Global Change Biology (2007) 13, 2052–2064, doi: 10.1111/j.1365-2486.2007.01426.x

Will northern fish populations be in hot water because of climate change?

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Abstract

Predicted increases in water temperature in response to climate change will have large implications for aquatic ecosystems, such as altering thermal habitat and potential range expansion of fish species. Warmwater fish species, such as smallmouth bass, *Micropterus dolomieu*, may have access to additional favourable thermal habitat under increased surface-water temperatures, thereby shifting the northern limit of the distribution of the species further north in Canada and potentially negatively impacting native fish communities. We assembled a database of summer surface-water temperatures for over 13 000 lakes across Canada. The database consists of lakes with a variety of physical, chemical and biological properties. We used general linear models to develop a nation-wide maximum lake surface-water temperature model. The model was extended to predict surface-water temperatures suitable to smallmouth bass and under climate-change scenarios. Air temperature, latitude, longitude and sampling time were good predictors of present-day maximum surface-water temperature. We predicted lake surface-water temperatures for July 2100 using three climate-change scenarios. Water temperatures were predicted to increase by as much as 18 °C by 2100, with the greatest increase in northern Canada. Lakes with maximum surface-water temperatures suitable for smallmouth bass populations were spatially identified. Under several climate-change scenarios, we were able to identify lakes that will contain suitable thermal habitat and, therefore, are vulnerable to invasion by smallmouth bass in 2100. This included lakes in the Arctic that were predicted to have suitable thermal habitat by 2100.

Keywords: climate change, general linear model, maximum surface water temperature, range expansion, smallmouth bass, thermal habitat

Received 24 April 2007; revised version received 10 May 2007 and accepted 11 May 2007

Introduction

Temperature is an important abiotic factor regulating many processes across numerous taxa, including ectothermic organisms such as fishes (Magnuson *et al.*, 1990). Most physiological processes in fishes are heavily influenced by temperature, including spawning, development, and growth (Magnuson *et al.*, 1979; Tonn, 1990). Temperature is the most important abiotic variable governing growth and survival of fishes (Christie & Regier, 1988). Climatic factors, such as temperature, affect community structure and limit species distribution because different species have different fundamental thermal niches (Magnuson *et al.*, 1979). The northern range limit of some species is largely influenced by temperature (Shuter & Post, 1990). For example, temperature plays a large role in determining the northern limit of smallmouth bass, because of its influence in regulating growth rate, timing and success in spawning and egg development, ultimately influencing young-of-year overwintering survival (Shuter *et al.*, 1980).

Global air temperatures are projected to rise between 1.4 and 5.8 °C over the next century (IPCC, 2001) with variability among estimates stemming from differences

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in expectations about economic development and assumptions in the General Circulation Models used to model temperatures. Northern regions of Canada are especially vulnerable to much larger increases in air temperatures compared with other regions of North America (Vaughan *et al*., 2003). For example, the Mackenzie River basin has already experienced increases in temperature up to 2 °C per decade since the mid-1970s (Stewart *et al*., 1998). Climate change will have profound impacts on thermal habitat, distribution and growth of aquatic organisms (Casselman, 2002). It is expected that some fish species will expand their range to the north (Rahel, 2002) by approximately 500 or 600 km (Magnuson *et al*., 1997; Jackson & Mandrak, 2002; Vander Zanden *et al*., 2004a). Invasion of non-native species and the northward range expansion of species may have serious consequences for native species (Casselman, 2002; Magnuson, 2002).

The northward range expansion of the smallmouth bass, in particular, is of concern, as this species has become established in many lakes in central Canada (Vander Zanden *et al*., 2004b; Dunlop & Shuter, 2006) and in numerous other countries (Jackson, 2002). This range expansion has been facilitated by previous stocking of lakes, unauthorized introduction by anglers and dispersal through drainage networks (Jackson, 2002; Vander Zanden *et al*., 2004b; Dunlop & Shuter, 2006).

As temperature increases and the thermal regime is shifted to the north, smallmouth bass populations are expected to follow the northerly shift in thermal habitat (Casselman *et al*., 2002; Jackson & Mandrak, 2002; Shuter *et al*., 2002) where they had been previously restricted by a cooler thermal habitat preventing successful overwintering (Shuter *et al*., 1980). Average July air temperatures are related to water temperatures which affect growth rate and therefore the size of young-of-year as they enter their first winter and the possibility of winter starvation (Shuter *et al*., 1980). The thermal range between 16 and 18 °C has been identified as being crucial because young-of-the-year smallmouth bass are likely to successfully overwinter if average July air temperatures reach 18 °C and unlikely to survive if temperatures reach 16 °C or less (Shuter *et al*., 1980). The northward range expansion of smallmouth bass is likely to have dramatic impacts on native cyprinids and lake trout populations (Jackson & Mandrak, 2002).

The presence of littoral predators like smallmouth bass, has been strongly associated with the lack of cyprinids (Harvey, 1981; Tonn & Magnuson, 1982; Jackson & Harvey, 1989; Jackson *et al*., 1992, 2001; Vander Zanden *et al*., 1999, 2004a; MacRae & Jackson, 2001; Jackson, 2002; Shuter *et al*., 2002). Establishment of smallmouth bass into an aquatic system may relate to the loss of entire species assemblages and contribute to the homogenization of fish fauna (Jackson, 2002). Jackson & Mandrak (2002) estimated that more than 25 000 local populations of four cyprinid species, specifically northern redbelly dace (*Phoxinus eos*), finescale dace (*Phoxinus neogaeus*), fathead minnow (*Pimephales promelas*) and pearl dace (*Margariscus margarita*), may disappear in ON, Canada, as climate warms and smallmouth bass colonize. Extending this approach to other species impacted by bass and increasing the geographic scope of the area considered shows the enormous impact that northern aquatic systems may undergo simply resulting from the range expansion of this species as suitable thermal habitat develops.

The objectives of our paper are fourfold. The first objective is to develop a statistical model linking current maximum lake surface-water temperatures to climate, lake geography, morphology, and water chemistry variables for lakes across Canada. The second objective is to predict maximum summer surface-water temperatures for lakes across Canada in the year 2100 under climate-change scenarios. The third objective is to identify current summer thermal habitat for smallmouth bass in lakes across Canada, and finally, the fourth objective is to predict suitable summer thermal habitat for smallmouth bass for lakes across Canada in 2100 under climate-change scenarios.

