A topographic index approach for identifying groundwater habitat of young-of-year brook trout (*Salvelinus fontinalis*) in the land–lake ecotone

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Abstract: We used a topographic index (TI) approach to link the presence of young-of-year (YOY) brook trout (*Salvelinus fontinalis*) at groundwater seepage and stream sites in the land–lake ecotone with subwatershed topography surrounding a set of 21 lakes in Algonquin Provincial Park, Ontario. A lakeshore site's TI value was positively related to the temperature difference between the substrate and lake surface, indicating higher TI values were associated with greater groundwater input. YOY brook trout tended to occupy lakeshore sites with relatively large TI values. Groundwater habitat available to YOY brook trout was relatively rare, with only a few sites used consistently on an annual basis. Larger lakes had fewer groundwater habitat sites per unit length of shoreline than smaller lakes. Logistic regression analysis and model selection (via Akaike's Information Criterion) indicated the odds of finding YOY brook trout increased significantly when a site was a stream and, in the summer, when there was a large difference in temperature between lake substrate and lake surface. Most of the stream sites used by brook trout were not on the Ontario base map system but were revealed by the TI approach.

Résumé : Nous avons utilisé une méthodologie qui emploie un indice topographique (TI) pour relier la présence de jeunes de l'année (YOY) de l'omble de fontaine (*Salvelinus fontinalis*) à des sites d'effleurement de la nappe phréatique et des sites d'eau courante dans l'écotone terre–lac, d'une part, et la topographie du sous-bassin versant autour d'un ensemble de 21 lacs au parc provincial Algonquin, Ontario, d'autre part. La valeur TI d'un site de rivage est en corrélation directe avec la différence de température entre le substrat et la surface du lac; ainsi, les valeurs plus élevées de TI sont associées à des apports plus grands d'eau souterraine. Les YOY de l'omble de fontaine ont tendance à occuper les sites du rivage qui ont des valeurs relativement élevées de TI. Les habitats phréatiques disponibles aux YOY de l'omble de fontaine sont relativement rares et seuls quelques sites sont utilisés de façon régulière au cours de l'année. Les grands lacs possèdent moins de sites d'habitat phréatique par unité de périmètre de rivage que les lacs plus petits. Une analyse de régression logistique et une sélection de modèle (d'après le critère d'information d'Akaike) indiquent que les chances de trouver des YOY de l'omble de fontaine augmentent de façon significative dans les sites d'eau courante et, en été, dans ceux où il existe une forte différence de température entre le substrat et la surface du lac. La plupart des sites d'eau courante utilisés par l'omble de fontaine ne se retrouvent pas sur le système de cartes de base de l'Ontario (Ontario Base Map System), mais ils ont été identifiés par la méthodologie TI.

[Traduit par la Rédaction]

Introduction

A multiscale approach linking site choices of fish at small scales to watershed processes that determine habitat distribution at larger scales is recommended for effective conservation of fish habitat (Folt et al. 1998; Caldow and Racey 2000; Jackson et al. 2001). Numerous studies highlight site choices of fish at microhabitat scales for assessing fish habitat. Scaling up can be difficult because processes linking habitat at different scales are themselves scale-dependent and complicated in nature (Bozek and Rahel 1992; Feist et al. 2003; Benda et al. 2004). Despite difficulties in linking habitat scales, recent research has demonstrated that fish distribution in watersheds is driven by multiscale factors (Thompson and Lee 2000; Rich et al. 2003). One fundamental multiscale feature of habitat for some fish species is the relationship between site-specific groundwater upwelling and watershed geomorphology and topography.

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Groundwater upwelling sites used by brook trout (*Salvelinus fontinalis*) for adult spawning and young-of-year (YOY) thermal refugia are essential habitats for lake-dwelling populations of this species (Curry et al. 1993; Blanchfield and Ridgway 1997; Biro 1998), though not in all locations throughout the species range (Curry et al. 2002). A large proportion of YOY brook trout cohorts in lakes occupy groundwater habitat in the form of seeps and streams at the lake margin (Curry et al. 1997; Biro 1998), an area we refer to as the land–lake ecotone. This habitat appears to be essential in the early development of brook trout cohorts in lakes. Mapping of these habitat locations is complicated by the scale mismatch between the geological features associated with seepage areas in the field (coarse sediment lenses sometimes less than 17 m; Curry and Devito 1996) and the scale of the available geologic information (e.g., the minimum size of mapping units of surficial geology in southern Ontario is approximately 50 m × 50 m).

Groundwater discharge zones around lakes are controlled by a number of physical parameters, including topography (Beven and Kirkby 1979), drainage basin geomorphology (Beven 1987; Devito et al. 1996), local geology (Quinn et al. 1991; Devito et al. 1996; Freer et al. 1997), and land use (Hartman et al. 1996; Johnson and Jones 2000). Local geology and bedrock topography appear to exert the greatest control on the dominant water flowpaths within lake basins on the Canadian Shield (Quinn et al. 1991; Power et al. 1999; Noguchi et al. 1999). This in turn affects small-scale factors such as water temperature in streams, seeps, and lake substrates at the land–lake ecotone.

Increased availability of digital elevation data has encouraged modeling of hydrologic and geomorphic processes at the landscape scale using topographic properties (Beven and Kirkby 1979; O'Loughlin 1986; Freer et al. 1997). This approach may be particularly appropriate on the Canadian Shield, where thin overburden (typically <1 m thick) and a close correlation between bedrock and surface topography means the latter provides a reasonable index of the hydraulic gradient for shallow groundwater systems (Buttle et al. 2001). This has direct relevance for mapping groundwater habitat used by brook trout, since their distribution and abundance are governed both directly by small-scale groundwater habitat and indirectly by large-scale habitat influenced by a basin's hydrogeologic and topographic characteristics.

Topographic indices (TIs) can be derived in a geographical information system (GIS) on the basis of some or all of the following aspects of basin morphology: elevation, flow direction, flow accumulation, gradient, and aspect. These parameters have been used to model hydrological processes within a basin and overall basin streamflow (e.g., Beven and Kirkby's (1979) TOPMODEL) and to describe ecological patterns as a function of physical process (Wilson and Gallant 2000). A commonly used TI is Beven and Kirkby's (1979) $\ln(a/\tan\beta)$ index of relative saturation within a basin, where a is the upslope area contributing water to a given cell per unit contour length, and β is the cell's slope angle. Correlations between $\ln(a/\tan\beta)$ and water table elevation across a range of landscapes suggest that the TI may assist in predicting groundwater discharge sites at the lake margin (e.g., Burt and Butcher 1985; Moore and Thompson 1996; Buttle et al. 2001). This GIS modeling technique is important given that there are presently no tools available to identify small-scale hydrological features at large spatial scales provided by base map systems (typically 1:10 000 or 1:20 000 scale). The TI method could potentially locate these groundwater habitats and delineate the catchment areas needed to support them.

The TI approach for determining groundwater sites in the land–lake ecotone can link different habitat scales that are relevant for conserving brook trout habitat. To establish this link, we first show the pattern of re-use of seep and stream habitats by YOY brook trout in two lakes over 3 years and demonstrate the relevance of the TI approach in mapping groundwater sites at a relatively fine scale (~25 m × 25 m) in the land–lake ecotone. We then determine the extent of groundwater habitat use by YOY brook trout (presence or absence) on a large spatial scale through a comparison of the subwatersheds of 21 brook trout lakes. A GIS model of Beven and Kirkby's (1979) TI is developed to map the subwatersheds contributing groundwater to sites at the land–lake ecotone.

Materials and methods

Study lakes and survey methods

Twenty-one lakes in Algonquin Park, Ontario, were surveyed in both spring and summer to determine the distribution and extent of groundwater habitat use by YOY brook trout (Table 1). A total of 273 km of shoreline was surveyed among all the lakes. Surveys in each year started with small lakes and moved to larger lakes as the spring season progressed because of the difference in littoral warming of small lakes relative to large lakes. Spring surveys took place between mid-May and early June in each lake, and the summer survey occurred in July. Two lakes in the 21 lake set, Mykiss Lake and Stringer Lake, were surveyed over a 3 year period (2000–2002) to assess the consistency of stream and seep habitat use among years during the spring and summer surveys.

