mean.

warm streams. PC3 was correlated most positively with percent urban development and percent sandy substrate and most negatively with elevation and percent boulder, implying a similar gradient as PC1. The thermal regime at most sites (Figure 2a) appeared suitable for Atlantic salmon growth (optimal temperature, ~19°C; Murphy 2003) but higher than the physiological optimum for rainbow trout (~17°C; Hokanson et al. 1977) and especially coho salmon (~15°C; Stewart et al. 1981).

For the biotic variables, the first three principal components accounted for about 61% (26.3, 18.6, and 16.3%, respectively) of the total variance in the original data set. PC1 was correlated most positively with invertebrate taxa richness, invertebrate diversity, and percent Ephemeroptera and most negatively with percent noninsects and GBI. Thus, PC1 implied a gradient from diverse macroinvertebrate assemblages predominated by mayflies and intolerant taxa to taxonomically depauperate assemblages predominated by crustaceans and tolerant taxa. PC2 was correlated most positively with percent Trichoptera and most negatively with fish taxa richness, fish density and biomass, wild salmonine density and biomass, and piscivore biomass. Thus, PC2 implied a gradient in fish community structure. PC3 was correlated most positively with piscivore density and biomass and most negatively with percent Diptera (Table 3; Figure 4b).

In all multivariate regressions modeling Atlantic salmon responses as functions of principal component scores derived from abiotic and biotic data, the best models as determined by stepwise selection were identical to those chosen using AIC and Shaw's (2003) criteria. The apparent survival of stocked Atlantic salmon was a function of all three habitat principal components and all three biotic principal components (overall model adjusted $R^2 = 0.89$, $P < 0.0001$; Table 4). The standing biomass of stocked Atlantic salmon was a function of habitat PC2, habitat PC3, and biotic PC2 (overall model adjusted $R^2 = 0.75$, $P < 0.0001$; Table 4). The proportional change in the biomass of stocked Atlantic salmon was a function of habitat PC2, habitat PC3, biotic PC2, and biotic PC3 (adjusted $R^2 = 0.84$; $P < 0.0001$; Table 4). The instantaneous growth rate of stocked Atlantic salmon was a function of habitat PC1, habitat PC3, and habitat PC4 (adjusted $R^2 = 0.58$; $P = 0.0011$; Table 4).

Discussion

Overall Survival and Growth Responses

The apparent survival estimates of stocked Atlantic salmon fell within the range previously reported in the Lake Ontario watershed (McCrimmon 1954; Murphy 2003; Stanfield and Jones 2003; Coghlan and Ringler 2004, 2005a, 2005b; Millard 2005) and elsewhere in the northeastern United States (Bley and Moring 1988; Orciari et al. 1994; Whalen and LaBar 1994; Nislow et al. 1999; Raffenberg and Parrish 2003). The apparent survival estimates of stocked rainbow trout and especially coho salmon were low compared with those obtained in studies in other geographic regions (e.g., Wentworth and LaBar 1984; Hume and Parkinson 1987; Close and Anderson 1992; Bilby and Bisson 1987; Bisson et al. 1988), but similar estimates in Lake Ontario tributaries are lacking—hence one rationale for conducting this study.

Species and Stocking Effects

Costocking putative competitors (i.e., rainbow trout and coho salmon) had no significant effect on the apparent survival or biomass of Atlantic salmon, although growth rates were slightly lower in the presence of stocked rainbow trout. Other authors have documented depressing effects of putative salmonine competitors on Atlantic salmon in laboratory and field settings (Gibson 1980; Hearn and Kynard 1986; Heland et al. 1997; Jones and Stanfield 1993; Coghlan