Materials and methods

Data acquisition

We collected data on maximum lake water temperature (based on surface or near-surface measurements) and corresponding lake morphology, water chemistry and climate data from a variety of academic and government institutions across Canada. We obtained data for 47 609 Canadian lakes for which 13 072 lakes had information on surface or near-surface water temperature (Fig. 1). We only included one water-temperature value for each lake selecting the temperature that was the maximum water temperature recorded for that lake. Variables for which we collected corresponding data for each lake included: latitude, longitude (expressed as a negative number to make it suitable for use in ArcGIS), surface area, volume, maximum depth, mean depth, shoreline perimeter, elevation, water temperature (near-surface from 0 to 2 m), water temperature measurement depth, conductivity, secchi depth, total phosphorous concentration, total dissolved solids concentration, pH, dissolved oxygen concentration, and sampling date. Climatic variables were obtained from

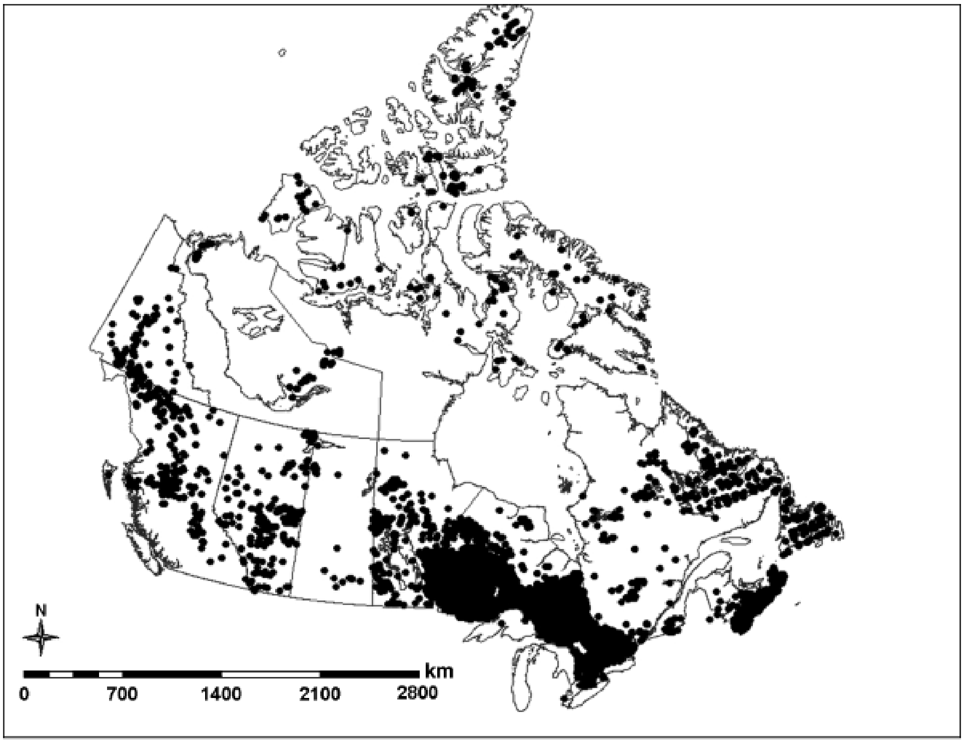

Fig. 1 Georeferenced surface-water temperature database describing 13 072 lakes in Canada.

IPCC Data Distribution Centre as 1961–1990 averages. The data were interpolated from meteorological stations using thin-plate splines and summarized on a $0.5 \times 0.5^{\circ}$ grid. The climatic variables we included were mean annual air temperature, mean July air temperature, mean August air temperature, monthly and mean annual precipitation, monthly and mean annual solar radiation, and monthly and mean annual cloud cover percent. We calculated the maximum number of daylight hours for each month and an annual mean using tables provided by the US Navy (http://aa.usno.navy.mul/data/docs/Dur_OneYear.html).

The dataset describing maximum lake surface-water temperatures was pruned to reduce some inherent sampling biases. Firstly, only water temperatures measured in June to mid-September sampled after 1960 were retained for the analyses. We reduced the Ontario and Nova Scotia datasets (these were substantially larger than all other provincial datasets) by only retaining lakes that had temperature values for July and August. In addition, lakes in Ontario and Nova Scotia were randomly subsampled, while stratifying for geography and lake morphology. Our decision to reduce the sample sizes from these provinces was to ensure that our models more accurately reflected relationships across the country rather than being dominated by a regional effect because of sample-size differences. Following the pruning, 2711 lakes remained in the dataset (Table 1). This dataset was randomly divided into two subsets while maintaining geographical and lake morphology gradients: a training dataset of 1726 lakes and an independent validation dataset of 985 lakes resulted.

Climate-change analyses – model and scenarios

The climate-change model that was selected for this study was Canadian General Circulation Model – Version 2 (CGCM2). The model was chosen because it estimates conservative increases in temperature and precipitation. Three scenarios are detailed by this model – IS92a, A2 and B2, each with different assumptions and predicting different future temperature outcomes. We obtained climate scenario data from the Canadian Centre for Modelling and Analysis for the three scenarios.

CGCM2–IS92a uses observed greenhouse gases from 1900 to 1990, which then increase at a rate of 1% per year until the year 2100 up to 1422 ppmv. This scenario includes the direct effect of sulphate aerosols. CGCM2–A2 is similar to the previous scenario, but estimates slightly lower greenhouse gas concentrations up to 1320 ppmv in 2100. CGCM2–B2 is the most conservative of the three scenarios assuming slower human popula-

Table 1 Summary statistics (count, minimum and maximum values, arithmetic mean) of parameters used in the multiple regression

