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Mixing Patterns and Plankton Biomass of the St. Lawrence Great Lakes under Climate Change Scenarios

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ABSTRACT. *This study is part of an assessment of potential effects of climate change on the St. Lawrence Great Lakes. Its purpose is to investigate potential future lake mixing patterns and primary production. Nested physical and biological models were applied to seasonal mixed layer depth, heat content, primary productivity, and to algal biomass measured as particulate chlorophyll. Two independent second generation General Circulation Models provided scenarios for future conditions of cloud cover, air temperature, humidity, and winds. The climate variables were used to force heat balance and surface mixed layer models for Lakes Superior, Michigan, Huron, Erie, and Ontario. Physical models of heat balance and mixed layer dynamics were coupled with a model of primary biological production and growth of phytoplankton. Simulated climate conditions were for time periods centered at 1975, 2030, 2050, and 2090. Climate projections from both GCMs lead to elevated mixed layer and bottom temperatures in all five lakes by as much as 5°C during this century. Both GCMs point to longer duration of thermal stratification in the five lakes, stronger stability of stratification, and deeper daily mixing depths during peak thermal stratification. For Lake Erie, no striking differences in algal biomass are likely according to climate projections of either model, but for the other lakes, either the duration of nutrient limitation of algal growth is projected to increase, or light limitation caused by deeper mixing is projected to limit the development of algal biomass.*

INDEX WORDS: *Irradiance, respiration, primary production, saturation light intensity, Great Lakes.*

INTRODUCTION

Climate variations may act as master variables for physical and biological processes in the Great Lakes. New understanding of climate dynamics and new projections of future climate conditions necessarily carry with them implicit consequences for the Great Lakes and their biota. Second generation General Circulation Models (GCMs) have recently produced projections of potential future climate conditions, but prospective climate details differ from model to model. In order to comprehend whether the different projections imply very different future conditions for the lakes, two of the models that generate the most widely divergent projections of climate conditions were selected for detailed study. Specifically, the question taken up for this work was whether and how projected climate conditions from different GCMs carry implications that are different with respect to lake temperatures, mixing dynamics, primary production, and algal biomass.

The only previous assessment of climate variations on plankton processes in the Great Lakes appears to be that of Blumberg and Di Toro (1990). The authors used weather conditions derived from first generation GCMs to drive a physical model of lake mixing and a 1970s-era lake nutrient model applied to Lake Erie. Model projections called for increased water temperatures, longer time of warm surface stratification, shallower depth of warming, and more extensive depletion of oxygen from deep waters. The authors ascribed projected declines in oxygen mainly to elevated temperature, which increases bacterial activity, rather than to the mixing patterns. They did not report rates of biological production, nutrient effects, or biomass.

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Other scenario projections from first generation GCMs have been applied to water balance and other issues of hydrology (Smith 1991, Mortsch and Quinn 1996). McCormick (1990) applied a physical mixing model (Garwood 1977, McCormick and Meadows 1988) to the question of potential future temperature structure of Lake Michigan. McCormick used simulated climate data generated by three first-generation General Circulation Models under two simulated states: (1) present condition and (2) doubled CO_2 concentration. The model used in this study is similar to that of McCormick (1990), and it is integrated on the same time and space scales. McCormick's model scenarios suggested that the surface waters of Lake Michigan might warm in the future, and that the summer depth of warming would thin. Model results suggested sharper temperature gradients at the thermocline, increased duration of summer stratification by up to 2 months, and reduced physical exchanges with deeper water. Under two of the three model scenarios investigated by McCormick (1990), Lake Michigan was projected not to mix thoroughly during the winter, and to develop a deep zone permanently isolated from water above it.

Based on model projections by McCormick (1990) for Lake Michigan and by Blumberg and Di Toro (1990) for Lake Erie, Magnuson *et al.* (1990) studied the potential implications for thermal habitats of Great Lakes fish. They concluded that the temperature changes were such that favorable thermal conditions would increase in Lake Michigan for cold, cool, and warm-water fish. In Lake Erie, favorable habitat would potentially increase only for cool and warm-water fish.

Hill and Magnuson (1990) projected water temperatures at nearshore sites by correlating water temperatures with air temperatures. They used air temperatures predicted by the three GCMs cited above to estimate water temperatures under CO_2 doubling scenarios. The scenarios were applied to physiological models of body growth by representative yearling fish: lake trout, yellow perch, and largemouth bass (cold, cool, and warm-water fish, respectively). Three nearshore sites were investigated in Lakes Erie, Michigan, and Superior. Water temperatures were projected to increase at all three sites under climate change scenarios. Model projections indicated that the fish would grow faster, provided that forage food levels increased; otherwise the growth rates might decrease. Furthermore, the prospect of oxygen depletion deep in Lake Erie meant that coldwater fish could not retreat there when otherwise lethal temperatures were projected at shallow depths. The authors concluded that (unknown) food web dynamics and possible oxygen depletion would "greatly influence the direction and magnitude of changes in fish growth as the climate warms." Hill and Magnuson (1990) cited the appendix of a 1989 EPA report in which primary production, zooplankton, and fish yields are projected to increase with climate warming by analogy with the chemical reaction rates of enzyme systems. They expressed reservations about whether the potential increases would be realized, owing to complexities of food web processes.

This report extends earlier work in two important ways. First, it relies on new model developments: second generation GCM climate projections with increased mechanistic and theoretical foundation. Second, it couples and integrates a physiological model of primary production with the vertical scales of mixing depth and light regime that result from physical processes.

METHODS

Data Sources

Projections from two second generation GCMs were selected for investigation. One of the model scenarios was CGCM1 produced by the Canadian Centre for Climate Modeling and Analysis (C) and the other was HadCM2 by the Hadley Centre (UK). Additional information on these models is available from Sousounis and Grover (2002) in this issue. Four time periods were investigated; each time period was centered at a different year: (1) the Base condition (BASE), 1975; (2) 2030; (3) 2050; and (4) 2090. BASE conditions represented archival monthly climate means measured over a 42-year interval (1954 to 1995). The GCM projections represented monthly means for 20-year intervals (e.g., 2041 to 2060).

The starting points for climate variables were GCM-projected climate conditions mapped to a coarse grid of points across the Great Lakes region. Because this study was part of a coordinated assessment effort, an effort was made to enforce uniformity of forcing variables. Research scientists at the NOAA Great Lakes Environmental Research Laboratory (NOAA/GLERL) in Ann Arbor, Michigan, selected geographically appropriate grid points from the global grids of projected climate variables produced by the two GCMs. The projected climate variables were then interpolated and averaged on a lake by lake basis (Lofgren *et al.* 2000). Thus there were specific projections of future climate variables for each lake, and those became the inputs for model developments in this study. Wind speeds measured over land are different from speeds over water because of different surface friction resulting from roughness differences. Consequently, GCM-projected wind speeds were transformed to over-lake speeds by NOAA/GLERL according to corrections reported by Croley (1989). This selection process was not capable of resolving any horizontal variations in the climate variables over a lake, owing to the coarse spatial nature of the GCM grids. The climate variables for each lake were thus regarded as horizontally averaged figures.

