

## Juvenile Rainbow Trout Production in New York Tributaries of Lake Ontario: Implications for Atlantic Salmon Restoration

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**Abstract.**—Three Pacific salmonid species *Oncorhynchus* spp. have replaced the extirpated Atlantic salmon *Salmo salar* as the main migratory salmonid in the Lake Ontario drainage. One of those species, the nonnative rainbow trout *O. mykiss*, has become widely distributed within the historical Atlantic salmon habitat, occupying an ecological niche similar to that of juvenile Atlantic salmon. Consequently, both a tributary's carrying capacity for Atlantic salmon and competition from established nonnative species are important when considering the feasibility of Atlantic salmon restoration. Estimation of juvenile rainbow trout production will help evaluate the capacity of tributaries to produce salmonids that occupy similar niches. Geostatistical methods were applied to standardized and efficiency-corrected electrofishing data from three of New York's best salmonid-producing streams to precisely estimate juvenile rainbow trout populations. Results indicated that each study stream could produce 20,000–40,000 age-0 and 4,000–10,000 age-1 and older rainbow trout per year. Statistical interpolation indicated areas of significantly different production potential and points of significant changes in productivity. Closer examination of the niche similarity and competitive potential of these two species is needed to properly interpret these estimates with regard to Atlantic salmon restoration.

The Atlantic salmon *Salmo salar* was enormously important historically in the native fish assemblage of Lake Ontario and its tributaries. In colonial and preindustrial times, Atlantic salmon were extremely abundant in Lake Ontario tributaries during both spring and fall runs (Webster 1982).

Records indicate that Atlantic salmon were present in every major tributary of Lake Ontario except the Niagara River (Webster 1982) and were the only native migratory salmonid in Lake Ontario. The decline of these Atlantic salmon populations began in the early 1800s and corresponds to the construction of dams on tributaries (Webster 1982; Smith 1985). However, a variety of factors combined to cause their extirpation from the Lake Ontario system by the early 1900s. Dams disrupted the life cycle by separating adult Atlantic salmon from their spawning grounds. Various forms of water pollution and habitat degradation further reduced Atlantic salmon production potential (Huntsman 1944; Christie 1974). Overexploitation added to the pressure on the spawning stock. Two additional factors greatly changed the ecological characteristics of the Lake Ontario ecosystem for

Atlantic salmon. The first was the invasion of the lake by alewives *Alosa pseudoharengus*. Declines of salmonid and other fish populations have been observed wherever these fish have become established as large components of the fish prey base (Smith 1970, 1972, 1995; Ketola et al. 2000). The cause appears to be “early mortality syndrome”—death of first-feeding larvae from thiamine-deficiency due to adults feeding heavily on alewives (Fisher et al. 1996; Ketola et al. 2000). The establishment of rainbow trout *Oncorhynchus mykiss* in these stream systems is another ecological change that may represent a major challenge to Atlantic salmon restoration because of potential competition between the stream-dwelling early life stages of these species.

Atlantic salmon restoration is of interest to fisheries management agencies due to its historical and ecological importance and its potential as a sport fish. The present salmonid sport fishery in Lake Ontario is supported by lake trout *Salvelinus namaycush* and four species of exotic salmonids: Chinook salmon *O. tshawytscha*, coho salmon *O. kisutch*, rainbow trout, and brown trout *Salmo trutta*. Substantial natural reproduction of the Pacific salmonids, especially rainbow trout, occurs in tributaries. Because rainbow trout are widespread and abundant in several Lake Ontario tributaries and have life history and juvenile habitat requirements similar to Atlantic salmon (Gibson 1981; Hearn

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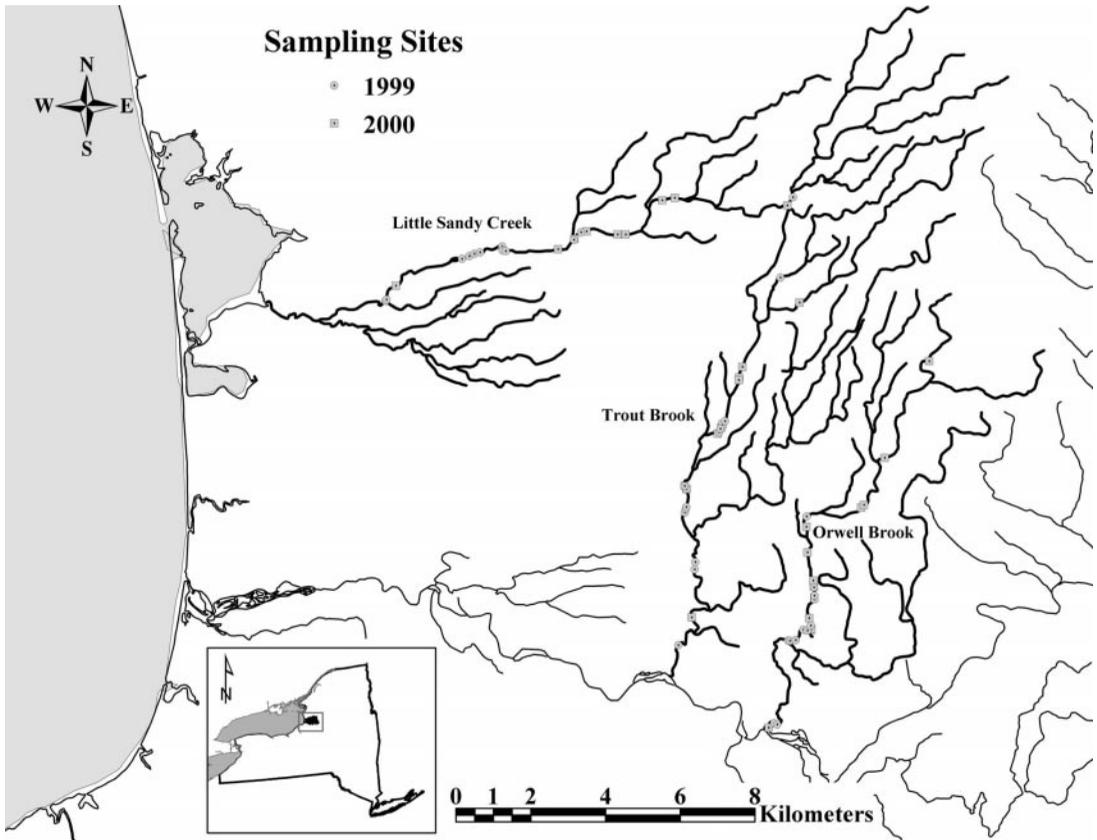


