TOPOGRAPHIC INDEX MODELING OF YOUNG-OF-YEAR BROOK TROUT (*SALVELINUS FONTINALIS*) HABITAT AND SELECTING CANDIDATE LAKES FOR WILD BROOK TROUT RE-INTRODUCTION

A Thesis

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by

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ABSTRACT

Adirondack brook trout (Salvelinus fontinalis) depend on locations of groundwater upwelling for spawning, nursery habitat and thermal refugia for both young-of-year (YOY) and adult fish. Landscape-scale anthropogenic disturbances, such as logging and road construction, have the potential to influence brook trout habitat by altering these groundwater regimes. We used a topographic index (TI) approach to link watershed-scale topography with groundwater-influenced tributaries and seeps and YOY brook trout presence in the littoral zone of three lakes in the Adirondack Mountains, NY. The TI value of shoreline locations was positively associated with the temperature difference between lake surface and substrate, indicating greater groundwater seepage at locations with a higher TI value. The TI value of shoreline locations was also positively correlated with YOY brook trout presence in the nearshore zone. TI represented a significant improvement in predictive capability over currently available groundwater-influenced habitat location and delineation methods. Akaike's information criterion indicated that TI value was the strongest predictor of: (1) the presence of groundwater-influenced tributaries or seeps, and (2) YOY brook trout presence and numerical abundance in the nearshore zone. However, TI-based metrics were unable to predict brook trout population reproductive status or density at an inter-lake scale, possibly because the effects of acid precipitation are the primary drivers of variability in brook trout population abundance at a regional scale within the Adirondacks. The TI model represents a useful management tool at the scale of an individual lake shoreline, but further refinement is required for applications at an inter-lake scale.

BIOGRAPHICAL SKETCH

Peter Merritt Stevens was born in Evanston, Illinois on May 5, 1981 to V. Arthur and Barbara Stevens. At the age of 13, the family moved to Libertyville, Illinois. He graduated from Libertyville High School in 1999. In 2003, he received a Bachelor of Arts Degree *magna cum laude* in Biology and Environmental Studies from Lawrence University (Appleton, Wisconsin). After graduation he completed an internship with the Bureau of Land Management in Idaho Falls, Idaho followed by a year as a Restoration Foreman for an ecological restoration firm in the Midwest. He started graduate work at Cornell University in the Department of Natural Resources in August 2005.

For my Parents who showed me the way and my Wife who helps me to walk it.

ACKNOWLEDGMENTS

First and foremost, I would like my committee, Dr. Cliff Kraft for advice and guidance throughout the process, Dr. Lars Rudstam for useful insights into icthyological and limnological question and Dr. Todd Walters for invaluable help in the development and de-bugging of the model. I would also like to thank Dan Josephson for logistical support and Maggie Kung (nee Newbold) and Errol Scheid for assisting me through many long hours of fieldwork. In addition, I would like to acknowledge my colleagues Dr. Dana Warren, Dr. Jesse Lepak, Beth Boisvert, Jason Robinson and Hannah Shayler for many useful discussions and much emotional support. This work would not have been possible without the generous support of the New York State Department of Environmental Conservation and the Kieckhefer Adirondack Felllowship. Finally, I would like to thank my Wife without whose love and support none of this would have been possible.

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INTRODUCTION

Brook trout (*Salvelinus fontinalis*) depend upon areas of groundwater upwelling during at least three critical life stages, as reproductively mature adults, young-of-year (YOY) and as eggs/alevin. Most lake-dwelling populations of brook trout require locations of groundwater upwelling for fall spawning habitat (Webster and Eriksdottir, 1976; Curry and Noakes, 1995; Ridgeway and Blanchfield, 1998). Groundwater at these locations provides a stable thermal environment (Needham and Jones 1959) and blocks the formation of anchor ice, which can cause high alevin mortality (Benson 1953). Also, areas of groundwater discharge provide nursery habitat with suitable thermal conditions for YOY brook trout (Curry et al. 1993, Biro 1998). This nursery habitat allows YOY brook trout to behaviorally thermoregulate while still providing them protection from predation (Biro et al. 2003b, Parkinson et al. 2004). Finally, in systems where summer temperatures frequently exceed brook trout thermal optima, areas of groundwater influx are critical to maintaining fish populations through the summer (Bilby 1984; Baird and Krueger, 2003).

Anthropogenic disturbances have the potential to severely alter groundwater regimes and, therefore, alter this crucial brook trout habitat. Logging has been shown to disrupt the hydrology of lake basins, thereby increasing temperatures in groundwater-influenced habitat and reducing flow volume (Curry et al 1993; Curry and Devito 1995; Curry et. al 2002). In addition, acid precipitation has caused upwelling groundwater to become acidic (Hultberg and Johansson 1981, Sebestyen and Schneider, 2004), resulting in complete reproductive failure of lake spawning brook trout (Warren et al. 2005). Finally, global climate change and its impacts on both groundwater flux and temperature pose a significant threat to brook trout populations (Meisner et al 1988; Meisner 1990a; Meisner 1990b)

Global climate change is expected to have long-term effects on salmonids at the local and regional scale. Biro et al. (2007) recently demonstrated that increases in lake temperature have the potential to cause both decreases in YOY rainbow trout growth due to increased metabolism and increases in mortality from predation. At a local scale, climate change models have predicted that increases in air temperature will result in increases in groundwater temperature, which approximates the mean annual air temperature for a region (Todd 1980). Such increases will shrink groundwater thermal refugia and will fragment brook trout habitat at lower elevations and latitudes (Meisner et al. 1988; Meisner 1990b). Increased groundwater temperatures will also result in high temperatures and lower dissolved oxygen concentrations in brook trout redds (Meisner et al. 1988). Finally, the loss of suitable thermal habitat will result in significant reduction in the distributions of brook trout near the southern margins of their native range (Meisner 1990b).

Well-defined groundwater discharge zones are vital to the reproduction and health of populations of lake-dwelling brook trout (Schofield 1993), especially in light of increased thermal stress expected from global climate change (Meisner et al. 1988; Meisner 1990a; Meisner 1990b). Understanding how watershed-scale topography influences groundwater discharge into lakes – and how this discharge influences brook trout populations – will provide information useful for sustaining and restoring these populations (Borwick et al. 2006). By developing and verifying an effective model of groundwater inputs into a suite of lakes and establishing relationships between groundwater discharge and fish abundance, fisheries managers will be better able to manage fish populations and identify anthropogenic disturbances to the broader landscape that are likely to impact essential fish habitat.

The goal of this study was to establish linkages between landscape-scale, hydrologic processes and fish abundance and distribution within Adirondack Lakes.

Specifically, we will 1) quantify the spatial extent and location of groundwater inputs into selected lakes using a GIS-based hydrologic model, 2) determine if locations of groundwater influx are predictably used as summer habitat by young-of-year brook trout and 3) determine if groundwater habitat can be used to predict variability in brook trout population reproduction and health among lakes.

MATERIALS AND METHODS

Study Sites and Timetable

Three lakes – Panther Lake, East Lake and Upper Sylvan Pond – were selected for intensive thermal and biological examination. All three lakes are high elevation, oligotrophic lakes that are fed through a combination of groundwater input, small tributaries and flow from higher elevation streams and lakes. Wild, self-sustaining brook trout populations are found in all three lakes. All three lakes have significant natural reproduction sufficient to sustain populations without supplemental stocking. Both East Lake and Upper Sylvan Pond thermally stratify in summer whereas Panther Lake remains unstratified. In order to expand the analysis to a broader set of candidate lakes for wild brook trout re-introduction, an additional twelve lakes in the south-central Adirondacks were included in this study (encompassing approximately 70 kilometers of shoreline); (Table 1). These lakes were selected to represent a range of Adirondack lake sizes, as well as a variety of physical, chemical and biological parameters.

