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Research Article

A Swedish case study of contemporary and possible future consequences of climate change on lake function

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Abstract. A physical lake model was employed to obtain a basis of discussing the impact of climate variability and climate change on the ecology of Lake Erken, Sweden. The validity of this approach was tested by running the PROBE-lake model for a 30-year period (STD) with observed meteorological data. The lake is adequately modelled, as seen in the comparison with actual lake observations. The validated lake model was then forced with meteorological data obtained from a regional climate model (RCM) with a horizontal resolution of 44 km for present (CLTR) and 2 × CO_2 (SCEN) climate conditions. The CLTR lake simulation compares reasonably with the STD. Applying the SCEN simulation leads to a climate change scenario for the lake. The physical changes include elevated temperatures, shorter periods of ice cover combined with two of ten years being totally ice-free, and changes in the mixing regime. The ecological consequences of the physical simulation results are derived from the historical dataset of Lake Erken. Consequences of a warmer climate could imply increased nutrient cycling and lake productivity. The results suggest that an application of RCMs with a suitable resolution for lakes in combination with physical lake models allows projection of the responses of lakes to a future climate.

Key words. Regional climate model; lake model; Lake Erken.

Introduction

Potential effects of climate on lake ecosystems would depend on the nature and magnitude of the climate change in the concerned region. To study how global warming (IPCC, 2001) might develop in the future, global climate change models (General Circulation Models, GCM) are used. However, with the rather coarse spatial resolution of present-day GCM-simulations (with a typical horizontal grid size of ~300 km), the simulation of climate on the scale of lake ecosystems is hardly possible. To increase the spatial detail in climate scenarios, regional climate models (RCM) can be used (e.g., Giorgi and Mearns, 1991; 1999; Christensen et al., 1997; McGregor, 1997; Christensen et al., 1998; Rummukainen et al., 2001). In such a simulation, a RCM with a resolution from 20 to 100 km is run over the targeted geographical area using time-dependent simulation results from a GCM as driving lateral boundary conditions.

To project the response of lakes to climate, deterministic simulation models based on "2 × CO_2" GCM scenarios have been applied to North American lakes (*cf.* De Stasio et al., 1996; Marsh and Lesack, 1996; Mortsch and Quinn, 1996). The lake model responded to the warmer climate with an earlier onset of stratification, increased summer epilimnetic temperature, and an

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increased intensity and longer duration of stratification, which is likely to change habitats of plankton and fish as well as their interactions (De Stasio et al., 1996). However, when the driving meteorology is derived from GCMs and when long-term observed data are scarce, the validation of lake model simulations becomes problematic (Arai, 2000) and requires historical data.

For the projection of future changes, it is beneficial to review the findings of climate-lake relationships found by using long-term datasets. The most distinct changes in lakes due to climate change were associated with a general tendency for lake temperature to become warmer (De Stasio et al., 1996; Schindler et al., 1996). The warming is also associated with shorter ice cover periods in the ELA regions (Schindler, 1996) and even over the Northern Hemisphere (Magnuson et al., 2000). Additionally, the increased temperature led to changes in the stratification pattern. In large, dimictic lakes, stratification might be expected to be stronger and shallower (De Stasio et al., 1996) or weaker (Schindler et al., 1996), depending on the color of dissolved organic carbon and the lake size together with its morphometry (King et al., 1999). Furthermore, a prolongation of the water renewal time has been found, which is likely to have critical effects on eutrophication, on the retention of nitrate (Schindler, 1996, and lit. therein) and increases in the relevance of internal processes. These physical and partly chemical changes induced by a warmer climate will affect the organisms and their interactions drastically, but the responses might differ between lakes.

Additionally to datasets gained from monitoring, there is now also considerable interest in using paleolimnology to determine how lakes have changed as a result of past climate changes and how these data can be used in conjunction with climate models (e.g., Felzer et al., 2000).

In this study, we will combine a long-term dataset with a model approach by forcing a physical lake model with the regional climate scenario derived from a RCM with a horizontal resolution of 44 km. The same approach has recently been applied for the Baltic Sea (Omstedt et al., 2000), where it was shown that the water temperature and the ice extent could be realistically modelled with a regional ocean model, using forcing fields from a RCM.

This paper is intended to be a synthesis-oriented case study on lake ecology and climate on one hand and on observations and modelling on the other. There is also a synthesis aspect in the use of a regional climate model and a free-running physical lake model. The regional climate model system, including the control and scenario run, used here is extensively discussed in Bergström et al. (2001), Rummukainen et al. (2001), Räisänen et al. (2001) and Christensen et al. (2001). The focus in this case study is related only to Lake Erken, Sweden, where we perform a quantitative evaluation of the model by validating the lake model against a long-term set of observed data.