FIGURE 1.—Map showing sampling sites for rainbow trout in the Salmon River basin, New York. Samples collected in 1999 are indicated by circles, and those collected in 2000 are indicated by squares.

and Kynard 1986), rainbow trout may pose a competitive impediment to Atlantic salmon restoration (Johnson and Wedge 1999).

Restoration of Atlantic salmon to the Lake Ontario watershed will require successful natural reproduction in tributaries. Consequently, in streams viewed as having Atlantic salmon restoration potential, determining juvenile production potentials is critical. However, few of the streams that historically provided Atlantic salmon spawning habitat retain their pristine quality, and fewer still allow unobstructed access to that habitat. A few streams in the eastern basin, particularly those in the vicinity of the Salmon River, New York, still have accessible habitat with the qualities necessary for Atlantic salmon spawning and juvenile survival. These streams currently produce unknown numbers of rainbow trout smolts annually. Rainbow trout production may serve as a surrogate measure of potential Atlantic salmon production because the niches of the two species are so similar (Hearn and Kynard 1986; Gibson 1988). Our study

objectives were to determine the extent of colonization of rainbow trout in three of New York State's best salmonid streams, quantify annual production of juvenile rainbow trout in those streams, assess bottlenecks that may be impeding production, and relate rainbow trout production to potential Atlantic salmon production.

### Methods

*Study sites.*—The study sites were contained within first-order to third-order streams of Lake Ontario's eastern basin (Figure 1). Two were tributaries of the Salmon River (Trout and Orwell Brooks). The other emptied into one of Lake Ontario's coastal ponds just north of the Salmon River. These typical cold-water streams with gravel-cobble-boulder streambeds are described in detail in Johnson (1978) and Kennen (1993).

Juvenile rainbow trout (and other species) were collected from 10–13 randomly located standardized electrofishing areas within Trout Brook, Orwell Brook, and Little Sandy Creek (Figure 1) in

TABLE 1.—Mean single-pass electrofishing capture efficiency in three study streams of eastern Lake Ontario, based on three-pass depletion estimate, for each commonly encountered species, by habitat quality (G = good, I = intermediate, P = poor).

Species	Habitat	Mean (%)
Blacknose dace <i>Rhinichthys atratulus</i>	G	55
	I	48
	P	71
Chinook salmon	G	69
	I	74
	P	67
Coho salmon	G	47
	I	55
	P	49
Creek chub <i>Semotilus atromaculatus</i>	G	61
	I	73
	P	69
Cutlip minnow <i>Exoglossum maxillingua</i>	G	77
	I	58
	P	43
Fantail darter <i>Etheostoma flabellare</i>	G	37
	I	22
	P	48
Rainbow trout (age 0)	G	31
	I	65
	P	55
Rainbow trout (age 1 and older)	G	49
	I	
	P	

August of 1999 and 2000. We expected optimal juvenile rainbow trout habitat to be concentrated in the middle reaches of each stream, based on prior knowledge of these systems. Because of limited sampling time and resources, random sampling locations were normally distributed ( $N[0, 1]$ ) and centered near each stream's midpoint. Sample sites spanned the main stem of each stream from near the mouth (third or fourth order) to first-order waters (Figure 1). The location of each sample reach was recorded in digital coordinate units by a handheld Garmin GPS45 Global Positioning System. The distance from the stream mouth to each sample location was then determined by measurement on the National Hydrographic Dataset stream coverage (1:100,000 scale) in the ArcView GIS program.

We used catch per unit effort (CPUE) from single-pass backpack electroshocking in 50-m reaches (with blocking nets) and adjusted for sampling efficiency to estimate rainbow trout population sizes. Single-pass species-specific efficiencies were determined for catches from each class of habitat quality by three-pass collections within preestablished stream segments (near some of the midstream sites subsequently sampled for this study) in 1998 (Table 1). Habitat quality for juvenile rainbow trout in late summer was classified as good, intermediate, or poor based on evaluation

of several criteria, including gradient, pool: riffle ratio, instream cover, substrate embeddedness, and maximum daily water temperature. All fish were identified to species, enumerated, and released. In addition, age-classes (young-of-the-year, age 0, or age 1 and older) of salmonids were recorded. The CPUE for each species and age-class was adjusted according to the sampling efficiency for that species and habitat to give the most precise estimate of the population size within the sample reach. Age-0 abundance is an index of annual production (Johnson 1980). Data from both years were combined for this analysis to provide the greatest power.