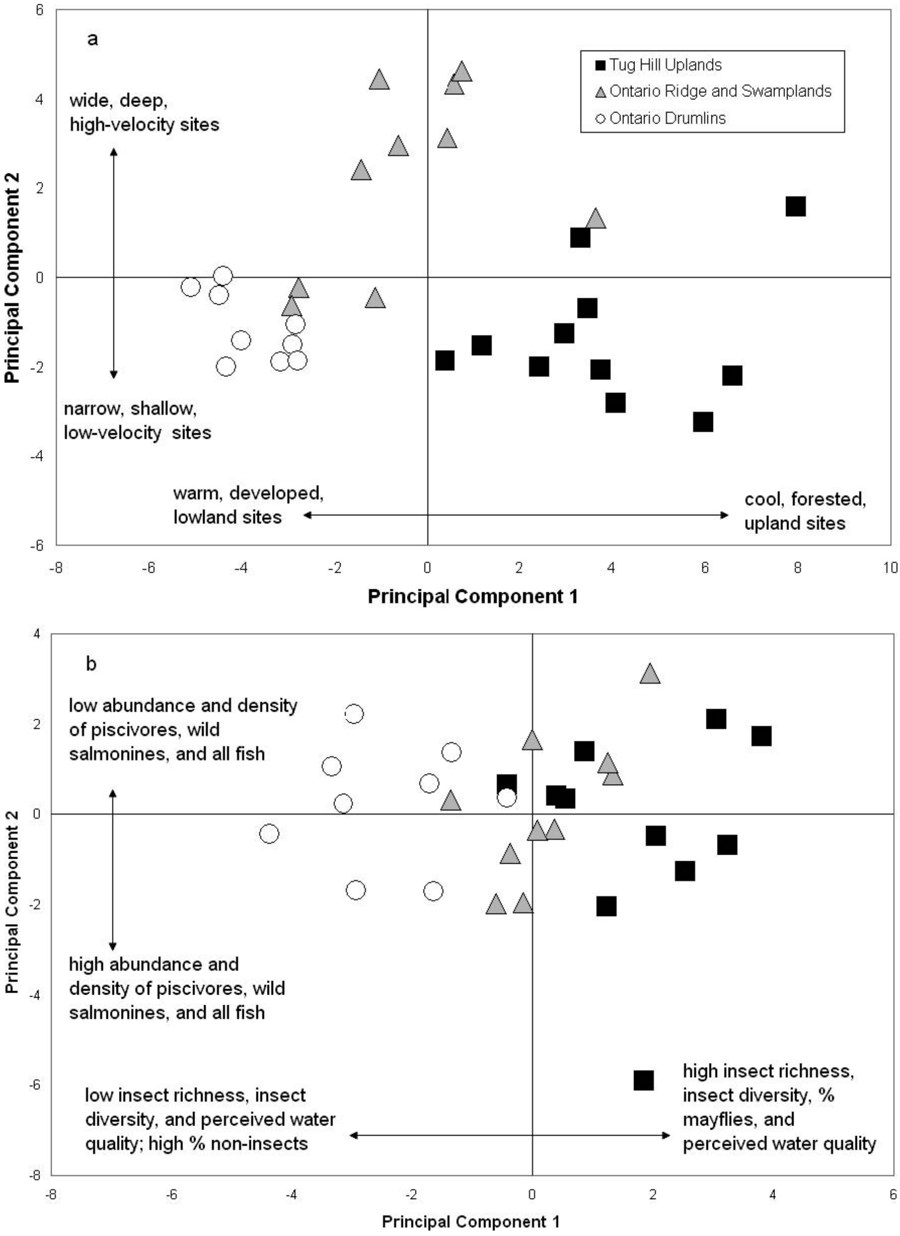

FIGURE 4.—Principal components analyses of **(a)** the abiotic and **(b)** the biotic variables used to characterize environmental gradients across tributaries of Lake Ontario in three physiographic regions. The implied gradients are indicated by arrows.

and Ringler 2005b). Substituting an equal number of heterospecifics for conspecifics (Fausch 1998) might have either enhanced or depressed Atlantic salmon responses, depending on the relative intensities of interspecific and intraspecific competition (Isely and Kempton 2000). Perhaps our initial stocking densities were lower than those at which interspecific competitive interactions overpowered intraspecific interactions and affected apparent survival. It is also possible that mortality or emigration of coho salmon and rainbow trout occurred immediately after stocking (e.g., Bilby and Bisson 1987; see below), rather than gradually over the summer, such that potential interspecific competitors were not present in numbers sufficient to affect Atlantic salmon apparent survival. Alternatively, the outcomes of any competitive interactions might

TABLE 3.—Pearson's product-moment correlation coefficients between biotic variables and biotic principal component (PC) scores for streams draining the eastern and southern shores of Lake Ontario. Correlations greater than 0.5 are shown in bold italics.