Variable	Count	Minimum	Maximum	Mean
Latitude	2381	42.13	82.51	53.51
Longitude	2381	−139.82	−53.27	−92.06
Surface area (ha)	1775	0.0002	2375 000	5788
Maximum depth (m)	2007	0.05	300.00	19.83
Mean depth (m)	1549	0.20	101.86	6.72
Surface water temperature (°C)	2471	0.00	28.86	17.76
Mean annual air temperature (°C)	2381	−26.51	9.18	−0.92
Mean July air temperature (°C)	2380	−3.40	22.30	15.22
Mean August air temperature (°C)	2380	−6.50	21.30	13.86
Conductivity ($\mu S\,cm^{-1}$)	952	3.70	59674	236.81
Secchi depth (m)	1328	0.20	36.60	3.31
Volume ($\times 10^4\ m^3$)	198	22.70	100 477 618	4 423 230
Perimeter (km)	1169	0.60	3788.00	42.73
Elevation (m)	1551	1.00	2243.00	395.93
Total dissolved solids ($mg\,L^{-1}$)	1094	4.00	84314	174.49
pH	1062	4.40	10.00	7.32
Year	2449	1942	2004	1984
Julian date	2449	145	259	208
Mean July precipitation (mm)	2379	0.40	4.70	2.52
Mean annual precipitation (mm)	2379	0.18	9.40	1.92
Mean July solar radiation ($Watts\,m^{-2}$)	2326	151.00	238.00	199.34
Mean annual solar radiation ($Watts\,m^{-2}$)	2326	63.67	132.58	111.31
Mean July cloud cover (%)	2378	42.00	80.00	60.30
Mean annual cloud cover (%)	2378	53.92	73.50	62.30
Water temperature sampling depth (m)	1707	0.00	5.00	0.79
January daylength (h)	2381	0.00	9.45	7.54
June daylength (h)	2381	15.25	24.00	17.47

The lakes summarized in this table only include those that were used in the analyses (the subset of 2711 lakes).

tion growth, rapid economic development and emphasis on environmental protection. CGCM2–B2 estimates greenhouse gas concentrations of 915 ppmv in 2100 (Canadian Centre for Modelling and Analysis; Canadian Institute for Climate Studies).

We used July 2100 air-temperature data and calculated mean annual air-temperature data for Canada in 2100 from the climate-change scenarios to predict future water temperature and smallmouth bass habitat suitability. Future projections in air temperature were summarized at a $3.75 \times 3.75^{\circ}$ grid level.

Data analysis

We generated models to predict: current and future maximum lake surface water temperature, and current and future smallmouth bass thermal habitat. This allowed us to best predict each of our response variables and increase the explained variability of the models. A summary of the general linear models generated in this study is provided in Table 2.

Model 1 – predicting maximum lake surface water temperatures

Multicollinearity between variables was evaluated using bivariate plots and correlation analyses before regression analyses in order to determine which variables should be retained. General linear models were constructed in SAS using PROC GLM to determine the relationships between maximum surface-water temperatures with lake morphology, physical habitat and water chemistry variables. This analysis will be referred to as Model 1 and was based on a stepwise approach using forward selection. Variables were required to be significant at $P < 0.05$ to enter and remain in the model.

Variables included in the model were: latitude, longitude, surface area, volume, maximum depth, mean depth, elevation, pH, total dissolved solid concentrations, water temperature measurement depth, sampling year, sampling date [Julian date and (Julian date)^2 to capture the seasonal dome shape of surface water temperature], mean annual air temperature, mean July

Table 2 A summary of the general linear models generated in the study

Model	Prediction	Variables in the model
1	Maximum surface water temperature	All variables
	Maximum surface water temperature under climate change	All variables. We set $\beta = 0$ and Julian date = 204.
2	Smallmouth bass thermal habitat	All except mean annual air temperature
	Smallmouth bass thermal habitat under climate change	All except mean annual air temperature. We set $\beta = 0$ and Julian date = 204.

All variables = latitude, longitude, surface area, volume, maximum depth, mean depth, elevation, pH, total dissolved solid concentrations, water temperature measurement depth, sampling year, sampling date, mean annual air temperature, mean July air temperature, mean solar radiation, mean cloud cover (the 1961–1990 average was used for the climatic variables), January day length and June day length.

air temperature, mean solar radiation, mean cloud cover (the 1961–1990 average was used for the climatic variables), January day length and June day length. The general linear models were constrained by sampling year in SAS using the term β to account for year to year variation in maximum near-surface water temperatures. Variables were log- or square-root transformed as required for normality.

Akaike information criterion (AIC), adjusted R^2 and root mean square error (RMSE) were calculated to assess the models. The model with the lowest AIC value was ultimately used to select the best model which was then evaluated using the independent, validation dataset in order to determine the amount of deviation and the root mean square error of the model for different regions across the country. Estimations from the general linear model were interpolated for the country and mapped using ArcGIS to determine the spatial distribution of maximum lake surface-water temperature values.

We used projected July and mean annual air temperatures for the year 2100 from the three climate-change scenarios in the general linear model to derive our predictions for maximum lake surface-water temperatures under climate change scenarios. We set $\beta = 0$ to apply the model in the year 2100. We determined that 23 July (Julian date = 204) yielded the maximum water temperature for the current time-period. Therefore, in order to estimate maximum temperatures for 2100, we set the Julian date term to 204 for the predictive models. The spatial distribution of maximum summer surface-water temperature values in 2100 were determined by extrapolating the general linear model for Canadian lakes.

Model 2 – predicting smallmouth bass thermal habitat

A general linear model similar to Model 1, including all variables except mean annual air temperature, was calculated to predict maximum surface-water temperature in order to identify suitable smallmouth bass thermal habitat (Model 2). Smallmouth bass thermal habitat has been linked with July air temperatures. Shuter *et al*. (1980) specified that suitable thermal habitat for smallmouth bass occurs where July air temperature is greater than 18 °C, potential habitat occurs at July air temperatures between 16 and 18 °C, and unsuitable thermal habitat exists in lakes where temperatures are less than 16 °C. The upper lethal temperature for smallmouth bass is known to be 35 °C (Scott & Crossman, 1973). The general linear model allowed us to make the link between July air temperatures and surface-water temperatures to predict thermal habitat for smallmouth bass across Canada. After developing the general linear model, we set July air temperature to be 16 and 18 °C in order to predict maximum surface-water temperatures and corresponding suitability of smallmouth bass habitat (Shuter *et al*., 1980). Thermal habitat distribution maps were created to identify suitable, potentially suitable, and unsuitable thermal habitat available to smallmouth bass across Canada.

July air temperatures in 2100 from the three climate-change scenarios were incorporated into Model 2 and extrapolated across the country to predict smallmouth bass habitat under climate-change scenarios. Spatial distributions of suitable, potentially suitable and unsuitable smallmouth bass thermal habitat in 2100 were mapped.