Typically, a stratified random approach is used to estimate population size or production. That technique takes advantage of differences in variability by sample stratum but assumes that the points are independent and variability is essentially constant, regardless of how far one point is from another (Snedecor and Cochran 1980). However, points near high fish concentrations are likely to have more fish than those farther away, and the range of that spatial influence varies (Journel and Huijbregts 1978; Maravelias et al. 1996). Streams, in particular, are essentially linear sequences of habitats and their associated biotic communities; the fish abundances are often serially autocorrelated (Maravelias et al. 1996). Therefore, we applied geostatistics to determine the best interpolation and most precise estimates of total stream productivity for each age-class of rainbow trout. This procedure takes advantage of the systematic change in variability with distance from any one point to another in the system. Modeling the autocorrelation of the response variable (rainbow trout abundance), produces precise estimates with much smaller variances than those from stratified random methods (Journel and Huijbregts 1978).

*Autocorrelation, spatial variance analysis, and kriging interpolation.*—In nature, attributes of ecological systems often vary continuously in space, rather than in discrete, independent steps. Points close together often have more similar attribute values than those that are farther apart. In such cases, there is an influence of distance, and the assumption that data points are independent is false. Variation of a variable has several components and is often scale-dependent. At large scales, overall system condition can be described by the average. Variation at the finest scale usually constitutes random "noise." However, at intermediate scales, the pattern of change may be spatially dependent.

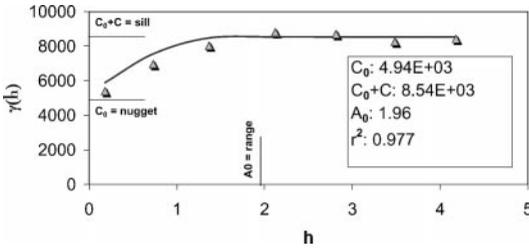


FIGURE 2.—General components of a semivariogram. Parameter values for the abundance of age-0 rainbow trout at Little Sandy Creek are shown, where  $\gamma(h)$  is the measure of systematic variability in abundance as a function of distance  $h$ ,  $C_0$  is the small-scale nugget variance,  $C$  is a measure of the increase in variability above the nugget value to the sill, and  $A_0$  is the distance to the sill. See text for more information.

Modern computational power allows us to take advantage of statistical techniques that may use this relationship to better estimate distributions of variables in space and their associated variance. Analysis of spatial autocorrelation with a semivariogram and interpolation by kriging are two such techniques. Kriging and semivariance analysis have been used to examine fisheries issues for nearly 20 years. However, these geostatistical techniques have not been widely applied. A detailed discussion is available in other works (e.g., Journel and Huijbregts 1978), but a brief overview and example may provide useful background. These methods were originally developed for geological exploration and mining, and several of the terms stem from that origin.

*Semivariance analysis and stationarity.*—Spatial autocorrelation analysis examines the dependence of values of a variable (e.g., temperature, clay content of soil, abundance of rainbow trout, etc.) at a point in space on the distance from a reference point(s). Any quantitative variable may be examined in this way. For this technique to work, a basic assumption must be made about the ecological system. That assumption is that the statistical properties of the spatially correlated variation are uniform throughout the system of interest (Burrough 1995). This simply means that statistical properties of variables, such as means, variances, and covariances, behave the same at one point in, for example, a grassy field as they do at a different point 100 m away, or anywhere else in the field. This is called statistical stationarity, and it operates in different degrees. Geostatistical methods usually need only invoke secondary stationarity, which assumes that only the mean and variance are constant. A weaker condition, identified as the

intrinsic hypothesis, assumes that the mean of differences in variable values over a given spatial interval is zero and that the variance is not dependent on location. This may be sufficient in many cases. These assumptions apply when modeling the change in variance of the variable of interest with distance.

Spatial variance is often modeled with the semivariogram because it is simple and robust to nonstationary variance (Robertson 1987). It takes the form

$$\gamma(h) = [1/2N(h)] \sum [z_i - z_{i+h}]^2;$$

$\gamma(h)$  = the semivariance for the distance interval class  $h$ ,

$N(h)$  = the number of sample pairs in the lag interval  $h$ ,

$z_i$  = the observed value at point  $i$ , and

$z_{i+h}$  = the observed value at the point  $i + h$ .

The stationarity requirement limits the types of models that are appropriate. There are six models that are typically used to model semivariance (though others exist). Spherical, linear with a sill, exponential, and Gaussian models apply when variance is stable (second-order stationarity). Linear and logarithmic models apply when variance is not stable (intrinsic hypothesis; Burrough 1995). Typical model structure is shown by the spherical isotropic model (Figure 2), which may be expressed as

$$\gamma(h) = C_0 + C [1.5(h/A_0) - 0.5(h/A_0)^3];$$

$h$  = the lag distance interval,

$C_0$  = the nugget effect (small-scale variability),

$C$  = the sill of the variogram that represents the maximum level of variability, and

$A_0$  = the range of the variogram beyond which data are no longer autocorrelated.

The semivariogram essentially models the increase in the variance of a variable as the distance from a measured point increases. It has three structural components (Figure 2): (1) the nugget ( $C_0$ ) or level of fine-scale noise (variance), (2) the sill or maximum level of variance, and (3) the range or distance from a measured point at which the variance is maximum.

This model of variance is in turn used for optimum interpolation. Interpolation by kriging uses the semivariance model to estimate the weight of the observed values applied to prediction of unsampled values based on their distance from the observed points. The general form of the interpolation is a weighted sum of the data, that is,

$$\hat{Z}(x_j) = \sum_{i=1}^N \lambda_i Z(x_i),$$

where  $\hat{Z}(x_j)$  = the predicted value of the response variable at an unsampled location ( $x_j$ ),  $Z(x_i)$  = the measured value at the  $i$ th sampled location,  $N$  = the number of sampled values, and  $\lambda_i$  = the weight applied to the measured value at the  $i$ th location.

