Projected impacts of climate warming on production of lake trout (*Salvelinus namaycush*) in southern Yukon lakes

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Abstract: We used existing models to predict changes in lake surface temperature and thermocline depth, in combination with a newly developed model to describe lake thermal profiles, to determine how thermal properties of a series of lakes located predominantly in the southern Yukon could change under three realistic climate-warming scenarios. We then used existing models to determine how relative changes in potential harvest of lake trout (*Salvelinus namaycush*) in southern Yukon lakes could change as availability of optimal thermal habitat was altered under the three warming scenarios. With warming, an overall decrease in availability of optimal thermal habitat and in lake trout potential harvest is predicted in southern Yukon lakes, although considerable lake-specific variation in direction and magnitude of change exists. For southern Yukon lakes overall, 2, 4, and 6 °C increases in mean annual air temperature lead to 12%, 35%, and 40% decreases in thermal habitat volume, respectively, and 8%, 19%, and 23% reductions in potential harvest, respectively.

Résumé : Nous avons utilisé des modèles préexistants pour prédire les changements de la température de la surface des lacs et de la profondeur de la thermocline, en combinaison avec un nouveau modèle pour décrire les profils thermiques des lacs, afin de déterminer de quelle manière les propriétés thermiques d'une série de lacs situés en majorité au sud du Yukon pourraient être modifiées selon trois scénarios réalistes de réchauffement climatique. Nous avons ensuite utilisé des modèles préexistants pour déterminer comment la récolte potentielle de touladis (*Salvelinus namaycush*) dans les lacs du sud du Yukon pourrait changer à mesure que la disponibilité de leur habitat thermique optimal est modifiée selon les trois scénarios de réchauffement. Avec le réchauffement, on s'attend à une réduction globale de la disponibilité de l'habitat thermique optimal et de la récolte potentielle de touladis dans les lacs du sud du Yukon, bien qu'il existe une variation considérable du sens et de l'amplitude du changement en fonction des lacs. En général pour les lacs du sud du Yukon, des accroissements de la température annuelle moyenne de l'air de 2, 4 et 6 °C mènent à des réductions du volume de l'habitat thermique respectivement de 12, 35 et 40 % et des diminutions de la récolte potentielle de 8, 19 et 23 %.

[Traduit par la Rédaction]

Introduction

Fish are heterothermic ectotherms with body temperatures, for most species, within a few tenths of a degree of the water temperature in which they live; thus habitat temperature directly influences their physiology and behavior (Magnuson et al. 1990). Fish exploit specific ranges of water temperature, depending on species, age, and thermal history (Crawshaw and O'Connor 1996), and appear to have an innate desire to remain within a preferred range (Mac 1985). A species' behavioral thermal regulation is characterized by a narrow range of temperatures into which it will ultimately gravitate with all other variables being equal or nonrestricting (Christie and Regier 1988). This temperature is the species "final preferendum" (Fry 1947) and is included in the species fundamental thermal niche (Christie and Regier 1988), which, in turn, defines optimum conditions for activity and growth (Christie and Regier 1988; Magnuson et al. 1979). For lake trout (*Salvelinus namaycush*), a cold-water species with a natural distribution that is primarily dependent on the species' requirements for cold water and relatively high concentrations of dissolved oxygen (Martin and Olver 1980), the fundamental thermal niche is identified as 10 ± 2 °C (Magnuson et al. 1990). Investigations by O'Connor et al. (1981), as well as results of a literature search completed by Christie (1986), suggest that lake trout growth is optimal within this temperature range. Volume of water within this fundamental thermal niche has been established as a strong predictor of lake

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trout yield (Christie and Regier 1988) or potential harvest (Payne et al. 1990). For this species, thermal habitat volume (THV), which is the volume of water in a given lake within the preferred thermal range of 8–12 °C, was the best predictor of yield (or potential harvest) compared with thermal habitat area, lake area, lake volume, or other indices of thermal habitat availability (Christie and Regier 1988).

Climate warming is expected to alter the size of this thermal niche by changing annual patterns of thermal structure simultaneously with other changes in precipitation, cloudiness, windiness, and ice cover that would influence other niche characteristics of fish (Magnuson and DeStasio 1997). It is generally agreed that temperate zone fish with moderate to high preferred temperatures should benefit (e.g., increased productivity) from climate warming through increased availability of thermal habitat in more northerly areas (Magnuson and DeStasio 1997; Shuter and Post 1990). Lake trout, on the other hand, will likely experience reduced availability of their preferred thermal habitat, particularly at the southern extent of their range, coupled with reductions in production (Meisner et al. 1987; Shuter and Meisner 1992; Shuter and Lester 2004) as lakes warm.

Climate-warming models predict greater warming at increasingly northern latitudes, yet existing lake-warming models are not able to quantify the magnitude of these changes on northern lake systems because they are calibrated to more southerly conditions where adequate meteorological data exist. For example, DeStasio et al. (1996) used the DYRESM model of Imberger and Patterson (1981, 1990), McCormick (1990) used Garwood's (1977) model, and the MINLAKE model of Riley and Stefan (1988) and Hondzo and Stefan (1993) was developed from a Minnesota data set. With the above models, it is often assumed that results can be extrapolated spatially because of the lack of topographic complexity in the region of study (e.g., MINLAKE model based on Minnesota data) and the relative lack of variability in meteorological conditions over vast distances. In the north, however, extensive meteorological data are often lacking (e.g., detailed wind-speed data at local scales), and in mountainous regions, considerable localized variation in meteorological conditions exists, rendering these models unreliable. Although it is difficult to predict impacts of climate warming with certainty, the approach taken here is an attempt to predict how warming could influence lake thermal characteristics of a subset of northern lakes, without the luxury of localized meteorological data.

The objectives of this study include development of a method to describe current lake thermal profile characteristics and approximate how thermal properties could be affected by climate warming given limited availability of both meteorological and lake thermal data for northern lakes. We then estimated current availability of lake trout thermal habitat and changes in habitat availability under increasing mean annual air temperatures. Finally, we estimated changes in lake trout potential harvest (Payne et al. 1990) under a series of warming scenarios using established relationships. These simulations allow estimation of both lake-specific and regional impacts of climate warming on potential harvest of northern lake trout populations.

Materials and methods

Study lakes

Potential effects of climate warming on lake thermal characteristics were evaluated from a data set of 33 Yukon lakes of various morphometries (Table 1), located predominantly in the southwestern portion of the Territory (Fig. 1) between 59°N and 63°N latitude. We included only lakes for which a midsummer thermal profile (late July to early August) and a previously digitized bathymetric map in geographic information system (GIS) format existed. When multiple profiles were available for a lake, the deepest was used in the analyses. All lake temperature data were collected with a regularly calibrated Datasonde 3 Hydrolab with Scout 2 (Hydrolab Corporation, Austin, Texas). The data set of lakes fitting the criteria for inclusion in this study is relatively representative of Yukon lake trout lakes in general (for which data exist) in terms of lake volume (Fig. 2*a*) and lake area (Fig. 2*b*). It should be recognized, however, that this is a small sample of all Yukon lakes, the majority of which have had no thermal or morphometric information previously collected.