Variable	PC1	PC2	PC3
Invertebrate taxa richness	***0.76***	−0.02	0.38
Invertebrate taxa diversity	***0.81***	−0.02	0.35
Percent Ephemeroptera	***0.86***	−0.25	0.13
Percent Plecoptera	−0.46	0.05	0.20
Percent Trichoptera	−0.15	***0.52***	0.29
Percent Diptera	−0.27	−0.38	***−0.70***
Percent non-insects	***−0.70***	−0.01	0.26
Generic biotic index	***−0.83***	−0.20	0.08
Fish taxa richness	−0.34	−0.43	0.40
Fish taxa diversity	0.28	−0.10	0.37
Fish density	−0.18	***−0.52***	−0.47
Fish biomass	−0.34	***−0.73***	0.15
Wild salmonine density	0.40	***−0.67***	−0.32
Wild salmonine biomass	0.45	***−0.66***	−0.30
Piscivore density	−0.19	−0.46	***0.72***
Piscivore biomass	−0.16	***−0.61***	***0.62***

vary along environmental gradients (e.g., Dunson and Travis 1991) and obscure detectable patterns in Atlantic salmon responses. Considering effects on growth, competition from the larger stocked rainbow trout could have forced the smaller Atlantic salmon into energetically unfavorable foraging microhabitats, thus reducing growth rates (e.g., Fausch and White 1981). Imre et al. (2005) found that intraspecific densities affected growth but not survival of Atlantic salmon at low population densities; perhaps in our study, interspecific effects from stocked rainbow trout exerted a similar effect (i.e., on growth but not apparent survival) of Atlantic salmon.

Atlantic salmon were more successful than rainbow trout in elaborating biomass, and both species outperformed coho salmon, which generally experienced a complete loss of cohort biomass. Temperature may play a role in mediating apparent survival and biomass elaboration during the summer for the less heat-tolerant *Oncorhynchus* species. Atlantic salmon are the most heat-tolerant of the juvenile salmonines (Grande and Andersen 1991) and, thus, should perform better in relatively warm sites. Thermal regimes at most sites appeared suitable for Atlantic salmon growth but higher than the physiological optimum for rainbow trout and especially coho salmon (Figure 2a). Furthermore, the summer average of mean daily temperature was correlated negatively and significantly with both B and ΔB of stocked rainbow trout; coho salmon survived and grew (albeit with a net loss in cohort biomass) only in the coldest site (Coghlan 2004). Coghlan and Ringler (2005b) demonstrated that temperature influenced the outcomes of interactions between Atlantic salmon and rainbow trout and that, as summer temperatures increased, Atlantic salmon biomass became increasingly favored at the expense of rainbow trout biomass.

Emigration

Movement of stocked salmonines from our study sites would have been interpreted as mortality and thus apparent survival would be downwardly biased. Gowan et al. (1994) stressed the importance of accounting for the migration of lotic salmonines because, although this phenomenon is probably widespread, it often remains undetected in studies encompassing small spatial and temporal scales. The literature on juvenile Atlantic salmon suggests extremely variable propensity for movement among individuals and populations. For example, Steingrimsson and Grant (2003) found that during the first summer of life, about 97% of all tagged Atlantic salmon remained within 5 m of their point of capture, similar to other findings (Juanes et al. 2000), in which

TABLE 4.—Regression models generated by stepwise selection relating Atlantic salmon responses to habitat and biotic principal component (PC) scores for streams draining the eastern and southern shores of Lake Ontario.

Dependent variable	Independent variable	Estimate	SE	Type II sums of squares	Partial R^2	F-value	P-value
Apparent survival	Habitat PC2	−0.082	0.0099	0.408	0.43	15.33	<0.0001
	Habitat PC3	0.0622	0.011	0.197	0.14	6.23	<0.0001
	Biotic PC2	0.054	0.011	0.136	0.25	25.05	0.0002
	Habitat PC1	0.027	0.0096	0.046	0.02	2.09	0.014
	Biotic PC1	0.036	0.016	0.03	0.023	2.56	0.0407
	Biotic PC3	0.027	0.015	0.015	0.025	3.38	0.0858
Standing biomass	Habitat PC2	−0.12	0.02	1.081	0.424	38.16	<0.0001
	Habitat PC3	0.1	0.022	0.58	0.183	20.46	0.0003
	Biotic PC2	0.07	0.024	0.298	0.145	10.51	0.0045
Proportional change in biomass	Habitat PC2	−0.969	0.13	58.37	0.43	58.81	<0.0001
	Habitat PC3	0.76	0.13	32.46	0.21	32.7	<0.0001
	Biotic PC2	0.59	0.14	17.52	0.19	17.65	0.0006
	Biotic PC3	0.28	0.19	2.23	0.02	2.25	0.05
Instantaneous growth rate	Habitat PC1	−0.0013	0.00032	0.0003571	0.33	17.1	0.0006
	Habitat PC3	0.0016	0.00059	0.0001532	0.18	7.33	0.0144

