

# Using a Landscape Approach to Identify the Distribution and Density Patterns of Salmonids in Lake Ontario Tributaries

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*Abstract.*—Effective management of salmonid populations in the Great Lakes basin requires understanding how their distribution and density vary spatially. We used a hierarchical approach to evaluate the predictive capabilities of landscape conditions, local habitat features, and potential effects from coinhabiting salmonids on the distribution and densities of rainbow trout *Oncorhynchus mykiss*, brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, and coho salmon *O. kisutch* within the majority of the Canadian tributaries of Lake Ontario. We collected fish assemblage, instream habitat, and water temperature data from 416 wadeable stream sites. Landscape characteristics were obtained for each site's catchment and summarized into six key attributes (drainage area, base flow index, percent impervious cover (PIC), reach slope, elevation, and location with respect to permanent fish barriers). Classification trees indicated that PIC in a catchment was a critical predictor of salmonid distribution, in that beyond a threshold of 6.6–9 PIC, all salmonids were predicted to be absent. Base flow index and barriers were also important predictors of the distribution of salmonids. Models generally provided higher classification success at predicting absence (86–98%) than predicting presence (63–87%). Landscape features were the best predictors of densities of rainbow and brook trout (adjusted  $r^2 = 0.49$  and  $0.30$  respectively), although the local habitat features were almost as effective for predicting brook trout ( $r^2 = 0.23$ ). Local habitat features (proportion of riffles and pools, substrate, cover, and stream temperature), and presence of other salmonids produced the best predictive model for brown trout. Coho salmon was only locally distributed in the basin, and the derived model was driven by spatial characteristics rather than ecological processes. Our models estimate 653,000 juvenile rainbow trout and 231,000 brook trout (all age-classes) in our study streams. Finally, we estimate that current brook trout distribution in our study area is only 21% of its historic range.

## INTRODUCTION

Traditionally, efforts to relate fish densities to habitat involved measures of local habitat features that were intended to capture both local morphology and the influence of larger scale fea-

tures and biotic interactions (Binns and Eiserman 1979; Bowlby and Roff 1986; Stoneman and Jones 2000). A hierarchical perspective of stream systems, whereby properties at the site level are constrained by processes occurring in the catchment, provides a useful analytical framework (Vannote et al. 1980; Frissell et al. 1986; Tonn 1990; Imhof et al. 1996). For

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example, substrate composition, water temperature, and some aspects of channel structure have been shown to vary predictably with topography, geology, and land use (Rabeni 1992; Sowa and Rabeni 1995; Richards et al. 1996; Regetz 2003). As a result, the landscape scale has been suggested as the appropriate scale for managing Great Lakes fisheries (Lewis et al. 1996). We believe that landscape conditions constrain the fish assemblage and range of densities expected at a site, while instream habitat and biotic interactions influence the realized species and densities. Recent advances in geographic information systems (GIS) have led to a rapid increase in our capabilities to quantify the importance of various landscape features in influencing aquatic assemblages (Wiley et al. 1997). A number of studies have shown the importance of landscape features in affecting assemblage composition and species distribution, in portions of the Great Lakes basin (Steedman 1988; Richards et al. 1996; Wang et al. 1997, 2000, 2001; Zorn et al. 2002). More recently, studies have included a number of composite metrics intended to quantify the overall disturbance from land use on the landscape. For example, Thompson and Lee (2000) used road density, Van Sickle et al. (2004) used total urban and agricultural land use/land cover within the riparian zone, and Stanfield and Kilgour (2006, this volume) among others used percent impervious cover (PIC).

In addition, instream habitat and biotic interactions structure fish assemblages (Bowlby and Roff 1986; Stoneman and Jones 2000; Stanfield and Jones 2003). Mullett et al. (2003) demonstrated that using a combination of landscape features (i.e., drainage area and geographic location) and biotic conditions provided a good predictor of sea lamprey *Petromyzon marinus* abundances across the Great Lakes basin. Therefore, analyzing both landscape and site level features provides a more holistic approach to assessing salmonid populations. Some studies have partitioned variation across scales (e.g., Wang et al. 2001); however, few, if any, have attempted to partition the variance associated with

landscape and local features related to Great Lakes fish populations. This information may help guide managers in taking actions needed to improve fish production.

We sought to first determine the relationships between landscape variables and the distribution and density of stream resident salmonids (i.e., rainbow trout *Oncorhynchus mykiss*, brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, and coho salmon *O. kisutch*). We then explored how much additional variation was explained by incorporating site level features into the landscape-density model. We combined the distribution and density models to identify the spatial distribution of salmonid populations. Finally, we used the outputs of landscape models to develop population estimates of salmonids in the study area and discuss management implications of these findings.

## METHODS

### Study Area

The Oak Ridges Moraine and the Niagara Escarpment provide source waters to the majority of the coldwater streams draining into the Canadian portion of Lake Ontario (Figure 1). These two physiographic features provide an abundance of groundwater discharge, ensuring that headwater segments are cold and that water temperatures gradually increase towards the mouth. The basin's landscape is dominated by agriculture in the east (e.g., row crop) and southwest (orchards), with an extensive band of urban area (GTA) in the west and central portion of the study area. Most forested areas are located on top of the moraine and escarpment. The tributaries draining the moraine consistently have coarse sands and gravels in the headwaters, while those draining the escarpment have fractured sedimentary rock with a shallow overburden of finer materials. Lower segments of all tributaries pass through finer grained glacio-lacustrine material (Chapman and Putnam 1984). This area is managed for six salmonid species: native brook trout

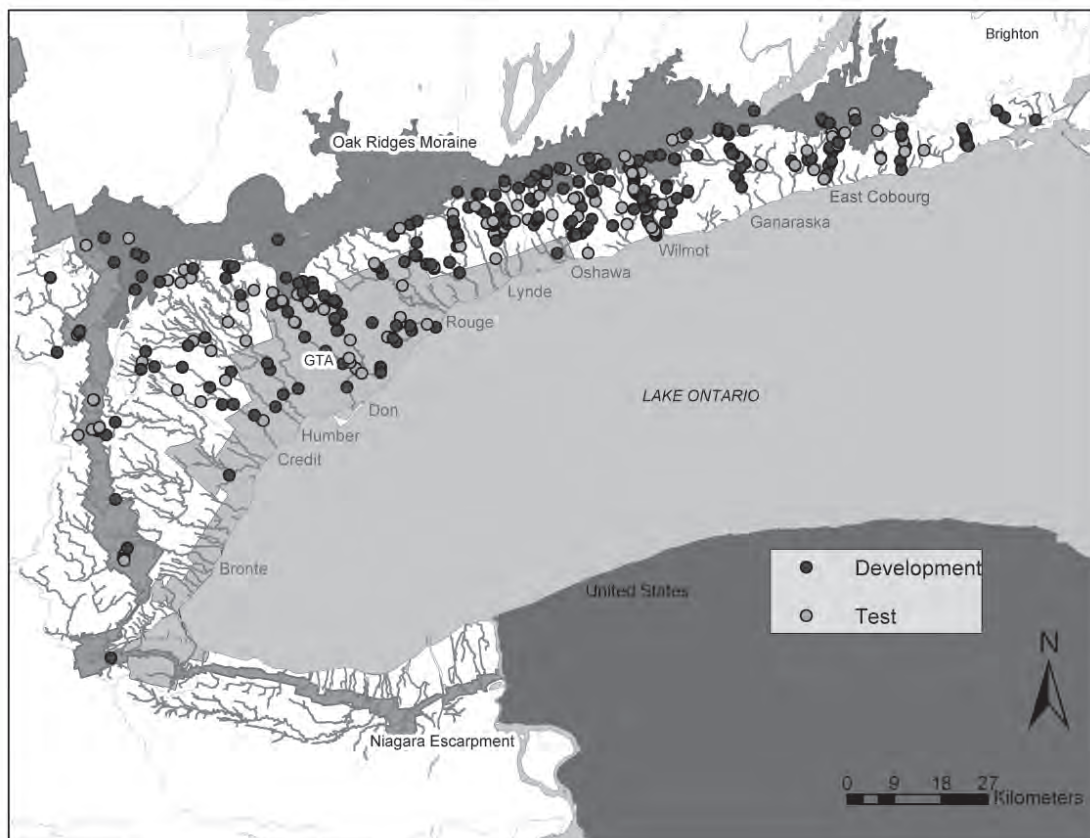


Figure 1. Major landform features and location of development and test sites used for development of the rainbow trout distribution models in this study.

and Atlantic salmon *Salmo salar* and naturalized nonnative rainbow trout, Chinook salmon *O. tshawytscha*, coho salmon, and brown trout.