The weight ( $\lambda_i$ ) is determined by the semivariogram model. Kriging provides the best linear unbiased estimate of the average value of a variable (Burrough 1995). Results from kriging should always be at least as precise as those from the more conventional stratified random approach. Kriging is also an exact interpolator (i.e., interpolated values coincide with the measure points).

*Water temperature example.*—Water temperature in a stream offers an example of how to apply these methods to a common variable that varies in space. Water temperature in a stream varies from place to place because of the influence of a number of factors, such as temperature of the inflowing water, exposure to the sun or shading by riparian cover, input of groundwater, etc. An overall average temperature can be computed to represent the entire stream system, and point measurements could be made every few centimeters (an absurd degree of detail) to clearly reveal the level of fine-scale noise. However, measurements at intermediate scale will probably show some degree of spatial dependence because of the factors sited above (and others). The following example uses randomly located point measurements of water temperature taken along the length of one of our streams (Orwell Brook) in 1999. The overall mean was 17.7°C; the variance was 1.4°C. The semivariogram shows spatial dependence to a range of approximately 1 km ( $A_0 = 917$ ) and was best fitted ( $r^2 = 0.985$ ) with a Gaussian model (Figure 3a). The nugget value (fine-scale noise) was 0.4 and about one-fourth the range over which semivariance responded to distance (0.4–2.1). The sill shows that maximum variance was roughly 2.1.

Measured points were no closer than 100 m. Thus, this example applies kriging to blocks of stream 100 m long. This technique estimates in-

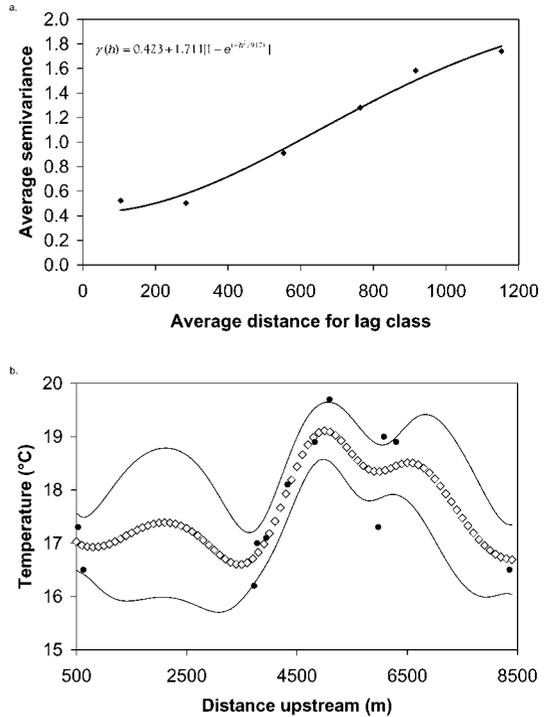


FIGURE 3.—Panel (a) depicts a semivariogram model of the dependence of stream temperature on the distance from measured points in Orwell Brook in 1999. Panel (b) shows a one-dimensional kriging-interpolated water temperature map developed from that model, where the circles indicate measured temperature values along the stream course, the diamonds represent kriging estimates of temperature in each 100-m reach, and the solid lines represent the 95% confidence limits around the kriging estimates.

terpolated values of average water temperature and their variances for each block over the entire sampled length of the stream, based on the predictions of the fitted semivariance model (Figure 3b). The overall average temperature (17.6°C) estimated by block kriging was nearly the same as that of the raw data, but the mean variance (0.87°C) of the estimate was 36% smaller than that of the raw data. This one-dimensional example shows how and where temperatures change along the stream course (in 100-m steps). One could then go back to the stream and measure riparian cover, incident radiation, groundwater flow, etc., to examine the causes of the temperature changes, compute a heat budget, and so on.

Simple computation of the mean and variance for the whole system (or large strata) from the raw data assume spatial independence of the points and estimate a variance that is considerably larger than

TABLE 2.—Isotropic semivariance models used in this analysis. Variables are defined as follows:  $\gamma(h)$  is the measure of systematic variability in abundance as a function of distance  $h$ ,  $C_0$  is the small-scale nugget variance,  $C$  is a measure of the increase in variability above the nugget value to the sill, and  $A_0$  is the distance to the sill. See text for more information.

Model type	Specification	
Exponential	$\gamma(h) = C_0 + C[1 - \exp(-h/A_0)]$	
Gaussian	$\gamma(h) = C_0 + C[1 - \exp(-h^2/A_0^2)]$	
Linear	$\gamma(h) = C_0 + [h(C/A_0)]$	
Linear; sill	$\gamma(h) = C_0 + [h(C/A_0)]$	for $h \leq A_0$
	$\gamma(h) = C_0 + C$	for $h > A_0$
Spherical	$\gamma(h) = C_0 + C[1.5(h/A_0) - 0.5(h/A_0)^3]$	for $0 < h \leq A_0$
	$\gamma(h) = C_0 + C$	for $h > A_0$

the kriging estimate. Also, that systemwide information tells us little about the internal structure or finer-scale changes within the system. The geostatistical approach may be applied to any spatially oriented continuous variable. Our study applied these methods to show both the distribution of juvenile rainbow trout densities within several streams and estimate their annual production for each stream.