Results

Model 1 – predicting maximum lake surface-water temperatures

The general linear model describing maximum lake surface-water temperatures was

$$\mathrm{SWT} = -57.88 + 0.79 \times \mathrm{MJT} + 0.26 \times \mathrm{MAT} - 0.00151 \times (J)^2 + 0.617 \times J - 0.019 \times \mathrm{longitude} + \beta$$

where J, Julian date; SWT, surface water temperature; MAT, mean annual air temperature (average of 1961–

Table 3 A list of partial R^2 for models one and two to describe the amount of variation accounted for by each variable

R^2 coefficient of parameter	Model 1	Model 2
Mean July air temperature	0.7	0.7
Mean annual air temperature	0.01	–
Year	0.052	0.057
Julian date	0.017	0.017
(Julian date)^2	0.019	0.011
Latitude	–	0.0096
Longitude	0.0026	0.0085

Table 4 Validation of surface-water temperature multiple-regression model (Model 1) using an independent dataset

	Mean Deviation	RMSE	*n*
Total	0.06	2.53	872
Alberta	−0.08	2.80	52
British Columbia	1.59	3.33	53
Manitoba	−0.16	2.63	80
Newfoundland	0.95	2.69	30
Nova Scotia	−0.09	2.31	59
Nunavut	1.15	3.33	56
Northwest territory	0.39	2.14	12
Ontario	−0.16	2.22	443
Quebec	−0.31	2.39	44
Saskatchewan	2.23	3.29	6
Yukon	−0.90	2.93	37

1990); MJT, mean July air temperature (average of 1961–1990); and β, coefficient describing inter-annual year variability.

The sample size used to construct the model was 1475 lakes and the model had an adjusted $R^2 = 0.80$. The root mean square error was 2.56 and its AIC value was 3161 – the lowest of all models using the various combinations of variables, thereby indicating that this model was the most parsimonious. Mean July air temperature was the most important variable in predicting maximum lake surface-water temperatures yielding a partial $R^2 = 0.70$. Inter-annual variability in surface-water temperatures accounted for approximately 5% of the variation. The partial R^2 values for all models retained in this study are listed in Table 3. The coefficients of β ranged from −3.35 to 3.22 with a standard deviation of 1.49 (Appendix A). The β coefficients are generally more positive in recent years and negative in the earlier years of this study suggesting that water temperatures have been increasing over the duration of the study (1960–2004).

An independent, validation dataset was used to test the model. Root mean square error (RMSE) and the deviations between observed and predicted temperatures were calculated for the country and by province. Based on the validation dataset comprised of 872 lakes, the overall mean temperature deviation was 0.057 °C with a RMSE = 2.53 (Table 4; Fig. 2) indicating similar results between the training and validation datasets. There is a strong latitudinal gradient in surface-water temperatures (Fig. 3a). The model incorporates differences in elevation, indirectly through air temperatures, as alpine lakes are cooler than lakes located at lower elevations in adjacent locations.

We extended Model 1 using July and mean annual air temperatures from the three climate-change scenarios (GCM2–IS92a, A2 and B2) in the year 2100, and by setting β to 0 and Julian date to 204 (Fig. 3b–d). Water temperatures in most of the country are expected to increase, with the greatest increase occurring in northern regions of Canada. The IS92a scenario predicted the greatest increase in water temperatures relative to other scenarios. By 2100, water temperatures in the majority of Canada are predicted to increase by 5–10 °C and northern regions of Canada could experience temperatures 10–18 °C warmer than current temperatures. The large increases in water temperature are comparable to the increases in air temperature as predicted by the General Circulation Model Version 2 scenarios. Note that these results are based on the predictions for year 2100 rather than the 30-year mean associated with that period which would provide slightly lower predictions.

Model 2 – predicting smallmouth bass thermal habitat

The general linear model describing maximum lake surface-water temperatures to determine suitable thermal habitat for smallmouth bass was:

$$\mathrm{SWT} = -44.72 + 0.76 \times \mathrm{MJT} + 0.59 \times J - 0.0015 \times (J)^2 - 0.034 \times \mathrm{longitude} - 0.23 \times \mathrm{latitude} + \beta$$

The sample size used to construct the model was 1475 lakes. The adjusted $R^2 = 0.80$ indicating that 80% of the variability in lake surface-water temperature could be explained by the multiple regression model. Mean July air temperature was the most important predictor in predicting lake surface-water temperatures yielding a partial $R^2 = 0.7$. Inter-annual variability in surface-water temperatures accounted for approximately 6% of the variation (Table 3). The coefficients of β ranged from −3.15 to 3.61 with a standard deviation of 1.53 (Appendix A). Again, the β coefficients are generally more positive in recent years and negative in the earlier years of this study suggesting that water temperatures have been increasing over the duration of the study (1960–2004). The RMSE of Model 2 was 2.55. Testing the

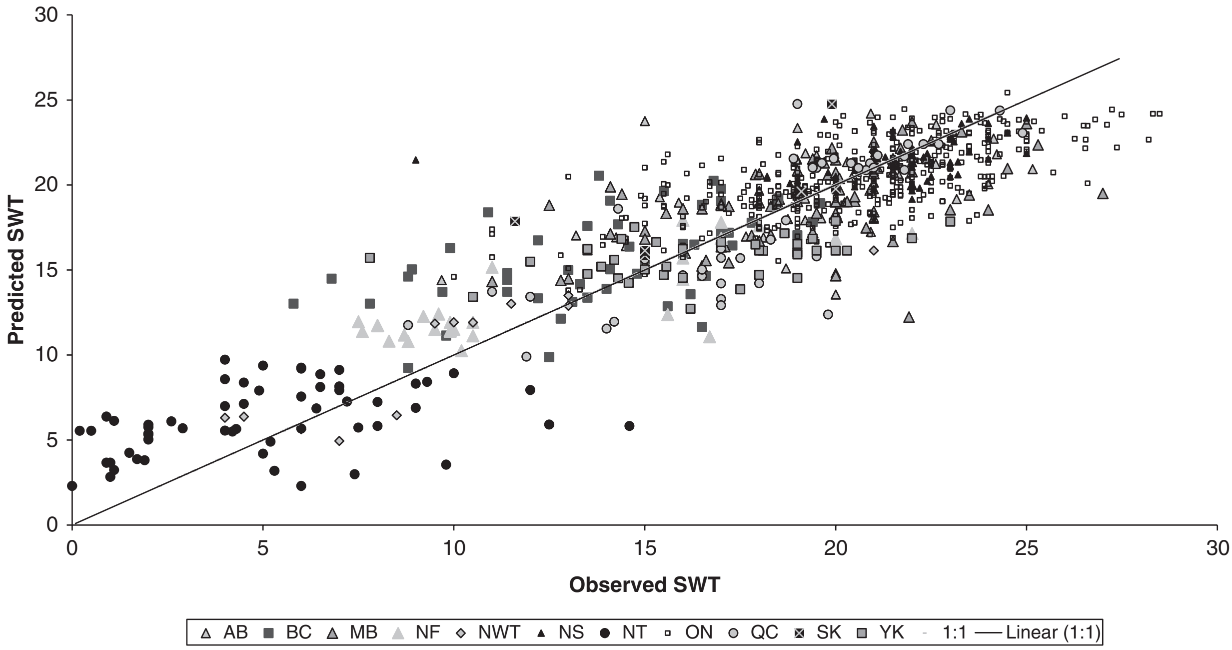

Fig. 2 Multiple-regression model evaluation with the independent validation dataset: deviations between predicted and observed surface-water temperatures for lakes across Canada.