Field data were collected by a variety of agencies and guidance on study design and site selection were provided by Stanfield et al. (1997). Each agency defined its own study area based on project objectives and whether stratification was necessary. Study areas were generally a subcatchment or landscape (i.e., the Oak Ridge Moraine study area), and most studies were stratified by stream size. Sampling intensity within each stratum was designed to meet the desired precision of each study. Sites were then randomly selected within each stratum. Sites began and ended at a cross-over (i.e., where the thalweg is in the middle of the channel) and were at least 40 m long.

### Fish Assemblage Data

Fishes were collected at 416 sites on 61 streams along the north shore of Lake Ontario (Figure 2). Sites were sampled between 1995 and 2002, with methods described in Stanfield et al. (1997). Only sites where effort exceeded five electrofishing seconds per square meter and sampling date was after June 21 (the earliest capture of a young-of-year rainbow trout in the region) were used in this analysis. Fish assemblage data were collected using single-pass electrofishing, which provides acceptable estimates of salmonid abundance in Lake Ontario streams (Jones and Stockwell 1995). Salmonids were identified, enumerated, weighed, and then released.

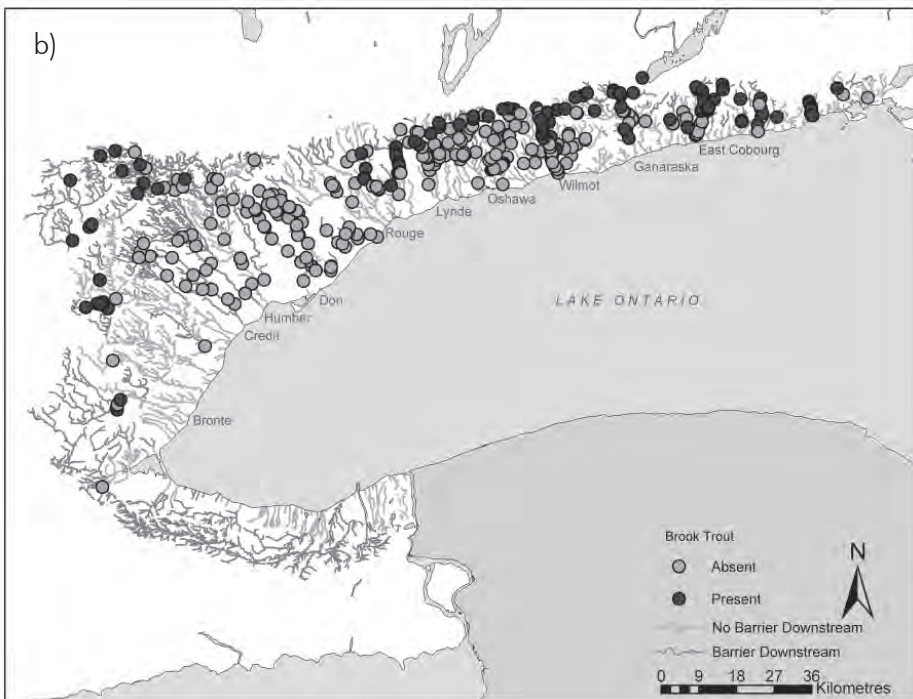
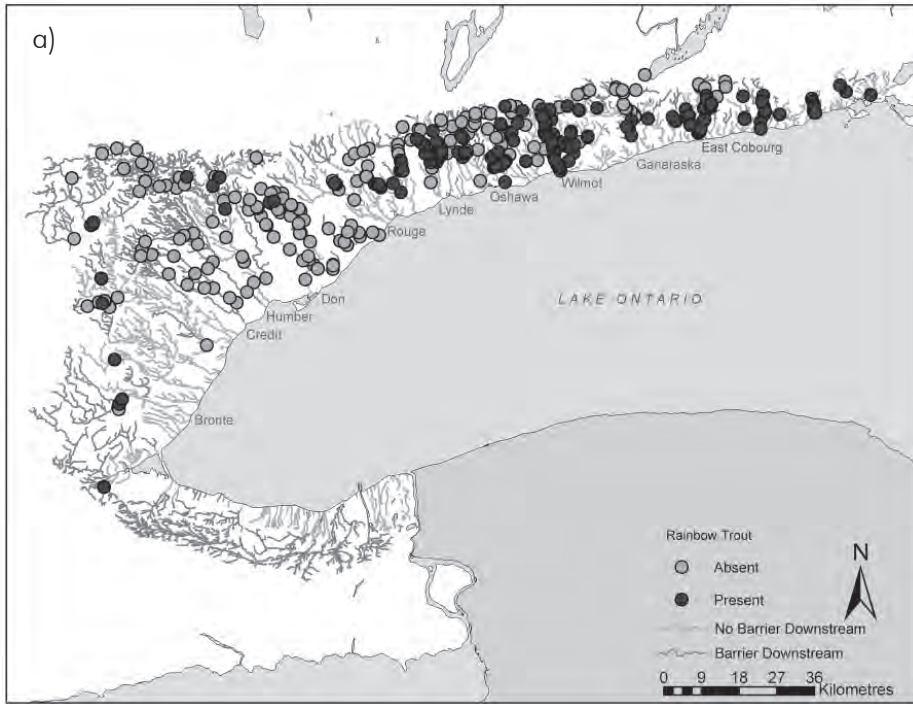


Figure 2. Distribution of rainbow trout (a), brook trout (b), brown trout (c) and coho salmon (d) at study sites where streams have been classified as being accessible (no barrier downstream) or inaccessible (barrier downstream) to rainbow trout from Lake Ontario.