Interpolated and transformed climate data were provided as monthly means by NOAA scientists (B. Lofgren and T. Hunter, personal communications). Climate variables used in this study were identical with those used by NOAA for projections of future water balance in the Great Lakes (Lofgren *et al.* 2002). BASE data were likewise supplied by NOAA scientists, and were taken from NOAA's archived empirical measurements. GCM outputs do not exactly match empirical regional conditions even at the BASE time. Consequently, each GCM climate variable was scaled by NOAA personnel so that GCM model output would conform with measured BASE conditions. For example, all GCM-projected air temperatures might be adjusted upward or downward by 10% in order to match the BASE conditions of the GCM with direct observations in the Great Lakes region.

The key model climate variables for this study were:

(1) maximum daily air temperature (°C)
(2) minimum daily air temperature (°C)
(3) cloud cover (percent)
(4) air vapor pressure (mb)
(5) wind speed (cm/sec)

Additional lake-specific climate data were required. The additional data were obtained from archival data and the empirical parameter set used by Croley (1989) to generate evaporation estimates for the Great Lakes. These additional parameters were:

(1) solar irradiance at ground level under clear skies (cal/cm^2/d)
(2) air density at lake surface level (g/cm^3)
(3) barometric pressure at lake surface level (mb)
(4) coefficient relating cloud cover to long-wave counter-radiation (dimensionless)

Several simplifying assumptions were used in the simulations, including:

(1) Each lake was modeled as a steep-sided rectangular basin of depth equal to the mean depth of the actual lake. Hence, the mixing model is a one-dimensional horizontally averaged model.
(2) Advective fluxes of heat and materials by river flow were not included in the equations for heat balance and mixing depth.
(3) Nutrient limitation of algal biomass was imposed by constraining the maximum possible chlorophyll attainable, on a lake-specific basis. Hence, nutrient dynamics were not modeled explicitly.
(4) The model time step was one hour and the vertical resolution was one meter.

Conceptual Overview

Climate scenarios are used here conceptually as a complex sensitivity analysis forced by variables developed by alternative groups of climate modelers. The scenarios are different, and they represent different visions of possible future conditions. The philosophy and approach adopted here is to let the different visions drive a simplified coupling of lake physics and biology in order to see if the visions lead to divergent, convergent, or surprising outcomes. These first order steps in analysis can uncover gaps in essential knowledge and more easily define subsequent directions of inquiry.

The tension in this approach is that it might seem to obscure the difference between scientist and fortune teller. Because climate projections are unverified, they could be wrong, and all the subsequent projections based on them may seem to be a house of cards. Nonetheless, the climate projections generated by GCMs are scientific deductions from theoretical constructs, and they can be legitimately used in further deductions which might expose weaknesses or inconsistencies in the original theories or in the theories that extend the projections.

With these points in mind, the models used here to extend the deductive reasoning of GCM scenarios are vastly simplified. Thus they are expected to have general comparative value only. If it is recognized that the GCMs themselves are unable to mimic accurately the current state of environmental variables at regional scale (see above), and that daily variation at regional scales are not a feature of the models, then the evolving state of the inquiry is clear.

The basic approach taken in this study was to blend the horizontally-averaged physical lake model equations of DYRESM (Imberger and Patterson 1990) with temporally and vertically explicit representation of photosynthetic primary production (Fee 1990). DYRESM model equations have been applied successfully to a wide range of lake mixing scenarios, including North American Great Lakes (Ivey and Patterson 1984, Patterson et al. 1985). Fee's primary production model has similarly been successfully applied to empirical data from large lakes (Burnet and Davis 1980). The coupled physical-biological model was forced by GCM scenarios of surface radiance, temperature, humidity, and wind. The interpolated GCM projections used here were for monthly mean conditions, not day-to-day weather variations. Hence, short-scale dynamics are not addressed by this study. Moreover, Lake Number (Imberger and Patterson 1990) calculations for these basins under typical wind friction velocities and incipient thermal stratification make it clear that one-dimensional models do not capture the richness of real lake physics. Similarly, the effects of the earth's rotation (Patterson *et al.* 1984) judged by the ratio of the internal Rossby radius of deformation to lake width are not captured. The modeling effort is intended simply to generate seasonal patterns of mixing depths from coarse-scale climate scenarios from seasonal and interannual variations, and to highlight differences among the lakes. To pretend to do more would be disingenuous given the limitations of the GCM projections.

Changes in heat content and seasonal mixing depth are consequences of heat and momentum fluxes, and they have been well described by others (Price 1981, Monismith 1985, Spigel *et al.* 1986, Spigel 1980, Spigel and Imberger 1980, Imberger and Patterson 1990). Heat is gained from irradiance and is lost to the atmosphere over time. The heat loss mechanisms are by long wave radiation, conduction, and evaporation. Net heat loss by long wave radiation depends on the counter radiation from the sky (Keijman 1974).

Variation in atmospheric water vapor or greenhouse gas can change the net long wavelength radiative heat flux from a lake surface. Heat loss by conduction and evaporation depends on wind speed and the gradients from lake surface to air, with provision for stability effects such as when the lakes are warmer than the air in the absence of wind (Croley 1989). The heat balance of surface waters is fundamentally self-correcting; any temporary decrease in heat loss is compensated by elevated water temperature, with resultantly increased heat flux by multiple heat loss mechanisms.

Heat Balance

Lake heat content is a balance among short wave and long wave radiative fluxes, evaporation, and heat conduction. The energy balance model is

$$\Delta \text{ Lake Heat} = SW_{net} + LW_{net} - LH - SH \qquad (1)$$

where SW is short wave radiation, LW is long wave radiation, LH is latent heat loss by evaporation and SH is sensible heat loss by free and forced convection. Net short wave radiation into the lake water is calculated as insolation measured at the ground (SW_0) reduced by lake albedo (α):

$$SW_{net} = (1 - \alpha)\, SW_0 \qquad (2)$$

where $\alpha = 0.07$ (Yin and Nicholson 1998). Heat losses by long wave radiation are estimated as gray body radiation from the lake surface

$$LW_{up} = \varepsilon\, \sigma\, T_L^4 \qquad (3)$$

where ε is emissivity (= 0.97 Strub and Powell 1987), σ is the Stefan-Boltzmann constant, and T_L is lake surface temperature in degrees Kelvin. Different formulas have been proposed for counter-radiation from sky and clouds (Keijman 1974, Maidment 1993, Strub and Powell 1987, Yin and Nicholson 1998). The formulation used here is from Keijman (1974)

$$LW_{net} = \sigma\, T_A^4\, (0.53 - 0.065\sqrt{e_A})(p + (1 - p)(1 - c)) - \varepsilon\, \sigma\, T_L^4 \qquad (4)$$

where $\sqrt{e_A}$ is the vapor pressure of the air expressed in mb (1013 mb = 760 mm Hg) and c is the fraction of sky that is covered by clouds. The coefficient p is empirical, and has been estimated for each of the Great Lakes (Croley 1989).

Heat losses by evaporation and conduction are computed from heat and vapor pressure gradients using bulk coefficients estimated for the turbulent atmospheric boundary layer over the lake. Bulk transfer coefficients were calculated by the iterative algorithm published by Croley (1989, his eqs. 1 to 10).