We expected a global trend and generally higher abundances in the middle reaches of the stream and fewer fish in headwaters or near the stream mouth. We tested universal kriging to see if the spatial model improved when the (suspected) global trend was explicitly included. However, there was little or no difference between ordinary and universal kriging results. In fact, the universal method produced slightly poorer results for Orwell Brook. These findings are similar to those from Zimmerman et al. (1999) who, using simulated data, specifically compared universal and ordinary kriging. Therefore, only ordinary kriging results are reported here.

The GS+ computer program (Robertson 2000) was used to fit variograms, conduct kriging interpolations, and produce maps. We tested each of the variogram models summarized in Table 2 and selected the model that best represented the observed data, based on maximum coefficient of determination ( $r^2$ ) and minimum residual sums of squares (RSS). Crossvalidation of each model was achieved with the jackknife procedure. We selected the jackknife regression results displaying regression coefficients closest to 1.0, maximum  $r^2$ , and minimum error reduction. This fitting procedure also provides an indication of the optimal kriging neighborhood. Kriging is a geostatistical method of precisely interpolating between georeferenced data points. Kriging interpolation is based upon the modeled spatial autocorrelation described by the fitted variogram (Journel and Huijbregts

1978; Robertson 1987). One-dimensional kriging was applied to interpolate and map age-0 and age-1 and older rainbow trout abundances at 100-m intervals for the sampled length of each stream. Population estimates were determined as the area under the curve of interpolated points. Variances of the population estimates were calculated in the same way as the stratified random estimates, treating each 100-m interval as a stratum.

Each stream was divided into several spatial strata to provide comparison of geostatistical results with the more conventional stratified random method. The strata were determined by identifying locations where the full multispecies fish assemblage changed most strongly. Those changes were determined at sampling locations along each stream course by use of a moving split-window multivariate distance technique (MSMD; Ludwig and Cornelius 1987). This technique entails computation of the squared Euclidean distance between the samples in the upper and lower halves of a window that is a specific number of samples wide. Seven samples per window were used in this analysis, which encompasses roughly one-third of the samples for each stream. Samples were ordered along the gradient (the stream course), and the first window was placed to include the seven most upstream samples. The computed squared Euclidean distance was assigned to the middle sample of the window. The window was then moved downstream one sample, losing the most upstream sample from the upper half of the window and gaining the next downstream sample in the lower window. The computation and movement cycle was repeated until the seven most downstream samples were enclosed within the window. The highest peaks (greatest Euclidean distances) separated by more than 1 km were chosen as the boundaries between strata. Stratified random population estimates were determined by the methods of Snedecor and Cochran (1980) after weighting the observations based

TABLE 3.—Dissimilarities of fish assemblages determined by the moving split-window multivariate distance analysis for each study stream. Dissimilarity, as measured by squared Euclidean distance, is given for each sample site from the middle of the most downstream window to the middle of the most upstream window. Values in bold italics indicate the approximate locations of substantial species assemblage changes.

Orwell Brook		Little Sandy Creek		Trout Brook	
Upstream distance (km)	Dissimilarity	Upstream distance (km)	Dissimilarity	Upstream distance (km)	Dissimilarity
3.72	18.28826	4.92	24.52763	4.72	19.84272
3.78	25.00187	5.13	18.13974	9.05	39.1336
3.94	29.23644	5.28	19.90838	9.16	39.81467
4.33	43.15162	5.44	20.81643	9.22	30.66549
<b>4.83</b>	<b>54.90278</b>	6.14	13.46731	9.72	21.49167
4.98	48.18633	6.26	13.88053	9.72	19.1954
5.00	22.60354	<b>6.36</b>	<b>24.68261</b>	9.83	18.28635
5.09	35.79403	7.79	21.56418	9.83	22.64816
5.40	38.42197	8.33	14.38269	11.79	16.93184
5.97	21.31085	8.37	7.038588	11.86	11.51167
6.03	8.271093	8.62	5.726161	11.97	7.387878
6.08	6.704015	8.77	6.779853	12.02	12.17901
6.30	9.638457	9.66	9.12225	12.12	10.59455
6.33	11.7509	9.76	15.5019	12.23	12.51595
6.50	16.29441	<b>9.88</b>	<b>19.42023</b>	13.41	8.55802
7.28	17.49528	11.48	12.97834	<b>13.48</b>	<b>16.19446</b>
8.03	20.89417				
8.36	26.77043				
<b>9.96</b>	<b>42.01358</b>				

on the inverse of the normal distribution used to randomly select sampling locations.

### Results

More than 5,500 salmonids were collected, 80% of which were rainbow trout. The fish bycatch included fantail darter (37%), blacknose dace (27%), cutlip minnow (3%), creek chub (3%), and an additional 24 species (7% combined). Three distinct regions were identified within each stream by the MSMD analysis (Table 3) and were used as the spatial strata for stratified random computations.

Semivariance analysis produced good isotropic models of spatial covariance in rainbow trout abundance within each study stream (Table 4). The first four or five points generally gave the most important structure. The active step (size of the lag interval used to group pairs of samples) used for each model ranged from 0.61 to 0.87 km. The active lag (range over which semivariance is calculated) ranged from 5.0 to 8.6 km. These settings provided a good balance between the number of points in each distance (lag) class and noise in the data and produced models that explained greater than 84% of variation in the semivariograms. Small-scale variability (nugget) was typically between 10% and 20%, but much higher for age-0 fish in Little Sandy Creek and lower for age-1 and older fish in Orwell Brook (Table 4). The range

over which distance significantly affected variability was typically 2–4 km but was nearly 8.5 km for age-0 fish in Trout Brook.