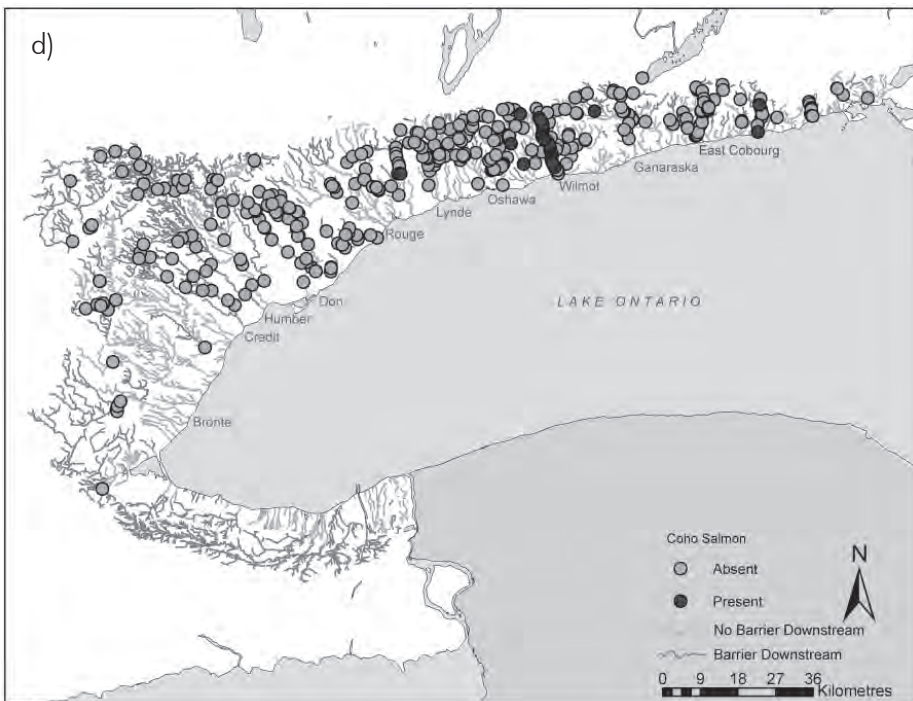
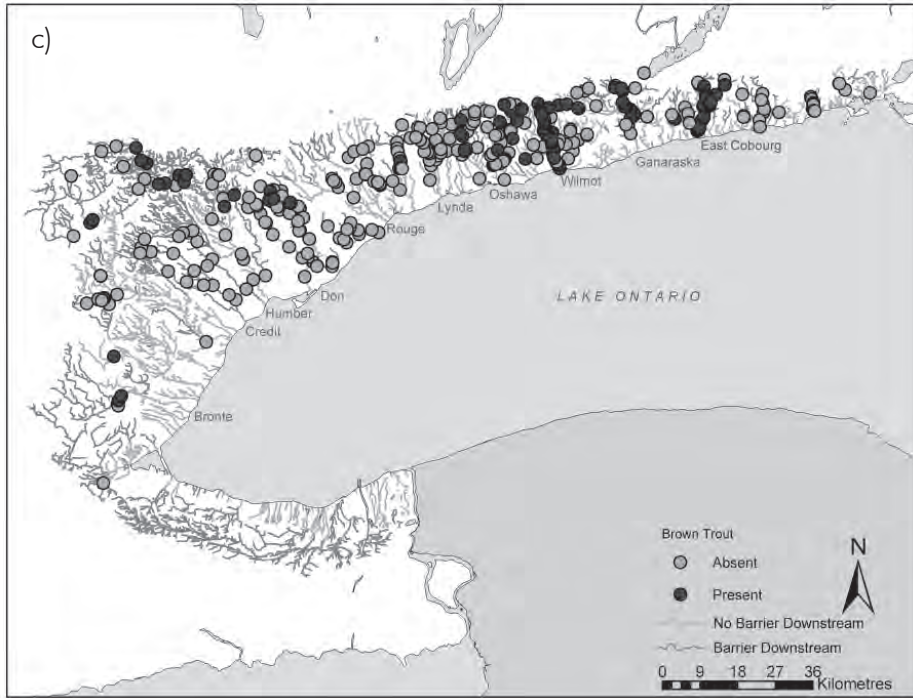


Figure 2 (continued)

## Landscape Data

For each site, we delineated catchment boundaries using a flow accumulation model based on a 1:10,000 digital elevation model (DEM) with 25-m resolution. We used GIS to attribute each site's catchment area, stream length, land use/land cover, quaternary geology, elevation, and stream slope. Additionally we developed a GIS layer locating the first impassable barrier to salmonids upstream from the lake for all streams in the basin. Each site was classified as to whether it was accessible to rainbow trout or coho salmon. To capture the full contrast in land use/land cover and quaternary geology, data were converted to composite measures of PIC and a base flow index (BFI). PIC was calculated by summing the ranked percent of each catchment occupied by each land use/land cover, following the rankings of Stanfield and Kilgour (2006), (i.e., forest [0.01], pasture [0.05], agriculture [0.1], urban [0.2]). Therefore, PIC varied between 1 (completely forested) and 20 (100% urban). Following the methods of Piggott et al. (2002), we calculated BFI by summing the ranked proportion of each catchment covered by quaternary geology types (Ontario Geological Survey 1997), where the ranking reflected a measure of its contribution to base flow. Rankings for our study area varied from 12 for silt-clay till to 77 for gravel-sand outwash material. These variables or their correlates related to the main landscape factors limiting fish distributions and assemblages in northern temperate streams (Wang et al. 2001; Zorn et al. 2002; Stanfield and Kilgour 2006). Drainage area was log transformed to approximate normalized data. The six variables were all weakly correlated ( $r < 0.46$ ) with one another and variance inflation factors for each were relatively low (1.2–1.6), (Neter et al. 1996; Graham 2003) indicating low multicollinearity among variables.

To aid in landscape modeling, streams were divided into segments based on changes in hydrography (i.e., confluence of tributaries with stream order less than three, or boundaries with

lakes and wetlands), access to Lake Ontario (i.e., barriers), and hydraulic conductivity (soil porosity), using an Arc GIS application. Landscape attributes, comparable to those collected for each site, were obtained for each segment's catchment. Stream segments of Strahler order less than three were combined.

## Site-Level Data

Physical habitat features and stream temperature were collected at 243 of the 416 sites with fish data. Variables included water temperature, substrate size, microhabitat type, riparian woodland width, percent rock cover, and percent wood cover (Table 1). Water temperature was standardized by determining the predicted temperature at an air temperature of 30°C for each site. Observed air and stream temperature for each site were used to select the most appropriate thermal class and algorithm as described by Stoneman and Jones (1996). The deviation from predicted temperature was added to the predicted temperature at 30°C to obtain the standardized temperature.

Microhabitat, cover, and substrate data were collected using a point transect sampling design (Stanfield and Jones 1998). Transects were equally spaced and oriented at right angles to current with typically six equally spaced points on each transect. Number of points per transect were reduced and number of transects increased on smaller streams to provide from 40 to 60 point observations per site. Depth and velocity data were used to classify the proportion of a site occupied by four velocity categories representing pools, glides, and slow and fast riffles. These data were summarized as a continuous variable corresponding to a gradient from pools to fast riffles, as determined by site scores along the first axis of a correspondence analysis (CA). This axis represented 71.7% of the variation in the microhabitat data. Rock and wood cover were measured as the proportion of observations, which contained a cover type with a median axis greater than 10 cm falling within a 15-cm radius of the observation point.

Table 1. Instream habitat and competition variables used in the density models.

Variable	Definition
Water temperature	Taken at 1545 and 1645 hours during a heat wave and standardized to 30°C air temperature using algorithms for reference cold-, cool-, and warmwater stream types. Log transformed.
Riparian	Summation of width of natural vegetation from both banks at four categories bounded by 1, 10, 30, and 100 m determined from a point transect survey.
Microhabitat	Summary statistic of the first CA axis based on percent of each of 4 microhabitat types (i.e., <3, 4–7, 8–17, >17 mm hydraulic head) where hydraulic head represents the height of water on a ruler held in the water at each point on transects.
Rock & Wood	Percentage of point observations where substrate particles or pieces of wood with median axis greater than 10 cm occur within 15 cm of the observation point.
D50max	Fiftieth percentile size of the distribution of maximum particles sampled from within a 30-cm ring. Sampling followed a point transect survey. Log transformed.
Number of salmonid species	Number of salmonid taxa at site.
Density of other salmonids	Density of salmonid taxa other than the target species for the analysis.