Saturation vapor pressure at the temperature of the lake surface was defined (Maidment 1993) as

$$e_L = 6.11 \exp(17.3\ T_L/(T_L+237.3)) \qquad (5)$$

The constants in previous equations were chosen to permit calculation of heat flux in cal/cm^2/d. Heat balance is thus a function of SW_0, T_L, T_A, e_A, c, and wind speed.

Theory of the Surface Mixed Layer

Credit for a modern synthesis for theory of the surface mixed layer belongs to Niiler and Kraus (1977). They drew on earlier studies to summarize how wind stress and buoyancy forces erode an existing seasonal thermocline. Considerable work has built upon these studies to extend the theory to the diurnal mixed layer.

Net incident solar radiation that penetrates a lake surface is ultimately absorbed and converted to heat. Because the specific volume of water, and alternatively its density, are nonlinear functions of temperature, the absorption of heat causes buoyancy changes. Light attenuates differentially according to wavelength. The solar irradiance at longer wavelengths (IR) is absorbed within the top 2 meters or less by water itself. Light at shorter wavelengths, particularly 400 to 700 nm (Photosynthetically Active Radiation, PAR), which is the photosynthetic and visible part of the spectrum, penetrates more deeply. Its attenuation rate varies strongly with dissolved and particulate matter in the water. In particular, PAR penetration varies inversely with algal biomass.

Heat loss occurs at the lake surface. The result is a cooled surface film. At temperatures greater than 4°C, the cooling generates convection cells that are denser than the water just below. The kinetic energy of these convection cells adds to kinetic energy produced by wind stress. The two sources of kinetic energy provide the turbulence velocity shears that work against any existing stable density gradient at the base of the turbulent mixed layer. During daytime, however, light absorption is a buoyancy generating mechanism that acts as a sink for this kinetic energy.

Light attenuation is strongly nonlinear, such that more light is absorbed at the top half of any water layer than in the bottom half of the same layer. The result is continual production of positive buoyancy while the sun is shining. Turbulence kinetic energy is either partially or completely expended by working to mix the water in opposition to these buoyancy forces. During sunlight hours the diurnal mixed layer shoals and mixing is contained much closer to the surface than during the night. Daytime mixed layer thickness can be predicted from irradiance, light attenuation, and the kinetic energy from wind and surface cooling.

Throughout the night, the mixed layer deepens as large convection cells, forced by the wind if it is present, entrain cool water at the base of the layer. The rate of layer deepening is set by the “generalized entrainment law” (Sherman *et al.* 1978), which considers available kinetic energy, convection cell size, and the potential energy represented by stable density stratification that opposes the entrainment forces. It takes energy to pull cooler, dense water from the bottom of the mixed layer and lift it upward against gravity. As a result of the overnight process driven by surface cooling, the maximum extent of vertical mixing is typically reached at or around dawn.

Diffusion Processes Below the Mixed Layer

Mixing processes below the turbulent mixed layer were modeled as eddy diffusion, using a constant diffusion coefficient of 0.02 cm^2/sec. Imberger and Patterson (1990) cite the value as a lower limit of diffusion rates below the mixed layer, and it is probably most appropriate to the region of high gradient diffusive fluxes immediately below the surface layer. This coefficient probably underestimates eddy diffusion in the bulk of the hypolimnion, but is inconsequential to mixed layer dynamics.

Primary Biological Production and Algal Growth in the Surface Mixed Layer

Primary production in the surface mixed layer is modeled by a modification of Fee’s (1990) numerical model (Lehman 1997). This application observes light variation by latitude, time of day, and depth in the water column. Light attenuation is an explicit function of algal biomass measured as particulate chlorophyll *a* based on empirical calibration data. The photosynthesis versus irradiance relationship is represented as a rectilinear model with a light-limited region of slope = P_{max}/I_K and a light saturated region where rate of photosynthesis = P_{max}. The light saturation parameter I_K represents the light intensity at which photosynthesis first reaches P_{max}. No provision is incorporated for inhibition at high light intensities. The resulting functions are integrated over depth and time to estimate primary production per unit of lake area.

Incident Solar Radiation

Model variation in solar irradiance with latitude, season, and time-of-day relied on formulas published by Fee (1990). Incident PAR (mE/m^2/min) was calculated from total incident short wave radiation (SW_0) according to Jerlov (1976). According to Jerlov, 43% of incident SW irradiance is PAR and the ratio of energy irradiance to quantum irradiance in the PAR region is essentially 1.0. Interconversion of short wave energy (E) and quantum flux (Q) from empirical data uses the following relations:

1 quantum/sec = 1987/(λ/10^{19} W), λ in nm

Q(350–700 nm, quanta/m^2/sec) = 1.2 •10^{18} •E(350–3000 nm, W/m^2)

1 cal/cm^2/d = 0.484 W/m^2

SW_0 (W/m^2) = 0.484• SW_0 (cal/cm^2/d)

PAR quanta/m^2/sec = 1.2•10^{18} W/m^2

PAR mE/m^2/min = PAR quanta/m^2/sec • 60 sec/min ÷ 6.023 • 10^{20} (6)

Total daily short wave irradiance at ground level (SW_0) was calculated from empirical total daily insolation under clear skies (max-SW_0) according to Croley (1989):

$$SW_0 = \text{max-}SW_0\ (0.355 + 0.68^*(1 - c)) \quad (7)$$

Photosynthesis Parameters and Integral Production

The P vs I function for gross primary production is simplified to a rectilinear model, with P increasing linearly from zero irradiance to I_K , and saturating at P_{max} for irradiances greater than I_K. Stoichiometry of carbon (C) to chlorophyll (Chl) is assumed = 120 by mass (mg C : mg Chl). Additional definitions are as follows:

P_{max} = maximum rate of light-saturated photosynthesis, mg C/(mg Chl)/h
I_K = light intensity at which photosynthesis saturates at P_{max}, mEin/m^2/min
Attenuation (ATTEN) = vertical attenuation coefficient for PAR, per m
CHL = biomass as particulate chlorophyll in the mixed layer, mg Chl/m^3
ZMIX = maximum vertical extent of mixing on a daily basis, m
RESP = algal respiration rate, mg C/(mg Chl)/h
σ = sinking rate, m/d
g = grazing rate, per d

Integral gross daily primary production (P_{INT}, mg C/m^2/d) and integral daily respiration (R_{INT}, mg C/m^2/d) through the mixed layer were calculated and used to derive algal growth parameters:

$$\mu = \text{intrinsic growth rate of algal biomass, per d} = P_{INT}/(CHL•120) \quad (8)$$

$$r = \text{net intrinsic growth rate, per d} = (P_{INT}–R_{INT})/(CHL•120) – \sigma/ZMIX – g \quad (9)$$

Equation 9 was used to calculate daily changes in algal biomass measured as chlorophyll concentration within the mixed layer. These changes were in turn used to calculate changes in light attenuation (see below).