Thermal habitat volume

To calculate thermal habitat volume (THV) for lake trout, it was necessary to describe current lake thermal profiles to determine the depth at which the upper (12 °C) and lower (8 °C) boundaries of lake trout optimal habitat occur, determine lake area at boundary depths, and subsequently calculate the volume of water in each lake within the optimal thermal range. To describe lake thermal characteristics in all lakes in which a thermocline was apparent, the shape of each lake thermal profile was described by

$$(1) \qquad T = T_\mathrm{b} + T_\mathrm{d}(D^\mathrm{STEEP}/Z_\mathrm{th}^\mathrm{STEEP} + D^\mathrm{STEEP}))$$

where T is the temperature (°C) at a given depth, T_b is the bottom temperature (°C) of the lake (profile), T_d is the difference in temperature from the surface to the bottom (i.e., $T_\mathrm{d} = T_\mathrm{surface} - T_\mathrm{b}$) of the profile, D is the given depth (m) in the profile, Z_th is the thermocline depth (m), and STEEP is a unitless parameter describing the degree of isothermality of the epilimnion (and hypolimnion) given the symmetrical nature of the function and describes the sharpness of the thermocline. The equation is a three-parameter sinusoidal function in which a constant parameter (T_b) has been added to ensure a non-zero intercept, with variable steepness (rate of temperature change) between high and low asymptotes. Equation parameters were fit using the SOLVER tool in Microsoft Excel® to achieve the closest fit to the empirical thermal profile by minimizing the sum of squared residuals. When SOLVER gave a negative (or <4) value for T_b, the T_b was set to 4 °C to ensure biologically reasonable parameter values. Equation 1 was solved at 8 and 12 °C (T) to determine the depth (D) at which these temperatures occurred.

Before volume calculations, it was necessary to calculate lake area at each of the optimal thermal habitat boundaries. An adjustment of the interpolation equation suggested by

Table 1. Climatological, thermal, and morphological characteristics of 33 southern Yukon lake trout (*Salvelinus namaycush*) lakes.

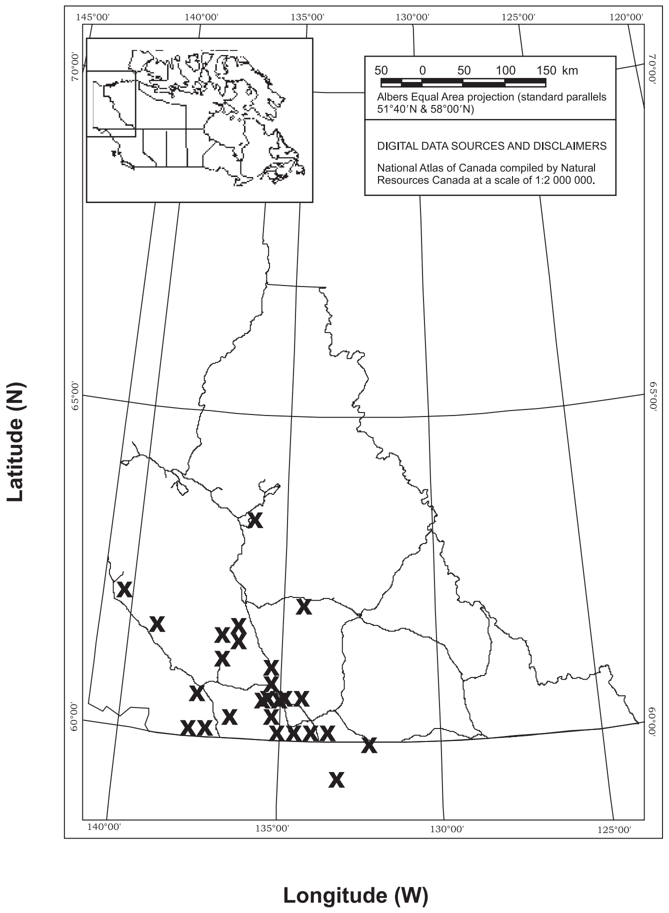
	Latitude	Longitude	Surface area (km^2)	FT (km)	Maximum depth (m)	$\overline{Z}$ (m)	TEMP (°C)	HRISE (°C)	THMZ (m)	Thermal group
Alligator	60°23′N	135°21′W	6.3	5.7	10	5.6	–1.4[a]	13.3	n/a	G1
Atlin	60°00′N	133°50′W	634.5	65.8	250	78.9	–2[a]	14.6 (13.2)	26.2 (22.3)	G4
Bennett	60°06′N	134°52′W	96.8	24.5	120	61.1	–1.4[a]	10.4 (10.0)	29.4 (30.5)	G2
Chadburn	60°03′N	134°57′W	1.9	2.2	42	14.5	–0.7[b]	16.1 (16.2)	9.8 (10.2)	G4
Dezadeash	60°28′N	136°58′W	82.5	19.5	6	4.1	–2.9[b]	17.3	n/a	G1
Ethel	63°22′N	136°06′W	47.3	18.8	60	30.7	–3.6[b]	14.4 (14.6)	9.9 (11.3)	G4
Fish	60°36′N	135°14′W	13.2	9.9	35	16.9	1[b]	15.9 (15.8)	9.5 (10.2)	G3
Fox	61°14′N	135°28′W	16.6	16.5	45	28.9	1[b]	19.6 (19.3)	9.9 (12.0)	G4
Frederick	60°23′N	136°40′W	4.5	6.4	40	22.3	–2.9[b]	14.6 (14.6)	13.5 (14.0)	G4
Granite	60°42′N	137°05′W	1.7	3.8	55	37.2	–2.9[b]	13.5 (13.6)	12.9 (13.6)	G4
Howard (N)	60°14′N	136°49′W	2.0	2.8	16	6.0	–2.9[b]	13.9 (13.6)	14.3 (14.0)	G3
Hutshi	61°08′N	136°35′W	3.2	4.2	16	5.0	–4.4[a]	15.5	n/a	G1
Jojo	60°34′N	136°21′W	6.4	9.3	60	28.3	–2.9[b]	12.0 (11.9)	19.6 (22.7)	G2
Kathleen	60°28′N	136°58′W	33.8	11.1	108	54.5	–2.9[b]	10.0 (9.8)	43.4 (43.0)	G2
Klukshu	60°19′N	136°59′W	1.5	3.1	30	13.3	–2.9[b]	13.0 (12.7)	17.6 (21.7)	G4
Kusawa	60°20′N	136°22′W	142.0	22.1	140	54.4	1[b]	16.5 (16.6)	25.9 (15.1)	G4
Laberge	61°11′N	135°12′W	201.0	50.2	140	52.9	1[b]	19.5 (18.0)	n/a (18.9)*	G4
Lewes	60°22′N	134°50′W	1.4	2.5	40	16.8	1[b]	15.3 (15.3)	14.1 (14.2)	G4
Little Atlin	60°15′N	133°57′W	37.9	15.3	45	11.0	1[b]	17.4 (16.7)	12.3 (12.9)	G3
Little Braeburn	60°30′N	135°49′W	0.8	1.9	40	12.8	–3.8[b]	17.2 (17.3)	7.1 (7.9)	G4
Little Fox	61°20′N	135°38′W	2.2	2.2	35	17.1	1[b]	17.2 (17.0)	7.6 (7.7)	G4
Little Salmon	62°11′N	134°40′W	62.1	28.8	140	93.1	–2.9[a]	14.7 (14.1)	16.0 (9.5)	G4
Long	61°21′N	136°41′W	13.9	9.4	50	16.8	–4.4[a]	10.2 (10.2)	28.1 (29.2)	G2
Louise (Jackson)	60°42′N	135°17′W	0.5	1.2	10	6.2	–2.9[b]	16.1 (16.1)	7.7 (8.2)	G3
Lower Snafu	60°11′N	133°26′W	2.9	1.5	25	5.9	–2[b]	17.0 (17.3)	9.4 (7.8)	G4
Marsh	60°25′N	134°18′W	96.3	22.3	50	12.8	1[b]	16.4 (15.6)	22.2 (22.2)	G3
Pine	60°49′N	137°27′W	5.5	5.7	25	14.9	–2.9[b]	15.6 (15.4)	12.4 (12.7)	G4
Tagish	60°10′N	134°20′W	354.6	31.6	300	61.2	1[b]	13.3 (13.3)	22.9 (25.2)	G4
Tarfu	60°03′N	133°43′W	4.2	4.3	30	11.9	1[b]	16.0 (15.7)	10.3 (10.6)	G4
Teslin	60°15′N	132°57′W	354.0	54.5	213	54.1	–2[b]	14.4 (14.0)	22.9 (21.9)	G4
Tincup	61°45′N	139°15′W	17.9	9.5	180	101.9	–4[b]	13.9 (14.3)	6.8 (8.3)	G4
Twin	61°42′N	135°55′W	1.6	1.8	40	16.3	–3.8[b]	18.7 (18.9)	7.0 (7.4)	G4
Wellesley	62°21′N	139°49′W	73.8	14.7	45	23.6	–6.3[a]	15.9 (15.8)	15.8 (16.4)	G4