Substrate was determined from measured particles at each observation point. The two biotic variables used in our analyses were the total number of salmonid species at a site and the total density of salmonids other than the target species at a site ( $\log_{10}$  transformed). These were included because other studies in the region have shown effects from competition among the different species of juvenile salmonids (Stoneman and Jones 2000; Stanfield and Jones 2003).

### Distribution Analyses

Catches of rainbow trout, brown trout, brook trout, and coho salmon were converted to presence/absence (distributional) data. In cases where sites had been sampled on multiple visits (in different years or seasons), the median value of the distributional data were rounded to the nearest integer (0 or 1). Species presence–absence models were created using classification and regression trees (CART) (Breiman et al. 1984), as it provided a reliable methodology for predicting the distribution of each species on the landscape. Classification trees assume no specific statistical distribution, do not assume linear relationships between predictor and response vari-

ables, can accommodate large complex datasets, incorporate a variety of response types, and are not influenced by severe outliers (De'ath and Fabricius 2000; Vayssieres et al. 2000). As such, CART models have become prevalent in the ecological literature, particularly for predicting species distributions on the landscape (Emmons et al. 1999; Magnuson et al. 1998; Rathert et al. 1999; Rejwan et al. 1999; Stoneman and Jones 2000; Stanfield and Jones 2003; Herlihy et al. 2006, this volume).

To evaluate model performance we split the data sets of each species into two groups, randomly assigning two-thirds of the sites for model development and one-third for testing. Data sets were first stratified based upon quaternary watersheds, such that there were equal proportions of sites with and without a species for each subwatershed, similar to Manel et al. (1999). Models were evaluated for the overall correct classification rate, model “sensitivity” (correct classification of presences), and model “specificity” (correct classification of absences) (Fielding and Bell 1997). In addition, Cohen's Kappa statistic  $K$  (Titus et al. 1984) was used to estimate how well the model performed compared to the expectations based simply on chance.

## Density Analysis

Catches of rainbow trout, brown trout, brook trout, and coho salmon were converted to densities (# fish/100 m<sup>2</sup>) and then  $\log_{10} + 1$  transformed. In cases where sites had been sampled on multiple visits (in different years or seasons), the median density was used. General linear models (GLM) (StatSoft, Inc. 1995) were used to develop relationships between landscape attributes and densities of the four species. This technique ensured that predictions for segments would be continuous, rather than categorical, and would therefore provide better contrast in suitability criteria between segments. To evaluate how much additional variance was explained by site-level habitat features and the presence of other salmonid species, we reanalyzed the landscape models on the sites that had landscape features, instream habitat, and biotic features. The residuals from this analysis represented any variation that could not be explained by the six landscape attributes. Thus, we used the residuals as the response variable and regressed these data against two sets of site variables: (1) six physical habitat metrics, and (2) two biotic metrics, representing effects from cooccurring salmonids at a site. The resulting adjusted  $r^2$  values provide a measure of the amount of independent variation that these variables explain. We then took the residuals from each of these analyses and regressed these against the opposite set of predictors (i.e., the residuals from the physical habitat were regressed against the two biotic variables and vice versa) to evaluate how much of the variance was explained by these variables alone. It was hypothesized that by the time the second set of residuals were used, there would be very little remaining variation to explain.

## Application of Models

We used models to predict the spatial distribution and densities of salmonids in sampled and unsampled segments across the basin. Predictions were confined to segments with drainage

areas less than 328 km<sup>2</sup>. This ensured that predictions were made only on segments where landscape attributes were within the same range as those from which the models were developed.

We used model results for species whose densities were predicted by landscape features, to develop coarse population estimates for our study area. We applied the CART models to determine which sites were predicted to have each species absent. The density models were applied to each remaining segment to derive a predicted log density. Results were used to classify each segment into four additional categories based on the quartiles of the predicted log densities (i.e., low, medium, high, and very high). Estimated stream width was determined for each segment using the model developed by Stanfield and Kilgour (2006), and each segment was then assigned a width category based on the quartiles of the distributions. Observed mean density and width were calculated for all five categories for which field data were available and were applied to each segment to determine population estimates (e.g., segment population = observed mean category width\*observed mean category density\*segment length).

## RESULTS

The 416 sites with fisheries data collectively covered most of the main salmonid waters on the Canadian side of Lake Ontario (Figure 1). Where salmonids occurred their densities varied considerably, regardless of whether they were isolated or in the presence of other salmonid species (Table 2). Brook trout tended to be more abundant in the absence of other salmonids although the four highest density sites were at locations where either brown trout (10 g/100 m<sup>2</sup>) or rainbow trout (11–43 g/100 m<sup>2</sup>) were also present, but not both. Brown trout and rainbow trout tended to be more abundant in the presence of other salmonids; however, interpretation of these results was confounded, as a much greater proportion of the sites had multiple species, compared with only a few having one species of



Table 2. Densities (#/100 m<sup>2</sup>) of four salmonid species when occurring by themselves and when cooccurring with other salmonid species.

	No other salmonids at site				Other salmonids at site			
	N	Min	Max	Median	N	Min	Max	Median
Rainbow trout	61	0.2	86.4	12.8	143	0.1	142.3	14.6
Brown trout	10	0.2	34.9	0.8	117	0.1	23.7	3.5
Brook trout	30	0.2	32.9	7.8	95	0.1	71.0	2.5
Coho salmon	0	–	–	–	34	0.1	16.1	1.2

salmonid present. Coho salmon densities were always low in our study area.

Rainbow trout was present at 49% of the sites and was widely distributed across the study area (Figure 2). Brook and brown trout were less common (30% of sites) and were generally captured in headwater areas. Coho salmon was caught at only 8% of sites and was restricted to Wilmot Creek and neighboring streams. All four salmonids were absent from 32% of the sites, most of which were located in the GTA.

Our data set included a wide range of catchment size, geology (BFI), slope, and land-use/land-cover conditions (Table 3). PIC ranged from 20 (100% urbanized catchments) to 1 (fully forested catchments), and 37% of sites had bar-

riers downstream, thus limiting access by migratory salmonids. While some confounding of the data exists (i.e., most forested catchments were in higher slope and higher porosity areas), there was sufficient contrast (Table 3), to test our hypotheses. There was also considerable contrast in instream habitat features in our data set (Table 3), such as proportions of pool versus riffle habitat (i.e., positive versus negative CA scores), substrate size, amount of both wood and rock cover, and water temperature.

### Distribution Models

The presence–absence models for the four species produced more than 80% correct classification rates for the test data sets (Table 4), and the rainbow trout model had the highest presence ratings (87%). The brook and brown trout models were more effective at predicting absence of these taxa (87% and 91%, respectively) than presence (68% and 63%). All four models had *K*-values greater than 0.55 (Table 4), indicating that model performance was moderately to substantially greater than that expected by chance (Landis and Koch 1977). Although the coho salmon model displayed the highest overall classification and absence, the unequal proportions of presence and absence sites may produce spurious results (Forbes 1995) and should be interpreted with caution.

The presence of barriers downstream and PIC were the two most influential variables in the species distribution models (Figure 3). Base flow index (BFI) was also highly influential as it was included in all but the rainbow trout model and,

Table 3. Minimum, maximum and median values of the six landscape features characterizing the upstream catchments and the six instream habitat variables used in this study ( $n = 416$  sites). Median density of other species is not presented as it varied among the four species. Na = not applicable.