### Population Estimates and Spatial Distributions

Rainbow trout population estimates in the sampled portion of each watershed ranged from 20,000 to more than 43,000 for age 0 and from 4,600 to 9,000 for fish age 1 and older (Table 5). There was a consistent increase in abundance from Trout Brook to Orwell Brook to Little Sandy Creek, which roughly parallels increase in stream size. Population estimates were similar using kriging or the stratified random approach and were generally within 10% of each other. However, variance associated with the stratified random method was 4 to 20 times greater than that produced by the geostatistical analysis.

Rainbow trout abundances typically increased from low levels at the headwaters to a peak around midstream (although this peak was skewed toward the upstream reaches in Trout Brook) and then declined again near the stream mouth (Figure 4). The interpolated maps indicate high production areas in the vicinity of the village of Orwell on Orwell Brook (Figure 4a), above the Sandy Creek–Lacona village area on Little Sandy Creek (Figure 4b), and near the upper reaches of Trout Brook (Figure 4c). They also show a sharp decline in

TABLE 4.—Parameter values and coefficients of determination ( $r^2$ ) for three different semivariogram models that fit the observed autocorrelation data from each study stream (sampled lengths are given in parentheses after stream names). Nugget percentage indicates the proportion of spatially dependent range accounted for by small-scale variability; see Table 2 for the definitions of the other variables. Parameter values for the best-fit models are shown in bold italics.

Age	Semivariogram model	$C_0$	Nugget percent	$C_0 + C$	$A$	$r^2$
<b>Little Sandy Creek (20.0 km)</b>						
0	Spherical	<b>4,940</b>	<b>57</b>	<b>8,540</b>	<b>1.96</b>	<b>0.977</b>
	Linear with sill	5,730	37	15,570	7.47	0.890
	Gaussian	6,240	50	12,481	3.20	0.774
≥1	Spherical	53	16	336	2.57	0.792
	Linear with sill	<b>57</b>	<b>17</b>	<b>329</b>	<b>1.87</b>	<b>0.878</b>
	Gaussian	87	26	339	1.30	0.788
<b>Orwell Brook (15.6 km)</b>						
0	Spherical	3,180	21	15,260	10.74	0.831
	Linear with sill	<b>1,270</b>	<b>13</b>	<b>9,410</b>	<b>2.24</b>	<b>0.897</b>
	Gaussian	2,500	21	11,900	2.15	0.828
≥1	Spherical	19	2	749	13.01	0.943
	Linear with sill	<b>1</b>	<b>&lt;1</b>	<b>583</b>	<b>6.94</b>	<b>0.945</b>
	Gaussian	80	10	771	6.17	0.940
<b>Trout Brook (18.9 km)</b>						
0	Spherical	90	<1	21,280	13.37	0.828
	Linear with sill	120	<1	21,340	9.15	0.834
	Gaussian	<b>1,450</b>	<b>8</b>	<b>18,500</b>	<b>8.42</b>	<b>0.869</b>
≥1	Spherical	46	17	274	5.6	0.784
	Linear with sill	<b>45</b>	<b>18</b>	<b>253</b>	<b>3.71</b>	<b>0.842</b>
	Gaussian	71	26	277	2.73	0.798

populations through the Sandy Creek–Lacona village on Little Sandy Creek and an apparent rebound below the village (Figure 4b).

**Discussion**

Effective application of hatchery production and releases depends greatly on knowledge of the carrying capacity of a managed system (Bagliniere and Champigneulle 1986; Hilborn and Walters 1992). Knowing the forage demands exerted by wild fish and the habitat areas that support the most productive populations is vital to analyzing the effects wild fish on other aspects of the Lake Ontario ecosystem, particularly that of the Salmon River system. Estimates of the natural production of rainbow trout in the study streams provide fish-

ery managers with a measure of the number of trout being contributed by wild production from these high-quality tributaries, in addition to that added by hatchery releases.

Before 1977, little information existed on the extent of natural reproduction of Pacific salmonids in Lake Ontario tributaries. Investigations on salmonid production in Orwell and Trout brooks, beginning in 1977, documented substantial reproduction of all three Pacific salmonids, especially coho salmon in Orwell Brook (Johnson 1980; Johnson and Ringler 1981). Almost a decade later Wisniewski (1990) documented a 48% increase in rainbow trout production in Orwell Brook. Our results indicate that this trend of increasing rainbow trout production was still occurring a decade

TABLE 5.—Rainbow trout population estimates ( $\pm$ SE) and variances based on stratified random and geostatistical methods for the three study streams.

System	Age	Kriging estimate		Stratified random estimate	
		Population	Variance	Population	Variance
Little Sandy Creek	0	39,299 $\pm$ 4.6	2,837	43,842 $\pm$ 46.5	47,689
	≥1	9,131 $\pm$ 0.9	112	9,460 $\pm$ 5.1	581
Orwell Brook	0	31,286 $\pm$ 4.6	3,249	31,670 $\pm$ 22.3	12,486
	≥1	6,741 $\pm$ 0.6	53	6,607 $\pm$ 16.3	1,126
Trout Brook	0	22,998 $\pm$ 2.1	684	20,301 $\pm$ 10.9	2,617
	≥1	4,652 $\pm$ 0.6	63	4,701 $\pm$ 3.2	228