Note: FT, lake fetch (km); $\overline{Z}$, mean depth of lake (m); TEMP, long-term mean annual air temperature (°C); HRISE, maximum summer surface temperatures (°C); THMZ, thermocline depth (m); asterisk (*) indicates reference to Mackenzie-Grieve (2005); n/a, not applicable. For each lake, the initial value in the HRISE and THMZ columns is the empirical measurement and the value in parentheses is that predicted by the relevant equation.

[a] TEMP from Canadian climate normals for 1951–1980.

[b] TEMP from Canadian climate normals for 1961–1990.

Fig. 1. The majority of the lakes included ($n = 33$) are located in the southern Yukon, Canada, and range from 59°N to 63°N latitude. Approximate locations of individual lakes are indicated by **X**. Major highways are indicated on the map.



Payne et al. (1990) was used (the area measurement was substituted for the temperature measurement) where

$$(2)\qquad A_t + A_1 + ((D_t - D_1)(A_2 - A_1)/(D_2 - D_1))$$

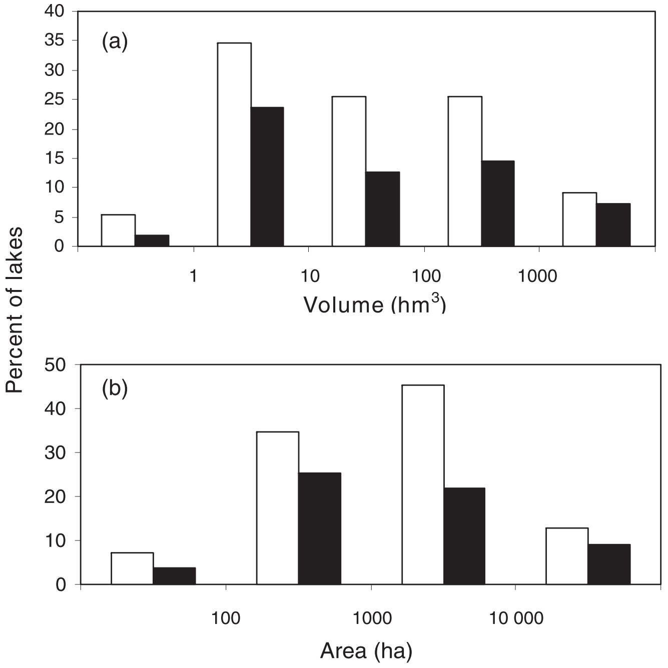
The equation was solved for A_t (area at either 8 °C or 12 °C) (km^2), where D_t is the depth (km) at either 8 °C or 12 °C, A_1 is the area (km^2) closest to, but greater, than A_t, A_2 is the area (km^2) closest to, but less than, A_t, D_1 is the depth (km) at A_1, and D_2 is the depth (km) at A_2. Areas of A_1 and A_2 were determined from bathymetric maps.

The volume (V) of habitat in a lake within the optimal thermal range for lake trout was calculated as follows, according to Welch (1948):

$$(3)\qquad V = (h/3)\left(A_1 + A_2 + \sqrt{A_1 \cdot A_2}\right)$$

where h is the vertical depth of the stratum (km), A_1 is the area of upper surface (km^2), and A_2 is the area of the lower of the lower surface of the stratum (km^2). Island volumes were subtracted from the water volume (as calculated above) to obtain an estimate of total volume of optimal lake trout habitat (THV) in each lake.

Fig. 2. Study lakes are reasonably representative ((*a*) by volume (1 hm^3 = 0.001 km^3) and (*b*) by surface area) of Yukon lake trout (*Salvelinus namaycush*) lakes overall (for which data exist). Study lakes include about 60% of all lake trout lakes for which data are available from Yukon Government files (all lakes, n = 55, open bars; study lakes, n = 33, solid bars).



Lake trout production

Current lake trout potential harvest was estimated following Payne et al. (1990) where July THV was related to potential harvest by

$$(4)\qquad \log_{10} H = 2.15 + 0.714 \log_{10} (\text{July THV})$$

where H is the potential harvest (kg·year^{-1}) and July THV (hm^3) (1 hm^3 = 0.001 km^3) is the thermal habitat volume calculated from July temperature data only.