Summer field surveys of these lakes took place between early-July and mid-August for all lakes and progressed from smallest to largest due to the lag in littoral warming between small and large lakes. Panther lake, East Lake and Upper Sylvan Pond were surveyed in summer 2006 and 2007 while the other 13 lakes were surveyed only in summer 2007.

Table 1: Location and selected physical and hydrologic statistics for 15 study lakes

Lake	Longitude (°N)	Latitude (°W)	Surface Area (ha)	Shoreline Length (km)	Watershed Area (ha)
Upper Sylvan Pond	43°36'47.16"	74°56'4.75"	5.40	0.92	31.00
Mountain Pond	43°42'24.03"	74°52'35.13"	6.22	1.15	63.45
Lower Sylvan Pond	43°36'30.87"	74°56'20.11"	6.79	1.06	48.64
Rock Pond	43°39'7.01"	74°58'28.70"	7.63	1.13	54.35
Chambers Lake	43°35'30.83"	74°56'21.35"	10.62	1.83	244.59
East Lake	43°41'38.65"	74°53'42.59"	13.90	1.62	226.14
Deer Lake	43°33'15.35"	74°45'42.33"	14.27	2.07	216.95
Panther Lake	43°40'43.83"	74°55'17.22"	16.90	2.07	86.28
Jones Lake	43°32'56.60"	74°46'41.36"	19.21	2.12	105.87
Wilmurt Lake	43°25'46.50"	74°43'34.64"	42.37	3.70	259.16
First Bisby Lake	43°36'14.56"	74°56'3.60"	60.18	5.07	296.11
Rock Lake	43°58'1.37"	74°52'9.44"	81.16	7.10	477.04
Canachagala Lake	43°36'18.77"	74°54'12.66"	139.51	10.41	350.94
Little Moose Lake	43°41'19.01"	74°55'38.45"	280.00	11.54	689.59
Honnedaga Lake	43°31'23.36"	74°49'1.96"	333.52	16.44	1066.63

Habitat Survey Methods

Surveys were conducted by foot and boat around the perimeter of all study lakes to identify groundwater-influenced shoreline habitat. The surveys identified two types of shoreline habitat: seeps and tributaries. Tributaries were defined as channelized inflows greater than 10 meters in length with base flow originating from lakes higher up in the drainage or groundwater sources. Seeps were defined as either a) channelized inflows less than 10 meters in length or b) point sources of groundwater flow. The point sources generally appeared as inundated terrestrial areas along the shoreline where flowing water could be either observed or heard. These definitions are consistent with those previously used by Borwick et al. (2006).

Physical, chemical and habitat variables were measured at each tributary and the location of the tributary mouth was recorded using a Garmin GPS72 hand-held global positioning system (GPS) unit. Stream depth and bankfull and wetted widths were measured in the thalweg at five meter intervals starting at the mouth of the tributary and progressing upstream to a distance of 20 m. Cover and cover type, embededness and substrate type were also summarized along the 20 m segment. Cover type was divided into five categories (undercut banks, large woody debris, plants, boulder and other). Substrate type was measured by estimating the proportion of five substrate types ranging from boulder (>256 mm) to fines (<2 mm) including sediment/detritus. In addition, water samples were collected in Nalgene high density polyethylene sample bottles for pH and ANC analysis at a distance 10 m upstream from the confluence with the lake. Bottles were rinsed with tributary water before being filled and capped underwater to prevent air bubbles from accumulating in the bottle. Samples were refrigerated and analyzed within one week of sampling according to US EPA titration methods.

Similar measurements were employed for evaluating seeps with the exception of measuring width, in the case of non-channelized seeps, and embededness. Width was excluded due to the difficulty in determining the width of a seepage face and embededness due to its lack of relevance in an in-lake context. Chemical sampling procedures were the same as with tributaries; water samples were collected as close to the inflowing seep as possible to indicate whether inflowing groundwater influenced in-lake, nearshore chemical conditions.

Biotic Survey Methods

Electrofishing surveys were conducted in Panther Lake, East Lake and Upper Sylvan Pond using three pass depletion surveys (Carle and Strub 1978). Block nets were place at the tributary mouth and a distance 10 m upstream. Surveys of seeps and non-habitat areas of lake shoreline were conducted by blocking an area on three sides with two nets extending two meters perpendicular to shore and one connecting net running parallel to shore for 10 meters. This blocking scheme ensured that similar sized areas were sampled in tributaries, seeps and non-habitat locations. All YOY brook trout collected during these surveys were measured for length and weight. In addition, a maximum of ten fish were retained for diet analysis from each sampling site. Retained fish were frozen until their stomach contents could be removed and preserved. All remaining YOY brook trout were returned alive upon completion of depletion runs.

Topographic Index Model Development

A topographic index (TI) is the measure of the topographic properties of a landscape including some or all of the following: elevation, flow direction, flow accumulation, slope and aspect (Wilson and Gallant 2000). Topographic indices are particularly applicable to systems dominated by shallow subsurface groundwater flow. This makes their application to the Adirondack Mountains particularly appropriate because most watersheds in this region are governed by shallow subsurface flow though thin to moderate glacial till (Shanley 1986; McHale et al. 2002). In this study we used the topographic index from Beven and Kirkby's (1979) TOPMODEL,

$$\mathrm{TI} = \ln\left(\frac{\alpha}{\tan\beta}\right)$$

where α is the upslope contributing area per unit width of contour and β is the slope of the given area.

The topographic index (TI) model was calculated using the TauDEM (Tarboton 2005) and spatial analyst toolboxes applied in the ArcGIS Modelbuilder application within ArcGIS 9.2 (ESRI, Inc.). The ArcGIS Modelbuilder application permits multiple spatial analyst and TauDEM functions to be linked together in series and then packaged in a single executable application with its own graphical user interface (GUI). A schematic for the TI model is presented below (Figure 1). The model has been packaged, along with necessary pre-processing steps, into an ArcToolbox toolbox that is available from the author (pms34@cornell.edu). More detailed explanation of the model structure and creation are available in Appendix A.

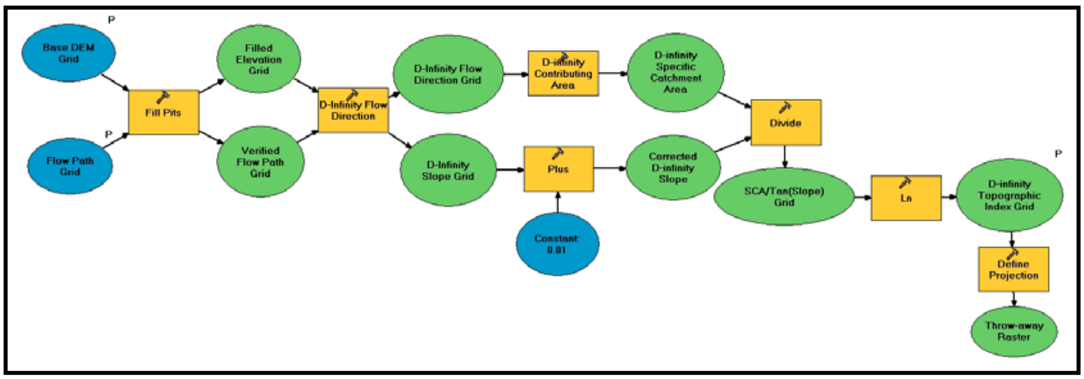

Figure 1: Flow Schematic for the TI model as applied within ModelBuilder in ArcGIS 9.2. Ovals represent raster layers and rectangles represent processes applied to input layers. "P" denotes a parameter that can be input by the user via a GUI or an output whose name and file path can be specified via the GUI.