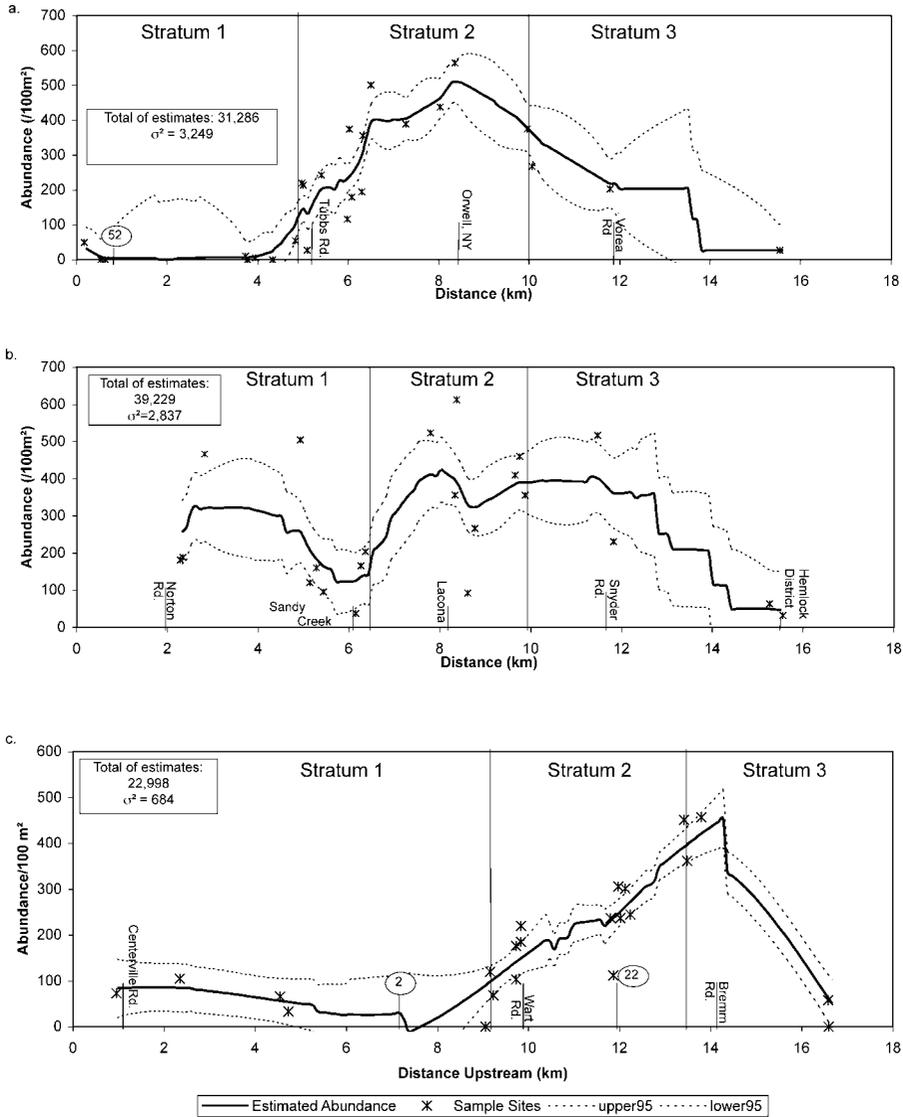


FIGURE 4.—One-dimensional kriging-interpolated maps of age-0 rainbow trout populations for (a) Orwell Brook, (b) Little Sandy Creek, and (c) Trout Brook. The heavy solid lines indicate estimated population sizes within 100-m stream reaches; the fine dashed lines indicate the 95% confidence limits. County road (circled numbers) and other road crossings and village locations are indicated along the horizontal axis.

later. The average density of age 1 and older rainbow trout in Orwell and Trout brooks in 1986 was 470/ha (Wisniewski 1990) compared with 1,010/ha observed in our work, a 53% increase. Reasons for the increase in rainbow trout production are unknown but might be attributed to fewer juvenile coho salmon in the streams. In 1977, Johnson (1980) documented juvenile coho production in Orwell Brook (5.9 g/m<sup>2</sup>, June 1–October 15) that was similar to the highest recorded values from the Pacific Northwest. In the mid-1980s, juvenile

coho salmon were the most abundant Pacific salmonids (200,489 or 53%) in 31 tributaries of Lake Ontario, followed by rainbow trout juveniles (118,267 or 31%) and chinook salmon juveniles (59,376 or 16%; Wildridge 1990). However, during our investigation in 1999 and 2000, coho salmon made up only 7% (783) of the juvenile salmonids in Orwell, Trout, and Little Sandy brooks, compared with 81% (8,951) for rainbow trout. This shift may potentially be attributed to a change in juvenile coho salmon hatchery release strategies

(i.e., from use of smaller tributaries, such as Orwell and Trout brooks, to larger tributaries and rivers).

Estimates of the number of age-1 and older rainbow trout juveniles produced in streams are useful as an index of fish production and are indicative of early life stage survivorship. Most of these fish will leave the streams as age-2 smolts the following spring, but a minor segment of the population (<10%) will leave as age-3 smolts (Johnson and Ringler 1981). However, estimates of the potential number of smolts produced are more helpful to fisheries managers. Seelbach (1987) found a relationship between rainbow trout smolt production from a tributary of Lake Michigan and severity of temperatures during the presmolt winter, overwinter mortalities ranging from 13% to 90%. If we assume similar presmolt mortalities for the populations in our study streams, using the age-1 and older densities we observed in these streams in 1999 and 2000, their contribution of smolts to Lake Ontario may be as few as 450 or as many as 7,800 (at 13–90% mortality, Little Sandy Creek = 931–7,944; Orwell Brook = 674–5,865; Trout Brook = 465–4,047). These values should be regarded as minimum smolt production estimates because they are based on observed parr densities over a 2-year period and may not represent full utilization of all suitable stream-rearing habitat by juvenile rainbow trout.