Perimeter surveys of each lake were conducted by foot and by canoe to locate groundwater habitat at the lake edge. Streams and seeps were the two types of groundwater habitat observed at the lake margins. A stream is a channelized inflow to the lake whose baseflow (background discharge between flood events; Hornberger et al. 1998) is from groundwater sources or a lake higher up in the drainage network. We define a seep as a point source (no greater than 10 m in length) of groundwater; generally, these are saturated zones where groundwater is discharged through seepage faces. Seep habitats were detected either by the presence of near-inundated, terrestrial habitat along the shore or by the sound of water percolating from land at the lake edge.

When a stream was encountered, depth, width, temperature, and location (using a global positioning system, GPS) were measured at the beginning of each stream segment in the thalweg. Streams were divided into sections (0–10, 10–30, 30–50, 50–70, 70–90, 90–120, 120–150, and 150–200 m) beginning at the lake's edge. These measurements were also made at seep habitats, with the exception of width given the difficulty of determining and measuring the seepage face width. Each stream segment was visually assessed for brook trout YOY presence by a single observer (J.A. Borwick) using polarized glasses, as well as by two

Table 1. Physical and hydrological characteristics of the 21 lakes surveyed.

Lake	Latitude (°N)	Longitude (°W)	Lake surface area (ha)	Perimeter (km)	Total watershed area (ha)	Maximum subcatchment area (ha)
Big Trout	45°50′04″	78°06′38″	1518.7	50.5	12 438.1	5205.3
Hogan	45°52′37″	78°29′51″	1303.2	48.8	7 106.5	3392.8
Dickson	45°46′52″	78°12′28″	974.7	33.3	4 380.0	1644.9
White Partridge	45°50′04″	78°06′38″	574.4	14.2	3 664.8	2001.1
Big Crow*	45°49′52″	78°26′11″	440.0	16.6	7 443.5	5604.7
Proulx*	45°46′37″	78°23′47″	339.1	15.7	4 589.7	2529.2
Redrock	45°46′01″	78°28′19″	287.6	9.9	1 791.4	978.4
McKaskill	45°43′37″	78°02′40″	278.0	21.6	1 018.8	147.3
Philip	45°55′12″	78°24′18″	181.9	8.7	10 831.4	6847.1
Harry	45°26′00″	78°27′00″	114.1	6.1	1 755.8	1454.2
North Grace*	45°26′37″	78°31′09″	102.7	12.3	922.9	284.6
Rence	45°24′59″	78°28′04″	95.6	6.4	1 454.2	579.4
Little Crow	45°48′47″	78°27′07″	73.8	5.5	5 523.1	4580.5
Nepawin	45°47′14″	78°27′55″	34.9	3.2	286.8	85.7
Stringer	45°25′44″	78°30′40″	33.5	3.6	262.3	94.5
Chipmunk	45°41′00″	78°12′00″	30.0	3.5	224.3	47.0
Scott	45°29′10″	78°43′22″	27.6	4.0	77.8	8.1
Frank	45°26′05″	78°28′23″	25.9	2.3	421.2	141.6
Mykiss	45°40′00″	78°14′00″	24.0	2.5	280.1	127.2
Florence	45°26′29″	78°28′32″	20.2	2.3	141.6	81.8
Charles	45°54′16″	78°23′53″	12.3	2.4	60.1	7.1

*Catchment area of upslope contributing lakes were manually added to the calculation of total watershed and maximum subcatchment areas.

field assistants as they obtained physical measurements of the previous habitat segment. If YOY presence was not determined immediately, each segment was observed for 15 min. Special attention was paid to undercut banks, slack water, and back eddies that YOY are known to inhabit and are habitats where the visual technique performs well (Heggenes et al. 1990). This visual technique has been used previously to determine habitat use (Dolloff and Reeves 1990; Heggenes et al. 1990), record behavioural observations (McLaughlin et al. 2000), and estimate abundance (Bozek and Rahel 1991; Knight et al. 1999). We assumed, as did the previous investigators, that YOY returned to normal holding behaviour throughout the course of the segment's survey 5–10 min after an initial approach to the habitat and that YOY would have been visually identified if present. Streams were surveyed to a maximum of 200 m upstream of the lake or until YOY were absent in two consecutive sections past a major barrier in the stream, such as a small waterfall. We calibrated our visual technique by electrofishing 51 stream segments (from eight streams) and two seeps in 10 different stream and seep habitats on eight different lakes in Algonquin Park. Our visual technique was 83% correct in identifying the presence or absence of YOY brook trout within stream reaches, correctly classifying 8 of the 10 habitats. However, our visual technique was least accurate in high-gradient streams, since electrofishing revealed YOY brook trout in seven segments from a large, high-gradient stream that were visually classified as not containing YOY.

The topographic index method

The $\ln(a/\tan\beta)$ TI was calculated using the Spatial Analyst extension of ARCVIEW 3.1 (ESRI Inc., Redlands, California) based on a 25 m unfilled, flow-corrected digital elevation model (DEM) for Algonquin Park. Slope (β, in degrees) of each grid cell was calculated as the greatest slope angle from each cell to its 3 × 3 neighbourhood (Quinn et al. 1991). Upslope area contributing water to a given cell (a) was calculated using the Eight Direction Pour Point Model (commonly referred to as D8). Direction of steepest descent (i.e., the direction water will flow out of each cell) was determined, and a single cell flow accumulation grid was then generated to determine a. This generated a flow accumulation area (henceforth referred to as FA) for each cell.

The most important assumption underlying our use of TIs to characterize basin hydrological conditions was the accuracy of the DEM and its representation of the local topography with few errors (Quinn et al. 1991). As in many other studies, surface topography is used as a surrogate for the hydraulic gradient across the landscape. We also assume that the water table for any given cell for which the TI was determined is at steady state (i.e., inflow of groundwater is equal to the outflow). Hydraulic conductivity and soil transmissivity are also assumed to be uniform throughout the basin. Finally, all cells with the same TI value are assumed to behave in a hydrologically similar fashion. These assumptions have been questioned elsewhere (e.g., Moore and Thompson 1996; Wise 2000; Beven and Freer 2001). We feel they are reasonable assumptions given the absence of detailed information on hydrological and geological conditions around the lake margins and our interest in predicting relative differences in potential for groundwater discharge to the surface rather than actual water fluxes.

Slope, FA, and TI values were calculated for each cell around the lake perimeters at the land–lake ecotone (i.e., the terrestrial cell nearest to the lake). The lake's perimeter was hydrologically corrected to remove DEM and resolution error based on the flow accumulation grid. For example, DEM elevations may cause water to flow along shorelines instead of discharging into the lake at the point of contact with inlet streams. The GPS locations of field-observed habitat were then superimposed on the spatial distribution of FA and TI, allowing the TI values of these habitats to be obtained. The shoreline cell adjacent to the GPS location of the field-observed habitat was assumed to contain the habitat. However, sometimes a given cell was designated as habitat as a result of DEM resolution, map inaccuracies, and GPS error when the adjacent cell clearly contained the seep or stream habitat. In these cases, cells assigned as habitat were moved one cell on either side of the original GPS-located cell to whichever had the larger TI value.

Calibrating the topographic index

The utility of the TI in identifying groundwater sites was assessed in the spring and summer of 2001 in Mykiss and Stringer lakes based on seepage rates and temperature differences between the lake water surface and substrate at sites with a range of TI values. Data were collected using seepage meters constructed and installed following Lee (1977), with modifications for use of plastic barrels (0.57 m diameter) and prefilling the collection bags with 1 L of water, as outlined in Blanchfield and Ridgway (1996). Seepage meters were installed in cells containing each of the field-observed habitats in Stringer and Mykiss lakes, in addition to randomly chosen cells encompassing a range of TI values. Meters were randomly placed within each cell at lake depths ranging from 0.25 to 0.84 m. Some TI values were not calibrated because of presence of bedrock or depth limitations associated with snorkeling. Difficulties encountered when trying to obtain a good seal between the barrels and the substrate in soft and gravelly sediments led to the installation of 9.8 cm diameter pipes in the calibration cells, which could be inserted deeper into the sediment than was possible with the barrels. Collection bags on the pipes were left for an average of 24 h compared with 3 hours for the barrels. Both pipes and barrels were installed in spring 2001, and measurements were taken bimonthly during the 2001 field season (May–July).