Topographic Index Model Calibration

Lake surface and substrate temperatures were measured from mid-June to late-August of 2007 at Panther Lake, East Lake and Upper Sylvan Pond using arrays of paired iButton (Dallas Semiconductor/Maxim Integrated Products, Inc.) temperature sensors: one at the lake surface (floating approximately 1-5cm below the lake surface) and one buried in the substrate to a depth of approximately 1 cm (directly below the surface logger). Arrays were installed at all field-identified locations of groundwater upwelling and randomly chosen locations around the lake. Previous studies have used the comparison of lake surface and substrate temperature as an index of groundwater discharge (Sorensen et. al., 1995; Essington et. al., 1998; Borwick et. al. 2006). Given that the temperature of shallow groundwater approximates the average annual air temperature of a region (Todd 1981), lake substrate temperatures at locations of groundwater discharge would be expected to be measurably cooler than the summer lake surface water temperature.

Linear regression was used to analyze the relationship between TI and locations of groundwater flux measured as the difference between surface and substrate temperatures at tributary, seep and selected non-habitat locations. The response variable, temperature difference, met the required normality assumptions of linear regression.

Data Analysis Methods

Logistic regression was performed on the groundwater-influenced shoreline habitat presence/absence data for all three study lakes to identify threshold TI values for use in later candidate lake comparisons. To assess correct classification rates of threshold TI values, the predicted probability of the presence or absence of groundwater-influenced shoreline habitat was compared with the observed presence/absence of this type of habitat. YOY brook trout habitat presence was predicted if classification probabilities were greater than 0.50 and absent if probabilities were less than 0.5.

The population estimates for YOY brook trout at each sampling location were non-normal with a significant right skew, owing to the high incidence of zero values for non-habitat locations. Therefore, a logistic regression analysis was used to assess the relationship between TI value and YOY brook trout presence/absence at all sampling locations for each study lake, rather than use population abundance as the dependent variable. Threshold TI values were calculated from these logistic regression analyses for use in later candidate lake analyses. Correct classification rates were assessed by comparing the predicted probability of YOY presence/absence to the observed YOY brook trout presence/absence. YOY brook trout presence was predicted if classification probabilities were greater than 0.50 and absent if probabilities were less than 0.5.

Akaike's Information Criterion (AIC) was used to evaluate the efficacy of TI model predictions to predict two response variables: 1) presence/absence of groundwater-influenced habitat and 2) presence/absence of YOY brook trout in the littoral zone. In both cases, four predictor variables were selected for evaluation. TI value was selected as a measure of the hydrologic properties of the surrounding landscape. Temperature difference between the surface and substrate at lakeshore sampling locations was a measure of groundwater inflow and thermal suitability for YOY brook trout. Habitat type – described as either tributary, seep or "non-habitat" – was included to represent a type of "expert knowledge". This predictor variable was excluded from the analysis of habitat presence/absence due to strong collinearity between the two variables. Finally, presence/absence of tributary, seep or non-habitat in USGS 1:24,000 quadrangle maps was included, despite very weak collinearity with habitat type. USGS quadrangle maps are useful in delineating fish habitat locations and informing management decisions regarding aquatic habitat. USGS hydrography layers and the New York State Department of Environmental Conservation stream layers were omitted from the analysis as they are derived from the USGS quadrangle maps, therefore making their inclusion redundant. We assumed that the USGS quadrangles act as a proxy for all maps available to managers.

Global models including all predictor variables were calculated for each response variable and non-significant p-values ($p > 0.05$) indicated reasonable goodness-of-fit for the global models. Overdispersion ($c \sim 1.0$) was not evident in either habitat presence/absence or YOY presence/absence data. However, the n/K ratio was less than 40 indicating that an AIC_C analysis was required. AIC_C is the conservative choice in any case since, if n/K is greater than 40, the AIC_C equation simply collapses to the basic AIC (Burnham and Anderson 2002).

Candidate models were ordered from highest to lowest by AIC_C value, then Δ_i and Akaike weights, or AIC_C w_i, were used to rank models. Δ_i is a measure of how much information is lost with each successive "worse" model. A $\Delta_i > 2$ indicates strong support for the model, Δ_i values ranging from 4 to 7 indicate much less support and $\Delta_i > 10$ indicates essentially no support. AIC_C w_i provides the likelihood that a model is, in fact, the best model of the candidate model set given the data. Higher values of w_i provide stronger "weight of evidence" that a given model is the best model (Burnham and Anderson 2004).

AIC was also used to evaluate a more complete suite of YOY brook trout littoral habitat factors, TI among them, for their effectiveness in predicting YOY brook trout abundance and distribution along lake margins. The estimated YOY brook trout population at each sampling location was used as the response variable for this linear model. Estimated population data was $\ln(x + 1)$ transformed to meet assumptions of normality for linear regression analyses. TI, temperature difference and substrate temperature were used as predictors of thermal habitat suitability. These variables were not used in combination in any of the models because they were strongly collinear. In these analyses habitat type served as a "universal" proxy for physical, chemical and biotic differences between the three types of sampling locations, non-habitat, seep and tributary. Cover level represents refuge habitat from potential predators. The chemical variables, pH and acid neutralizing capacity (ANC), and one physical variable , substrate composition , were examined for inclusion but did not contribute to model fit and were therefore removed from further analysis. AIC_C was again used and candidate models were ranked and compared as described above.

Finally, a regional scale analysis was used to evaluate the effects of landscape-scale hydrologic, chemical and physical factors on the brook trout reproduction and population abundance across a suite of lakes. Logistic and linear regression were used to assess a variety of response measures of brook trout reproduction and population abundance as a function of predictor variables selected to capture the effects of landscape-scale hydrologic, chemical and physical factors. Four response measures were selected for modeling: (1) reproduction designated as a good/poor binomial based on redd counts from the suite of lakes, (2) catch per unit effort (CPUE) within spring gill net surveys, (3) the mean number of redds observed during fall 2005-2007 surveys, and (4) the mean number of redds per unit shoreline length (providing an approximate measure of the amount of spawning relative to potential littoral spawning habitat). Reproduction, as a binomial, was modeled using logistic regression and CPUE; total number of redds and redds per unit shoreline were modeled using linear regression.

The model set included eight TI-based predictor variables including: a) mean TI value for the lake shoreline, b) maximum TI value found along the shoreline, c) the number of cells greater than either the habitat or YOY presence/absence threshold calculated for the intensive study lakes, d) the proportion of cells greater than either the habitat or YOY brook trout presence/absence thresholds and e) the mean of the top 5% or 10% of TI values found along a given lake shoreline. TI variables were never used in combination in the same regression due to strong collinearity. In addition, pH and ANC were selected to represent chemical conditions in the study lakes, summer thermal stratification was included as a “yes/no” binomial to capture lake-wide thermal conditions, and a lake classification category – developed according to the method employed by the Adirondack Lakes Survey Corporation (Gallagher and Baker 1990) – was included to account for alternative classification schemes. Global models were calculated for each of the four response variables and tested for goodness-of-fit.

RESULTS

Topographic Index Model Calibration

A significant linear relationship was found between TI values and the difference between surface and sediment temperature for Upper Sylvan Pond (r^2 = 0.68, p = 0.0002) (Figure 2), East Lake (r^2 = 0.48, p = 0.0007) (Figure 3) and Panther Lake (r^2 = 0.59, p < 0.0001) (Figure 4). Given the shallow nearshore range of depths surveyed (0.25-1m), these differences did not likely result from thermal stratification.