	Min	Max	Median
<i>Landscape attributes</i>			
Drainage area (km <sup>2</sup> )	0.1	328	22
Percent impervious cover (PIC)	1.1	20	7
Reach slope (%)	0	10	1
Elevation (masl)	75	403	156
Base flow index (BFI)	14	77	46
Dams downstream (binary)	0	1	0
<i>Instream habitat</i>			
d50max (mm)	0.01	340.0	80.0
Wood (%)	0	35	2
Rock (%)	0	100	38
Forested riparian width (m)	0	200	60
Microhabitat (CA1)	-1.24	0.85	-0.091
Water temperature (°C)	10.3	36.3	20.9

Table 4. Measures of classification success based on the classification tree models for each species. Classification success based on independent data set and expressed as a percentage of the total. Cohen’s Kappa expressed as a percent.

	Coho salmon	Rainbow trout	Brown trout	Brook trout
Number of sites with species	34	204	127	125
Overall correct classification rate	97.1	86.2	82.4	81.6
Specificity (correct absences)	98.4	85.9	90.6	87.4
Sensitivity (correct presences)	82.0	87.0	63.0	68.0
Cohen’s Kappa (K)	87.9	73.2	55.0	55.5

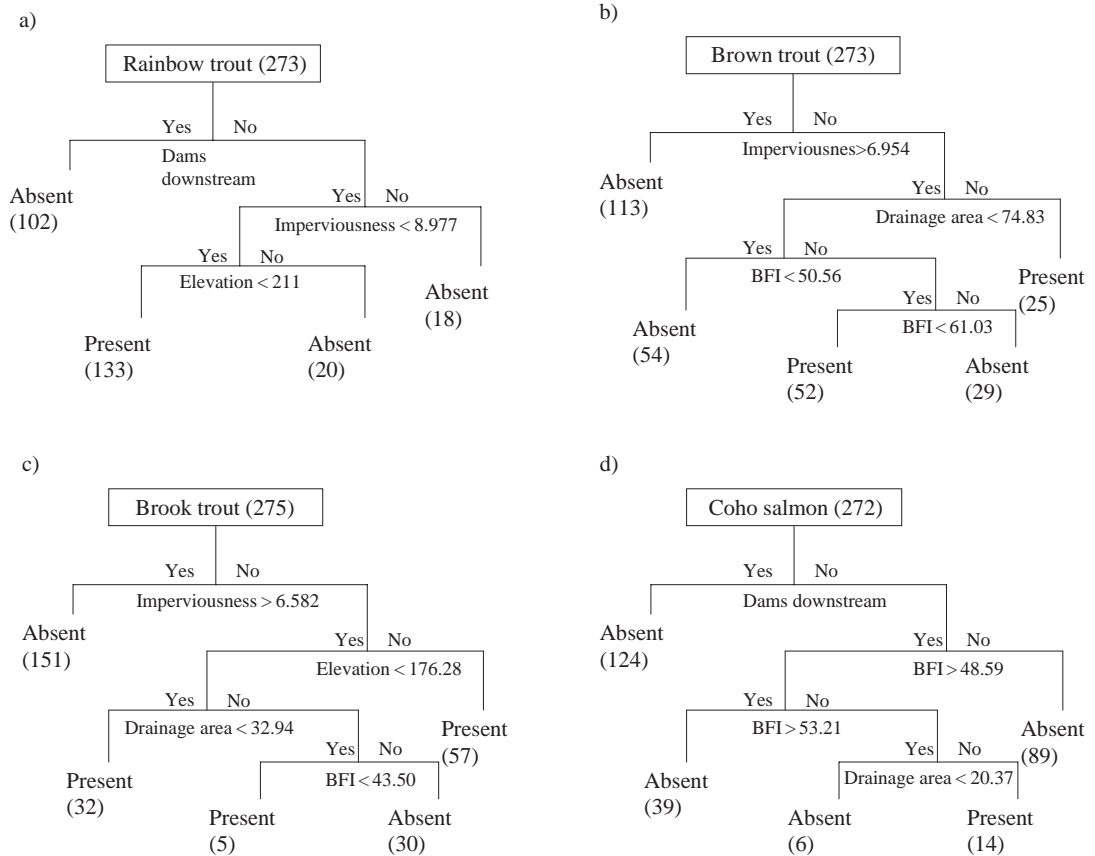


Figure 3. Classification trees for rainbow trout (a), brown trout (b), brook trout (c) and coho salmon (d). Numbers at the ends of each branch are the number of sites with the predicted response based on landscape conditions. Criteria for each split are given at each node.

in some cases (i.e., brown trout and coho salmon), was used as the split criteria twice in the model. Rainbow trout was predicted to be present at sites with no barriers downstream, in catchments with PIC less than 9, and in the lower

segments of streams (i.e., lower elevations). Brown trout were predicted in catchments with PIC less than 7 and moderate catchment size (i.e., <74.8 km<sup>2</sup>), or in smaller well-drained catchments. Brook trout was predicted in smaller

catchments, provided PIC did not exceed 6.6. Not surprisingly, coho salmon was predicted for a very restricted group of streams lacking barriers, BFI values between 49 and 53, and drainage area greater than 20 km<sup>2</sup>.

### Density Models

Correlation between the landscape predictors and densities of rainbow trout provided the strongest model ( $r^2 = 0.491$ ; Table 5), with dams, PIC, and elevation having the greatest influence on the model (Table 6). The biotic variables alone were found to explain 35.8% of the variation in rainbow trout density (Table 5) and an additional 12.9% of the residual variation left over from the landscape models. Whether modeled individually (adjusted  $r^2 = 0.156$ ) or in conjunction with landscape features, the instream habitat features did not relate well to rainbow trout density, explaining only an additional 2.8% of the residual variance.

Landscape models were able to explain 30% of the variation in brook trout densities (Table 5). PIC and the size of the drainage area were the dominant variables in the model (Table 6). Instream habitat variables explained a smaller amount of the variance in brook trout density (adjusted  $r^2 = 0.23$ ), and water temperature was the most influential variable in this model. Biotic models were very poor predictors of brook trout density (adjusted  $r^2 = 0.074$ ). However, there was similar explanatory power of brook trout density between the landscape model (adjusted  $r^2 = 0.37$ ) and the combination of site features and cooccurring salmonids model

(adjusted  $r^2 = 0.38$ ). All residual analyses on the brook trout models produced adjusted  $r^2$  of less than 0.04, indicating that the addition of either cooccurring salmonids or site habitat features to landscape models did not substantially increase their predictive performance.

The landscape features were poor predictors of brown trout density (adjusted  $r^2 = 0.115$ ) and BFI and PIC were the only variables contained in the model (Table 6). The instream habitat models explained more variance (adjusted  $r^2 = 0.219$ ), however, the biotic models were found to be the best predictors (adjusted  $r^2 = 0.413$ ). Instream habitat could increase landscape models by 11.9%, while biotic variables were shown to improve the landscape model predictive performance by 35.5%. Thus, landscape models may not be the best approach to predict brown trout densities in Lake Ontario tributaries.

Coho salmon models were quite poor when using landscape (adjusted  $r^2 = 0.062$ ), instream habitat (adjusted  $r^2 = 0.126$ ), and biotic (adjusted  $r^2 = 0.192$ ) variables. Residual models were able to explain an additional 11.0–18.7% of the variation but were not enough to justify inclusion in a combined model. Evidently, factors other than the landscape variables included in this study are influencing coho salmon density in the study area.

### Application of Models

Landscape models provided good predictive power (adjusted  $r^2 > 0.3$ ) for rainbow trout and brook trout; thus, subsequent analyses focused

Table 5. Results of the density models for the four species. Numbers are adjusted  $r^2$  values. Residuals were used as the response variable and regressed against the specified suite of variables in the last two models. Landscape indicates data derived from GIS. Site represents data collected in the field.