Lake surface temperatures were compared with sediment temperatures beside the seepage meters concurrent with seepage meter measurements. Shallow groundwater temperatures often approximate the local mean annual air temperature (Todd 1980), and groundwater discharge into a lake during the open water period would be expected to reduce sediment temperatures relative to the warmer lake surface water. Sediment temperatures were taken at approximately 1–3 cm into the sediment with a hand held thermometer (±0.5 °C). Essington et al. (1998) and Sorensen et al. (1995) also used comparisons of water surface and sediment temperatures as an index of groundwater upwelling.

All field sampling periods during this study were warmer than the 30-year mean (Environment Canada 1993), with the exception of July 2000, July 2001, and May 2002. All three field seasons were extremely dry compared with the 30-year normal monthly precipitation for May, June, and July. Months with notable precipitation deficits were June 2000 and 2001, April 2001, and July of all 3 years (43.5–65.0 mm below the 30-year normal rainfall for July; Environment Canada climate station, 45°95′N, 77°31′W).

Data analysis and model selection

Logistic regression was used to evaluate the presence or absence of brook trout as a function of landscape and mapped and field-based information at sites with groundwater flow in the land–lake ecotone. Four parameters were used in the set of logistic regression models. First, the TI of each shoreline cell was used because it incorporated important watershed variables, such as slope and contributing area. Second, presence or absence on the Ontario base map (OBM) was used because it is the basis for designating habitat protection in Ontario watersheds. Third, site designation as a seep or stream (Inflow), regardless of its presence in the OBM, was used. Habitat type (stream or seep) was correlated with presence on the OBM (streams more likely to be present), but site presence or absence on the OBM was still included to determine the relative contribution of the OBM map information towards site designation. Finally, water temperature difference between the seep or stream in the land–lake ecotone and the adjacent lake surface (Δtemp) was used to represent site differences in the relative coolness of seeps or streams.

The global model (all parameters present) was evaluated for goodness-of-fit (GOF) as a first step in model analysis. A Pearson χ^2 GOF statistic was calculated for the model and a nonsignificant P value ($P > 0.10$) indicated reasonable fit. Pearson χ^2 residuals were plotted against predicted probabilities from the global model to identify outliers. This identified six sites that were removed from analysis (see below). The fit of the global model was adequate (Pearson χ^2 GOF, $P = 0.35$) so the model set was also assumed to provide an adequate fit (Burnham and Anderson 1998).

Models were evaluated based on the information-theoretic approach (Burnham and Anderson 1998):

$$\mathrm{AIC} = -2\ln[L(\hat{\theta}\,|\,\mathrm{data})] + 2k$$

where $\ln[L(\hat{\theta}\,|\,\mathrm{data})]$ is the maximized log likelihood of the parameters given the data, and k is the number of estimated parameters in the model. The quasi-likelihood method of Akaike's Information Criterion (i.e., $\mathrm{QAIC_c}$) was used, adjusted for sample sizes.

$$\mathrm{QAIC_c} = \frac{-2\ln[L(\hat{\theta}\,|\,\mathrm{data})]}{\hat{c}} + 2k + \frac{2k(k+1)}{n-k-1}$$

where n is the sample size and $\hat{c}$ is the variance inflation factor (χ^2 GOF from the global model divided by degrees of freedom) (Burnham and Anderson 1998). The brook trout presence or absence data showed evidence of overdispersion ($c > 1.0$), so QAIC was employed.

Models were ranked based on the difference between the model with the lowest value of $\mathrm{QAIC_c}$ and the $\mathrm{QAIC_c}$ for each candidate model. The $\Delta\mathrm{QAIC_c}$ values were then used to order models (Burnham and Anderson 1998), and the weight of evidence for each model, r, was based on the Akaike weights, w_i.

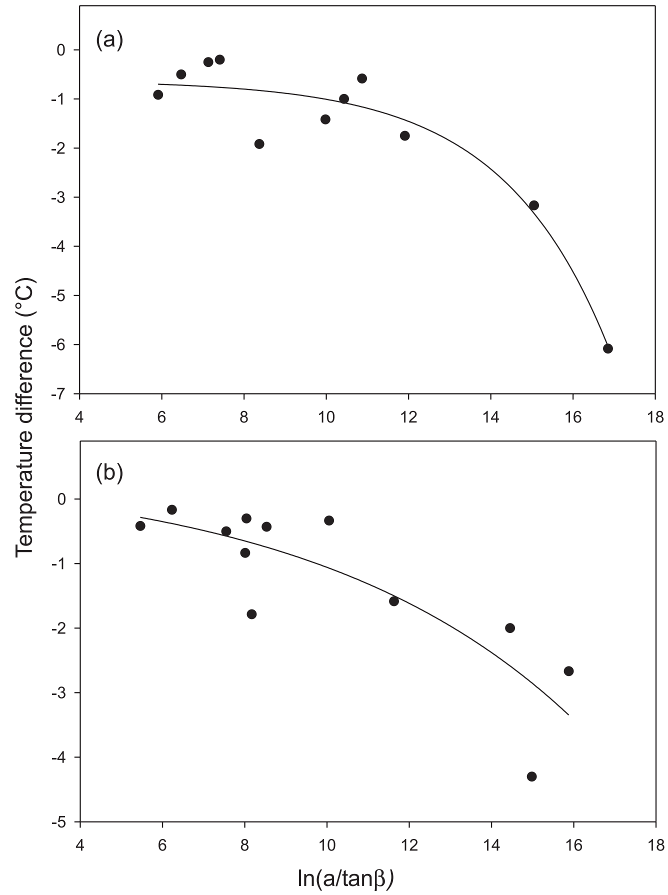
$$w_i = \frac{\exp(-\Delta \mathrm{QAIC}_{c_i}/2)}{\sum_{r=1}^{R} \exp(-\Delta \mathrm{QAIC}_{c_r}/2)}$$

Akaike weights provide a means of comparing the relative weight of evidence for selecting one model over another. Specifically, the Akaike weight refers to the $L(M_i | \text{data}) / L(M_{\Delta \mathrm{QAIC}=0} | \text{data})$, where M_i refers to model i, and $M_{\Delta \mathrm{QAIC}=0}$ refers to the best model in the candidate model set.

Akaike weights also allow for model-averaged parameter estimates and associated standard errors (SEs). A weighted average value for each logistic regression coefficient (and SE) was calculated from all relevant models in the candidate set that contained the specific parameter, paying particular attention to recalculating weights for each parameter from the model set that contained the parameter (i.e., weights for a particular parameter sum to 1.0; Burnham and Anderson 1998). The SE for model-averaged parameter estimates was calculated using a variance inflation equation (eq. 4.11, p. 135, Burnham and Anderson 1998). This approach incorporated model uncertainty in the error estimate.

Confidence intervals for odds ratios from the logistic regression analysis were used to determine the significance of each variable in the model. In this case, this is equivalent to testing $\beta = 0$ or in odds ratio format, $e^0 = 1$ (Hosmer and Lemeshow 2000). Confidence intervals (CI, 90%) were calculated as $\exp(\beta_i \pm 1.64 \times \mathrm{SE}(\beta_i)$, with estimates of β_i and $\mathrm{SE}(\beta_i)$ (SE, standard error) for the composite model based on model averaging (Burnham and Anderson 1998). Following Rich et al. (2003), we interpreted the magnitude of statistically significant predictors at the lower bound (for positive coefficients), mean, and the upper bound (for negative coefficients).

Fig. 1. Mean difference between sediment and surface water temperatures at the seepage meter barrels vs. ln(a/tanβ) for Mykiss (a) and Stringer (b) lakes during 2001.



Results

Calibration of the topographic index

No relationship between flow amount or direction and the TI value for each cell was observed using seepage meters in the shallow littoral zone. Seepage rates were highly variable from week to week and from barrel to barrel, and no association between rainfall events and seepage amounts or direction was evident. There was a significant ($R^2 = 0.92$, $p < 0.0001$ for Stringer Lake; $R^2 = 0.71$, $p < 0.0004$ for Mykiss Lake) nonlinear relationship between TI and the difference between sediment and lake surface water temperatures for both lakes, with a stronger relationship for Mykiss Lake (Fig. 1). Temperature differences were not the result of thermal stratification of the water column, since the maximum water depth at which meters were installed was 0.84 m. Unexplained variation in differences between surface and sediment temperatures was likely associated with variations in sediment type as well as the amount of overburden at and near the calibration site, which combined to determine the site's ability to sustain groundwater flow. Larger TI values suggested relatively greater groundwater upwelling, particularly for TI values ≥8–9.