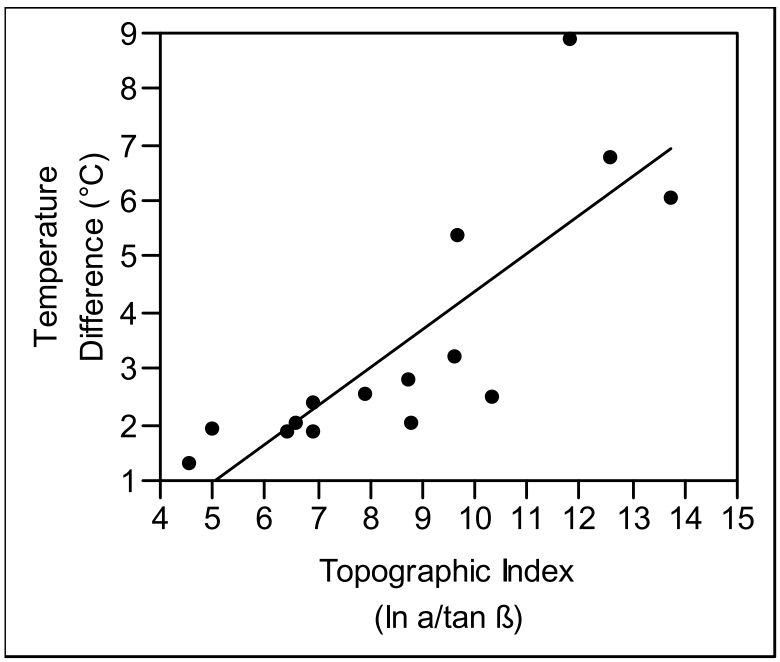

Figure 2: Mean difference between surface and sediment water temperatures at tributary, seep and non-habitat cells vs. topographic index values for Upper Sylvan Pond for mid-June through August 2007

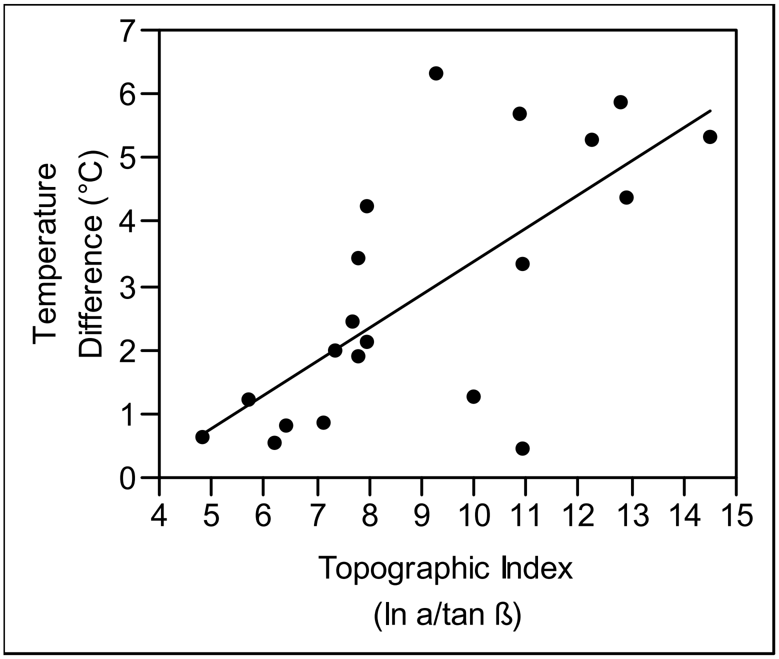

Figure 3: Mean difference between surface and sediment water temperatures at tributary, seep and non-habitat cells vs. topographic index values for East Lake for mid-June through August 2007

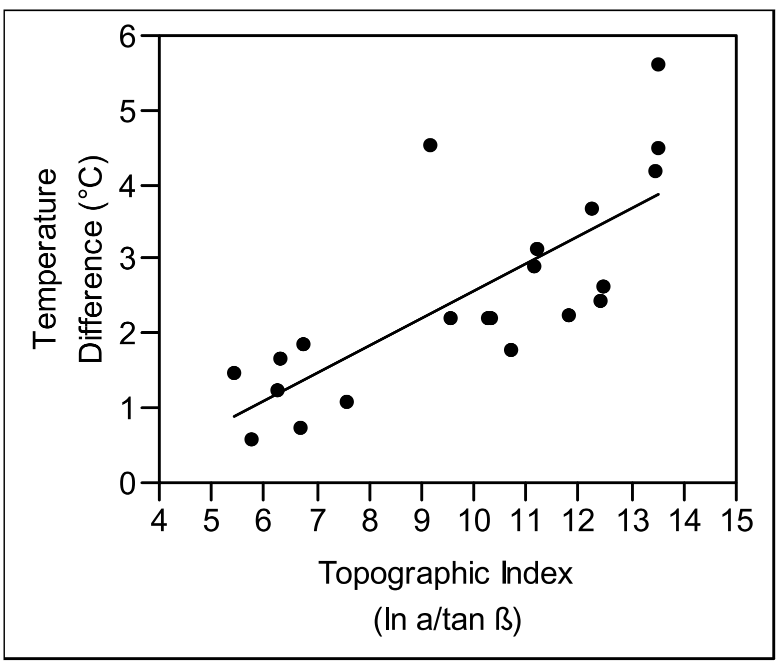

Figure 4: Mean difference between surface and sediment water temperatures at tributary, seep and non-habitat cells vs. topographic index values for Panther Lake for mid-June through August 2007

YOY Habitat Use

A significant logistic relationship was found between TI values and YOY brook trout presence/absence for Upper Sylvan Pond ($r^2 = 1.00$, $p < 0.0001$) (Figure 5), East Lake ($r^2 = 0.77$, $p < 0.0001$) (Figure 6) and Panther Lake ($r^2 = 0.56$, $p = 0.0027$) (Figure 7). The inflection points describing this relationship for each lake occurred at different TI values: 10.8, 9.5 and 6.2 for Upper Sylvan Pond, East Lake and Panther Lake, respectively. TI values correctly classified YOY brook trout presence or absence at 100%, 87% and 83% of the locations sampled in Upper Sylvan Pond, East Lake and Panther Lake, respectively.

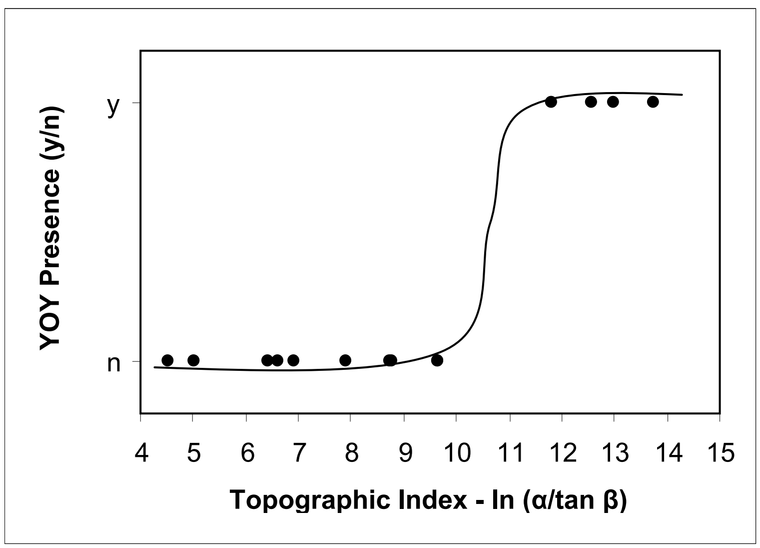

Figure 5: Logistic regression of YOY brook trout presence/absence at tributary, seep and non-habitat cells vs. topographic index values for Upper Sylvan Pond.