90% of all tagged fry moved less than 20 m. However, individual fish that did migrate often traveled long distances (up to 400 m; Juanes et al. 2000). Some confusion exists regarding fitness correlates of resident individuals versus those that moved. Elliott (1994) suggested that emigrating age-0 brown trout were competitively weak individuals that could not establish or maintain a feeding territory, whereas Gowan and Fausch (2002) found that emigrating brook trout *Salvelinus fontinalis* were most likely dominant individuals in search of new energetically profitable foraging stations, especially as hydrologic conditions changed. Although there are many conditions that favor emigration (e.g., floods or droughts, high density of conspecifics, inadequate invertebrate production or drift, lack of suitable physical habitat, unsuitable temperatures), it is clear that the frequency and magnitude of movements are related inversely to the quantity and quality of available habitat (Belanger and Rodriguez 2002; Gowan and Fausch 2002). Those sites that provide the most habitat or highest quality habitat should contain and retain the most fish (e.g., Urabe and Nakano 1999; Nislow et al. 2000).

Our estimates of apparent survival most likely include losses from emigration, but we do not have the data to distinguish between movement and mortality. However, the objective of our study was to compare the relative productive potentials of many sites over a wide geographic range, rather than to quantify actual production at any one site. As such, our estimates of SURV, B, and ΔB are indices of the capacity of each site to retain a given density or biomass of salmonines, assuming high-quality sites would retain more salmonines (whether measured by density or biomass) than would low-quality sites. Belanger and Rodriguez (2002) argue that movement patterns provide a better measure of habitat quality than does density. Because our sites received an initial stocking of salmonines, the magnitude of emigration of individuals from each site would indicate habitat quality, even if we measured the net effect of emigration (and mortality) in terms of resultant density. Because stocking densities were low, intraspecific interactions were probably negligible (Millard 2005), and few significant differences were found that could be attributed to the presence of stocked *Oncorhynchus*; considering that, variation in Atlantic salmon responses would be a function of site quality as determined by habitat parameters.

A related objective was to rank sites in terms of their potential to retain stocked Atlantic salmon fry so that we could identify the most suitable areas for future restoration attempts. Even if a site was ranked as low quality because of high emigration rates rather than outright mortality, emigrating fish probably would have lower survival and growth rates than would resident fish (Hartman 1959; Elliott 1994; Nislow et al. 2000; but see Gowan and Fausch 2002; Steingrimsson and Grant 2003), such that overall site quality still would be poor. Similarly, our regression analyses were simply attempts to identify important abiotic and biotic factors related to stocked salmonine apparent survival and growth rather than to predict those attributes at any specific location.

Emigration of stocked *Oncorhynchus* spp., which also would have been interpreted as mortality, may have occurred, as it did in the case of Atlantic salmon. Close and Anderson (1992) concluded that such emigration is density-dependent for steelhead stocked in Lake Superior tributaries, although their stocking densities were 5–10 times greater than ours. Emigration rates of steelhead fry stocked in British Columbia streams at densities similar to our study were negligible compared with losses from mortality (Hume and Parkinson 1987). Bisson et al. (1988) stocked coho salmon in volcanically perturbed streams at higher densities than we did in our study, but they obtained higher survival and biomass estimates. Temperatures in many Lake Ontario tributaries exceeded the physiological optimum for rainbow trout and coho salmon (Figure 2; Coghlan 2004), which may have caused early emigration or high mortality (e.g., Hartman 1959), but those temperatures did not exceed temperatures observed by Bisson et al. (1988).

The virtual failure of coho salmon in this study may have resulted from artificial selection within hatchery populations. Most coho salmon returning to the Salmon River hatchery were stocked originally in Lake Ontario as smolts (New York State Department of Environmental Conservation, unpublished stocking data) and experienced no prior stream residence. Therefore, selection for high lacustrine survival could be significant within hatchery-derived populations, but selection pressures associated with lotic survival are probably relaxed (Kostow 2004). Furthermore, because the Salmon River Hatchery rears fish in cold, thermally stable groundwater (~5–7°C), there are no selective pressures or acclimation regimes favoring adaptation to the high, variable temperatures found naturally in many Lake Ontario tributaries. Other authors have documented the importance of woody material and deep pools to juvenile coho salmon (e.g., Hartman 1965; Nielsen 1992), and the relative paucity of such habitat in our study sites could have contributed to either emigration or mortality of this species. However, exploratory sampling in seemingly suitable reaches adjacent to our study sites yielded no coho salmon. Clearly, additional studies are needed to identify the mechanism behind this high apparent mortality in some Lake Ontario streams, but temperature probably is important.