	Coho salmon	Rainbow trout	Brown trout	Brook trout
Landscape only ( $n = 416$ )	0.06	0.49	0.12	0.30
Landscape reduced ( $n = 243$ )	0.04	0.48	0.07	0.37
Site-level only (6 variables)	0.13	0.16	0.22	0.23
Cooccurring salmonids only (2 variables)	0.19	0.36	0.41	0.07
Site and Competition (8 variables)	0.26	0.58	0.44	0.38
Landscape residuals on site-level	0.11	0.03	0.12	0.03
Landscape residuals on cooccurring salmonids	0.19	0.13	0.36	0.02

Table 6. Model results for the four species density models based on the six landscape features, the six instream habitat features, and the two biotic features. The *B* coefficients represent the coefficients used in the predictive model, whereas the beta coefficients provide a measure of the relative contribution of each variable to the model. Bolded values are significant at  $p < 0.05$ .

		Coho beta	Coho <i>B</i>	Rainbow beta	Rainbow <i>B</i>	Brown beta	Brown <i>B</i>	Brook beta	Brook <i>B</i>
<i>Landscape models</i>									
<i>n</i> = 416	Constant		0.0098		<b>1.7531</b>		-0.0508		0.1245
	Percent impervious cover	-0.0731	-0.0026	<b>-0.3570</b>	<b>-0.0585</b>	<b>-0.2036</b>	<b>-0.0185</b>	<b>-0.2579</b>	<b>-0.0263</b>
	Slope	0.0124	0.0015	<b>0.1106</b>	<b>0.0590</b>	0.0173	0.0051	<b>0.1066</b>	<b>0.0354</b>
	Elevation	0.0882	0.0002	<b>-0.2968</b>	<b>-0.0032</b>	0.1005	0.0006	<b>0.1851</b>	<b>0.0012</b>
	Base flow index	0.0393	0.0005	<b>-0.1232</b>	<b>-0.0070</b>	<b>0.1585</b>	<b>0.0050</b>	<b>0.1547</b>	<b>0.0055</b>
	Drainage area <sup>a</sup>	0.0618	0.0159	<b>0.1573</b>	<b>0.1831</b>	0.0813	0.0525	<b>-0.2651</b>	<b>-0.1920</b>
	dams downstream	<b>-0.2651</b>	<b>-0.0753</b>	<b>-0.3472</b>	<b>-0.4579</b>	-0.0708	-0.0518	0.0858	0.0704
	df	6,404		6,404		6,404		6,404	
	adjusted $r^2$	0.0620		0.4910		0.1150		0.3010	
	<i>p</i> -value	0.0000		<0.00001		<0.00001		<0.00001	
<i>Site habitat features</i>									
<i>n</i> = 243	Constant		0.1251		<b>1.3869</b>		<b>1.2206</b>		<b>2.2199</b>
	Riparian	-0.1176	-0.0002	<b>-0.1667</b>	<b>-0.0016</b>	-0.0329	-0.0002	<b>0.1768</b>	<b>0.0011</b>
	Microhabitat	-0.1219	-0.0191	<b>-0.3195</b>	<b>-0.3345</b>	<b>-0.2807</b>	<b>-0.1581</b>	-0.0153	-0.0109
	Rock	<b>-0.2506</b>	<b>-0.0780</b>	-0.1110	-0.2304	<b>-0.2039</b>	<b>-0.2275</b>	0.0519	0.0731
	Wood	<b>0.2557</b>	<b>0.3325</b>	-0.0899	-0.7801	0.1047	0.4884	<b>0.1364</b>	<b>0.8032</b>
	D50max <sup>a</sup>	0.1619	0.0220	0.1360	0.1233	<b>0.2074</b>	<b>0.1012</b>	-0.0046	-0.0029
	Stream temperature <sup>a</sup>	-0.0893	-0.0878	-0.0983	-0.6447	<b>-0.2464</b>	<b>-0.8694</b>	<b>-0.3659</b>	<b>-1.6290</b>
	df	6,233		6,233		6,233		6,233	
	adjusted $r^2$	0.1660		0.1560		0.2190		0.2300	
	<i>p</i> -value	<0.00001		<0.00001		<0.00001		<0.00001	
<i>Biotic features</i>									
<i>n</i> = 243	Constant		-0.0149		<b>0.1879</b>		<b>0.0166</b>		<b>0.1884</b>
	Number of salmonid species	<b>0.6544</b>	<b>0.0550</b>	<b>0.9281</b>	<b>0.4613</b>	<b>0.9273</b>	<b>0.2479</b>	<b>0.5388</b>	<b>0.1805</b>
	Density of other salmonids	<b>-0.2950</b>	<b>-0.0498</b>	<b>-0.5841</b>	<b>-0.6847</b>	<b>-0.4708</b>	<b>-0.2530</b>	<b>-0.4626</b>	<b>-0.3046</b>
	df	2,240		2,240		2,240		2,240	
	$r^2$	0.2200		0.4410		0.4680		0.1240	
	<i>p</i> -value	<0.00001		<0.00001		<0.00001		<0.00001	

<sup>a</sup>Variable was  $\log_{10}$  transformed.

on these species only. The predicted distributions of rainbow trout and brook trout demonstrate little overlap in species presence (Figure 4). The majority of the sampling has been conducted in stream segments classified as having low to medium densities of rainbow trout and brook trout (Table 7). Rainbow trout were predicted to be absent from a large portion of the study area (~80%), particularly in the western tributaries, where wadeable streams were, for the most part,

predicted to be unoccupied by this species. The central part of the basin contains the highest predicted densities of rainbow trout in the Lake Ontario basin. Analyses also identified several potentially productive segments where sampling has not occurred. Our models suggest that there are approximately 653,000 juvenile rainbow trout in the Ontario portion of the Lake Ontario basin. The majority of rainbow trout (39%) are produced in the eastern tributaries. This estimate