Parameter Estimation

The empirical relationship between light attenuation and algal biomass measured as chlorophyll was determined from measurements for Lakes Erie, Huron, Michigan, and Superior from 1995 to 1997. PAR attenuation was measured with a 4-π sensor deployed with a Seabird 9/11 CTD.

$$\text{ATTEN (per m)} = 0.075\ (SE = 0.005) • CHL + 0.107\ (SE = 0.007) \quad (10)$$
$$r^2 = 0.713,\ N = 104$$

Numerical values for parameters in the model of biological production were chosen from literature reports or unpublished data archives. Rates of respiration, sinking, and grazing loss exhibit wide ranges of variation in the literature, and consequently the choice of single values for simulation was purposely arbitrary. The objective of this project was to examine the potential interactions among mixing depth, light, and primary production. Consequently, the model emphasized the photosynthesis-irradiance relationship in relation to mixing depth; variable loss rates associated with higher order trophic interactions were ignored. Actual numerical values used in the simulations are reported in Table 1.

Among other things, no provision was made for

TABLE 1. Parameter values for the biological production model.

Parameter	Value	Units	Applicable Lakes	Source
P_{max}	2.8	mg C/(mg Chl)/h	E	Brooks and Sandgren unpub.
P_{max}	2.3	mg C/(mg Chl)/h	H, M, O, S	Fahnenstiel *et al.* 1989
I_K	7.3	mEin/m^2/min	E	Brooks and Sandgren unpub.
I_K	7.0	mEin/m^2/min	H, M, O, S	Fahnenstiel *et al.* 1989
Resp	$0.1 \cdot P_{max}$	mg C/(mg Chl)/h	All	Arbitrary
Sinking	1	per d	All	Arbitrary
Grazing	0.01	per d	All	Arbitrary
CHL_{max}	10	mg/m^3	E, O	Lehman unpub.
CHL_{max}	3	mg/m^3	M	Lehman unpub.
CHL_{max}	2.8	mg/m^3	H	Lehman unpub.
CHL_{max}	1	mg/m^3	S	Lehman unpub.

seasonal variation in photosynthesis coefficients, even though real variation in both P_{max} and I_K is probable. The knowledge base for modeling seasonal changes in the various Great Lakes is limited, and proliferation of poorly constrained additional variables could only obscure the circumscribed focus of inquiry. Seasonal variations in nature are contemporaneous with species changes and with nutrient limitation effects. Owing to the simplified treatment of both nutrients and trophic dynamics, simplification of the photosynthetic parameters was adopted, as well.

The effects of multiple simplifying assumptions about biological dynamics deserves further attention beyond the present report. Sensitivity of the mixing model to variations in climate variables has been investigated for a tropical lake application (Lehman 2002); cloud cover and wind speed emerged as the most influential factors in that analysis. Sensitivity of model responses to variations in photosynthesis and respiration parameters is the subject of on-going investigation.

Application to the St. Lawrence Great Lakes

In order to minimize complications owing to ice dynamics (latent heat of fusion, albedo), simulations were run from 1 March to 1 January in Lakes Ontario, Huron, Michigan, and Superior, and from 1 April to 1 January in Lake Erie. The initial condition at start of each simulation was an isothermal, holomictic water column at the temperature predicted by the NOAA/GLERL water balance model (Croley 1989; B. Lofgren and T. Hunter personal communication) for that date using identical model climate conditions as inputs. Initial chlorophyll concentration for each simulation was uniform with depth at 0.1 mg/m^3.

The model was constructed as a spreadsheet in Excel™, with Visual Basic™ macro subroutines for iteration, root-finding, and other numerical operations.

RESULTS

Summaries of simulation results by lake are reported in Figures 1 to 6. The graphs compare predictions generated by using output from Canadian (C) and Hadley (UK) GCMs. Several generalizations emerge.

Duration of Thermal Stratification

Model projections using both climate models are in agreement about the likelihood that all five Great Lakes will experience extended periods of thermal stratification in the future. The magnitudes of change projected by climate scenarios of the Canadian model are greater than those of the Hadley model (Fig. 1). The relative magnitudes of change are smallest in Lake Erie and largest in Lake Superior. By 2030, the Hadley model (UK2030) leads to projected increases of about two weeks in the total time that the 4 deepest lakes might maintain thermal stratification. With the Canadian model (C2030) the projected increases are about one month.

Under current conditions (BASE) the four lower lakes are projected to exhibit thermal stratification for about 5 months each summer, whereas Lake Superior becomes stratified for little more than 3 months. Under climate change scenarios, however, the mixing duration of Lake Superior is projected to become more similar to the other lakes, and under climate conditions of the Canadian model, it rivals

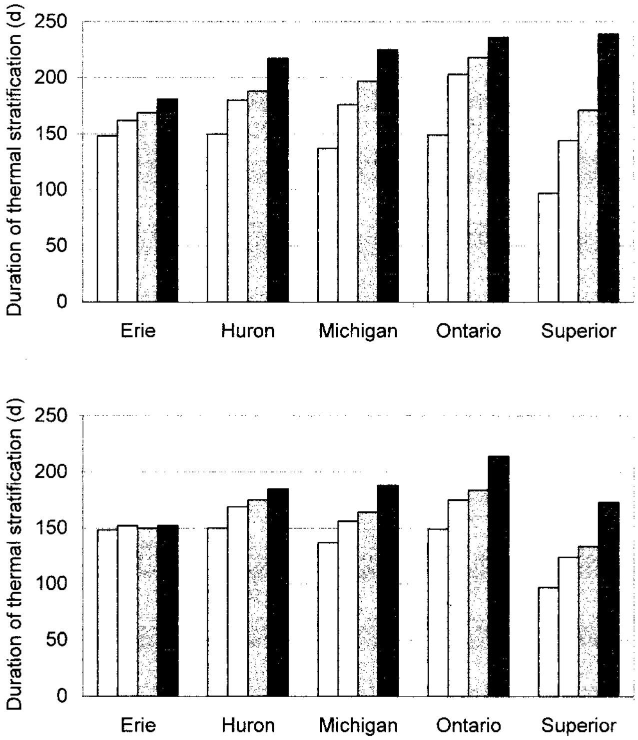

FIG. 1. Projected duration of thermal stratification under Canadian Climate Centre (upper panel) or Hadley Centre (lower panel) climate scenarios. See Figures 4 or 6 for legend key.

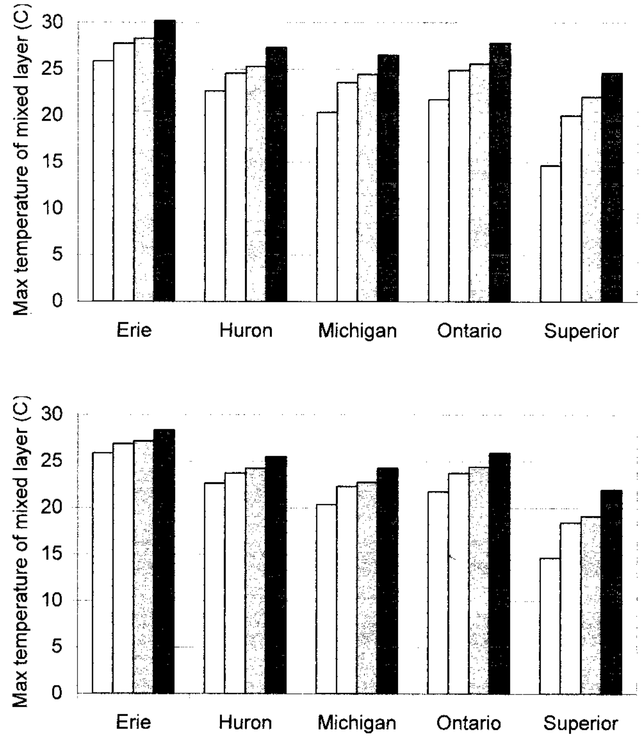

FIG. 2. Projected maximum temperature of the mixed layers during summer under Canadian Climate Centre (upper panel) or Hadley Centre (lower panel) climate scenarios. See Figures 4 or 6 for legend key.