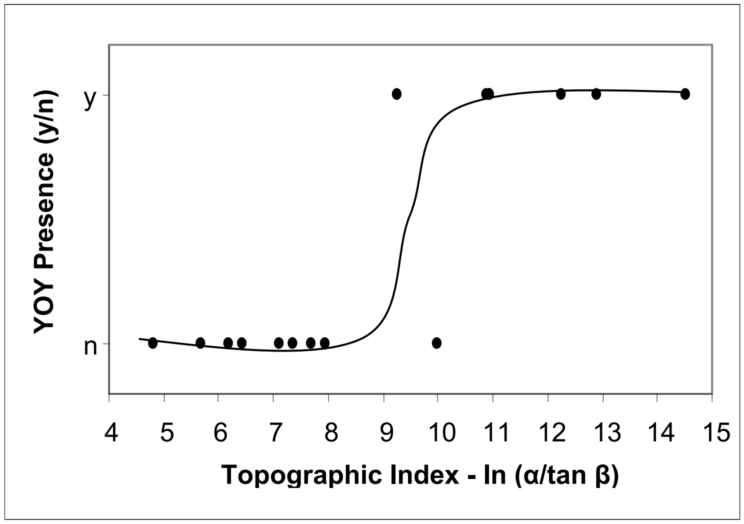

Figure 6: Logistic regression of YOY brook trout presence/absence at tributary, seep and non-habitat cells vs. topographic index values for East Lake.

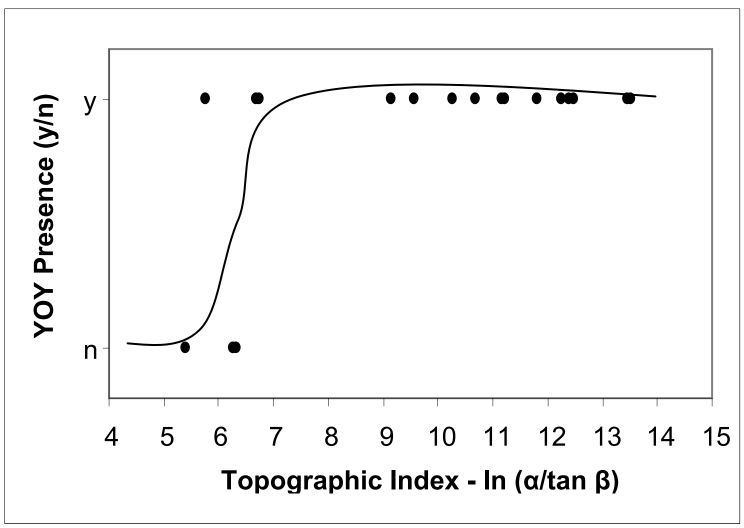

Figure 7: Logistic regression of YOY brook trout presence/absence at tributary, seep and non-habitat cells vs. topographic index values for Panther Lake.

Topographic Index Thresholds and Classification Rates

When combined across all three intensive study lakes, a significant logistic relationship was found between both TI values and groundwater-influenced habitat presence/absence ($r^2 = 0.55$; $p < 0.0001$) (Figure 8) and TI values and YOY brook trout presence/absence ($r^2 = 0.48$; $p < 0.0001$) (Figure 9). The inflection points describing this relationship were 9.7 and 8.8 for habitat presence/absence and YOY presence/absence, respectively. TI values classified habitat presence/absence and YOY presence/absence correctly at 90% of the 48 locations sampled for both variables.

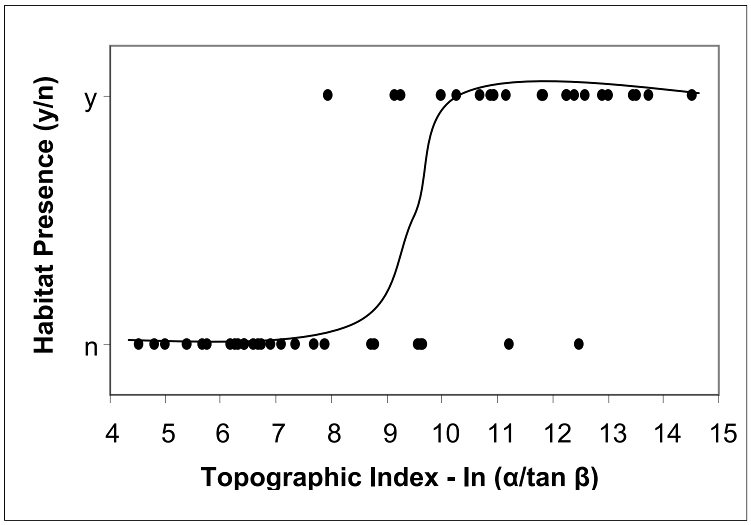

Figure 8: Logistic regression of presence/absence of tributary or seep habitat at a particular shoreline location vs. topographic index value at tributary, seep and non-habitat locations for all intensive study lakes.

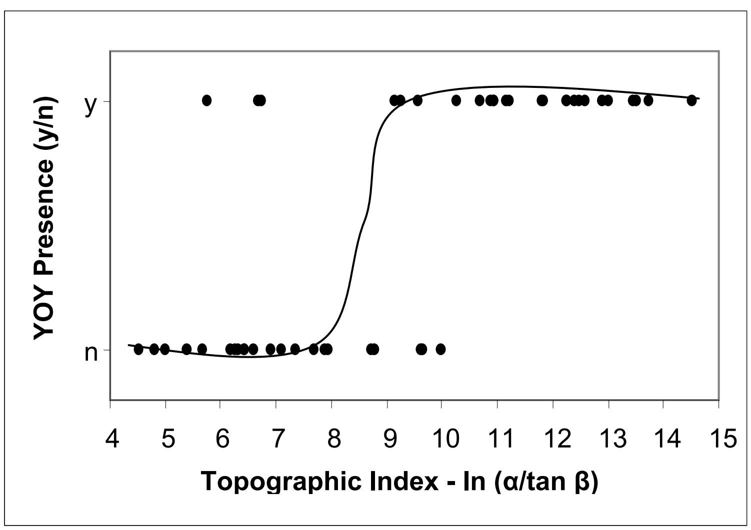

Figure 9: Logistic regression of presence/absence of YOY brook trout vs. topographic index value at tributary, seep and non-habitat locations for all intensive study lakes.

Topographic Model Analysis

TI value alone represented the most effective and parsimonious model for both groundwater-influenced habitat and YOY brook trout presence/absence response variables, and other models failed to capture large amounts of the observed variation in these response variables. Based on Δ_i values and the AIC_C w_i, TI value alone was the predictive variable most strongly supported by the data. This result corresponds with r^2 values of 0.51 and 0.48 for the logistic regression of habitat presence/absence or YOY brook trout presence/absence as a function of TI. It is also important to note that for both habitat and YOY brook trout presence/absence, the presence of tributary, seep or non-habitat on a USGS quadrangle map represented the single worst model with high Δ_i values, 35.5 and 29.3, respectively, indicating extremely poor fit of the data to the model.

Table 2: AIC model selection results for habitat presence/absence using predictor variables recorded at tributary, seep and non-habitat cells for all three intensive study lakes. The complete set of models tested is shown.

Model	*n*	K	Δ_i	AIC_C w_i
TI	47	3	0	0.915
TI, USGS Quad	47	5	4.79	0.0836
TI, ΔT(°C)	47	3	14.84	0.000548
ΔT(°C), USGS Quad	47	5	19.36	5.74×10^{-05}
USGS Quad	47	5	35.49	1.80×10^{-08}

Table 3: AIC model selection results for YOY brook trout presence/absence using predictor variables recorded at tributary, seep and non-habitat cells for all three intensive study lakes. Only the top five models evaluated are shown.