Payne et al. (1990) developed eq. 4 by linear regression of the original 15 lakes used by Christie and Regier (1988) plus an additional five lakes with surface areas less than 60 km^2 (6000 ha). The Payne et al. (1990) equation was used in our analyses as the majority of Yukon lakes included here are less 60 km^2 (Table 1). Payne et al. (1990) also found that using a geometric average of July THVs, rather than the 10-day summer averages used by Christie and Regier (1988), improved the precision of the model. We assumed that a single-lake July or early August thermal profile was representative of average July temperatures in a given lake.

Climate warming

Climate warming models predict mean annual surface air temperature increases of between about 2 °C and 5 °C by the year 2100 in the southwestern Yukon (http://www.cccma.bc.ec.gc.ca/eng_index.shtml). We evaluated the effect of climate warming on lake thermal characteristics under three different temperature scenarios: current mean annual air temperature at each of the lakes was increased by 2, 4, and

6 °C. We assumed that mean annual air temperature was the driver of changes in lake thermal profiles with climate warming. We assumed that these changes incorporated the mechanics of lake warming explicitly considered in other, more-complicated lake-warming models (e.g., Hondzo and Stefan 1993).

Shuter et al. (1983) used mean annual air temperature, lake mean depth, and lake fetch to determine thermocline depth according to

$$(5)\qquad \ln(\mathrm{THMZ}) = 0.220\ln(\mathrm{FT}) + 0.213\ln(\bar{Z}) - 0.0263(\mathrm{TEMP}) + 1.550$$

where THMZ is the thermocline depth (m), FT is lake fetch (km), $\bar{Z}$ is the mean depth of lake (m), and TEMP is the long-term mean annual air temperature (°C). Data from a wide latitudinal range (41°N–75°N latitude) were included in the analyses used to develop these predictive equations and should therefore be appropriate for use here where latitudes of database lakes range from 59°N to 63°N latitude. Hanna (1990) suggested that of the 17 models of mixing depth that she evaluated, the Shuter et al. (1983) model, although slightly biased (overestimates thermocline depth), was the best available for predicting mixing (thermocline) depth.

Shuter and Post (1990) used mean annual air temperature (TEMP; °C) and mean depth ($\bar{Z}$; m) to predict maximum summer surface temperatures (HRISE; °C) according to

$$(6)\qquad \log_e(\mathrm{HRISE}) = 0.0437(\mathrm{TEMP}) - 0.002(\mathrm{TEMP})^2 - 0.108\log_e(\bar{Z}) + 3.158$$

To assess how climate warming (i.e., increase in TEMP) impacts lake thermal characteristics, T_{surface} ($T_{\mathrm{d}} = T_{\mathrm{surface}} - T_{\mathrm{b}}$) and Z_{th} parameters of the sinusoidal function fitted to observed data were adjusted by the difference in values predicted by the above equations with increases in TEMP from current conditions. For example, if the HRISE (T_{surface}) predicted under current climatic conditions was 15 °C and the HRISE predicted under a 2 °C increase in mean annual air temperature was 17 °C, then the value of the T_{d} parameter of the sinusoidal function was increased by 2 °C from the current fitted value. The sinusoidal equation (eq. 1) was then resolved at depths in the original profile to allow comparison of lake thermal profiles under the various climate warming scenarios. We assumed that increases in TEMP would have little effect on T_{b}, consistent with results of other lake-warming models (Hondzo and Stefan 1993; Stefan et al. 1993). We also assumed that neither the STEEP parameter in eq. 1 nor $\bar{Z}$ and FT in eqs. 5 and 6 would change under climate warming.

Although THV for each of the study lakes under climate warming was calculated as previously described for current lake thermal profiles, we interpreted changes in potential harvest in terms of relative percent changes because lake productivity in northern regions is generally lower than in southern regions (where the majority of the data on which the equation was based originates).

Three of the study lakes were approximately isothermal based on their midsummer profiles. Although there were small temperature differences in lake surface and bottom temperatures (<2 °C), we assumed that surface temperature was representative of average lake temperature. For these three lakes, maximum surface water temperature under increased TEMP was calculated using eq. 6. Current maximum surface temperatures were then adjusted by the difference between equation predictions and current conditions. Potential harvest calculations were not performed as no appreciable volume of optimal thermal habitat currently exists in any of these three lakes.

Results

Thermal profiles and habitat volume

The 33 Yukon lake trout lakes were divided into four groups based on lake thermal properties (Fig. 3): group 1 (*n* = 3), lakes where there is currently no thermal habitat in the main basin of the lake (i.e., lakes are isothermal); group 2 (*n* = 4), lakes where there is currently no water warmer than the upper optimal thermal limit for lake trout of 12 °C; group 3 (*n* = 5), lakes where there is currently no habitat colder than the lower optimal thermal boundary of 8 °C; and group 4 (*n* = 21), lakes where there is currently water colder and warmer than the lower (8 °C) and upper (12 °C) optimal thermal boundaries for lake trout.

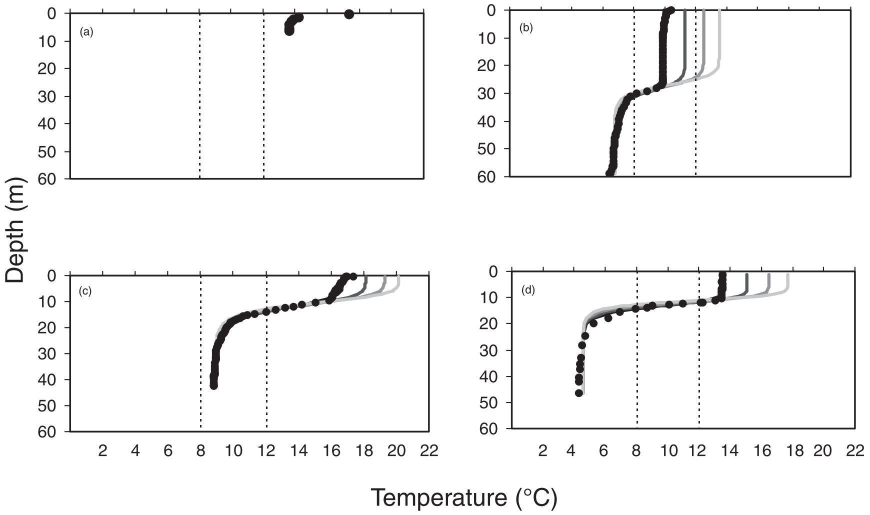
The sinusoidal function used to describe characteristics of lake thermal profiles provided a good fit to most of the lake data, although the fit was poorer in lakes with secondary (temporary) thermoclines or where the epilimnion was less well mixed (e.g., surface warming on a warm, calm day). There were generally only small differences in fitted versus empirical thermocline depths and surface temperatures (Table 1). The fitted thermocline depth (eq. 1) did slightly overestimate empirical thermocline depth, although differences were usually less than 0.5 m. Any differences in fitted and empirical surface temperatures (eq. 1) were almost always less than 0.5 °C. These model fits provided the template for current thermal profiles to which warming scenarios were applied.