TI values for YOY brook trout habitat

Frequency distributions of TI for lakeshore cells in both Mykiss and Stringer lakes were right-skewed (Fig. 2), with a minimum of 5.29 for both lakes, means of 7.95 ± 1.76 (Mykiss Lake) and 7.97 ± 1.63 (Stringer Lake), and maxima of 16.85 (Mykiss Lake) and 15.88 (Stringer Lake). Also indicated is the percentage of cells with a given TI used as habitat by YOY brook trout at least once during the 3-year survey period (Fig. 2). The smallest TI of YOY habitat was 8.17 (Stringer Lake) and 8.97 (Mykiss Lake). Lakeshore cells with large TI were used by YOY as habitat at least once during 2000–2002.

Water temperature at groundwater habitats in the land–lake ecotone

Habitat temperatures on Stringer and Mykiss lakes for spring and summer 2001 were greater than for either 2000 or 2002 (Fig. 3), coinciding with warmer climatic conditions in 2001. The surface temperatures during a survey were similar between the lakes, with seeps generally cooler than stream habitats for brook trout (Fig. 3). Stream and seep habitats for YOY in Mykiss Lake were colder than those of Stringer Lake in all seasons of all years, suggesting that habitat conditions on Mykiss Lake were more stable and indicative of greater groundwater inputs. Water flow ceased in four seeps

Fig. 2. Frequency distributions of topographic index (TI; ln(a/tanβ)) for lakeshore cells in Mykiss (a) and Stringer (b) lakes and the percentage of cells in a given TI range (solid circles) that were used as young-of-year brook trout (*Salvelinus fontinalis*) habitat at least once during the 2000–2002 period.

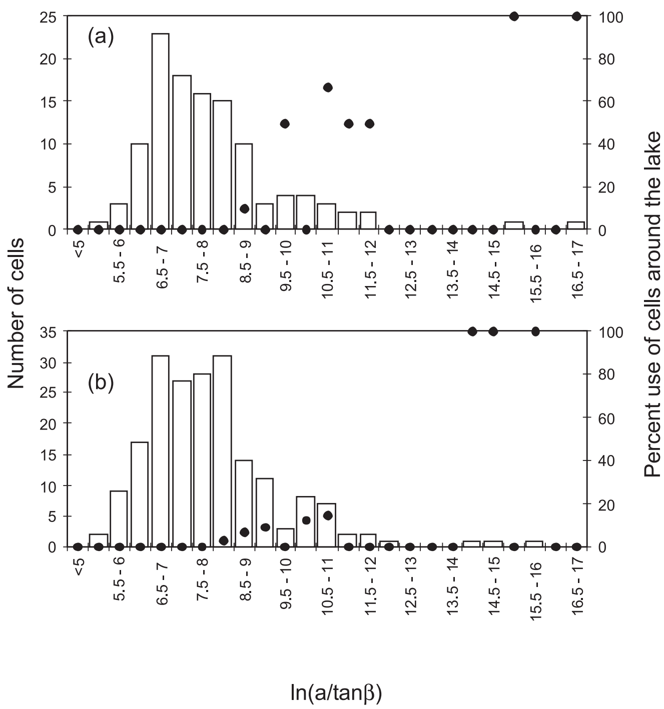
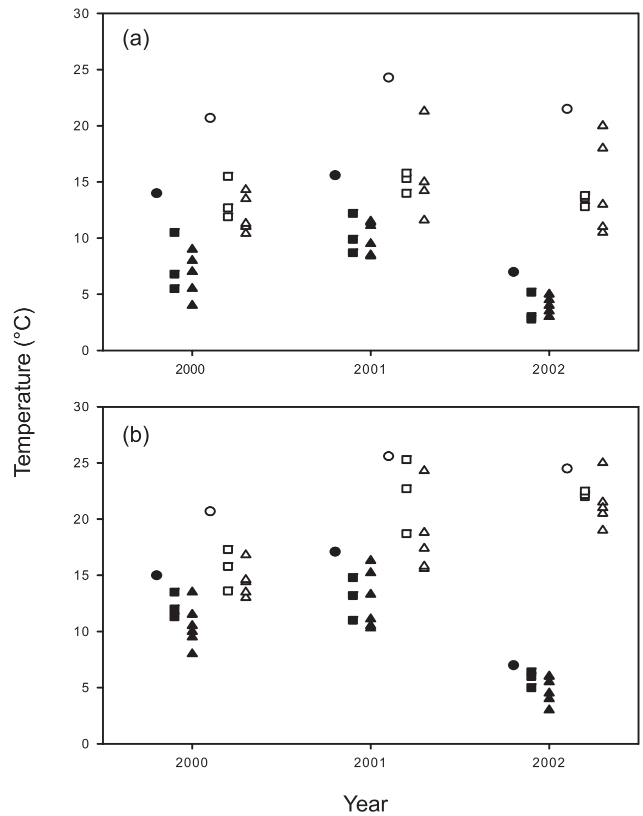


Fig. 3. Lake surface (circles), stream (squares), and seep (triangles) temperatures measured in 2000, 2001, and 2002 for Mykiss (a) and Stringer (b) lakes. Spring, solid symbols; summer, open symbols.



at various times during summer surveys. One site on Stringer Lake (Stringer #8) was dry in summer 2000 and 2001 and did not dry up in 2002. Another site (Stringer #5) dried in 2002 that had not dried previously. Two seeps in Mykiss Lake (Mykiss #5 and Mykiss #7) were dry in summer 2001 only.

Patterns of YOY groundwater habitat use among years

In Mykiss and Stringer lakes, seepage and stream sites provided a range of available habitat from sites present in spring and summer of each year to sites that were used infrequently or dried during summer. All Mykiss Lake stream and seep sites and eight of nine sites in Stringer Lake were used in spring and (or) summer by YOY during the 3-year survey (Table 2). Only two sites in Mykiss Lake (Mykiss #2–3 and #4) were used each spring and summer, while only one site in Stringer Lake (Stringer #10) was used each spring and summer. These sites had relatively large contributing areas to the groundwater habitat (Table 2; Mykiss #2–3, 15.3 ha; Mykiss #4, 127.19 ha; Stringer #10, 20.19 ha). The clearest difference between lakes was the more widespread use of seep and stream habitat in summer in Mykiss Lake relative to Stringer Lake, possibly reflecting a greater groundwater flux in Mykiss Lake.

All habitats found on Mykiss Lake in 2000 were used by YOY in either the spring or summer (Table 2). This was generally the case in the other years in Mykiss Lake, except for two sites that ceased to flow in 2001. One of Stringer Lake's habitats (Stringer #2) was never used by YOY in any year (Table 2), while Stringer #4 was used by a single YOY only in summer 2002. Stringer sites #2 and #4 had the smallest TI values in the two-lake data set (Table 2).

It is difficult to discern a pattern among sites with small contributing areas and the presence or absence of seepage. This may be indicative of a lower threshold for groundwater flow (based on TI) in small subwatersheds at the land–lake ecotone. In Mykiss Lake, two sites not occupied in some summers had relatively small contributing areas (Mykiss #5, 3.63 ha; Mykiss #7, 1.0 ha), while other sites occupied in two or more seasons also had small contributing areas (Mykiss #9, 1.31 ha; Mykiss #10 2.06 ha). The lack of any clear pattern among sites with small contributing areas was also observed on Stringer Lake with some sites rarely used (Stringer #2, 0.69 ha; Stringer #4, 0.56 ha), while other sites appeared to be important based on the frequency of YOY occupation (Stringer #3, 0.19 ha; Stringer #7, 1.31 ha). Overall, only a few seepage stream sites provided habitat for YOY brook trout on a consistent basis in spring and summer.