Model	*n*	K	Δ_i	AIC_C w_i
TI	47	3	0	0.646
TI, Habitat Type	47	6	2.97	0.146
Habitat Type	47	4	3.34	0.122
TI, USGS Quad	47	5	4.79	0.0590
ΔT(°C), Habitat Type	47	6	7.69	0.0138

Shoreline Habitat Modeling

TI value combined with habitat type represented the most predictive yet parsimonious model for predicting YOY brook trout abundance in the littoral zone. The AIC_C w_i indicates that this model had substantial support as the best model. This result is corroborated by an r^2 value of 0.70 given by the linear regression of the transformed estimated population as a function of this model. TI appears as a predictor variable in both of the top two models. It is also important to note that the direct measures of temperature, temperature difference and substrate temperature, either singly or in combination with other habitat variables, performed relatively poorly compared to the TI variable in predicting the availability of shoreline groundwater habitat.

Table 4: AIC model selection results for linear regression of ln(estimated population + 1) using habitat variables recorded at tributary, seep and non-habitat cells for all three intensive study lakes. Only the top five models tested are shown.

Model	***n***	**K**	Δ_i	AIC_C w_i
TI, Habitat type	47	5	0	0.616
TI, Habitat type, Cover level	47	6	1.57	0.280
Substrate Temperature (°C), Habitat type	47	5	5.18	0.0463
Habitat type	47	4	6.89	0.0196
Substrate Temperature (°C), Habitat type, Cover level	47	6	7.14	0.0174

Regional Scale Modeling

No global model incorporating any combination of response and predictor variables produced a model fit adequate to justify further analysis. Logistic regression using reproduction as a measure of brook trout population viability yielded significant p-values ($p < 0.05$) for Pearson χ^2 goodness-of-fit values for all possible global models, thereby indicating inadequate fit. In addition, stepwise regression for all combinations of response and predictor variables showed no significant effects ($\alpha >$

0.05) for any predictor variable or combination of variables and very low r^2 values (0.03-0.29) indicating extremely poor fit.

DISCUSSION

This study found that larger TI values were associated with greater differences in temperature between lake surface and substrate temperatures at nearshore locations along lake shorelines, suggesting a positive, linear relationship between TI value and groundwater influx in the littoral zone. We also found that YOY brook trout exhibited a preference for sites with larger TI value. Interestingly, the threshold values used to predict both the presence of groundwater-influenced habitat and YOY brook trout presence/absence (TI ~ 9.4) correspond closely to predictions from more complex hydrologic modeling efforts that have identified TI values < 10 as representing the cut-off for areas with shallow, subsurface groundwater flow (Agnew et al. 2005). This suggests that our model results are consistent with previous hydrologic modeling efforts and are biologically relevant.

These results demonstrate that TI modeling represents a new and effective method for locating and delineating important groundwater-influenced YOY brook trout habitat in Adirondack lakes. TI modeling clearly out-performed alternative methods we tested such as measuring shoreline areas for adequate temperature ranges or "expert knowledge" in the form of knowing the position of tributary and seep habitat along a lake shoreline. Most notably, USGS 1:24,000 topographic maps, acting as a proxy for other management maps, consistently provided the least informative method for identifying groundwater-influenced habitat or the presence or absence of YOY brook trout. This result was corroborated by Borwick et al. (2006) who found that their TI model results identified many seeps and streams along lake shorelines that were omitted from provincial maps (Ontario base maps). We therefore conclude, as did Borwick and colleagues, that currently available maps are insufficient for the purpose of identifying important fish habitat in Adirondack lakes and rivers, therefore the TI model represents a substantial advance in our ability to locate and delineate critical groundwater-influenced shoreline habitat.

We were also able to successfully use the TI model to predict the abundance of YOY brook trout in the littoral zone of three study lakes. The TI value and habitat type (non-habitat, seep or tributary) combined represented the most predictive yet parsimonious model for predicting YOY brook trout abundance. Similarly, TI, habitat type and cover level represented the second most predictive model and was only lower in the ranking due to a penalization for additional parameters. TI values appeared in both of the top two models, indicating the significant explanatory utility of this variable which corresponds with previous studies that have related groundwater to trout abundance (Latta 1965). However, this result contrasts with previous work conducted by Borwick at al. (2006) in which they found that TI values, while increasing the probability of locating seep or stream habitat along a lake shoreline, did not improve the odds of finding YOY brook trout along lake margins.

The improved ability of our model to identify the presence or absence of YOY brook trout likely resulted from several model improvements that reduced errors and improved the routing of flow within drainage basins and along lake margins. We describe five such modifications of the TI framework used by Borwick et al. (2006). First, our TI model used higher resolution 10 m digital elevation models (DEMs) that are available for New York State. Second, the digital elevation models (DEMs) were pre-processed to remove spurious sinks and pits in the data. These imperfections originally resulted from errors in the remote sensing or interpolation procedures used to create the DEMs and are well documented (Garbrecht and Martz 2000). Third, a verified flow path was used to enforce drainage along existing streams and tributaries. Fourth, we utilized the D-Infinity flow direction algorithm that assigns a flow direction based on the steepest slope along triangular facets (Tarboton, 1997). This allows bi-directional flow, which creates a more realistic aggregation and dis-aggregation of flow paths through the landscape. Finally, the TauDEM extension was used to calculate flow across flat areas of the landscape using the method of Garbrecht and Martz (1997). This method imposes two gradients – one towards lower terrain and the other away from higher terrain – which prevents the erroneous routing of flow along lake shorelines that can create inappropriately high TI values for shoreline cells close to the outlet.

Direct measures of thermal habitat – such as the difference in temperature between the surface and substrate, or substrate temperature by itself – were substantially less effective in predicting YOY brook trout presence/absence or abundance than were TI values. This is a somewhat counter-intuitive result since this study and others (Borwick et al. 2006) have demonstrated a clear relationship between increasing TI values and lower water temperatures, and therefore a more favorable thermal regime, at locations with field-observed groundwater-influenced habitat. Additionally, other studies have demonstrated the strong influence of cooler water temperatures on YOY brook trout density (McRae and Diana 2005) and trout biomass (Bowlby and Roff 1986). This could indicate that the availability of suitable thermal conditions is not the primary driver of YOY brook trout abundance in these systems. However, it seems more likely that TI values incorporate a combination of thermal characteristics and additional factors associated with groundwater-influenced habitat to form a more robust measure of habitat suitability for YOY brook trout.

A topographic index represents a measure of shallow-subsurface groundwater flow that incorporates the lake shoreline thermal conditions as one component of groundwater's overall influence along with other chemical, spatial and biotic factors. Groundwater-influenced locations are known to provide chemically stable brook trout habitat owing to the chemical buffering capacity of groundwater (Gunn, 1986; Curry et al. 1995). This is a critical factor in our study systems due to the presence of widespread episodic pH depressions resulting from acid deposition in lakes within this region of the Adirondacks. These pH depressions occur mainly during the spring snowmelt, which represents a critical time in the brook trout life cycle as fry are in the early stages of exogenous feeding (Curry et al. 1993). Also, episodic pH depressions can occur throughout the open water season following significant rain events, such as occurred in early-July 2006 (P. Stevens unpublished data). High TI values that represent locations of groundwater-influenced habitat may therefore also provide YOY brook trout with a stable chemical regime that allows these fish to survive episodic pH depressions.

Groundwater-influenced habitats along the lake margin also may reduce the predation risk faced by YOY brook trout. Presence of piscivorous fish has been shown to correlate negatively with trout biomass (Bowlby and Roff 1986b). Also, predation risk to YOY trout decreases with increased body size until a size dependent survival threshold is reached (Parkinson et al. 2004), and attainment of this threshold size corresponds to YOY movement into deep littoral and pelagic habitats in late summer (Biro et al. 2003a, Biro et al 2003b, Parkinson et al. 2004). Groundwater-influenced habitat along lake margins provides YOY brook trout with an opportunity to behaviorally thermoregulate (Biro 1998) without forcing them to move prematurely into deeper, thermally-stratified habitat where the predation risk would substantially increase.