model on the validation dataset comprised of 872 lakes yielded an overall mean temperature deviation was 0.11 °C and a RMSE = 2.51 indicating similar results between the training and validation datasets.

We incorporated July air temperatures between 16 and 18 °C in Model 2 to determine the maximum surface-water temperatures required for suitable, potentially suitable and unsuitable smallmouth bass thermal habitat. Current suitable thermal habitat for smallmouth bass is restricted to the southern regions of Canada (Fig. 4a). The majority of Canada does not currently contain suitable thermal habitat for this warmwater species as summer temperatures are too cool to permit successful growth and overwintering survival of young-of-year smallmouth bass.

Smallmouth bass thermal habitat suitability was predicted for July 2100 using the three climate-change scenarios: CGCM2–GHG + A, A2 and B2 (Fig. 4b–d). By July 2100, the majority of the lakes in the country could potentially contain suitable thermal habitat for smallmouth bass. The extent of the potential thermal habitat distribution varies between the three climate-change scenarios and depends upon the degree of climate warming.

Discussion

Water temperature has a myriad of effects on limnological processes (Magnuson *et al*., 1997) and plays an important role in the distribution and life history of many aquatic organisms, including fishes. A comprehensive model for predicting maximum lake surface-water temperatures across Canada does not exist. Several surface-water temperature models are available in the literature (e.g. Shuter *et al*., 1983; Shuter & Post, 1990; Pienitz *et al*., 1997; Snucins & Gunn, 2000; Edmundson & Mazumder, 2002), but they tend to be region specific, based on a small number of lakes and are not generally good predictors of surface-water temperature for lakes across large areas (e.g. Canada). The empirical lake surface-water temperature models developed in our study were based on a very large dataset, encompassing a vast distributional gradient and explained approximately 80% of the variability in maximum lake surface-water temperature.

Mean July air temperature was the most important predictor variable and explained approximately 70% of the variability in maximum lake surface-water temperatures – matching the critical temperature period identified by Shuter *et al*. (1980) for determining the northern boundary of smallmouth bass. Mean annual air temperature, latitude, longitude, sampling year and sampling date were significant variables in predicting maximum lake surface-water temperatures, but only explained approximately 10% of the variation. Although the IPCC 1961–1990 average values for July air temperature were used in this study to model surface-water temperatures and to subsequently permit climate-

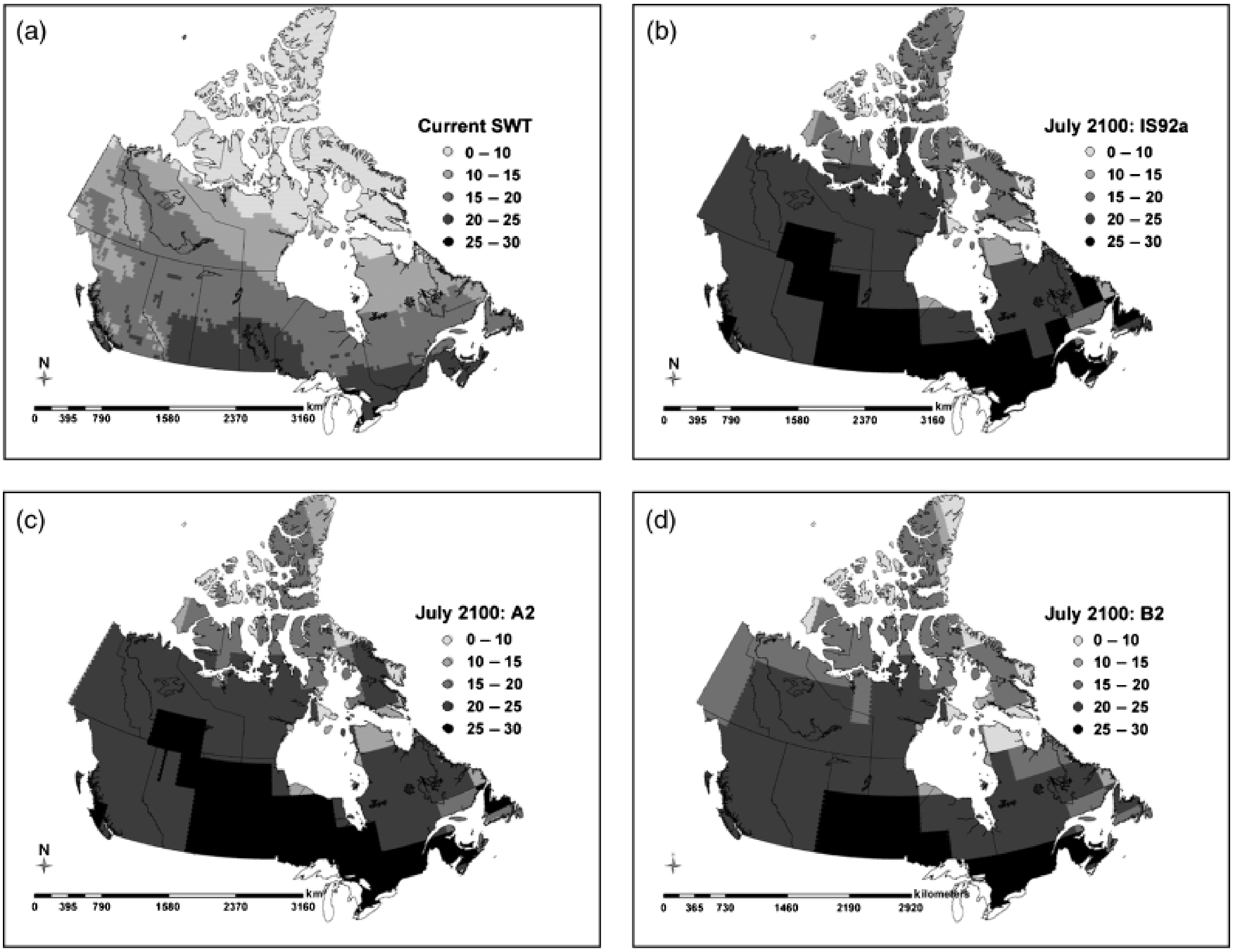

Fig. 3 (a) Current lake surface-water temperatures in Canada based on multiple-regression Model 1. (b–d) Predicted future lake surface-water temperatures in Canada based on multiple-regression Model 2 and climate-change scenarios CGCM2–IS92a, A2 and B2 in July 2100.