Lake Ontario for the longest period of thermal stratification by 2090 of all the lakes.

Maximum Lake Surface Temperatures

For each scenario year (2030, 2050, or 2090) the climate projections of the Canadian Centre GCM lead to higher predicted maximum (Fig. 2) temperatures in the mixed layer of all five lakes compared with parallel results with the Hadley model. The projections have surface temperatures in Lake Superior approaching or exceeding 20°C by 2030 (Canadian), or 2050 (Hadley).

Mean Mixed Layer and Bottom Temperatures

Both models lead to average mixed layer (Fig. 3) temperatures elevated above BASE conditions in all five lakes by from 3 to 8°C within a century. Mean bottom temperatures are projected to increase, as well (Fig. 4). The changes in bottom temperature are more modest than those of the mixed layer, generally no more than 2°C even by 2090. However, these projected increased temperatures of lake hypolimnia could portend increased metabolic rates of invertebrates and microbes that would accelerate consumption of dissolved oxygen during the extended periods of stratification. It is important to bear in mind that the more modest changes in bottom temperatures are imposed upon initial BASE conditions of 4°C or less in most cases. Hence, the relative temperature changes imposed on a perennially cold environment, with their potential for acceleration of metabolic processes, are worthy of further study.

Mixed Layer Thickness

Climate variables produced by both the Hadley and the Canadian GCMs imply the possibility of deeper daily mixing depths during peak thermal stratification in the future (Fig. 5). The Canadian model generally predicts deeper mixing depths than does the Hadley model. Mixing depth interacts strongly with algal biomass and rates of primary production owing to the vertical attenuation of light

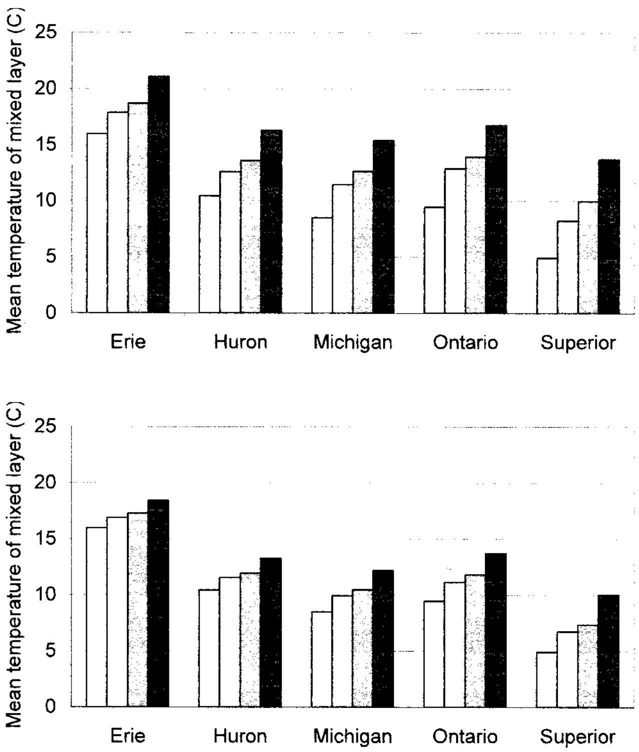

FIG. 3. Projected average temperatures of surface mixed layers under Canadian Climate Centre (upper panel) or Hadley Centre (lower panel) climate scenarios. See Figure 4 for legend key.

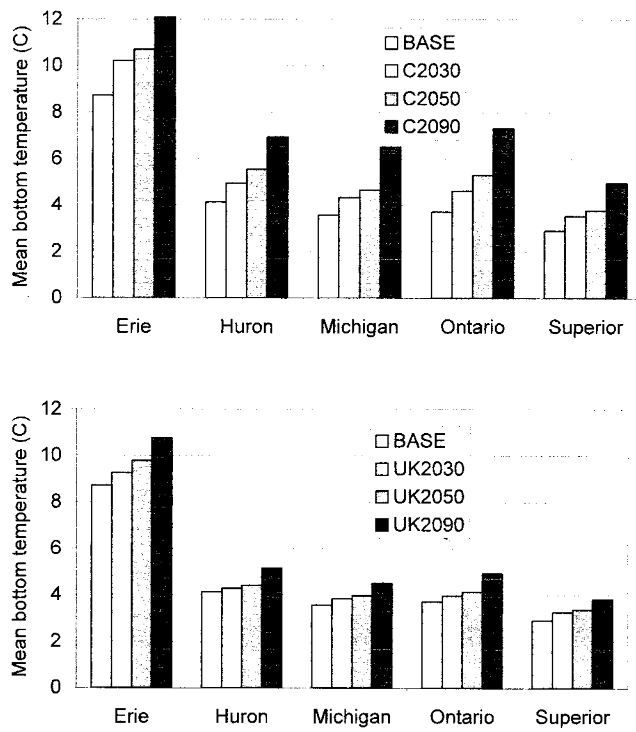

FIG. 4. Average bottom temperatures at lake mean depth under Canadian Climate Centre (upper panel) or Hadley Centre (lower panel) climate scenarios.

in the water column. Consequently, the projected trends in mixing depth raise the prospect of increasing important of light limitation of algal growth under climate change scenarios.

The causes of the deeper mixing depths under future climate scenarios are two-fold. In Lake Michigan, minimum daily mixing depths are typically achieved during late June to early July. Both the Canadian and Hadley GCMs project positive anomalies for over-lake mean wind velocities in both June and July compared with BASE conditions (Table 2). As a result of the higher wind speeds, water surface friction velocities are greater, and there is more kinetic energy transferred to the lake surface by wind stress.

Secondly, climate conditions projected by the GCMs lead to larger surface buoyancy fluxes, which in turn generate higher rates of convection in the surface layer. Calculations indicate that mean daily lake surface temperatures will increase relative to minimum and maximum daily air temperatures, and that saturation vapor pressure at the lake surface will correspondingly increase faster than over-lake vapor pressure (Fig. 2). These projected trends in temperature gradients and vapor pressure gradients imply increased heat loss by both conduction and evaporation, relative to BASE conditions. The heat loss is maintained owing to reduced cloud cover, particularly in the Canadian Centre model projections, with corresponding increased *in situ* heating from solar irradiance.

Buoyancy flux is calculated from the net surface heat flux. Loss of heat at the surface causes surface cooling, and convective stirring of the mixed layer. Both wind shear and night-time convection resulting from buoyancy flux thus deepen the mixed layer under projected climate conditions. The minimum mixed layer thickness of Lake Michigan increases from BASE in these climate change scenarios because the GCMs project conditions that would make future over-lake winds increase from present values at the critical time of the year, and because night-time heat loss with resulting convection is projected to increase.