Habitat rarity

Few sites around Mykiss and Stringer lakes served as possible groundwater-based habitat in the land–lake ecotone during spring and the critical summer months when littoral zone temperatures were high (7.9% (9/114) of total cells around Mykiss Lake; 4.6% (9/196) of total cells around Stringer Lake). The rarity of this habitat type was more pronounced in summer, when fewer sites were occupied in 2 or more

Table 2. Young-of-year brook trout (*Salvelinus fontinalis*) presence or absence at seepage and stream sites at the land–lake ecotone of Mykiss and Stringer lakes, 2000–2002.

				2000		2001		2002	
Site no.	Type	Subcatchment area (ha)	ln(a/tanβ)	May	June	May	June	May	June
Mykiss Lake									
1	Seep	10.81	10.73	○	●	●	●	○	●
2–3*	Stream–seep	15.31	11.91	●	●	●	●	●	●
4	Stream	127.19	16.85	●	●	●	●	●	●
5	Seep	3.63	11.00	●	●	○	X	●	●
6	Seep	6.56	10.87	●	○	●	●	○	○
7	Seep	1.00	9.69	●	○	○	X	●	●
8	Stream	53.81	15.05	●	○	○	●	○	●
9	Seep	1.31	9.98	●	●	●	○	●	●
10	Seep	2.06	8.97	●	○	●	●	●	●
Stringer Lake									
2	Seep	0.69	8.01	○	○	○	○	○	○
3	Seep	0.19	8.53	●	●	●	○	●	●
4	Seep	0.56	8.17	○	○	○	○	○	●
5	Seep	7.25	10.05	●	○	●	○	●	X
6	Stream	21.13	14.45	●	○	●	●	●	○
7	Seep	1.31	9.16	○	●	○	●	●	●
8	Seep	2.44	10.95	●	X	○	X	●	○
9	Stream	94.50	15.88	○	○	●	○	●	○
10	Stream	20.19	14.98	●	●	●	●	●	●

Note: Solid circles represent sites where brook trout are present; open circles represent sites where brook trout are absent. An X represents sites that were dry.

*Adjacent sites.

Table 3. The number of cells (25 m × 25 m resolution) on the perimeter of each lake where brook trout (*Salvelinus fontinalis*) were observed in nearshore habitat.

Lake	No. of lake cells	No. of cells with streams	No. of cells with seeps	Percentage of lake cells as stream or seep habitat	No. of stream–seep habitats used by brook trout	Percentage of lake cells occupied by brook trout
Big Trout*	2627	12	8	0.8	3	0.1
Hogan	2350	8	4	0.5	4	0.2
Dickson	1589	9	9	1.1	9	0.6
White Partridge	704	8	5	1.8	3	0.4
Proulx*	809	8	6	1.7	1	0.1
Redrock	674	9	4	1.9	6	0.9
McKaskill	994	3	8	1.1	2	0.2
Philip*	473	8	5	2.7	2	0.4
Harry*	275	3	3	2.2	4	1.4
Rence	351	8	2	2.8	7	2.0
Little Crow*	256	3	3	2.3	1	0.4
Nepawin	155	2	5	4.5	2	1.3
Stringer†	196	3	6	4.6	6	3.1
Chipmunk	189	6	5	5.8	8	4.2
Scott*	194	0	7	3.6	2	0.5
Mykiss*†	114	3	6	7.9	7	6.1
Charles	93	0	5	5.4	5	5.4

Note: Data represent the relative representation of stream or seep habitat in the land–lake ecotone and the percent occupancy by young-of-year brook trout.

*One or more cells around the lake contained two field-observed habitats.

†2001 survey results.

years of the survey (6.1% (7/114) of total cells around Mykiss Lake; 3.1% (6/196) of total cells around Stringer Lake).

The survey of 21 lakes revealed relatively few groundwater habitats (seeps and streams) around lakes. For individual lakes, the number of observed streams ranged from 0 to 12 and the number of seeps from 2 to 9 (Table 3). In total, 93 stream and 91 seepage habitats were detected among the lake set (N = 184 habitats). These sites range from 0.5% to 7.9% of the total lake margin habitat (Table 3). YOY brook trout were found in 72 of these sites (streams and seeps combined, 39.1%) in either spring or summer, with brook trout found in 49 of 93 (52.7%) streams and in 25 of 91 (27.5%) seeps. Only 34 of the 72 occupied stream or seep sites (47.2%) had YOY brook trout present in both spring and summer (34 sites represents 18% of all sites surveyed). Not all habitats observed in the spring were present in the summer, with eight streams (7.0%) and 42 seeps (35.9%) becoming dry as the season progressed.

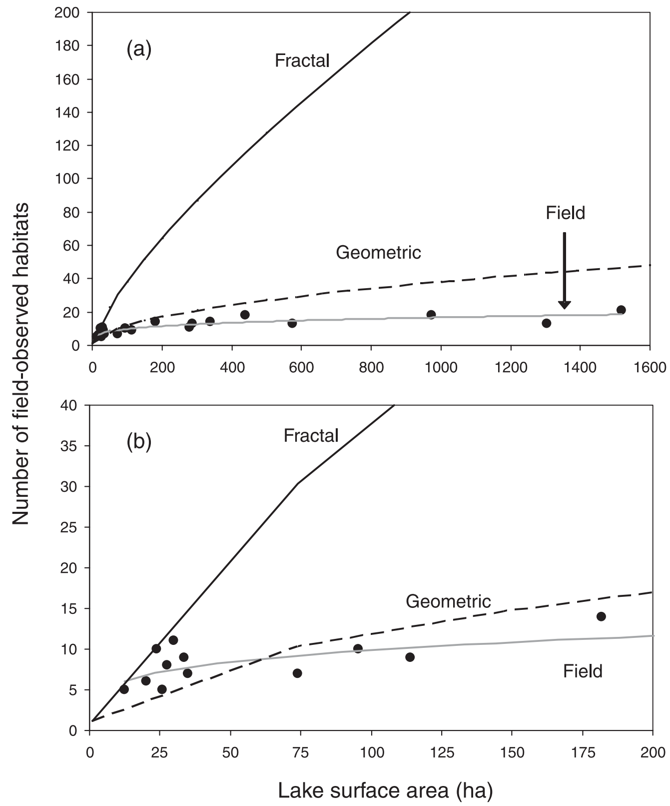
Lake size comparisons

Relatively few of the groundwater habitats (streams or seeps) in the land–lake ecotone were used by YOY brook trout during the lake surveys (Table 3), which may be a function of lake surface area. Lakes with surface areas <100 ha had more stream and seep habitats occupied by YOY brook trout (mean proportion of sites used = 0.53; N = 9 lakes) than 100 ha lakes (mean proportion of sites used = 0.30; N = 8 lakes). Big Crow, North Grace, Frank, and Florence lakes were excluded from this comparison because YOY brook trout were not observed using shoreline habitats (Table 1). Brook trout are relatively rare in three of these lakes (North Grace, Florence, and Frank), which may account for not finding YOY during the spring and summer surveys. Big Crow Lake has a large river inlet and outlet, and YOY may have resided in these systems and their tributaries rather than in the lake itself.

To further examine this lake size effect, we compared the detected number of stream and seep habitats with lake surface area. The rate of increase in groundwater habitats in the land–lake ecotone declined with increasing lake surface area (Fig. 4*a*). Declines in the frequency of this habitat type could be expected with increasing surface area based on two models of scale. First, habitat frequency along lakeshores can decrease in a fractal relationship based on Kent and Wong's (1982) observed change in shoreline complexity with increasing lake size (exponent = 0.75). Alternatively, habitat frequency can decline in a simple geometric pattern related to changes in a circle's area as a function of an expanding circumference (exponent = 0.5). Our lake survey data did not fit either of these alternatives (Fig. 4*a*), and frequency of groundwater habitats in the land–lake ecotone declined with increasing lake surface area to a larger extent than suggested by either of the alternative models (number of habitats = $3.42 \times \text{surface area}^{0.23}$; SE exponent = 0.035).

This general pattern does not hold for lakes <200 ha (Fig. 4*b*), which fall between the fractal and geometric models of increasing habitat frequency with increasing lake area. The number of field-observed habitats departs from a fractal relationship beyond a lake surface area of ~50 ha while diverging from the geometric relationship at ~200 ha.