change modeling, this variable still explained the majority of variation in surface-water temperature. Greater amounts of variation may have been explained if local air and surface water temperatures were recorded simultaneously, but this was not possible because of the retrospective nature of our study. Air temperatures have been empirically linked to surface-water temperatures in the literature (e.g. McCombie, 1959; Shuter *et al.*, 1983; Livingstone & Lotter, 1998; Livingstone & Dokulil, 2001). Although more extensive datasets exist for air temperature, which is closely associated with surface-water temperature (albeit indirectly), it is imperative to predict lake surface-water temperatures as water temperatures are more relevant to aquatic processes and organisms (Livingstone & Lotter, 1998).

Other variables included in the analyses, such as lake morphology, physical habitat and water chemistry did not play a significant role in predicting maximum lake-surface water temperatures at such a large scale. In contrast, surface-water temperature models reported in the literature typically incorporated lake morphology (e.g. Shuter *et al.*, 1983; Shuter & Post, 1990; Snucins & Gunn, 2000; Edmundson & Mazumder, 2002; Kettle *et al.*, 2004) and water chemistry variables, such as turbidity (e.g. Snucins & Gunn, 2000; Edmundson & Mazumder, 2002). However, these studies were generally conducted at smaller spatial scales and with fewer lakes. Variables describing patterns at a smaller scale (e.g. tens to several hundreds of kilometers) may not have contributed explanatory or predictive power in our study because the conditions were dominated by patterns that occur at larger spatial scales (e.g. large-scale climatic patterns, geographic patterns in lake size). Large spatial scale studies, such as this

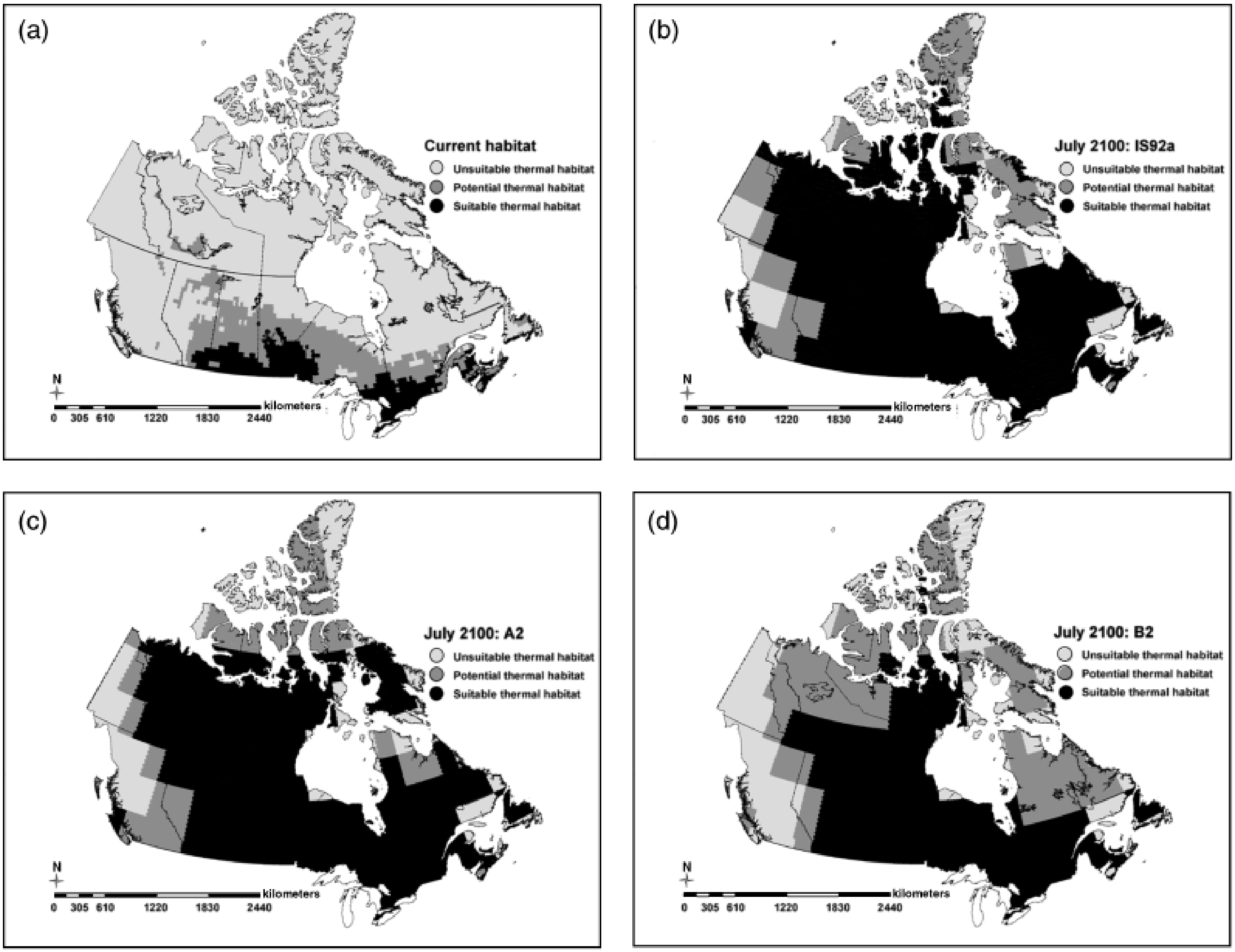

Fig. 4 (a) Current potential smallmouth bass thermal habitat in Canada based on multiple-regression Model 2. (b–d) Predicted potential smallmouth bass thermal habitat in Canada based on multiple-regression Model 4 and climate-change scenarios CGCM2–IS92a, A2 and B2 in July 2100.

one, emphasize a large range of variation, whereas smaller-scale studies are more limited in the range of variables. Other variables (such as lake morphology and water chemistry) increase in their relative importance at smaller regional scales given the more restricted range of climatic conditions involved (sensu Jackson *et al*., 2001).