In the 30 Yukon lakes in which thermoclines were identified (groups 2, 3, and 4), thermocline depth became increasingly shallow with increasing TEMP, although the magnitude of the surfaceward shift was not the same for each 2 °C increase in TEMP. As the thermocline was shifted up in the water column with increases in TEMP, optimal thermal habitat boundary depths also shifted in the water column, although neither the direction of change (i.e., up or down in the water column) nor the changes in THV were consistent across all lakes.

Group 1 lakes (nonstratified) currently have no appreciable volume of midsummer optimal habitat (Table 2). With increases in TEMP, average lake temperatures in the warmest part of the summer further increased, pushing temperatures even further beyond the optimal range for lake trout throughout the warmest part of the year.

Group 2 included some of the larger, colder lakes in the southern Yukon, where there was currently either no 12 °C isotherm or this isotherm was at the lake surface. In lakes of this type, THV generally decreased slightly with a 2 °C increase in TEMP (Table 2). In two of the four lakes, slight increases in THV were predicted, and in the other two lakes,

Fig. 3. Empirical and temperature measurements, fitted thermal profiles, and warmed midsummer thermal profile of four Yukon lakes typical of each of the four groups of lakes based on spatial patterns of lake trout (*Salvelinus namaycush*) thermal habitat volume as defined by habitat between 8 and 12 °C (indicated by dotted vertical lines). (*a*) Thermal group 1 (*n* = 3); (*b*) group 2 (*n* = 4); (*c*) group 3 (*n* = 5); and (*d*) group 4 (*n* = 21). See text for details on thermal groups. Solid circles indicate empirical data; lines indicate the current fitted profile, dark shaded lines indicate the predicted profile under a +2 °C increase in mean annual air temperature, medium shaded lines indicate the +4 °C profile, and light shaded lines indicate the +6 °C profile.



decreases in THV were predicted (Table 2). With 4 °C and 6 °C increases in TEMP, large reductions in THV occurred (Table 2) as the 12 °C isotherm developed (generally with a 4 °C increase in TEMP) deep in the water column, leading to an overall reduction in THV in these lakes through vertical compression of the extent of lake trout habitat.

In group 3 lakes, no 8 °C isotherm currently existed as lake temperatures exceeded 8 °C in midsummer. The THV predictions for these lakes varied little with increases in TEMP compared with lakes of groups 2 and 4 (Table 2) as there was little change in the position of the 12 °C isotherm. With a 2 °C increase in TEMP, a reduction in mean THV of only 6% was predicted, whereas under a 6 °C TEMP increase scenario, a slight increase in the mean THV (1.2%) was predicted compared with current conditions. Increases in THV were predicted for four of the five lakes of this type. Little change in THV occurs in these lakes because lake warming occurs in the epilimnion of the lakes and the 12 °C isotherm in group 3 lakes is deeper and therefore less affected by surface warming.

With increases in TEMP, THV in the group 4 lakes (where 8 °C and 12 °C isotherms currently exist) was compressed as the dimension (height) of the optimal habitat layer decreased in all cases, resulting in a decrease in THV with increasing TEMP. The majority of lakes in our data set are of this type (21 of 33). The optimal thermal habitat is almost always a small proportion of total lake volume (Table 2) and is generally restricted to the metalimnetic region in these lakes. The compression of THV in group 4 lakes occurs by one of two mechanisms. Thermal habitat is reduced either by a deepening of the 12 °C isotherm combined with a shallowing of the 8 °C isotherm or by a shallowing of the 12 °C isotherm combined with a shallowing of the 8 °C isotherm. In the latter case, the magnitude of the shallowing of the 8 °C and 12 °C isotherms (and associated increase in lake area at depth) is not enough to counter the reduction in height of the optimal thermal habitat layer, thus results in an overall decrease in THV. Specifically, under a 2 °C increase in TEMP, an average 13% reduction in THV occurred, and under a 4 °C increase in TEMP, an average 20% reduction in THV occurred, whereas under a 6 °C increase in TEMP an average reduction in THV of 27% is expected (Table 2).

Pooling all data for the southern Yukon lakes database for each of the three warming scenarios suggested an overall decrease in THV for lake trout in Yukon lakes, where magnitude of the decrease in THV was greater with increasing changes in TEMP. With a 2 °C increase in TEMP, a mean 12% decrease in THV was predicted, and with a 6 °C increase in TEMP, more than a 40% decrease in THV was predicted (Table 2).

Warming and lake trout potential harvest

In group 1 lakes, no appreciable volume of preferred thermal habitat currently exists. We assumed, as in the other lakes, that the late July – early August profile was representative of July thermal habitat conditions and therefore related to potential harvest by the Payne et al. (1990) equation. With essentially no optimal thermal habitat in group 1 lakes, the Payne et al. (1990) equation could not be applied. Lake trout production in lakes of this type is probably already limited by elevated water temperatures.

In group 2 lakes, there was a small overall average decrease in *H* by 12% with a 2 °C increase in TEMP. This overall decrease was the result of a large decrease in *H* in a single lake, as other lakes in this group actually showed small increases or decreases in *H*. As TEMP further increased, large decreases in *H* resulted in all cases. With a 4 °C increase in TEMP, an average decrease of 61% was predicted, and with a 6 °C increase in TEMP, an average decrease of 67% was predicted (Fig. 4).

Table 2. Current and predicted changes in July thermal habitat volume (THV) for 33 southern Yukon lake trout (*Salvelinus namaycush*) lakes under warming scenarios where current mean annual air temperature was increased by 2, 4, and 6 °C.