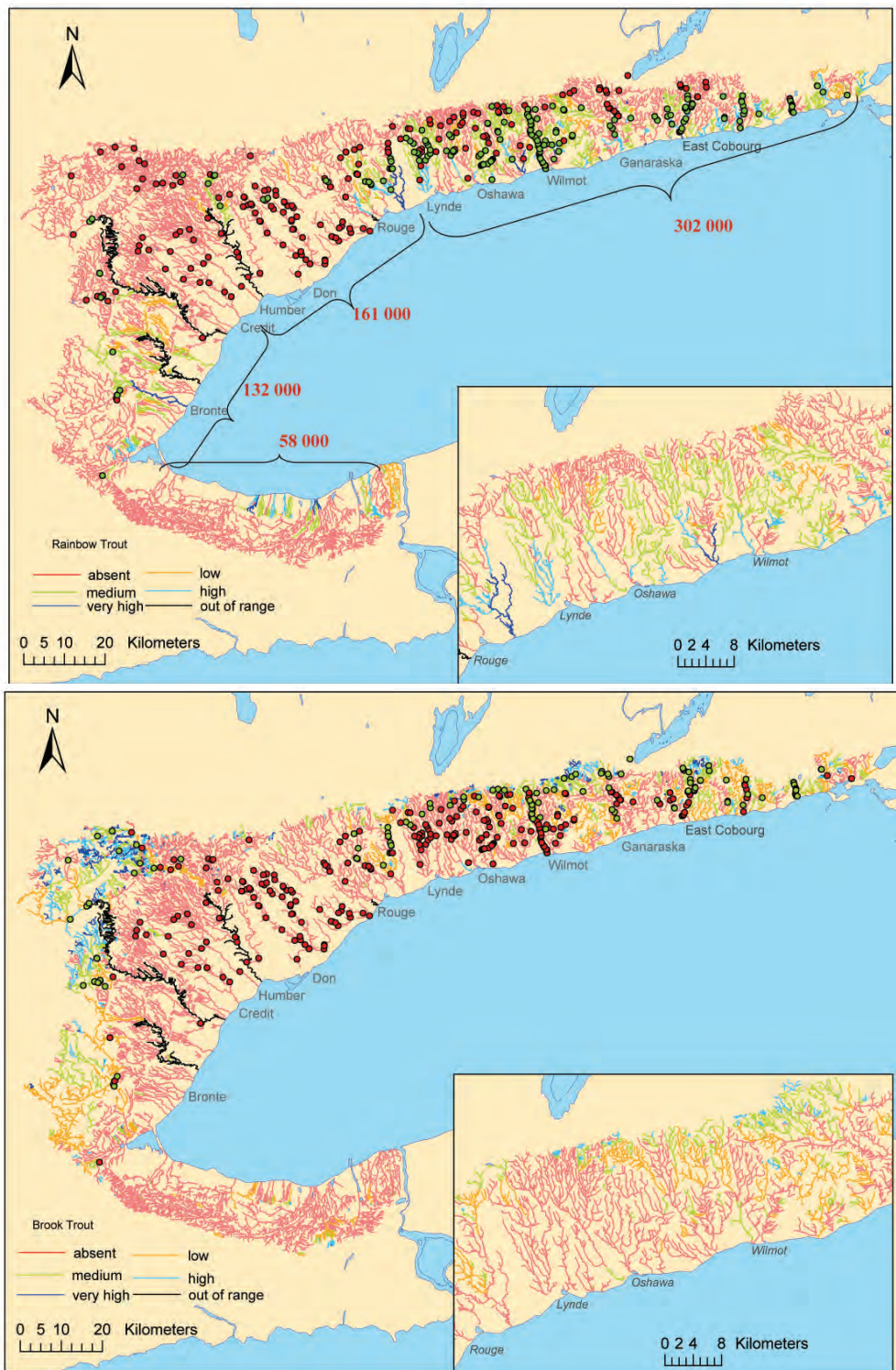


Figure 4. Predicted distribution and densities of rainbow trout and brook trout in stream segments of the Canadian waters of Lake Ontario and study sites classified by the presence or absence of this species. NA = not applicable because drainage areas were greater than 328.1 km<sup>2</sup> and, thus, outside the model range.

Table 7. Model thresholds for classifying stream segments and observed densities and standard deviations (in brackets) of rainbow trout and brook trout for Canadian tributaries to Lake Ontario.

Density categories	Model thresholds for rainbow trout	Densities of rainbow trout	Number of observations	Model Thresholds for brook trout	Densities of brook trout	Number of observations
Absent	0	0.12 (0.36)	65	0	0.04 (0.36)	66
Low	<4.11	1.97 (7.33)	161	<1.70	1.16 (4.59)	281
Medium	<6.52	13.15 (16.99)	63	<3.50	8.53 (13.22)	53
High	<9.44	20.05 (23.31)	68	<6.26	9.63 (9.89)	13
Very high	>9.44	23.58 (17.30)	59	>6.26	18.86 (16.98)	3

is conservative since it does not include segments from larger catchments (>328 km<sup>2</sup>) or for any waters in the eastern tip of the basin.

Brook trout are predicted to be present and abundant in the upstream segments of northwest (Bronte, Credit, and Humber rivers) and eastern (Cobourg and Shelter Valley) tributaries, and the overall population in the study area is estimated to be approximately 231,000 individuals (Figure 4).

## DISCUSSION

The PIC, access from Lake Ontario, BFI, and drainage area were important predictors of the distribution and density of salmonids in our study area. In addition, salmonid species differed in their response to instream habitat and presence of other salmonids. Instream habitat conditions and densities of other salmonids added little explanatory power to landscape models for rainbow trout and brook trout, but were important for brown trout. The limited distribution of coho salmon in the basin diminished our ability to explore the role of landscape features for it. We have also demonstrated how the model results can be used to predict distribution and density in unsampled segments across the basin. We found that brook trout distribution is currently restricted to smaller catchments and areas with low levels of impervious cover (i.e., high forest cover). Finally, there is considerable natural reproduction of rainbow trout occurring in

streams across the basin. However, disproportionate numbers of these fish are produced from a small number of stream segments. These analyses may guide future fisheries management within and across tributaries of Lake Ontario.

### Landscape Relationships

The primary landscape relationships we found were consistent with those of Zorn et al. (2002) and Wang et al. (2003), although the explanatory power and the relative importance of the individual attributes differed. For example, in our study, salmonid distribution and densities were more influenced by land use/land cover than catchment size, BFI, or slope. We found a clear signal indicating that development (PIC) in a catchment is a strong modifier of the salmonid distribution and densities in a catchment. Others have demonstrated that development has a modifying effect on the distribution of salmonids (Steedman 1988; Wang et al. 2003) and Van Sickle et al. (2004) demonstrated that the amount of agriculture in the riparian zone effects cutthroat trout *O. clarkii* densities, but to our knowledge, this is the first paper to demonstrate effects of catchment level development on salmonid densities. Zorn (2003) found that low flow yield was a more important predictor of fish abundances in lower Michigan streams than land use/land cover. Zorn et al. (2004) suggest that reasons for these results are related to their dataset having much larger gradients in river temperature and hydrologic conditions than in

land use/land cover. Few sites in their study area were from highly urbanized catchments.

Our measures of BFI and catchment area are comparable to the components that contributed to the low flow yield used in the Michigan study, further supporting the importance of these variables as predictors of salmonid assemblages. The importance of PIC as a predictor in this study reflects the high range of development in our study area (Wang et al. 2006, this volume). Van Sickle et al. (2004) also demonstrated that land use/land cover in the riparian network affected cutthroat trout only slightly better than catchment land use/land cover. We agree with Van Sickle et al. (2004) that confounding between land use/land cover and geology are inevitable with this kind of study and make interpretation challenging. In our study area, development pressure is greater on lands where soils support farming and urban areas and less on soils that have low productivity, high erodibility, or high water tables, such as those in the Oak Ridges Moraine and the Niagara Escarpment. This inherent bias is difficult to control in a landscape analysis and inevitably results in models having inflated  $r^2$  values. The large sample size in our study and the observation that the patterns were consistent across the landscape give confidence that the data support our conclusions. Additionally, Stanfield and Kilgour (2006) demonstrated that the effect of PIC on the residuals of a variety of instream variables, including fish assemblages, was significant, even after accounting for primary landscape features.

Other studies have confirmed that barriers constrain fish distributions (Joy and De'ath 2001; Moyle et al. 2003); however, few studies within the Great Lakes basin have documented the influence of barriers on salmonid distributions. Our study confirmed that barriers are, for the most part, an effective means of segregating tributary systems into rainbow trout and brook trout waters. Our results suggest that our efforts to identify furthest upstream barriers will underestimate distribution of rainbow trout, likely due to either residual problems with our dam

data or as a result of anglers passing fish. Given our results, more emphasis should be placed on maintaining an accurate record of barriers across the basin. However factors influencing the distribution of these species are complicated. Catchment size, geology, location relative to barriers, and the amount of development in the basin interact to determine which species are likely to occur in a particular stream segment. Many of these factors primarily affect measures of hydrology/groundwater that others have reported as having a primary influence on the distribution or density of salmonids (Seelbach et al. 1997; Zorn et al. 2002; Wang et al. 2003).

We do not suggest that instream habitat conditions are not important to rainbow trout and brook trout. Rather, we suggest that landscape conditions define the range of densities for a species, likely through their influence on the overall hydrologic and geomorphic conditions, while site-level conditions define the actual densities at a site. Provided landscape conditions are suitable for a species, that is are below a minimum threshold, local habitat and biotic conditions determine whether a species will occur at high or low densities.