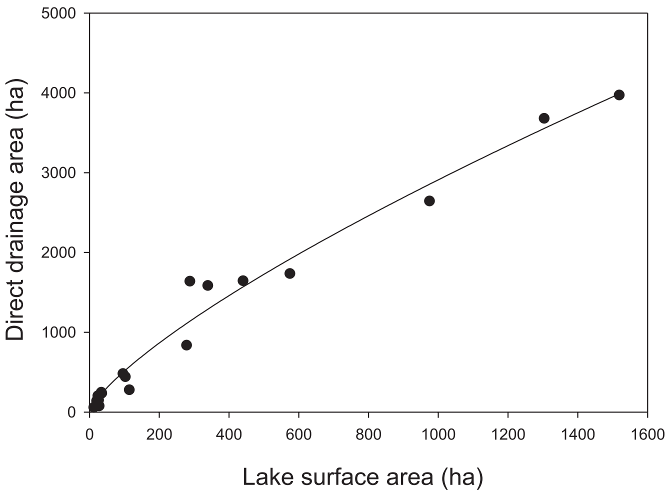
Fig. 4. The relationship between lake surface area and the number of streams and seeps at the lake edge under a fractal (exponent = 0.75), geometric (exponent = 0.5), and field-observed patterns: (*a*) the entire data set across all lakes; (*b*) the observed pattern closer to the origin in the lake data set.



One explanation for this relationship between lake surface area and habitat frequency is an increase in the complexity of drainage networks of streams discharging to larger lakes relative to small lakes. We assessed this by relating the direct drainage area of each lake (the addition of all subcatchments draining into a given lake, not including the catchments of other lakes higher up in the drainage network) to lake surface area. This direct drainage area represents the maximum local recharge area that contributes groundwater discharge to the lake at streams and seeps. The significant positive relationship between direct drainage area and lake surface area (direct drainage area = $15.97 \times \text{lake surface area}^{0.75}$; SE (exponent) = 0.042; Fig. 5) indicates that this maximum local recharge area does not increase in direct proportion to lake surface area, which would be indicated by an exponent of 1.0. There was a positive correlation between lake area and the number of streams, which includes streams draining lakes and their catchments higher up in the drainage network (r_s = 0.74; p < 0.001; N = 21), but not between area and number of seeps (r_s = 0.34; p = 0.133; N = 21). Therefore, the number of groundwater habitats around lakes increases with lake surface area until a surface area is reached, above which subcatchments are increasingly drained by higher-order stream networks. In smaller lakes, individual subcatchments drain directly to the lake as either seeps or first- or second-order streams.

We combined all stream and seep habitats for those lakes in which YOY brook trout were found (Table 3; total N =

Fig. 5. The relationship between lake surface area and direct drainage area. Removal of North Grace and Philip lakes improved the fit of the relationship.



184) to assess the feasibility of TI thresholds for designating sites as potential groundwater-based habitats for YOY brook trout along the lake edge. The minimum TI or FA associated with a stream or seep in each lake was taken as the lower threshold for detecting a site used by YOY brook trout in each lake (Table 4). Minimum TI values with brook trout present ranged from 7.62 (Redrock Lake) to 15.74 (Little Crow Lake). For the lake set, most of the seep and stream habitat in the land–lake ecotone was below the minimum observed TI value for brook trout presence for each lake (mean 89.4% of lake cells below minimum; 95% CI, 83.2%–95.6%). A similar pattern was observed for FA to cells at the lake edge. The minimum contributing area of subwatersheds connected to lake edge cells with YOY brook trout present was highly variable (mean, 39.6 ha; 95% CI, 4.4–74.8 ha) but consistently fell within the top percentiles of contributing subwatershed areas in most lakes (Table 4; mean 89.9%; 95% CI, 82.0%–97.8%). Clearly, subwatersheds contributing to the single outlet cell of seeps and streams at the land–lake ecotone and supporting the presence of YOY brook trout represent a small proportion of all subwatersheds draining to a lake. In most cases, 80%–90% of all lake edge cells do not have subwatersheds generating seeps or streams for use by YOY brook trout.

Model analysis

Logistic models of YOY brook trout presence or absence in seeps and streams were used to assess the relative influence of variables capturing large-scale features of the watershed present at the land–lake ecotone as well as variables that reflect site-specific features. At the larger watershed scale, TI and presence or absence of a site on the OBM represented variables capturing landscape elements contributing to lakeshore sites. Inflow (0 = seep, 1 = stream) and Δtemp (difference between lake and seep–stream temperatures) represented conditions encountered by YOY brook trout at the site-specific scale.

The initial model runs indicated that the TI had a negative coefficient ($\beta = -0.256$; SE = 0.113; both model averaged) and a significant odds ratio (0.774; 90% CI = 0.643–0.931). The analysis indicated that a unit change in TI resulted in at least a 7.5% (1/0.931) decrease in the odds of finding YOY brook trout and on average would result in a 29% (1/0.774) decrease in the odds of finding YOY brook trout. This was puzzling, since other analyses showed stream habitats were important for YOY brook trout in lakes (Curry et al. 1997; see below). Six sites with TI > 17 were large streams in which no brook trout were observed near the lake margin. In our experience, the absence of brook trout in these locations could be attributable to detection problems associated with observing brook trout in relatively deep habitats. Because these sites likely represented a sampling problem of this kind, the analysis was rerun, excluding the six sites with TI > 17.

For spring and summer model sets (Table 5), AIC weights indicated that a number of models could plausibly account for brook trout presence or absence, since the difference among weights was relatively small. Only the variable Inflow (0 = seep; 1 = stream) significantly increased the odds of finding brook trout, with at least a 35% increase in the odds during spring (1.35/1.0) and a 274% increase in the odds during summer (2.74/1.0) in favour of streams over seeps (Table 6). This seasonal difference likely reflects the importance of stream habitats as refuge in the land–lake ecotone during summer and points to the relative importance of small streams over seeps as important habitat. The variable Δtemp had a significant odds ratio in summer only. There was at least a 10% decrease (1/0.9056) in the odds of finding brook trout in the summer with every 1 °C decrease in the difference between the lake and nearshore site water temperatures (i.e., seepage and stream sites becoming warmer relative to lake temperature). On average, however, the decrease in the odds of finding brook trout was 20% (1/0.8275) for every 1 °C decrease in the difference between lake and stream–seep temperatures (Table 6). The temperature difference between lake and stream–seepage sites that did not contain brook trout in the summer (mean –3.9 °C; 95% CI –4.9 °C, –2.8 °C; N = 88) was less than the difference between lake and stream–seepage sites with brook trout present (mean –7.1 °C; 95% CI –8.0 °C, –6.1 °C; N = 48).

Ontario base map vs. topographic index

Topographic information in the form of TI or presence of a stream in the OBM system did not increase the odds of finding brook trout in the spring or summer (Table 6). The current resolution of mapped information is therefore insufficient on its own for designating brook trout rearing habitat. This is particularly interesting since Inflow did permit sites with and without YOY brook trout to be distinguished in both seasons. The discrepancy between field-based observations of streams and mapped-based information on streams in the land–lake ecotone is the result of small streams used by brook trout being absent from the OBM.

Stream numbers around each lake based on the OBM system did not match the field-observed count of 16 of the 21 lakes. The OBM-based streams were derived from field observation and air photo interpolation, and the discrepancy noted here indicates a systematic underestimation in the interpretation of stream presence using air photo interpretation. A sharper discrepancy between the OBM information system and our field survey emerges if the number of seeps

Table 4. Minimum values for the topographic index (TI = ln(a/tanβ)) and flow accumulation and the percentage of total lake perimeter cells below these minimum values occupied by young-of-year brook trout (*Salvelinus fontinalis*).

Lake	Minimum ln(a/tanβ) value for lake cells occupied by brook trout	Percentage of lake cells below minimum ln(a/tanβ)	Minimum summer flow accumulation cells occupied by brook trout	Percentage of lake cells below minimum flow accumulation
Big Trout	13.06	97.5	763	99.4
Hogan	12.10	97.0	1187	99.5
Dickson	9.17	76.0	4	46.2
White Partridge	10.71	93.2	75	94.3
Proulx	16.35	99.6	4452	99.8
Redrock	7.62	55.0	5	60.7
McKaskill	12.80	97.4	1119	99.6
Philip	13.73	96.4	944	98.3
Harry	10.45	96.4	77	94.9
Rence	11.49	96.6	230	97.2
Little Crow	15.74	98.8	1356	98.8
Nepawin	8.16	81.9	11	74.2
Stringer	9.16	81.1	21	92.3
Chipmunk	12.06	96.8	415	97.9
Scott	10.28	88.7	64	97.9
Mykiss	8.96	73.7	33	88.6
Charles	10.15	93.5	27	89.2

Table 5. Model selection results for logistic regression using habitat variables recorded at streams or seeps in the 21 lake set.