Increases in water temperatures resulting from climate change are predicted to have a dramatic impact on the water quality and availability of suitable fish habitat. By July 2100, many lakes may experience water temperatures as high as 30 °C. As temperatures warm, there is an expected increase in the rate of evapouration and evapotranspiration which may result in decreased runoff and a decline in water levels (Mortsch & Quinn, 1996). Holomixis is predicted to decrease as the duration of stratification increases, thus reducing hypolimnetic oxygen concentrations and negatively impacting many aquatic organisms, particularly fishes (Stefan & Fang, 1993; Stefan *et al*., 1993; Rouse *et al*., 1997; Lehman, 2002).

Limnological changes in response to climate change may affect ecosystem productivity and fish biology. Changes in climate will affect all members of the foodweb, for example declines in diatom production (Schindler *et al*., 1996) and changes in the production of phytoplankton and zooplankton (Mortsch & Quinn, 1996). A decline in water levels and low flow could negatively affect spawning, nursery and feeding grounds in shallow regions (Meisner *et al*., 1987; Schindler *et al*., 1996). Such water-level reductions could lead to reduced access to spawning regions, increased exposure to turbidity, wave action and an alteration in habitat necessary for developing eggs and larvae (Meisner *et al*., 1987). As temperatures increase and dissolved oxygen levels decline, respiration rates and metabolism in aquatic organisms could increase and stages of embryonic development could be impaired (Lehman, 2002). It is expected that fish populations most sensitive to winter conditions may be the first to be affected by climate change contributing to increased survivorship, whereas fishes that are sensitive to fall/spring conditions may be the least and lastly affected by climate change (Shuter *et al*., 2002). If forage-food levels increase, fishes are expected to exhibit greater growth rates at higher temperatures (Magnuson *et al*., 1997; Brandt *et al*., 2002; Lehman, 2002).

Increased water temperatures may lead to the increased colonization and range expansion of non-native species (Casselman, 2002; Magnuson, 2002; Jackson & Mandrak, 2002; Vander Zanden *et al*., 2004b). This could occur by a northward range expansion of warmwater and some coolwater species, as the amount of suitable thermal habitat increases (Magnuson *et al*., 1997; Casselman, 2002). Additionally, the environment may become more suitable for exotics arriving in ballast waters from Eurasia (Magnuson *et al*., 1990). Mandrak (1989) predicted that the likelihood of invasion would increase for 27 of 58 fish species that could potentially invade the Great Lakes region today from both the south and the east. The probability of inland lakes becoming invaded increases dramatically once a species has invaded the Great Lakes (Vander Zanden *et al*., 2004b).

We focused on the potential for northward range expansion of smallmouth bass under climate-change scenarios and identified a boundary zone that represents theoretical suitable summer thermal habitat for smallmouth bass. Our study linked July air temperatures to maximum summer surface-water temperatures in order to predict suitable summer thermal habitat for smallmouth bass. Currently, suitable thermal habitat appears to be restricted to the southern regions of Canada as temperatures are too cool to permit successful overwintering survival of young-of-year smallmouth bass (Shuter *et al*., 1980). There is uncertainty about the exact current northern distribution limit of smallmouth bass due to uncertainties in specific abiotic and biotic conditions present in each lake. Inter-annual variability in summer temperature contributes to failed recruitment in some years along the northern boundary. As this inter-annual variability may interact with lake morphological and chemical conditions, thereby impacting localized thermal conditions and productivity, lakes along the northern range boundary may vary in their suitability among years and also spatially at a local level (i.e. scale of tens of kilometers). There may be additional physical or chemical abiotic conditions that prevent the successful recruitment of smallmouth bass, such as the absence of suitable spawning substrate although suitable thermal habitat exists (Scott & Crossman, 1973; Olson *et al*., 2003).

As temperatures increase and the thermal regime is shifted northward, smallmouth bass populations are expected to follow the northerly shift in thermal habitat (King *et al*., 1999; Casselman *et al*., 2002; Jackson & Mandrak, 2002; Shuter *et al*., 2002) where they had been previously restricted by a cooler thermal habitat preventing successful overwintering (Shuter *et al*., 2002). We have shown that climate change has the potential to greatly influence the smallmouth bass distribution by increasing the amount of thermal habitat available to the warmwater fish species over thousands of kilometres. By July 2100, the majority of the lakes in Canada could potentially contain suitable thermal habitat to sustain smallmouth bass populations.

Recent work (Austin & Colman, 2007) has shown Lake Superior water temperatures to become warmer than expected due to a shorter ice-cover period, thereby reducing the albedo effect and leading to a net warmer of the lake. Given the high albedo of Arctic systems, this effect may contribute to increased warming of lakes in the northern regions relative to what our model predicts. The extent of the northerly shift in thermal habitat varied between climate-change scenarios and depends upon the degree of climate warming. Even the least conservative climate change scenario did not predict maximum surface water temperatures to exceed 35 °C by 2100 suggesting that there will not be thermally lethal regions in Canada for smallmouth bass. Although the business as usual climate scenario predicts that suitable thermal habitat could exist in the High Arctic, the marine systems should prove an effective barrier to dispersal.

While suitable thermal habitat may exist, a major factor in determining a species distribution is its ability to disperse into new areas. Aquatic organisms are typically viewed as being more limited in their dispersal capabilities because of the constraints imposed by the landscape. However, the range of fish species and other aquatic organisms has been shown to expand considerably either through human introductions of species (e.g. Litvak & Mandrak, 1993; Dextrase & Mandrak, 2006), or their own abilities to colonize into adjacent waters (Jackson & Mandrak, 2002). One major factor that may contribute to accelerated expansion northwards is the direction of drainage systems. To date, the northern boundary of smallmouth bass (and many exotic species) has been contained within river systems draining to the south into the Great Lakes basin. However, once environmental conditions are suitable north of this continental divide, the northward expansion of smallmouth bass may be further assisted by the northward direction of flow for the river systems further north. This acceleration in potential dispersal may be offset somewhat because if water levels decline as climate warms, the northward dispersion of smallmouth bass may be hindered as some drainage systems become fragmented. However, the importance of the change in direction of water flow from south to north above the continental divide cannot be underestimated in affecting the future expansion of species into northern Canada.