Groundwater-influenced habitats corresponding to locations of large TI values may also provide increased opportunities for foraging and growth by YOY brook trout. These locations tend to occur near either tributaries at the interface of lotic and lentic environments or groundwater seepage zones along the lake margin. Lakes with tributaries have been shown to have high abundances of invertebrates and aquatic macrophytes (Hrabik et al. 2005), therefore these locations may provide increased opportunities for brook trout to forage on lotic prey items. In addition, groundwater-influenced habitat has also been shown to increase algal biomass (Hagerthey and Kerfoot 1998, Hagerthey and Kerfoot 2005) and invertebrate taxonomic richness (Malard et al 2003). Such increased food availability may lead to increased growth by YOY brook trout utilizing habitat at the mouth of tributary systems (Curry et al 1993).

Finally, lake-scale TI modeling efforts failed to identify any correspondence between a TI-based metric of groundwater influx and relevant measures of brook trout reproduction or population abundance in a larger set of 15 lakes from which data were available. One potential explanation of this lack of correspondence is the failure to properly identify and parameterize a TI-based metric that adequately captures groundwater-influenced habitat at the spatial scale of an entire lake. This is unlikely, however, as a large number of TI-based metrics were tested that represented as many *a priori* arguments as could be found to have a logical hydrologic and biological rationale. While *a posteriori* "data dredging" could potentially produce a useful explanatory variable, as a general rule, such procedures should be avoided (Burnham and Anderson 2004). Also, without a justifiable biologic or hydrologic explanation for the efficacy of a TI-based metric, the validity of such results would be speculative at best.

An alternative and more likely explanation for the failure of a lake-wide TI-based metric is that groundwater-influenced habitat is not the primary driver of variability and population abundance of brook trout at a regional scale. Acid precipitation and the resultant mobilization of inorganic monomeric aluminum is a significant current and historic threat to wild brook trout in the Adirondack Mountains (Jenkins et al. 2007). Inorganic monomeric aluminum causes abrasion and mechanical destruction of fish gills that result in mortality from the loss of iono- and osmoregulatory capacity (Schofield and Trojnar 1980; Exley et al. 1991). This process has resulted in the local extirpation of wild brook trout populations throughout the Adirondack Mountains and chronic or episodic habitat limitation in many of the remaining populations (Baker et al. 1993; Baker et al. 1996). While groundwater-influenced habitat represents a chemical refuge from episodic acidification (Baker et al. 1996), the recent appearance of documented instances of acidic groundwater (Sebestyen and Schneider 2004; Warren et. al 2005) indicates that acidification remains a threat. Acidification of lake surface water and groundwater inflow likely represents the single largest influence on Adirondack brook trout populations and provides a likely explanation for the failure of TI-based metrics to differentiate between lakes with varying levels of brook trout reproduction and population abundance.

In conclusion, TI has proven to be a useful predictive tool for identifying YOY brook trout nursery habitat in the littoral zone of lakes and explaining YOY abundance and distributions along lake margins. However, TI predictive efficacy did not carry over to lake-scale TI metrics for predicting brook trout reproduction and population abundance at a regional scale. This is likely the result of biogeochemical factors acting as the strongest control over brook trout populations throughout the Adirondack region of New York.

APPENDIX A

Detailed explanation of topographic index model design

A topographic index (TI) is the measure of the topographic properties of a landscape including some or all of the following: elevation, flow direction, flow accumulation, slope and aspect (Wilson and Gallant 2000). Topographic indices are particularly applicable to systems dominated by shallow subsurface groundwater flow. This makes their application to the Adirondack Mountains, where most watersheds are governed by shallow subsurface flow though thin to moderate glacial till, particularly appropriate (Shanley 1986; McHale et al. 2002). The equation used to calculate TI is given below:

$$TI = \ln\left(\frac{\alpha}{\tan\beta}\right) \qquad \text{Equation 1}$$

where α is the upslope contributing area per unit contour length and β is the slope of the given area.

The topographic index (TI) model was calculated using the TauDEM (Tarboton 2005) and spatial analyst toolboxes applied in the ArcGIS Modelbuilder application within ArcGIS 9.2 (ESRI, Inc.). The ArcGIS Model builder application permits multiple spatial analyst and TauDEM functions to be linked together in series and packaged in a single executable application with its own graphical user interface. The TI model is available by contacting the author (pms34@cornell.edu) and may be imported and edited at the user's convenience. The flow schematic for this process is provided below (Figure A.1).

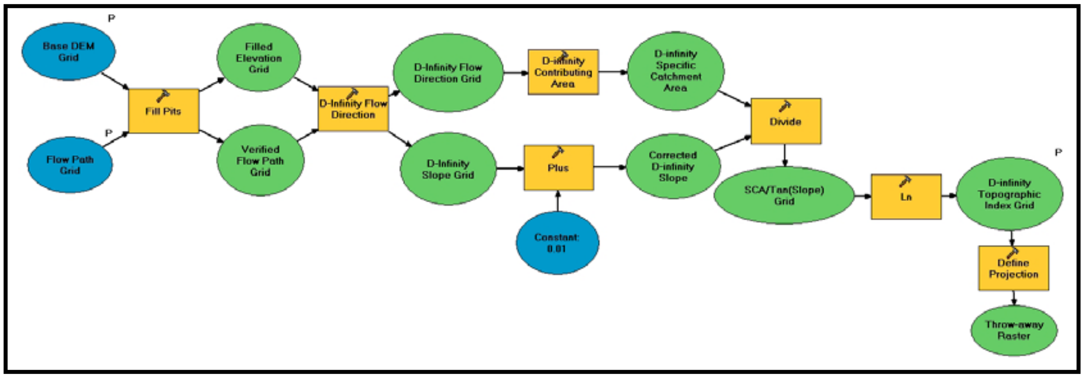

Figure A.1: Flow Schematic for the TI model as applied within ModelBuilder in ArcGIS 9.2. Ovals represent raster layers and rectangles represent processes applied to input layers. “P” denotes a parameter that can be input by the user via a GUI or an output whose name and file path can be specified via the GUI.

The modeling process begins with two input raster layers: a 10m resolution digital elevation model (DEM) that has been converted to an ArcGIS raster grid and a flow path grid. This flow path grid is derived from available hydrography data and enforces flow routing along established flow paths where known. This is the most appropriate approach when hydrography information is believed to be more accurate than elevation data (Tarboton 2005) as considerable bias can be introduced into the TI model if drainage networks are not accurately depicted (Quinn et al. 1995). The use of high resolution DEMs and a verified flow path grid represents the first of a series of model updates implemented to reduce errors and improve flow routing and connectivity.

These raster layers are input into a standard “Fill Pits” function that removes spurious pits and sinks from the DEM. These pits and sinks are often the result of errors in the remote sensing or data interpolation process (Quinn et al. 1991) and must be filled in order to ensure connectivity and accurate flow routing throughout the surface. Filling pits represents another model update implemented in this project. This function outputs a “filled” elevation grid and a verified flow path grid.

These newly derived grids are input into the Flow Direction function. This function calculates flow direction using the "Deterministic Infinity" or D∞ method proposed by Tarboton (1997) and applied using the TauDEM toolbox (D. Tarboton person. comm.). Most commercially available GIS programs utilize the "eight-direction deterministic", or D8, algorithm (O'Callahan and Mark 1984) which routes flow from the center of a focal cell to a single, downslope neighbor determined by the steepest slope from cell center to cell center (Figure A.2a). This results in flow along only the four Cardinal and four diagonal directions. D∞, however, is a multiple flow direction algorithm that permits bi-directional flow from the center of a focal cell to two adjacent, downslope neighbors. The flow direction is determined by steepest downward slope along triangular facets centered on the focal cell (Figure A.2b). Flow is apportioned between the two cells according to the angle of flow along the triangular facet. D∞ was selected for use in this model as it represents a compromise between single flow direction, which tends to aggregate flow too strongly, and true multiple flow direction which tends to disperse flow too strongly. Also, where D8 allows only parallel and convergent flow, D∞ allows parallel, convergent and divergent flow which is critical to accurate depiction of natural flow paths (Brasington and Richards 1998).