One caveat to bear in mind is that the mean cloud cover projections do not distinguish between day and night. Because Great Lakes generate their own

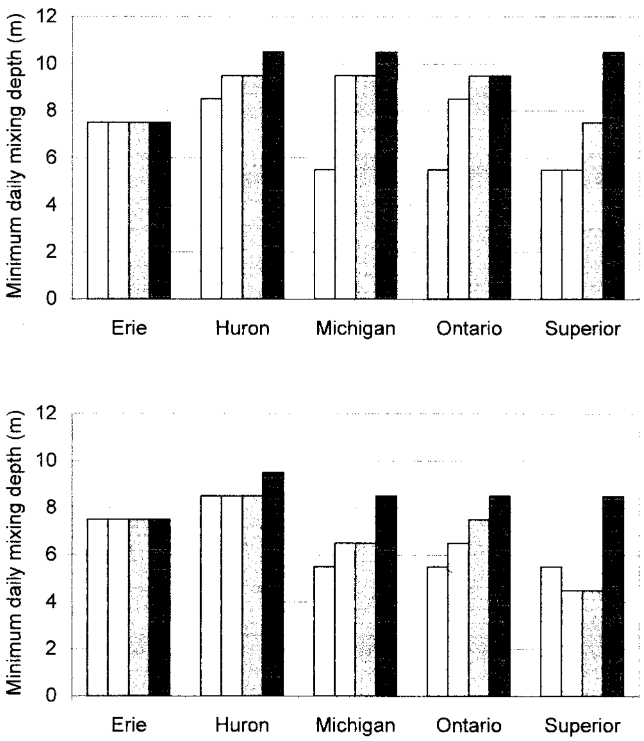

FIG. 5. Minimum mixing depth under Canadian Climate Centre (upper panel) or Hadley Centre (lower panel) climate scenarios. See Figures 4 or 6 for legend key.

weather, including clouds, diurnal shifts in mean cloud cover could have significant unanticipated effects on heat balance and mixing dynamics, as Yin and Nicholson (1998) demonstrated for Lake Victoria.

Algal Biomass and Nutrient Limitation

For both Lakes Erie and Ontario, the maximum mixed layer chlorophyll concentrations specified in Table 1 were never achieved in any of the simulations. Thus, algal biomass can be interpreted as being limited by the interaction of light limitation and loss processes. In both lakes there were no substantial differences in maximum mixed layer algal biomass predicted by either model, the maxima being roughly 6 to 6.5 mg Chl/m^3 for Lake Erie and 4.5 to 5 mg Chl/m^3 for Lake Ontario. For Lakes Huron, Michigan, and Superior, the duration of nutrient limitation of algal growth is predicted to increase sharply in all climate change scenarios (Fig. 6). As was also true of projected physical variables, the magnitudes of change projected using climate variables from the Canadian model were larger than those from Hadley. And as was true for the physical factors, the largest relative changes are expected to occur in Lake Superior. Additional detail about projected changes in algal biomass and primary pro-

TABLE 2. Mean monthly anomalies for Lake Michigan with respect to BASE conditions for GCM predictions. Wind speed predicted by the GCMs is corrected to over-lake speed according to Croley (1989). Lake surface temperature (T_L) and lake surface saturation vapor pressure (e_L) are daily means.

L. Michigan	Vapor mb	Wind m/sec	Cloud Cover percent	Max Air °C	Min Air °C	T_L °C	e_L mb
C2030- Jun	3.1	0.2	–1.8	1.7	1.5	9.1	8.0
C2030- Jul	2.0	0.2	–2.5	1.9	1.5	3.9	5.9
C2050- Jun	4.2	0.1	–3.4	2.4	2.3	11.2	10.6
C2050- Jul	2.9	0.3	–4.0	2.7	2.3	4.8	7.4
C2090- Jun	7.3	0.3	–4.7	4.6	5.3	14.8	15.6
C2090- Jul	5.9	0.5	–5.1	4.2	4.7	7.2	11.8
UK2030- Jun	1.7	0.0	–1.1	0.6	0.7	4.6	3.5
UK2030- Jul	1.7	0.2	0.0	0.6	0.8	2.1	3.0
UK2050- Jun	2.4	0.1	–1.2	0.9	1.1	6.1	4.9
UK2050- Jul	2.4	0.2	–0.3	0.9	1.3	2.9	4.2
UK2090- Jun	4.1	0.2	–0.8	2.1	2.3	10.2	9.3
UK2090- Jul	4.3	0.4	0.0	2.1	2.6	4.5	6.9

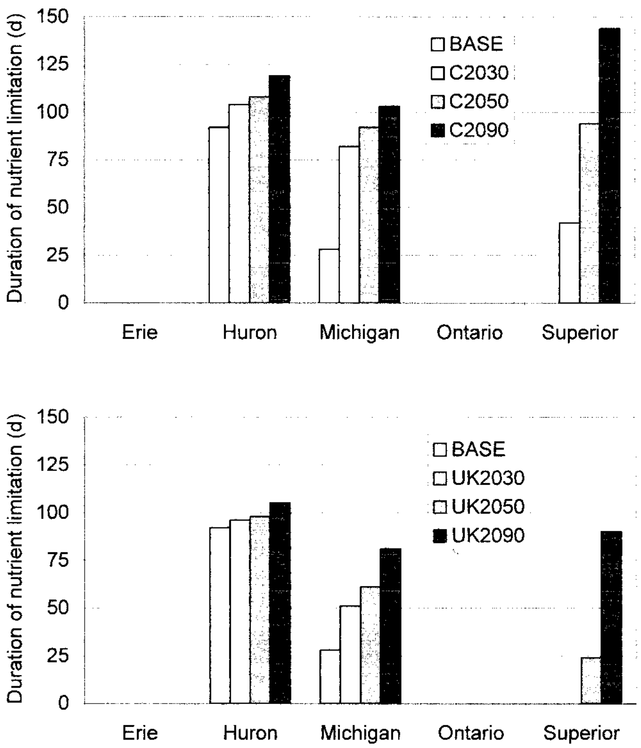

FIG. 6. Duration of nutrient limitation for Lakes Huron, Michigan, and Superior under Canadian Climate Centre (upper panel) or Hadley Centre (lower panel) climate scenarios. Algal biomass in Lakes Erie and Ontario is assumed not to be limited by nutrients per se in the simulations (see text for further explanation).

ductivity is provided by Brooks and Zastrow (2002) in this issue.

DISCUSSION

Climate variables projected by two different GCMs imply extended thermal stratification and elevated water and sediment temperatures in the Great Lakes. These potential changes could lead to important habitat changes. Rates of respiration by deep water animals and microbes would necessarily increase in response to elevated temperatures. Extended duration of stratification would reduce holomixis thereby reducing ventilation of the deep water with oxygen. Hypolimnetic oxygen concentrations would be expected to decrease, with possible negative effects for coldwater fish.