			Predicted change in July THV (%)		
Lake	Total lake volume (hm^3)	Current July THV (hm^3)	with 2 °C increase	with 4 °C increase	with 6 °C increase
Group 1					
Alligator	34.0	—	—	—	—
Dezadeash	337.0	—	—	—	—
Hutshi (S)	17.0	—	—	—	—
Group 2					
Bennett	5 990.0	2 514.7	–0.6	–81.8	–86.2
Jojo	196.0	132.6	–67.9	–73.3	–75.9
Kathleen	1 864.0	1 110.3	1.7	–82.4	–87.5
Long	259.0	189.7	10.5	–52.9	–65.1
Average			–14.1	–72.6	–78.7
Group 3					
Fish	218.0	120.8	–2.2	–1.6	0.7
Howard (N)	15.0	1.0	–6.7	–0.7	10.3
Little Atlin	402.0	140.6	1.2	4.3	8.8
Louise (Jackson)	4.0	0.3	–7.4	–4.5	4.9
Marsh	1 220.0	98.2	–14.9	–19.7	–18.9
Average			–6.0	–4.4	1.2
Group 4					
Atlin	54 400.0	6 290.9	–18.3	–28.2	–34.9
Chadburn	28.0	1.4	–3.2	–9.8	–16.4
Ethel	1 462.0	168.3	–16.0	–26.4	–34.3
Fox	475.0	72.4	–6.8	–12.8	–18.4
Frederick	101.0	10.5	–15.2	–24.0	–30.0
Granite	66.0	3.9	–21.1	–32.3	–39.4
Klukshu	0.0	7.2	–36.4	–49.4	–56.0
Kusawa	7 668.0	1 781.7	–5.4	–6.5	–12.0
Laberge	10 800.0	1 523.4	–6.3	–11.9	–17.0
Lewes	23.0	1.4	–8.5	–13.1	–16.9
Little Braeburn	11.0	1.0	–9.7	–16.6	–22.0
Little Fox	24.0	0.9	–8.6	–14.7	–19.6
Little Salmon	5 750.0	208.8	–18.2	–29.3	–37.4
Lower Snafu	18.0	1.0	–7.7	–11.9	–14.2
Pine	81.0	10.5	–7.3	–11.8	–15.0
Tagish	21 800.0	2 866.4	–16.8	–25.1	–30.2
Tarfu	49.0	3.4	–9.2	–14.7	–18.3
Teslin	20 800.0	1 461.6	–16.9	–26.7	–33.4
Tincup	1 844.0	72.5	–19.8	–34.5	–46.8
Twin	26.0	2.0	–8.8	–16.0	–22.2
Wellesley	1 757.0	233.3	–12.0	–20.0	–25.8
Average			–13.0	–20.7	–26.7
Yukon total[a]	137 351.0	26 376.7	–11.90	–34.50	–40.2

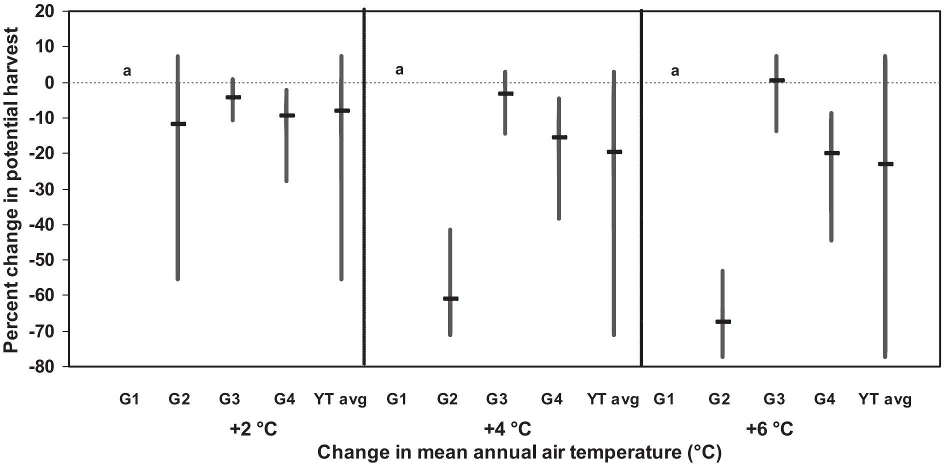
Note: Dash (—) indicates that THV is absent.

[a] Yukon total does not include group 1 lakes.

Our analyses suggest the impact of climate warming on the group 3 lakes will be minimal; slight increases in H are predicted in some lakes under the various levels of climate warming and slight decreases in H are predicted in others. Our analyses suggest that any increases in H will be less than 6% and any decreases will be less than 15% of the current H (Fig. 4). Our analyses predict that an increase in TEMP of 2 °C would lead to the greatest overall reduction in H (4.4%). When TEMP was increased by 4 °C, a 3.3% reduction in H in group 3 lakes resulted, whereas under a 6 °C increase in TEMP, an increase in H of 0.7% resulted (Fig. 4), with slight increases occurring in four of five lakes.

In group 4 lakes, decreases in H are predicted under all three warming scenarios, and the magnitude of these reduc-

Fig. 4. Predicted percent change in lake trout potential harvest (*H*) for 33 Yukon lake trout (*Salvelinus namaycush*) lakes with increasing mean annual air temperature. Mean (short horizontal bars) and range (vertical bars) in percent change in *H* for each of the thermal groups under the applied climate warming scenarios are indicated: G1 (*n* = 3), lakes in which there is currently no optimal thermal habitat (i.e., "a"); G2 (*n* = 4), lakes in which there is currently no thermal habitat beyond the upper optimal thermal boundary; G3 (*n* = 5), lakes in which there is currently no thermal habitat colder than the lower optimal thermal boundary; and G4 (*n* = 21), lakes in which 8 and 12 °C isotherms currently exist. YT avg, Yukon Territory averages.



tions increased with increasing TEMP. For example, under a 2 °C increase, *H* decreased by 9.5% on average, under a 4 °C increase in TEMP, *H* decreased by a little more than 15% on average, and under a 6 °C increase in TEMP, *H* decreased by about 20% on average (Fig. 4).

Overall, lake trout potential harvest in southern Yukon lakes is expected to decrease with increasing TEMP. Under increases in TEMP of 2, 4, and 6 °C, mean decreases in *H* of about 8%, 19%, and 23%, respectively, are expected (Fig. 4).

Discussion

Probably the most important physical characteristic of a lake is its seasonal stratification pattern (Stefan et al. 1993). Application of the Shuter et al. (1983) model, which uses lake fetch, lake mean depth, and local mean annual air temperature to predict thermocline depth, shows that thermocline depth will become increasingly shallow with increasing mean annual air temperature. The directional change in thermocline depth as a result of climate change is equivocal in the literature, although predictions of our study are consistent with empirical data for Lake Opeongo (King et al. 1999) and Lake Huron (King et al. 1997) where shallower thermoclines have been associated with warmer climatic conditions. The greater density difference between surface and bottom water with increased surface layer warming is responsible for this stratification pattern. The shallower, stronger stratification predicted for lakes in our Yukon database is consistent with results of DeStasio et al. (1996) for small north-temperate lakes, Magnuson et al. (1990) for the Great Lakes, and McCormick (1990) for Lake Michigan, assuming that little change in wind energy occurs with climate warming.

Thermocline depth is relevant in the discussion of lake trout thermal habitat because optimal habitat is often restricted to this metalimnetic zone, particularly in our group 4 lakes, which were the most common lake type in our data set. The stronger stratification (i.e., increased thermal gradient) predicted under climate warming and predicted for our group 2 and group 4 lakes, in particular, implies a reduction in the vertical extent of the thermal niche during the summer stratification period. Our results are consistent with the a priori expectations of Magnuson et al. (1990) where this squeeze on the thermal niche was expected to increase (and affect habitat availability for lake trout more negatively) with climate warming, although their results did not support it. The group 3 lakes are less affected by changes in the depth and the strength of the thermocline because optimal habitat in these lakes is normally deep in the hypolimnion where changes in the upper lake profiles have little impact on temperatures near the bottom of these lakes.