TauDEM's D∞ flow direction function also utilizes an improved approach to routing flow across flat areas. Most common flow direction functions route flow over flat terrain towards low areas, in this case the lake outlet. This causes the "parallel flow" problem where flow entering a flat surface, such as a water body, will travel along the edge of higher terrain, the shoreline, until the high terrain recedes from the flow line producing the common problem of erroneous shoreline accumulation of TI values (Garbrecht and Martz 1997). However, an improved technique pioneered by Garbrecht and Martz and employed by the TauDEM toolbox utilizes an additional decision rule that routes flow away from high areas in addition to towards low areas. Employing this dual criterion prevents erroneous accumulation along lake shoreline cells. Using this criterion, flow contacts the shoreline, flows out into the middle of the flat lake surface and then leaves the lake through the outlet resulting in more realistic flow routing through the surface.

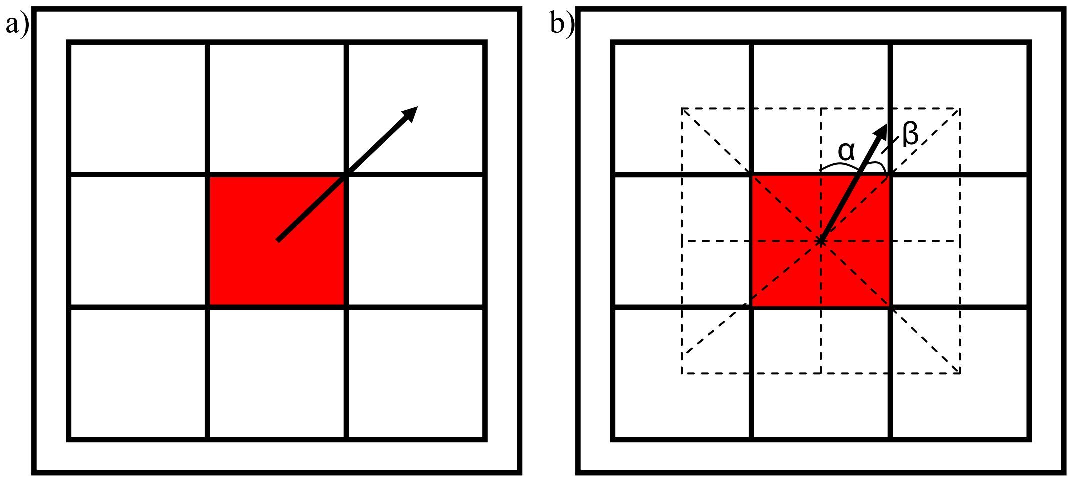

Figure A.2: Diagram of a) D8 and b) D∞ flow routing algorithms. Arrows represent flow direction through the surface. α and β represent angles used to apportion flow using D∞.

The flow direction grid output by the flow direction function is then input into contributing area function. This calculates the flow accumulation of every cell in the surface and then calculates the specific catchment area (SCA) using the grid cell area ($100m^2$) and grid cell size (10m) according to equation 2:

$$SCA = \frac{(flow\_accumulation)(100m^2)}{10m^2} \qquad \text{Equation 2}$$

In this case, SCA is equivalent to α in equation 1 when a raster grid is used to calculate TI. The SCA grid is then output for later use.

Next, the slope grid output generated by the flow direction function must have a small constant added to it to prevent null set values for flat surfaces. As equation 1 demonstrates, any flat surface will result in a zero slope in the denominator which will cause a null set error for the TI equation. This is a known problem with this type of hydrologic modeling and a common and widely accepted fix is simply to adjust all slope values by some small constant, 0.01 in this case (T. Walter, person. comm.). This makes a uniform adjustment to the entire surface, thereby preventing any systematic bias or error from emerging in the resulting TI model.

The SCA grid and corrected-slope grid are then input into a series of simple raster math functions to produce the TI grid. First, the SCA grid is divided by the corrected-slope grid. Next, the natural log (ln) of the resulting SCA/Slope grid is calculated to produce the final TI grid. Finally, the TI grid must have its projection re-defined because the original projection information is lost when using the TauDEM functions. This produces the final TI model grid which can then be used for further prediction and analysis (Figure A.3).

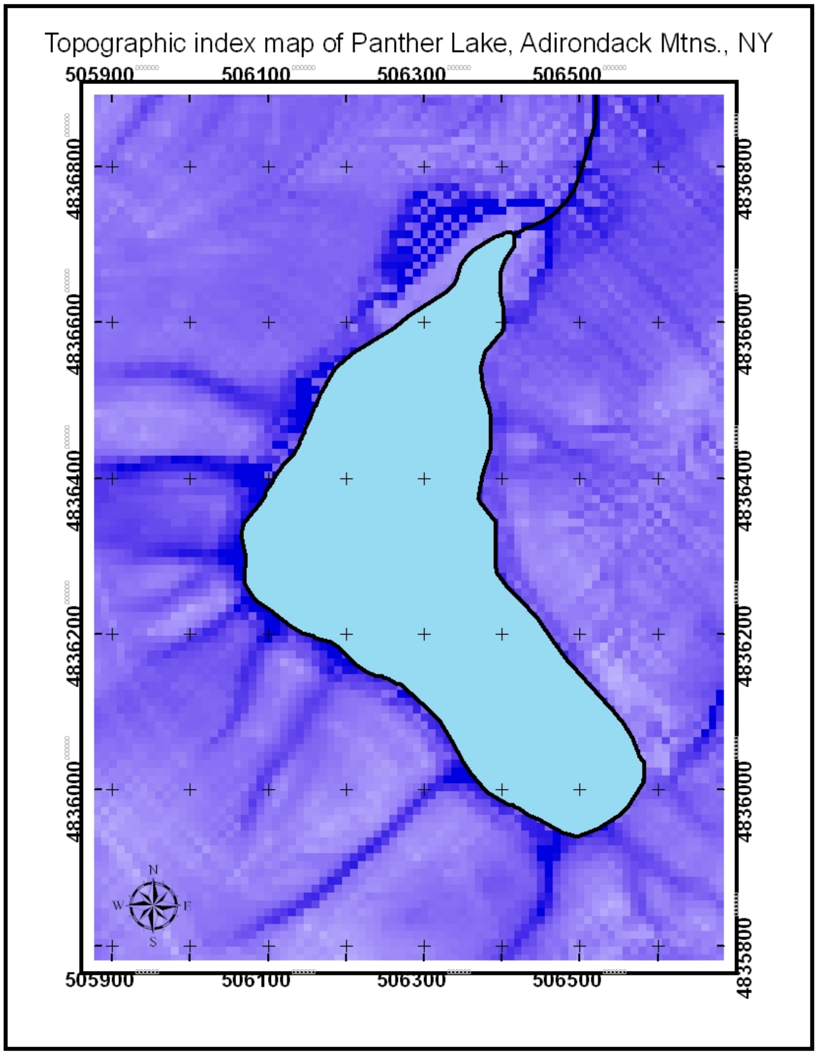

Figure A.3: A representative TI model map of Panther Lake. Dark shoreline cells correspond to higher TI values and greater likelihood of soil saturation and shallow, sub-surface groundwater flow at those locations.

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