Variable	Parameters (K)	$\Delta QAIC_c$	AIC weights
Spring model set			
Inflow, ln(a/tanβ)	3	0	0.174
Inflow, Δtemp	3	0.299	0.149
Inflow, OBM	3	0.312	0.148
ln(a/tanβ), OBM	3	0.658	0.125
Δtemp, OBM	3	0.780	0.118
ln(a/tanβ), Δtemp	3	1.544	0.080
Inflow, ln(a/tanβ), OBM	4	1.896	0.067
Inflow, ln(a/tanβ), Δtemp	4	2.062	0.062
Inflow, OBM, Δtemp	4	2.380	0.053
Inflow, ln(a/tanβ), OBM, Δtemp	5	3.995	0.024
Summer model set			
Inflow, Δtemp	3	0	0.188
Δtemp, OBM	3	0.314	0.161
ln(a/tanβ), Δtemp	3	0.839	0.124
Inflow, ln(a/tanβ)	3	0.953	0.117
Inflow, OBM	3	0.963	0.116
ln(a/tanβ), OBM	3	1.344	0.096
Inflow, Δtemp, OBM	4	1.997	0.069
Inflow, ln(a/tanβ), Δtemp	4	2.129	0.065
Inflow, ln(a/tanβ), OBM	4	3.050	0.041
Inflow, ln(a/tanβ), OBM, Δtemp	5	4.164	0.024

Note: Models are ranked based on the difference between the model with the minimum value for $\triangle QAIC_c$ (quasi-likelihood Akaike's Information Criterion) and the rest of the candidate model set. OBM, Ontario base map.

is included with the field-based stream count. Thus, most groundwater habitats used by YOY brook trout are not identified by current mapped information.

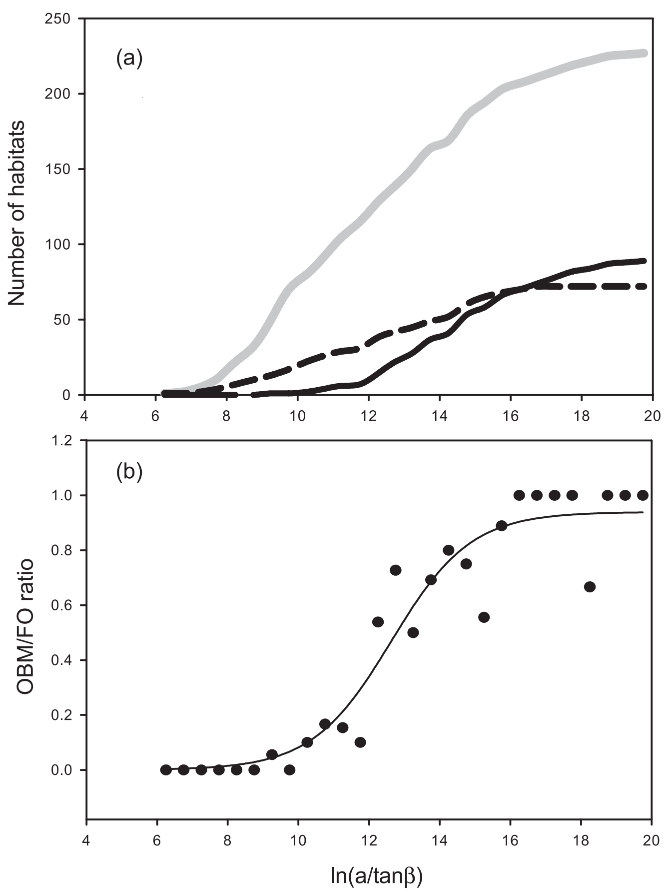
There appears to be a systematic omission of smaller habitat sites in the OBM system, as shown by comparing the cumulative count of lake perimeter cells with field-observed streams and seeps and the cumulative count of cells with either OBM-based streams or sites with YOY brook trout present (Fig. 6*a*). The OBM does not fully represent all available or occupied shoreline habitats with groundwater

Table 6. Model-averaged estimates and odds ratios from logistic regression models of brook trout (*Salvelinus fontinalis*) presence in springs and seeps.

Variable	Parameter estimate	SE	Odds ratio	90% CI for odds ratio
Spring				
Intercept	–0.3243	0.4343	0.7230	(0.3546, 1.4740)
Inflow	0.9829	0.4163	2.6722	(1.3501, 5.2890)
OBM	0.6834	0.6052	1.9806	(0.7341, 5.3438)
Δtemp	0.0237	0.0362	1.0240	(0.9650, 1.0866)
$\ln(a/\tan\beta)$	–0.0999	0.1257	0.9049	(0.7364, 1.1121)
Summer				
Intercept	–2.8044	1.7319	0.0605	(0.0035, 1.0366)
Inflow	2.1516	0.6968	8.5986	(2.7424, 26.9599)
OBM	1.2619	0.8972	3.5321	(0.8110, 15.3836)
Δtemp	–0.1894	0.0550	0.8275	(0.7561, 0.9056)
$\ln(a/\tan\beta)$	0.0524	0.1828	1.0534	(0.7808, 1.4222)

Note: SE, standard error; CI, confidence interval; OBM, Ontario base map.

Fig. 6. (*a*) The relationship between the topographic index (TI; ln(*a*/tanβ)) for streams and seeps observed at the lake edge and (*i*) the cumulative frequency distribution of field-observed stream and seepage sites (shaded line), (*ii*) the cumulative frequency distribution of sites occupied by young-of-year brook trout (*Salvelinus fontinalis*, broken line), and (*iii*) the cumulative frequency distribution of sites on the Ontario base map (solid line). (*b*) The relationship between TI and relative change in the concordance of field-observed (FO) streams and seeps and their presence in the Ontario base map (OBM). A low ratio of OBM sites to FO sites indicates absence of the site from the OBM system.



seepage at lower TI values (generally indicative of smaller habitats). However, stream habitats are not used as frequently as the OBM count of potential brook trout habitats at TI > 16 (Fig. 6*a*).

Another way to express the effect of under-representation of the field-observed habitats using the OBM system is to relate the number of habitats appearing on the OBM at a given TI value to the field-observed habitats at that TI (Fig. 6*b*). Few field-observed habitats appear on the OBM at small TI values, while essentially all field-observed habitats are mapped by the OBM at large TI values. The proportion of field-observed habitats that are used by YOY also increases significantly ($r^2 = 0.39$; $p < 0.002$) with increasing TI (TI range from 6.5 to 17) until TI = 17, beyond which habitats used by YOY were not detected by our field methods.

Discussion

Brook trout use groundwater habitat in a number of life history stages (Power et al. 1999), although not in all locations throughout their species range (e.g., Curry et al. 2002). Subadult brook trout (<20 cm in length) occupy habitat in the shallow nearshore zone of lakes and streams in spring and early summer (Curry et al. 1993; Venne and Magnan 1995; Biro 1998). A shift to cooler habitat occurs later in summer, in part because of competitive interactions (Tremblay and Magnan 1991) but certainly because of temperature requirements. Remaining in shallow habitat at groundwater discharge sites in the land–lake ecotone through warm summer months may be a response by YOY brook trout to predation risk in cooler littoral and sublittoral habitats of a lake. Groundwater habitat is relatively rare in the land–lake ecotone (Biro 1998; Curry et al. 1997; this study). Many of the streams and seeps that serve as YOY brook trout habitat in the Algonquin Park region of central Ontario do not appear on provincial map systems (e.g., OBM). This makes the protection of this unmapped habitat difficult.