Environmental Gradients

Principal components and regression analyses suggested that several important environmental gradients affected Atlantic salmon responses. These gradients most likely were a product of interactions at several spatial scales (e.g., geomorphic variables affecting microhabitat characteristics; Poff and Huryn 1998). The first habitat PC axis (representing a distinct geomorphic transition from high-elevation, forested sites to low-elevation, developed sites and corresponding changes in temperature regime, pH, and conductivity), explained much variation in growth rates. Although not measured here explicitly, nutrient concentration and, hence, benthic macroinvertebrate productivity usually are correlated positively to the variables we measured, such as agricultural development and conductivity (e.g., Krueger and Waters 1983; Hunsaker and Levine 1995; Aguiar et al. 2002; Shieh et al. 2003). Therefore, our measures of GBI, conductivity, and percent agricultural development probably provide an adequate, albeit rough, estimate of potential benthic macroinvertebrate productivity across our sites. Thus, moderate increases in agricultural development, nutrient enrichment, or benthic productivity can stimulate juvenile salmonine growth rates, as other studies suggest (e.g., Kennedy et al. 1983; Bowlby and Roff 1986; Bergheim and Hesthagen 1990; Richardson 1993; Weng et al. 2001; Nislow et al. 2004). Presumably no sites exceeded the level of deforestation, organic enrichment, or temperature beyond which salmon growth would be reduced, either due to metabolic stress or shifts in the macroinvertebrate assemblage towards taxa that do not provide many foraging opportunities for young salmonines (e.g., Scott et al. 1986; Rader 1997; Kilgour 1998; Wang et al. 2003; Coghlan and Ringler 2005a). Furthermore, relatively high temperatures might have favored growth in Atlantic salmon by excluding potentially competing wild or stocked rainbow trout (Coghlan and Ringler 2005b), provided that adequate food was available.

The second habitat PC axis appeared to reflect stream size and was related inversely to the apparent survival, biomass, and proportional change in biomass of Atlantic salmon. Small streams replete with shallow, low-velocity habitats provide Atlantic salmon fry with energetically profitable foraging habitats (Nislow et al. 1999, 2000) and exclude large piscivores (McCrimmon 1954; Bowlby and Roff 1986), thus favoring survival or retention of young fish. Principal components derived from biotic (fish and invertebrate) data exhibited less explanatory power than those derived from habitat data. Biotic PC axis 2 was significant in three of four regression models and represents a gradient in density and biomass of all fish, wild salmonines, and piscivores. Here, we interpret apparent survival, biomass, and proportional change in biomass as inverse functions of the density and biomass of potential competitors and predators. Taken together, these regression analyses suggest that apparent survival and biomass elaboration responded to somewhat different predictor variables than did growth rate.

Stream-Specific Assessments

Distinct gradients in abiotic and biotic variables corresponding to geomorphology were apparent across our study region (Figure 4; Coghlan 2004) and probably were responsible for the patterns seen here. Furthermore, significant regional differences exist in production potential of wild salmonines in the southern catchment of Lake Ontario (Wildridge 1990). Northeast-to-southwest gradients exist (i.e., from Tug Hill to Ontario Ridge and Swamplands to Ontario Drumlins), such that stream temperature, organic enrichment, and total fish community biomass (which presumably are all correlated with benthic productivity; Krueger and Waters 1983) increase with a concomitant decrease in wild salmonine biomass (Wildridge 1990; Coghlan 2004). These gradients may be affected by climatic, geomorphic, and anthropogenic variation (Cressey 1966; Sly 1971; Wildridge 1990; Coghlan 2004). Densities and production of wild salmonine juveniles in several Tug Hill streams may approach or exceed those of high-quality Pacific coast tributaries (Johnson and Ringler 1980). Wildridge (1990) considered Tug Hill streams to have the greatest production potential of all New York tributaries of Lake Ontario. Growth rates of stocked Atlantic salmon were lowest in Tug Hill streams, presumably due to low temperatures and perhaps low nutrient levels. However, apparent survival in many Tug Hill streams was high enough to offset slow growth and resulted in the greatest biomass elaboration. Skinner, Lindsey, and Deer creeks may offer the best juvenile rearing habitat for future Atlantic salmon restoration efforts because summer temperatures appear to be optimal for Atlantic salmon but slightly higher than optimal for wild rainbow trout (Coghlan and Ringler 2005b). However, these streams are relatively small, so absolute production potential is probably limited. The prospect for restoring Atlantic salmon to the coldest streams in Tug Hill may be limited by the abundance of wild rainbow trout and the desire to manage accordingly for that species (Johnson and Wedge 1999; McKenna and Johnson 2005;