There is additional uncertainty about the potential for smallmouth bass to successfully establish in a lake depending on future conditions, such as duration of ice-cover, and available hours of sunlight. We based our smallmouth bass thermal habitat suitability model on Shuter *et al*., (1980). The model predicted that July air temperatures over 18 °C are required for young-of-year smallmouth bass to attain a sufficient size for successful overwintering (Shuter *et al*., 1980). However, the mechanism underlying the empirical model has not been evaluated at high latitudes due to the currently unsuitable thermal conditions. The summer thermal regime may theoretically provide suitable thermal habitat for smallmouth bass and an increased potential for growth, particularly during the 24 h light period. However, the continual darkness period over several months may result in arduous winter conditions that may prevent the young-of-year smallmouth bass from overwintering successfully at high latitudes. Such similar effects exist in the modeling exercises for northward range expansions of other animal and plant species too. For lakes in which smallmouth bass successfully invade, the northward range expansion of smallmouth bass will have dramatic impacts on fish community composition (Jackson, 2002). The presence of littoral predators like smallmouth bass has been strongly associated with the lack of cyprinids (e.g. Tonn & Magnuson, 1982; Jackson & Harvey, 1989; MacRae & Jackson, 2001; Jackson, 2002; Jackson & Mandrak, 2002; Vander Zanden *et al*., 2004a). Invasion of smallmouth bass into an aquatic system may relate to the loss of entire assemblages, leading to the homogenization of fish fauna (Jackson, 2002). These effects on cyprinids appear to be more pronounced in smaller lakes (Jackson & Mandrak, 2002). MacRae & Jackson (2001) found that lakes with smallmouth bass and largemouth bass (*Micropterus salmoides*) contained on average 2.3 fewer smaller-bodied species than similar-sized lakes without bass and attributed the reduction to predation by bass. Jackson & Mandrak (2002) estimated that more than 25 000 local populations of four cyprinid species, specifically northern redbelly dace, finescale dace, fathead minnow and pearl dace, may disappear in Ontario, Canada as climate warms and smallmouth bass invade. For lakes in which smallmouth bass and lake trout co-occur, the invasion of smallmouth bass may affect lake trout populations. In the absence of pelagic forage fish, lake trout must shift their diet to less energetically efficient prey items, thereby negatively implicating the growth and reproduction of the native, cold-water fish species (Vander Zanden *et al*., 1999).

The northward range expansion of the smallmouth bass may have major consequences on the native fish community, particularly under climate-warming scenarios. Despite the large, negative ecological impacts of smallmouth bass invasion, there has been little concern from resource managers regarding the introduction of this species; the ‘out of sight – out of mind’ effect (Jackson, 2002). The range expansion and impact on native systems has been facilitated by governmental agencies through stocking, unauthorized and accidental introductions by anglers, and dispersal through drainage networks (Jackson, 2002; Vander Zanden *et al*., 2004b). Regulations and public education can help limit the unauthorized and accidental introduction of smallmouth bass into watersheds. However, should changes to climate approximate those found in any of the standard scenarios that we examined, the impact of northern range expansions of species such as smallmouth bass will have major detrimental impacts on extensive numbers of aquatic systems.

Acknowledgements

We thank the numerous organizations that contributed data to this study including: University of Toronto, Ontario Ministry of Natural Resources, Ontario Ministry of Environment, Department of Fisheries and Oceans Canada, Canadian Centre of Inland Waters, Laurentian University, Experimental Lakes Area, University of Calgary, University of Regina, Université du Québec à Montréal, and Université de Montréal. We thank the numerous scientists who published their data in scientific journals, theses or in online databases. Many thanks to Dan Giang for providing assistance with the figures. Thank you to Ann Zimmerman, two anonymous reviewers and the Subject Editor for their comments on an earlier version of the manuscript. Funding for this research was provided by a Natural Sciences and Engineering Research Council of Canada Research Discovery Grant to D. A. J.

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Appendix A

Appendix A1 β Coefficients used in Model 1 and 2 to describe inter-annual variability in near-surface water temperatures

Model 1			Model 2		
Year	β coefficient	n	Year	β coefficient	n
2004	−0.87	24	2004	−0.78	24
2003	0.93	37	2003	1.07	37
2002	1.19	7	2002	1.43	7
2001	1.54	47	2001	1.68	47
2000	0.088	35	2000	0.52	35
1999	0.39	5	1999	0.56	5
1998	2.29	44	1998	2.24	44
1997	0.57	33	1997	0.98	33
1996	−0.73	29	1996	−0.49	29
1995	3.22	76	1995	3.61	76
1994	0.89	18	1994	1.39	18
1993	0	1	1993	0	1
1992	−0.39	17	1992	0.47	17
1991	−1.94	26	1991	−1.84	26
1990	1.75	16	1990	2.15	16
1989	2.39	22	1989	3.27	22
1988	0.82	17	1988	1.21	17
1987	0.28	10	1987	0.13	10
1986	−0.49	36	1986	−0.26	36
1985	−0.15	79	1985	−0.05	79
1984	1.16	65	1984	1.36	65
1983	0.86	86	1983	0.95	86
1982	−1.01	107	1982	−0.96	107
1981	0.55	110	1981	0.82	110
1980	0.24	118	1980	0.29	118
1979	0	69	1979	0	69
1978	−0.87	46	1978	−1.34	46
1977	−1.38	54	1977	−2.78	54
1976	−2.76	23	1976	−0.87	23
1975	−0.98	32	1975	−0.06	32
1974	−0.3	35	1974	−0.06	35
1973	−0.16	27	1973	−0.26	27
1972	−1.52	13	1972	−1.43	13
1971	−2.53	23	1971	−2.38	23
1970	−0.3	25	1970	−0.2	25
1969	−1.9	15	1969	−1.7	15
1968	−1.38	12	1968	−1.1	12
1967	−0.67	12	1967	−0.68	12
1966	−1.95	2	1966	−1.28	2
1965	−3.35	4	1965	−3.15	4
1964	0.4	6	1964	0.61	6
1963	2.09	2	1963	2.18	2
1962	1.68	8	1962	1.85	8
1961	−1.07	3	1961	−0.74	3
1960	−2.92	1	1960	−2.47	1