The geostatistical approach applied here produced estimates that were similar to those yielded by the conventional stratified-random procedure but that were much more reliable because of small variances (Journel and Huijbregts 1978; Burgess and Webster 1980; Isaaks and Srivastava 1988; Rossi et al. 1992). The particularly high or low abundances identified within each stream may warrant closer examination. For example, the sharp decrease through the Sandy Creek–Lacona village area may be indicative of a pollution-related habitat degradation problem or excessive undocumented harvest of sublegal parr in that reach of Little Sandy Creek.

Like most streams, those studied contain a wide variety of habitats, ranging from sluggish marshy areas to high-gradient boulder and bedrock areas. Salmonid stream habitat requirements are quite specific and relatively few areas of optimal salmonid habitat are likely to exist in a given stream. Of 31 Lake Ontario tributaries surveyed, Wildridge (1990) classified only Orwell Brook, Trout Brook, and Little Sandy Creek as excellent in terms of salmonid production potential. She found

that these three streams produced 87% of the salmonids from the surveyed streams; 97% of that salmonid production occurred in the third-order and fourth-order segments of those streams. This spatially differential production was demonstrated in our study by the longitudinal pattern of rainbow trout abundance along the stream course. The kriging-interpolated maps clearly show low abundances in the upper and lower reaches of each stream and a peak of abundance within the middle reaches. In general, headwaters are expected to be less than optimal simply because that habitat is smaller and less extensive (median of stream widths at sample locations are Little Sandy Creek = 6.9 m, Orwell Brook = 5.9, Trout Brook = 5.2). The observed decrease in abundances in the lower reaches of the streams were probably associated with less than optimal thermal and flow conditions in those areas during the nursery period (mean velocity by stratum was upper = 15.2 cm/s, middle = 27.2 cm/s, lower = 19.5 cm/s). Identification of factors supporting the high production in the vicinity of the village of Orwell would be valuable information for any manager of these or similar streams, particularly in light of the fact that optimal production appears to occur in few places within each stream.

Population estimates from this study apply to the main stem of each stream only, but many smaller branches exist. Our sampled areas represent about 25% of the stream area in each watershed. However, we probably sampled the most productive habitat within the watershed. The smaller branches probably contain much less high-quality habitat than the main stems, by virtue of their smaller size, but have the potential to significantly contribute to the production from each stream system because of their combined extent. In the Pacific Northwest, juvenile salmonid production in smaller stream systems has been found to be substantial (Bramblett et al. 2002; Rosenfeld et al. 2002). Construction of models of production as a function of stream size may be possible but would require more extensive sampling than conducted in this study.

After examining the available literature, Fausch (1998) found insufficient evidence to judge interspecific competition between juvenile Atlantic salmon and other salmonids, including rainbow trout. However, Raffenberg and Parrish (2003) found no evidence that age-0 Atlantic salmon were affected by the presence of rainbow trout. Conversely, Volpe et al. (2001) found that juvenile Atlantic salmon did not perform well after being

released in habitat already occupied by juvenile rainbow trout and that interspecific agonistic behavior between the two species varied between diurnal and nocturnal periods.

Our estimates of rainbow trout parr and smolt production from these three Lake Ontario tributaries may provide some insight into potential for juvenile Atlantic salmon production in these streams because of similar juvenile life history requirements for these two species (Gibson 1981; Hearn and Kynard 1986; Jones and Stanfield 1993). However, there are some differences in the niches of juvenile rainbow trout and Atlantic salmon. For example, there is evidence that Atlantic salmon fry prefer faster flowing riffle habitat than do rainbow trout (Hearn and Kynard 1986) and are superior competitors in such microhabitat because of morphological adaptations (Gibson 1988; Johnson and Wedge 1999). This advantage is largely derived from the larger pectoral fin of juvenile Atlantic salmon, which when placed in contact with the substrate, allows them to better maintain station in fast water (Kalleberg 1958). Because Atlantic salmon spawn and emerge earlier, they may also have a size advantage, up to age 1, over rainbow trout (Volpe et al. 2001).

Restoration of a natural spawning population of Atlantic salmon in the Lake Ontario basin would undoubtedly reduce juvenile rainbow trout production in the tributaries because of competition for limited nursery habitat. However, increased total salmonid production, as a result of interactive segregation between two closely related salmonid species, has been demonstrated (Nilsson 1967; Bjornn 1978). If interactive segregation occurs between juvenile Atlantic salmon and rainbow trout in Lake Ontario tributaries, the result may be an overall increase in total salmonid production in those streams. The presence of rainbow trout in Lake Ontario tributaries may pose an obstacle to restoration of a self-sustaining Atlantic salmon population. The severity of that obstacle will depend upon the true differences between the niches of these two species, the intensity of competition, and the availability of alternative microhabitats for each species. Our estimates of rainbow trout production in these streams provides fisheries managers with bounds when considering future restoration strategies for Atlantic salmon in eastern Lake Ontario tributaries.

### Conclusions

The streams we studied are some of the highest-quality, most productive salmonid streams in the

eastern basin (probably all of Lake Ontario). Each produces at least 20,000–40,000 age-0 rainbow trout each year or roughly 2,000 fish/km. Annual age-1 and older rainbow trout production was approximately 4,500–9,000 fish or roughly 450/km. This represents a rough minimum estimate of potential Atlantic salmon production for these tributaries. However, more research is needed to determine the similarity of juvenile rainbow trout and Atlantic salmon niches and what kind of competitive obstacle rainbow trout represent for Atlantic salmon restoration. This work highlights the need to focus on protecting and enhancing the stream habitat (Seelbach 1993) to promote effective management of the rainbow trout populations in eastern Lake Ontario tributaries.

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