Coghlan and Ringler 2005b). Another Lake Ontario tributary in the Tug Hill region, the main-stem Salmon River, was the subject of a previous study (Coghlan and Ringler 2004). Although apparent survival of stocked Atlantic salmon was relatively low there, the sheer amount of available habitat provided by this large river makes it a likely candidate for restoration attempts.

The virtual failure of Atlantic salmon in Ontario Ridge and Swamplands streams is puzzling. Johnson and Wedge (1999) mentioned that poor water quality may render Grindstone Creek unsuitable for Atlantic salmon, but they did not elaborate. Coghlan and Ringler (2005a) found that variation in water quality could alter the energy balance of juvenile Atlantic salmon and reduce apparent survival and growth. Biotic indices derived from invertebrate communities indicated slightly impacted water quality in Ontario Ridge and Swamplands streams compared with Tug Hill streams (Coghlan 2004), but one would expect streams in the highly perturbed Ontario Drumlins region, rather than in the Ontario Ridge and Swamplands region, to be most affected in this manner. Because of the poor drainage capacity of soils in the region, Ontario Ridge and Swamplands streams may experience extreme fluctuations in discharge after a storm (S. M. Coghlan and M. J. Connerton, personal observations)—that is, freshets large enough to displace newly planted fry (e.g., Egglishaw and Shackley 1980) or reduce the amount of energetically profitable foraging habitat (Nislow et al. 2004). However, although many Ontario Ridge and Swamplands streams possess seemingly suitable thermal and physical habitat for juvenile Atlantic salmon, our results and previous evidence (Wildridge 1990; Johnson and Wedge 1999; Murphy 2003) clearly indicate that most streams in the region offer little or no potential for future restoration attempts.

The Ontario Drumlins region demonstrates high variability in rearing potential among streams, which may result from the high intensity and occurrence of agriculture and other human activities in the landscape (e.g., Kilgour 1998). All streams studied in the region contain at least one artificial barrier and impoundment, and water diversion for agricultural and municipal purposes is widespread. At least some of these streams contain high-quality salmonine habitat, provided adequate flow is available. For example, Atlantic salmon were relatively successful in Eightmile and Rice creeks during our study. However, in a pilot study during the previous year (summer of 2002), drought and municipal water diversions dried both streams to standing pools, and no stocked salmonines survived (Coghlan 2004). This region also contains streams with relatively poor water quality; improvements in water quality in the most impaired streams (e.g., Wolcott Creek) might increase the potential for Atlantic salmon restoration (Coghlan and Ringler 2005a). In addition, the numerous low-head dams in these streams increase water temperatures downstream (e.g., England and Fatora 1978), favor invertebrate assemblages relatively invulnerable to salmonine predation (Rader 1997; Tiemann et al. 2005), and prevent upstream migrations of spawning adults and juveniles. Removal of these dams may improve downstream habitat accordingly (but see Mistak et al. 2003) and also open up suitable habitat upstream for future colonization.

Management efforts applied towards maximizing the salmonine biomass produced in eastern and southern Lake Ontario streams should account for thermally marginal or unsuitable conditions (Coghlan and Ringler 2005b). Given existing physiological information on each species (e.g., Hokanson et al. 1977; Stewart et al. 1981; Murphy 2003), summer temperatures at most sites appeared to be nearly optimal for Atlantic salmon but above optimal for rainbow trout and especially coho salmon. Perhaps the cold Tug Hill streams such as Trout Brook, Orwell Brook, and Little Sandy Creek (Johnson and Ringler 1980; Wildridge 1990; McKenna and Johnson 2005) could continue to be managed solely for natural reproduction of wild salmonines, whereas Atlantic salmon restoration efforts might target the more thermally marginal streams that have less potential for producing other salmonines, especially in the Ontario Drumlins region. Based on our results, tributaries of Lake Ontario along its southern and eastern shores, such as Skinner, Lindsey, Deer, Black, Rice, Eightmile, and Red creeks, appear to be promising candidates for Atlantic salmon reintroduction programs.

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