In contrast to southern lakes in which lake trout are often restricted to metalimnetic and hypolimnetic areas in an effort to remain within the optimal thermal range (Ryan and Marshall 1994), the epilimnion of northern lake trout lakes is currently often within the optimal range for lake trout, as in our group 2 lakes. Under climate warming, however, our results suggest optimal habitat availability in northern lake trout lakes may further resemble that in southern lake trout lakes as temperatures in the epilimnion warm above 12 °C, leading to a vertical compression in optimal habitat as suggested by analyses on our group 2 lakes.

Hypolimnetic oxygen depletion has been less of a concern in northern systems compared with southern ones as lake trout are not usually restricted to this zone as in southern lakes. Dissolved oxygen (DO) concentrations rarely limit availability of optimal habitat for lake trout in northern lakes because temperatures are cold and lakes are usually oligotrophic. In our data set, DO concentrations of less than 6 $mg{\cdot}L^{-1}$, which is often considered to be the lower DO limit for optimal lake trout habitat (MacLean et al. 1990), occurred in the hypolimnion of only one basin in each of two lakes.

Under climate warming, oxygen depletion is expected to be of increasing concern in northern waters. Higher lake temperatures would result in reduced DO saturation values

(Blumberg and DiToro 1990). The likely increases in primary production with warmer water temperatures (Rouse et al. 1997) increase the potential for summer oxygen depletion (Marshall 1996). Longer periods of stratification and more stable systems predicted from several models (DeStasio et al. 1996; Hondzo and Stefan 1993; Stefan et al. 1993) and observed in northern Ontario (Ryan and Marshall 1994) show that this will also lead to more pronounced oxygen depletion, increasing the frequency of anoxia in bottom waters in mid- and late summer and reducing DO habitat availability for lake trout. Such changes would place marginal populations at increased risk of population adverse processes.

A habitat model for lake trout developed by Dillon et al. (2003) used this DO concentration of 6 $\mathrm{mg \cdot L^{-1}}$ as the lower optimal habitat boundary, whereas we employed the thermal measure (8 °C). The Dillon et al. (2003) model used data on lake morphometry, total phosphorus (TP) concentration, and secchi depth (or dissolved organic carbon concentration) to predict depth of the upper boundary of lake trout optimal habitat (10 °C isotherm) and depth of the lower habitat boundary as described above. Although this model is useful in estimating optimal habitat volume for lake trout in some cases, it was not the best model given our study objectives. Specifically, data on TP and secchi depth are not readily available for several lakes in our data set. Also, the optimal habitat volume as defined by Christie and Regier (1988) and by Payne et al. (1990) was strongly linked to measures of lake trout production, whereas the Dillon et al. (2003) model was not.

Of particular concern to Schindler (1997) when considering effects of climate warming on lake trout and other cold stenotherms was their presence in cold monomictic lakes with no summer thermal refugia. The shallow nature of these lakes predisposes them to warmer summer conditions and the optimal thermal habitat restrictions that follow. Although there is suitable thermal habitat in the spring and fall, the duration of “no thermal habitat” conditions in the summer is likely to increase with climate warming. Schindler (1997) suggested that for lakes that are isothermal in midsummer, even a temperature increase of a few degrees could lead to population extirpation of cold-water species such as lake trout. Localized extirpations of lake trout populations as a result of limited optimal summer habitat have already been reported in a number of lakes in central and eastern Ontario (MacLean et al. 1990).

Our analysis of changes to lake trout habitat volumes under reasonable warming scenarios suggests that climate warming will render most southern Yukon lakes less suitable for lake trout, resulting in overall decreases in potential harvest. Analyses by Minns and Moore (1992) suggest that the areas currently supporting the highest fish yields will become the areas with low or marginal yields under climate change and areas with the highest yields will be relocated northward. Our analyses, which have been restricted to southern Yukon lakes (because of limited data available for more northerly lake trout lakes), suggest that any increase in species productivity will be further north than the southern Yukon. Under climate warming, cold-water species such as lake trout would be restricted to lakes that are further north or at higher altitudes than where populations are currently found; an 8° shift in latitude or a 1500 m shift in altitude is predicted (McLain et al. 1994). Overall range shifts for lake trout are also likely in the long term, provided previously unusable habitat becomes accessible.

As with any modeling exercise, the validity of our results depends on the realism of the assumptions made in our models and the quality of the data used in the simulations. Even though there are uncertainties involved in predicting the magnitude of climate change, managers of renewable resources, including fisheries, must assess the scope of potential impacts of global warming and prepare for a range of future conditions (Minns and Moore 1992). This study provides a framework for continued analyses of these possibilities and identifies southern Yukon lake trout populations and lake types that could be at the greatest risk from climate warming in terms of preferred habitat reductions and subsequent decreases in lake trout potential harvest and population viability. The importance of enhanced data collection in Canada’s north is clear, as according to ideas initiated by Minns and Moore (1992), potential harvest in Canada’s far north should increase compared with current conditions.

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References

Blumberg, A.F., and DiToro, D.M. 1990. Effects of climate warming on dissolved oxygen concentrations in Lake Erie. Trans. Am. Fish. Soc. **119**: 210–233.

Christie, G.C. 1986. Measures of optimal thermal habitat and their relationship to yields for four commercial fish species. M.Sc. thesis, University of Toronto, Toronto, Ont.

Christie, G.C., and Regier, H.A. 1988. Measures of optimal thermal habitat and their relationship to yields for four commercial fish species. Can. J. Fish. Aquat. Sci. **45**: 301–314.

Crawshaw, L.I., and O’Connor, C.S. 1996. Behavioral compensation for long-term thermal change. *In* Society for Experimental

Biology seminar series 61: global warming and marine fish. *Edited by* C.M. Wood and D.G. McDonald. Cambridge University Press, Cambridge, UK. pp. 371–376.

DeStasio, B.T., Hill, D.K., Klenhans, J.M., Nibbelink, N.P, and Magnuson, J.J. 1996. Potential effects of global climate change on small north-temperate lakes: physics, fish, plankton. Limnol. Oceanogr. **41**: 1136–1149.

Dillon, P.J., Clark, B.J., Molot, L.A., and Evans, H.E. 2003. Predicting the location of optimal habitat boundaries for lake trout (*Salvelinus namaycush*) in Canadian Shield lakes. Can. J. Fish. Aquat. Sci. **60**: 959–970.