McCormick (1990) used climate scenarios from three different first generation GCMs He projected effects of an instantaneous doubling of atmospheric carbon dioxide. He applied a one-dimensional mixed layer model to Lake Michigan and forced it with realistic hour-scale weather conditions. However, there was no biological dimension to the study. McCormick's (1990) projections for Lake Michigan were far more dramatic than those generated by this study. Under two of his GCM scenarios, Lake Michigan became permanently stratified, and thus presumably anoxic or even meromictic at depth. Even under the least dramatic scenario of the three, however, the mixing period in Lake Michigan was projected to decrease to nearly 2 months. If realized, such severe reductions in mixing and ventilation would likely be catastrophic. The dire projections of the earlier model are not confirmed by second generation GCM projections used in this study.

Maximum mixed layer temperatures projected by McCormick (1990) for Lake Michigan are, however, indistinguishable from projections under the present study. McCormick projected maximum summer surface temperatures in excess of 24°C from all three of his climate models. In this study, the maximum surface temperature of Lake Michigan is projected to approach (Hadley) or exceed (Canadian) 25°C by 2090. Side-by-side comparison of the climate forcing variables applied by McCormick with those used here reveal several differences. Wind speeds generally decreased in the projections used by McCormick, whereas over-lake wind speeds are elevated at critical times in the second generation GCMs. Furthermore, reductions in cloud cover projected by first generation GCMs were far more extreme than those used here. Both of these factors can account for increased physical stability with the earlier models.

Mortsch and Quinn (1996) summarized studies that relied on four first generation GCMs and probed their potential implications for Great Lakes hydrology and water balance. They cited previously unpublished calculations by T. E. Croley that used the GCM output to project mean annual surface water temperature in the lakes. In general, the largest temperature increases, both in absolute and in relative terms, were for Lake Superior, and the smallest increases were projected for Lake Erie. Both findings are consistent with this study. Moreover, the magnitudes were quite comparable, ranging from a minimum of 3°C (Erie) to a maximum of 7.4°C (Superior). The reason for this consistency across models appears to be the fact that long-term surface water temperatures are directly related to long-term average air temperatures (Hondzo and Stefan 1996a, 1996b), and that the projected air temperatures by the different GCMs are not markedly different in aggregate.

Stefan *et al.* (1996) investigated the potential effects of one first-generation climate scenario (GISS) for doubled atmospheric carbon dioxide on inland lakes of northern Minnesota. They point out that projected lake temperatures depend on lake geometry, and that bottom temperatures are projected to change less than surface temperatures. Their conclusions are confirmed by this study. Stefan *et al.* (1996) further point out that lake geometry ratios should influence rates of hypolimnetic oxygen depletion. They use as their metric of lake geometry the ratio of the 4^{th}-root of lake surface area to maximum depth based on criteria proposed by Gorham and Boyce (1989). Based on this criterion, Lake Ontario should be the most sensitive of the Great Lakes to hypolimnetic oxygen depletion, followed closely by Lake Superior, and then Lake Michigan. The place of Lake Superior in this ranking is noteworthy.

The magnitudes of predicted temperature changes are large enough to raise the prospect of significant biological changes. Rather than looking for changes in the metabolism and growth of resident species, it is likely that there will be substantial species change by invasions. Successful range expansion northward by traditionally southern species has to be expected even in Lake Superior. Average surface temperatures of that deepest and coldest Great Lake could potentially rise by more than 5°C within the century, and maximum surface temperatures during summer may rise by as much as 10°C, to well over 20°C. The period of thermal stratification in Lake Superior may increase from roughly 3 months at present to well over 5 months, thus providing habitat and growth opportunity for many warm water species. At the same time, its relatively small lake geometry ratio (1.7) marks it as a lake that will dramatically reflect in its deep waters any increases in production that occur above.

There is convergence of opinion that surface temperatures would increase more than bottom temperatures, and hence that thermal stratification would be more intense as well as of greater duration than at present. The projected trend points to diminished ventilation of deep water and reduced levels of dissolved oxygen. Elevated rates of primary production in the surface waters may aggravate the problems, because particulate organics that sink into the hypolimnia will not be accompanied by downward mixing of oxygen.

Responses by zooplankton and other secondary consumers to changes in temperature and primary production are confounded by multiple influences that are not yet quantitatively defined. Elevated temperatures would increase metabolism and rates of both embryonic and post-embryonic development, hence shortening the generation times of most invertebrates. Because both herbivores and carnivores experience accelerated metabolism and resource needs, net changes in community composition are not intrinsically predictable. The four deepest lakes would continue to have cold water refuges, so unique fauna of the Great Lakes would not be lost on account of temperature changes alone. Whether resulting changes in oxygen levels or fish community cause changes to these taxa is a question beyond the scope of the current study, but it is an important matter worth future attention.

Increases in water temperature lead not only to incremental changes in physiological processes like metabolism, but there may be threshold changes as well. For example, optimum temperatures for spawning by lake trout in the autumn (8 to 11°C) and northern pike in the spring (4 to 12°C) are breeding windows that may be shifted or compressed. These changes in the breeding patterns of fish would affect the rates of predation on their prey. Other possible threshold temperature effects could result from developmental responses that are cued by temperature, such as hatching of resting eggs and resting stages, or induction of changes in body shape that affect predator-prey interactions.

Any discernible changes in the zooplankton fauna are likely to be in the direction of increased small bodied Cladocera (*Bosmina*) and cyclopoid Copepoda in the warmer mixed layers. The expectation is based on analogy with warm water lake communities elsewhere. Ultimate causation for the changes is believed to be elevated rates of predation by fish in warmer water.

The Canadian model, more so than the Hadley model, projects that evaporation rates from all the Great Lakes will be higher than at present in the late fall and winter. There are important feedbacks of these lake changes on regional climate that have not been explored.

Emerging Challenges

This study was undertaken in an effort to answer what seems a reasonable and important question:

What are the implications of different projected climates for mixing patterns, temperatures, and primary production of the Great Lakes? While assembling model components and parameters to answer the question, a great many physiological and ecological processes were reduced to simplistic representations. The magnitudes of bias introduced into model results by these simplifications is unknown at present. One value of the study has therefore been to highlight present uncertainty, and to identify fruitful areas of research. It is obvious that additional inquiry is required for a comprehensive climate change assessment, and that some needs are especially pressing. In some cases suitable data sets and models may already exist in unpublished form; in many other cases original data will have to be collected and new theory will be needed.

There are many ways in which the models used in this study can be refined and extended. Some of the most pressing and immediate needs include the following:

1. Oxygen dynamics need to be incorporated in future studies in order to assess the magnitudes of change in that critical chemical property.
2. Improved empirical information is needed about magnitudes and seasonal variation of photosynthetic parameters P_{max} and I_K among lakes. Basic information is needed about rates of respiration in these lakes and variation of the rates with temperature.
3. Review is needed to identify the maximum levels of algal biomass sustainable by nutrients in the five lakes.
4. Structural refinements to the models are possible by incorporating actual lake morphometry, heat advection by river discharge, and ice dynamics; their effects, if any, on key model outcomes warrant investigation.
5. A review is needed to characterize the magnitudes of variation in net intrinsic growth rates of Great Lakes algae and zooplankton with water temperature.