We found greater TI values were associated with an increased difference between lake water and nearshore sediment temperatures, suggesting a positive, though nonlinear, relationship between TI and groundwater flux. Detailed surveys in two lakes also revealed that brook trout YOY preferred to use sites with large TI as habitat. Surveys of 21 lakes in Algonquin Park showed that small streams and seepage sites around lakes generally fell into the highest percentiles of TI values around lake perimeters. The frequency of YOY brook trout habitat declined as a function of lake size, likely because of the increasing order of stream networks in larger basins containing larger lakes (Benda et al. 2004). Our results demonstrate that small streams and seeps used by YOY brook trout in lakes can be identified using a TI based on a digital elevation model of Precambrian Shield landscapes. Many of these seeps and streams are present around a lake's shoreline but are missing from the OBM system. Given the large area of Precambrian Shield landscapes in central and eastern Canada (Gunn and Pitblado 2004), developing TI models of watersheds will provide a substantial step towards mapping fish habitat in lakes and rivers.

Although our results suggest that increasing TI values are associated with relatively cooler water temperatures and presumably greater groundwater fluxes, no YOY brook trout were observed in streams with TI > 17. There are two possible explanations. First, fish may not have been detected either because they moved upstream of the 200 m limit we used in our surveys or, if a barrier to upstream passage existed and YOY brook trout were in fact present, they could not be observed because of the stream depth and width. Second, streams with large TI values at the lakeshore represent higher-order stream networks in larger watersheds. YOY brook trout may not reside in habitat near the lakeshore in such networks, but may occupy more upstream locations.

Our results have general implications for identifying brook trout habitat. Not all groundwater-based seep and stream habitats around a lake are occupied by YOY brook trout. Model-averaged parameters showed the odds of finding young brook trout increased significantly if the site was a small stream rather than a seep. Although seeps are used by brook trout, they can dry out during summer months. Small streams appear to be important habitat particularly during summer months, as reflected in the significant contribution by the model-averaged parameter Δtemp. In smaller lakes (with smaller catchments), seeps can provide the only thermal refuge for YOY brook trout cohorts (see Biro 1998). Although the TI was relatively successful in predicting the location of seeps and streams, it did not improve the odds of actually finding brook trout in this study. This may be a result of colinearity between this variable and the presence of seeps and streams in the field survey.

Studies of fish distributions in watersheds provide contrasting results when comparing the role of large- vs. small-scale variables influencing fish abundance. Fish presence or absence has been linked to a suite of traditional watershed variables in large-scale studies (Thompson and Lee 2000). Small-scale variables such as stream elevation, velocity, and substrate characteristics also perform well in predicting fish presence or absence when compared among geological categories (Nelson et al. 1992) or used within geographic areas (Sheldon and Meffe 1995). However, studies that have incorporated multiscale variables reveal the relatively poor ability of small-scale variables in predicting fish abundance (e.g., Fausch et al. 1994; Feist et al. 2003). The relative influence of habitat variables on fish presence or absence or abundance can change with the scale of observation. Accounting for habitat use at one scale relative to another can produce scale inconsistencies when considering a suite of watershed variables across multiple scales (Folt et al. 1998; Feist et al. 2003). These scale inconsistencies are the basis for the "habitat–population conundrum": the mismatch between the scale at which habitat is potentially characterized on one hand and the functional linkages between fish populations and essential habitat that must exist in some form on the other (Feist et al. 2003).

We have shown that small-scale features, such as the classification of a site as a stream or seep and the difference between lake surface and substrate temperatures, are important in locating YOY brook trout in lakes. This would seem to contradict the appeal of using large-scale landscape features to characterize habitat for management purposes. However, the difference between ambient lake temperature and that of the stream or seepage site in the land–lake ecotone was shown to be a function of a topographic index that integrates watershed slope and upslope contributing area. Both of these subwatershed characteristics exert a strong influence on the location of small streams and seeps along lake shorelines in the Algonquin Park region. The success of the TI approach in determining the distribution of YOY brook trout in this landscape provides a means of linking small- and large-scale variables that influence the role of habitat in sustaining fish populations, thus avoiding the habitat–population conundrum.

Topographic index: limitations and future directions

The TI was not clearly associated with estimates of groundwater flux obtained from seepage meters, likely as a result of problems of using these meters on a lake-wide scale and in a variety of sediment types where it was often difficult to insure a proper seal around the meters (Sebestyen and Schneider 2001). Other studies have had limited success in relating TI values to groundwater properties (see review in Buttle et al. 2001). Nevertheless, this and other studies illustrate that TIs can indicate spatial patterns of near-surface groundwater and are valuable in identifying seepage zone locations across the landscape (O'Loughlin 1986; Burt and Butcher 1985; Moore and Thompson 1996).

Until this study, there was no way of identifying potential brook trout habitat sites other than through field observation. The TI approach offers a valuable screening tool for eliminating portions of a lake's margin as potential habitat sites, such that efforts can be focussed in areas more likely to contain habitat with groundwater flux. Shoreline cells below the minimum TI value of habitat used by YOY brook trout in Mykiss and Stringer lakes identified 81% and 74% of the shorelines, respectively, as habitat without major groundwater flux. Although these threshold TI values did not eliminate as much potential shoreline habitat on Mykiss Lake as on Stringer Lake, most of the potential habitat shoreline cells on the former lake were contiguous and could be managed as a single habitat. Use of additional information (e.g., geology) may help distinguish between nonhabitat and potential habitat sites that exceed these TI thresholds. Regardless, we suggest that the TI approach can provide important hydrological and ecological insights.

Limitations related to the TIs used here are scale dependent. Smaller basins at the upper reaches of flow networks (e.g., first-order streams) are more sensitive to data resolution, errors, and the various algorithms used to model the landscape than are larger basins (Wise 2000). We have assumed that our DEM had few errors; however, even small errors may propagate through calculations of primary and secondary attributes, such as slope, FA, and the $\ln(a/\tan\beta)$ index (Wise 2000). Some DEM errors relate specifically to lakes (the focus of this study), which are essentially local depressions or large sinks that must be preserved in the DEM. Nevertheless, spurious sinks on the terrestrial landscape will trap water and prevent its further passage downslope, and our inability to fill all sinks in the DEM automatically complicates topographic modelling and introduces error to the estimated FA values (Martz and Garbrecht 1998). In addition, lack of lake bathymetric data introduces an unknown error to the estimated aspect and slope of shoreline cells. Obvious errors in the FA network of all 21 lakes were corrected manually as recommended by Wise (2000); however, manual correction of the entire Algonquin Park DEM covering our lake set may be impossible given the hundreds of lakes within the Park's boundaries.

The 25 m DEM used here was the finest resolution available at the time, but may have been too coarse to capture small-scale habitat features properly. Considerable improvement in TI performance occurs when using a 10 m compared with a 30 m DEM (Zhang and Montgomery 1994; Quinn et al. 1995). Nevertheless, the improved estimates of TIs associated with finer-resolution DEMs must be weighed against the exponential decrease in the amount of topographic information revealed as DEM resolution increases (Brasington and Richards 1998). DEM resolution can also affect the performance of the slope (Zhang and Montgomery 1994; Zhang et al. 1999) and FA algorithms (Zhang and Montgomery 1994), and some authors have suggested alternatives to the D8 algorithm used to calculate these properties. Most of these suggest a multiflow direction algorithm that allows water to flow out of one cell in several downslope directions. However, the D8 method is acceptable for a 25 m resolution DEM (Quinn et al. 1991).

Future work should examine differences in predicted habitat locations obtained from a 10 m DEM versus a 25 m DEM, identify TI differences derived from using various algorithms, and improve flow connectivity through lake networks. The potential for the incorporation of data on surficial and bedrock geology, soil, and vegetation type may also improve predictions of habitat locations with groundwater flux in the land–lake ecotone. Whatever improvements result from increased spatial resolution or different landscape model algorithms, the TI approach provides a useful tool for locating and protecting previously unmapped groundwater habitats. This task is made even more important given the critical role these groundwater discharge sites play for many fishes' requirements for spawning sites, summer and winter thermal refugia, and nursery habitat (Power et al. 1999) and also given the potential for land use change to alter the stability of groundwater habitats (Wright et al. 1990; Curry and Devito 1996). By linking the aquatic environment to its terrestrial counterpart, the TI approach facilitates the need to protect the terrestrial basins sustaining these important groundwater habitats (Curry and Devito 1996) and to recognize important hydrological units rather than placing simple "donuts" around lakes (Buttle 2002).

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