#### Constraints on Species Distributions and Densities

We believe that rainbow trout can reside in nearly any Lake Ontario tributary, provided no barriers are present to limit access, and PIC is less than 9. At this threshold, it is possible that the stream hydrology becomes unsuitable for rainbow trout. Our findings differ from those of Stoneman and Jones (2000), in that rainbow trout densities were higher in areas with higher numbers of other salmonids. This suggests that in Lake Ontario tributaries, high quality salmonid habitat is suitable for a variety of species. This may not be the case in other tributaries of the Great Lakes. In our study, instream habitat features were less important than reported by Stoneman and Jones (2000) or Wang et al. (2003). Although instream habitat features are important to these fish, the

landscape attributes and salmonid assemblage are better predictors of rainbow trout densities in the Lake Ontario basin.

It is clear that natural reproduction is contributing a substantial, but not equally distributed number of rainbow trout to the basin. A disproportionate amount of production is occurring in the eastern portion of the study area. While we acknowledge that our results do not include tributaries east of Brighton or rivers wider than 15 m, we do not believe that production from these waters would greatly increase the overall population estimate for this species. Finally, geospatial analysis identified a number of segments where no data have been collected, but are predicted to contain high densities of rainbow trout and therefore should be considered in future monitoring programs.

Our results were similar to those of Wang et al. (2003) in that brook trout was generally found in sites with smaller catchments and low development. Stream temperature was the dominant variable in the site-level model, which is not surprising given that it is highly influenced by landscape features (Stanfield and Kilgour 2006). Therefore, the similarity in predictive capabilities between the landscape and site level models was expected. Our study confirmed that brook trout densities decreased with increasing densities of other salmonids; however, this variable added very little to the predictive capabilities produced by landscape models alone.

Larson and Moore (1985) observed that brook trout densities and distribution declined in the presence of rainbow trout in the southern Appalachian Mountains and speculated that eventually brook trout would be restricted to headwater areas or areas where rainbow trout lacked access. In most of our study area, brook trout is restricted to headwater areas or stream segments where other salmonids are absent or only one species is present. These observations give credibility to Larson and Moore's (1985) prediction, although the mechanisms are still uncertain. Brook trout distribution and densities were depleted by logging and farming prac-

tices, following European colonization. As such, it is difficult to separate historic effects from recent interactions with Pacific salmonids. Our findings also conform to those of Stoneman and Jones (2000), suggesting the overall importance of both stream temperature and the presence of cooccurring salmonids in providing suitable conditions for brook trout. However, our findings also suggest that rainbow trout now occupies many habitats in Lake Ontario tributaries that may be suitable for brook trout, and in the majority of the cases, brook trout is now absent. At this point, it is unknown if this is the result of competitive interactions or historic alterations to the landscapes.

We provide the first comprehensive assessment of the current distribution of brook trout in the study area, and the results are not encouraging. Ricker (1932) and Dymond (1965) suggested that brook trout was historically common in the study area and was found in all tributaries with cool clean water, including the main stem of streams where migratory salmonids currently reside. In estimating the preEuropean range of brook trout, we assumed that its range would include segments suitable for rainbow trout if forest cover was 100% and there were no barriers in the system. Our analysis indicated that historically, every segment in our data set would have been suitable for brook trout. With this assumption, the current distribution represents only 21% of its historic range. This reduction in distribution is an underestimate, given that our analyses assumed brook trout was absent in nonwadeable streams, despite its occasional capture in these waters recently.

We found that brown trout was only slightly less sensitive to the effects of PIC than brook trout. Below 6.9 PIC, its current distribution reflects historic stocking upstream of barriers and areas where streams could be populated by spawning fish from Lake Ontario. Our density models confirmed that instream habitat features and the densities and number of cooccurring salmonids are the best predictors for brown trout, corroborating the findings of Mortensen (1977)



and Stoneman and Jones (2000). We found that many of the features important to brown trout (i.e., abundant wood, deep pools, finer substrates, low amounts of rock cover, and cold/cool water) are not well correlated with landscape features. It is also likely that some of these features covary with biotic factors (i.e., number and densities of cooccurring salmonids). For example, rainbow trout tends to be more common in areas with abundant rock cover (Stanfield and Jones 2003).

Populations of coho salmon in the study area were low and were restricted to Wilmot Creek and its surrounding catchments. Coho salmon migrates great distances in the fall and winter in search of deep pools with wood and backwater habitats to overwinter (Bustard and Narver 1975). Wilmot Creek generally contains more wood than most other tributaries in the study area, has long stretches without barriers, and also has several backwater habitats/side channels that are used by this species (L. Stanfield, personal observation). These features are not easily captured with existing GIS information. Additional work is required to better understand the conditions influencing the distribution and abundance of this species in Lake Ontario.

### Management Implications

Generally, our distributional models illustrate that brook trout and rainbow trout distributions do not overlap. Barriers, PIC, and coinhabiting salmonids play an important role in this segregation, however, the reasons for this segregation are still unclear. Migratory salmonids were present in the lower segments of streams, where productivity would generally be higher and impacts from historic land uses would be greater. Therefore, this confounding effect may have masked any negative effect of rainbow trout on brook trout. Clarifying the degree to which competition from other salmonids influence the distribution and densities of brook trout should precede stocking into waters where brook trout currently reside.

Both brook and rainbow trout were sensitive to fairly low PIC, with populations absent at greater than 6.6 and 8.9, respectively. These PIC values translate to approximately 33% urban or 65% agriculture. The thresholds identified here provide a lower PIC threshold than that described by Stanfield and Kilgour (2006) for a general fish assemblage index. It is clear that many tributaries in the greater Toronto area have lost the potential to produce salmonids because of excessive development in their catchments. This may in part explain why brook trout were only found in headwater segments, since in much of the study area, these are the only areas where PIC are below this threshold. The combination of the threshold response and the decline in densities that occur below the threshold for brook trout and rainbow trout provide a powerful management tool that can be used to set targets and predict changes associated with proposed development of a watershed.

Fisheries management in Canadian tributaries of Lake Ontario is complicated by the migratory pattern of salmonid populations. Management objectives are established to balance the provincial objective of maximizing the reliance on self-sustaining natural populations while optimizing fishing opportunities for non-native naturalized fishes (OMNR 1992). In the tributaries, the objectives then recognize the need to protect native species such as brook trout, while optimizing production of naturalized non-natives such as rainbow trout, brown trout, or coho salmon (OMNR 1992; Stewart et al. 1999). Various strategies, including barrier management, instream habitat enhancement, stocking, and land stewardship are used to address the objectives in each management zone.

Our results provide tools for evaluating the benefits of various strategies for managing salmonid populations. For example, instream habitat restoration should be targeted in streams where brown trout are present, and PIC thresholds are useful for preserving constrained populations (i.e., brook trout). Catchments where land management plans ensure that PIC values

exceed the brook trout threshold and do not reach the rainbow trout threshold, may be candidates for increasing access for rainbow trout. Segments that still contain salmonids, even though the catchment is close to the PIC threshold, represent segments in need of immediate assistance to protect the remaining populations or to evaluate populations for genetic conservation.

This study expanded our understanding of the factors that influence the distribution and density of salmonids within the Great Lakes basin and can be used to strategically guide future management action. These results support the work of Seelbach et al. (1997) who suggested that landscape measures of slope, area, hydrography, and geology were critical factors determining fish assemblages in streams. Our findings suggest that in addition to these natural attributes, anthropogenic factors such as access to a Great Lake and the amount of impervious cover in the catchment should also be incorporated in classification strategies.

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