Despite simplification of the model processes, it seems fair to conclude that GCM projections imply the North American Great Lakes will be substantially affected during this century. Becoming warmer, less well mixed through the year, and with longer periods of nutrient limitation, the lakes seem susceptible to a host of biological changes.

Assessment of potential future conditions in ecosystems is fraught with uncertainty. Projections are surely inaccurate or incomplete either because the climate scenarios may not be realized, or because model assumptions were too idealized. For these reasons, model projections should be tailored to reveal not so much whether they are wrong, but how and why they are wrong, so that better formulations and better simplifying theories can be adopted. The models used here make specific predictions about trends and magnitudes of surface water temperatures and stratification periods, for example, that should be testable on time scales of a decade or two. In short, the predictions are falsifiable by direct test using archival and continuing future sources of lake data.

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REFERENCES

Blumburg, A.F., and Di Toro, D.M. 1990. Effects of climate warming on dissolved oxygen concentrations in Lake Erie. *Trans. Am. Fish. Soc.* 119:210–213

Brooks, A., and Zastrow, J. 2002. The potential influence of climate change on offshore primary production in Lake Michigan. *J. Great Lakes Res.* 28: 597–607.

Burnet, A.M.R., and Davis, J.M. 1980. Primary production in Lakes Rotorua, Rerewhakaaitu, and Rotoiti, North Island, New Zealand, 1973–78. *N. Z. J. Mar. Freshwater Res.* 14:229–236.

Croley, T.E. 1989. Verifiable evaporation modeling on the Laurentian Great Lakes. *Water Resources Research* 25:781–789.

Fahnenstiel, G.L., Chandler, J.F., Carrick, H.J., and Scavia, D. 1989. Photosynthetic characteristics of phytoplankton communities in Lakes Huron and Michigan: P-I parameters and end-products. *J. Great Lakes Res.* 15:394–407.

Fee, E.J. 1990. *Computer programmes for calculating in situ phytoplankton photosynthesis.* Canadian Technical Report of Fisheries and Aquatic Science.

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

Gorham, E., and Boyce, F.M. 1989. Influence of lake surface area and depth upon thermal stratification and the depth of the summer thermocline. *J. Great Lakes Res*. 15:233–245.

Hill, D., and Magnuson, J.J.. 1990. Potential effects of global climate warming on the growth and prey consumption of Great Lakes fish. *Trans. Am. Fish. Soc*. 119:265–275.

Hondzo, M., and Stefan, H.G. 1996a. Dependence of water quality and fish habitat on lake morphometry and meteorology. *J. of Water Resources Planning and Management* 122:364–373.

______, and Stefan, H.G. 1996b. Long-term lake water quality predictors. *Water Research* 30:2835–2852.

Imberger, J., and Patterson, J. C. 1990. Physical Limnology. *In* Hutchinson, J. W. and Wu, T. Y. [eds], *Advances in Applied Mechanics* 27:303–475.

Ivey, G.N., and Patterson, J.C. 1984. A model of the vertical mixing in Lake Erie in summer. *Limnol. Oceanogr*. 29:553–63.

Jerlov, N.G. 1976. *Marine Optics.* Elsevier Oceanography Series, 14.

Keijman, J.Q. 1974. The estimation of the energy balance of a lake from simple weather data. *Boundary Layer Meteor.* 7:399–407.

Lehman, J.T. 1997. *A modification of Fee's numerical primary production model for spreadsheets.* IDEAL Technical report 97-1.

______. 2002. Application of satellite AVHRR to water balance, mixing dynamics, and the chemistry of Lake Edward, East Africa, pp. 235–260. *In* Odada, E. and Olago, D. [eds.], The East African Great Lakes: Limnology, Paleolimnology, and Biodiversity. Kluwer.

Lofgren, B.M., Quinn, F.H., Clites, A.H., Assel, R.A., and Eberhardt, A.J. 2000. Water Resouces, pp. 29–37. *In* Sousounis, P.J. and Bisanz, J.M. [eds.], Preparing for a changing climate: Great Lakes Regional Assessment. ISBN 0-9705619-0-3.

______, Quinn, F.H., Clites, A.H., Assel, R.A., Eberhardt, A.J., and Luukkonen, C.L. 2002. Evaluation of potential impacts on Great Lakes water resources based on climate scenarios of two GCMs. *J. Great Lakes Res*. 28:537–554.

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

Maidment, D.R. [ed.] 1993. *Handbook of hydrology*. McGraw-Hill.

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

______, and Meadows, G. A. 1988. An intercomparison of four mixed layer models in a shallow inland sea. *J. Geophysical Res*. 93:6774–6788.

Monismith, S.G. 1985. Wind-forced motions in stratified lakes and their effect on mixed-layer shear. *Limnol. Oceanogr*. 30:771–783.

Mortsch, L.D., and Quinn, F.H. 1996. Climate change scenarios for Great Lakes Basin ecosystem studies. *Limnol. Oceanogr.* 41:903–911.

Niiler, P.P., and Kraus, E.B. 1977. One-dimensional models of the upper ocean. *In* E.B. Kraus [ed.], Modelling and prediction of the upper layers of the ocean, pp. 143–172. Pergamon.

Patterson, J.C., Hamblin, P.F., and Imberger, J. 1984. Classification and dynamics simulation of the vertical density structure of lakes. *Limnol. Oceanogr*. 29: 845–861.

______, Allandson, B.R., and Ivey, G.N. 1985. A dissolved oxygen budget model for Lake Erie in summer. *Freshwater Biology* 15:683–94.

Price, J.F. 1981. Upper ocean response to a hurricane. *J. Physical Oceanogr.* 11:153–175.

Sherman, F.S., Imberger, J., and Corcos, G.M. 1978. Turbulence and mixing in stably stratified waters. *Ann. Rev. Fluid Mech.* 10:267–288.

Smith, J.B. 1991. The potential impacts of climate change on the Great Lakes. *Bulletin of the American Meteorological Society* 72:21–28.

Sousounis, P.J., and Grover, E.K. 2002. Potential future weather patterns over the Great Lakes region. *J. Great Lakes Res.* 28:496–520.

Spigel, R.H. 1980. Coupling of internal wave motion with entrainment at the density interface of a two-layer lake. *J. Physical Oceanogr*. 10:144–155.

______, and Imberger, J. 1980. The classification of mixed-layer dynamics in lakes of small to medium size. *J. Physical Oceanogr*. 10:1104–1121.

______, Imberger, J., and Rayner, K.N. 1986: Modeling the diurnal mixed layer. *Limnol. Oceanogr*. 31: 533–556.

Stefan, H.G., Hondzo, M., Fang, X., Eaton, J.G., and McCormick, J.H. 1996. Simulated long-term temperature and dissolved oxygen characteristics of lakes in the north-central United States and associated fish habitat limits. *Limnol. Oceanogr*. 41:1124-1135.

Strub, P.T., and Powell, T.M., 1987: The exchange coefficients for latent and sensible heat flux over lakes: dependence upon atmospheric stability. *Boundary Layer Meteor*. 40:349–361.

Yin, X., and Nicholson, S.E. 1998: The water balance of Lake Victoria. *Hydrological Sciences Journal* 43: 789–811.

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