Fry, F.E.J. 1947. Effects of the environment on animal activity. Univ. Toronto Stud. Biol. Ser. **55**: 1–62.

Garwood, R.W., Jr. 1977. An oceanic mixed layer model capable of simulating cyclic states. J. Phys. Oceanogr. **7**: 455–468.

Hanna, M. 1990. Evaluation of models predicting mixing depth. Can. J. Fish. Aquat. Sci. **47**: 940–947.

Hondzo, M., and Stefan, H.G. 1993. Regional water temperature characteristics of lakes subjected to climate change. Clim. Change, **24**: 187–211.

Imberger, J., and Patterson, J.C. 1981. A dynamic reservoir simulation model — DYRESM: 5. *In* Transportation models for inland and coastal waters. *Edited by* H. Fischer. Academic Press, New York. pp. 310–361.

Imberger, J., and Patterson, J.C. 1990. Physical limnology. Adv. Appl. Mech. **27**: 303–475.

King, J.R., Shuter, B.J., and Zimmerman, A.P. 1997. The response of the thermal stratification of South Bay (Lake Huron) to climate variability. Can. J. Fish. Aquat. Sci. **54**: 1873–1882.

King, J.R., Shuter, B.J., and Zimmerman, A.P. 1999. Signals of climate trends and extreme events in the thermal stratification pattern of multibasin Lake Opeongo, Ontario. Can. J. Fish. Aquat. Sci. **56**: 847–852.

Mac, M.J. 1985. Effect of ration size on preferred temperature of lake charr (*Salvelinus namaycush*). Environ. Biol. Fishes, **14**: 227–231.

Mackenzie-Grieve, J.L. 2005. Climate warming and northern lake trout (*Salvelinus namaycush*): energetics, production and conservation under climate warming. M.Sc. thesis, University of Calgary, Calgary, Alberta.

MacLean, N.G., Gunn, J.M., Hicks, F.J., Ihessen, P.E., Malhiot, M., Mosindy, T.E., and Wilson, W. 1990. Genetic and environmental factors affecting the physiology and ecology of lake trout. Lake trout synthesis. Ontario Ministry of Natural Resources, Toronto, Ontario.

Magnuson, J.J., Crowder, L.B., and Medvick, P.A. 1979. Temperature as an ecological resource. Am. Zool. **19**: 331–343.

Magnuson, J.J., and DeStasio, B.T. 1997. Thermal niche of fishes and global warming. *In* Global warming: implications for freshwater and marine fish. Society for Experimental Biology, seminar series 61. *Edited by* C.M. Wood and D.G. McDonald. Cambridge University Press, Cambridge, UK. pp. 375–408.

Magnuson, J.J., Meisner, J.D., and Hill, D.K. 1990. Potential changes in the thermal habitat of Great Lakes fish after global climate warming. Trans. Am. Fish. Soc. **119**: 254–264.

Marshall, T.R. 1996. A hierarchical approach to assessing habitat suitability and yield potential of lake trout. Can. J. Fish. Aquat. Sci. **53**(Suppl. 1): 332–341.

Martin, N.V., and Olver, C.H. 1980. The lake charr, *Salvelinus namaycush*. *In* Charrs: salmonid fishes of the genus *Salvelinus*. *Edited by* E.K. Balon. D.W. Junk Publishers, The Hague, Netherlands. pp. 205–277.

McCormick, M.J. 1990. Potential changes in thermal structure and cycle of Lake Michigan due to global warming. Trans. Am. Fish. Soc. **119**: 183–194.

McLain, A.S., Magnuson, J.J., and Hill, D.K. 1994. Latitudinal and longitudinal differences in thermal habitat for fishes influenced by climate warming: expectations from simulations. Verh. Int. Ver. Theor. Angew. Limnol. **25**: 2080–2085.

Meisner, J.D., Goodier, J.L., Regier, H.A., Shuter, B.J., and Christie, W.J. 1987. An assessment of the effects of climate warming on Great Lakes basin fishes. J. Gt. Lakes Res. **13**(3): 340–352.

Minns, C.K., and Moore, J.E. 1992. Predicting the impacts of climate change on the spatial pattern of freshwater fish yield capability in eastern Canadian lakes. Clim. Change, **22**: 227–246.

O'Connor, D.V., Rottiers, D.V., and Berlin, W.H. 1981. Food consumption, growth rate, conversion efficiency, and proximate composition of yearling lake trout. Great Lakes Fish. Lab. Ann Arbour, Michigan, Admin. Rep. No. 81-5.

Payne, N.R., Korver, R.M., MacLennan, D.S., Nepszy, S.J., Shuter, B.J., Stewart, T.J., and Thomas, E.R. 1990. The harvest potential and dynamics of lake trout populations in Ontario. Lake trout synthesis. Ontario Ministry of Natural Resources, Toronto, Ontario.

Riley, M.J., and Stefan, H.G. 1988. A dynamic lake water quality simulation model. Ecol. Model. **43**: 155–182.

Rouse, W.R., Douglas, M.S.V., Hecky, R.E., Hershey, A.E., Kling, G.W., Lesack, L., Marsh, P., McDonald, M., Nicholson, B.J., Roulet, N.T., and Smol, J.P. 1997. Effects of climate change on the freshwaters of Arctic and subarctic North America. Hydrol. Process. 11: 873–902.

Ryan, P.A., and Marshall, T.R. 1994. A niche definition for lake trout (*Salvelinus namaycush*) and its use to identify populations at risk. Can. J. Fish. Aquat. Sci. **51**: 2513–2519.

Schindler, D.W. 1997. Widespread effects of climatic warming on freshwater ecosystems in North America. Hydrol. Process. **11**: 1043–1067.

Shuter, B.J., and Lester, N.P. 2004. Climate change and sustainable lake trout exploitation: predictions from a regional life history model. *In* Boreal shield watersheds: lake trout ecosystems in a changing environment. *Edited by* J.M. Gunn, R.J. Steedman, and R.A. Ryder. Lewis Publishers, CRC Press, Boca Raton, Florida. pp. 281–291.

Shuter, B.J., and Meisner, J.D. 1992. Tools for assessing the impact of climate change on freshwater fish populations. GeoJournal, **28**: 7–20.

Shuter, B.J., and Post, J.R. 1990. Climate, population viability, and the zoogeography of temperate fishes. Trans. Am. Fish. Soc. **119**: 314–336.

Shuter, B.J., Schlesinger, D.A., and Zimmerman, A.P. 1983. Empirical predictors of annual surface water temperature cycles in North American lakes. Can. J. Fish. Aquat. Sci. **40**: 1838–1845.

Stefan, H.G., Hondzo, M., and Fang, X. 1993. Lake water quality modeling for projected future climate scenarios. J. Environ. Qual. **22**: 417–431.

Welch, P.S. 1948. Limnological methods. Blakiston Co., Philadelphia.