The mesotrophic Lake Erken has neither undergone anthropogenic eutrophication, nor have there been detectable changes or disturbances in the surrounding catchment. As the lake conditions have been monitored over a considerable period of time, we feel that this lake is well suited for a study of potential impacts of climate change on natural lake ecosystems.

The aims of this paper are (i) to investigate the usefulness of physical lake modelling for lake studies on various time scales, (ii) to attempt the use of RCM-driven simulations for a study of climate-driven consequences in the contemporary and possible future physical lake conditions ($2 \times CO_2$), and (iii) to discuss climate-driven ecological consequences of such influences based on the long-term dataset.

Background

Lake Erken is a mesotrophic lake in eastern Sweden (59°25′N, 18°15′E) at 11 m above sea level with a surface area of 24 km^2, a maximum depth of 21 m, mean depth of 9 m and a turnover time of 7 years. The lake is always ice-covered in winter and the ice break-up, registered since 1954, occurs between March and early May. Water samples have been taken since 1954 with more intensive sampling both in the 1970s and from 1993 onwards. Thus, at least 20 years of data from Lake Erken are available. Climate impacts on Erken have previously been analysed by Weyhenmeyer et al. (1999), Blenckner et al. (2002) and Pettersson and Grust (2002). These investigations document a one month earlier ice break-up during the later period, compared with the 1960s, and a decrease of springtime snow cover. These changes, in turn, can explain a shift in the timing of the spring phytoplankton bloom, which now occurs one month earlier than in the 1960s and 1970s. Additionally, a warmer winter seems to shift the phytoplankton species composition towards a dominance of diatoms. Furthermore, a longer ice-free period at present has led to an increase in water temperature, especially in May, which may stimulate bacterial activity (Goedkoop and Törnblom, 1996). The resulting enhanced remineralization of nutrients combined with the longer ice-free period has increased the availability of nutrients to algae. Indeed, a significantly higher summer phytoplankton biomass has occurred during the late 1990s (Blenckner et al., 2002).

We are aware that a time series of 20–30 years is still quite brief from a climate point of view and reflects only annual and decadal variations. From an ecological point of view, the time series is still relatively long.

The findings listed above indicate that since the 1980s the lake ecosystem has been responding to different forcing conditions compared with the 1960s. The ecological consequences that may follow from a future climate change of a greater magnitude is clearly a topical issue.

The models and the analytical method

The RCM employed in this work is the Rossby Centre Atmospheric model, version 1 (RCA1), developed within the SWEdish regional CLImate Modelling programme (SWECLIM). RCA1 is based on the international limited area forecast model HIRLAM (Källén, 1996; Eerola et al., 1997). Compared with HIRLAM, the land surface and snow schemes have been modified in RCA1 and the regional sea surface temperatures and sea ice are now calculated in an interactive fashion (Rummukainen et al., 2001). Results from two more recent RCA1 simulations, both with a 44 km horizontal resolution over a domain covering most of Europe and some of the North Atlantic, are used to drive physical lake simulations for Erken. In the following these are called the "control" (CTRL) simulation (where the greenhouse forcing in the driving GCM, the ECHAM4/OPYC3, *cf.* Roeckner et al. (1999), corresponds nominally to the present-day) and the "scenario" (SCEN) simulation (where the so-called equivalent CO_2 concentration has reached a doubling, compared with the control). The RCA1-simulations are made as 10-year "time slices" extracted from one long transient GCM-simulation nominally running from 1860 to 2100. The difference in the global mean warming between the 10-year time slices is 2.6 °C, which is rather a modal estimate from the overall set of climate scenarios for the global mean temperature rise from 1990 to 2100, i.e., the range of 1.4–5.8 °C (IPCC, 2001).

For the lake simulations, 6-hourly meteorological data were extracted from the regional RCA1-simulations for the Erken location. The data required are the 2 m air temperature, the 2 m relative humidity, the 10 m wind speed and direction, and the total cloudiness.

In addition, a 30-year lake simulation ("standard" STD) was performed, in order to check the performance of the lake model. In STD, observed meteorological data for 1970–98 were used from the 1° × 1° SMHI meteorological database (L. Meuller, SMHI, personal communication). The same variables as from RCA1 were used, with the exception of wind data. As the actual 10 m wind is not available in the meteorological database, the geostrophic wind was used instead, reduced to 10 m wind by a reduction coefficient of 0.36, without any turning angle modification. The choice of the reduction coefficient was based on a comparison between observed wind data at Lake Erken and the meteorological database.

The physical lake model, the PROBE-lake

The lake model used for the Erken runs is the same PROBE-based lake simulation tool (Ljungemyr et al., 1996; Omstedt, 1999) as is included in the RCA1. The PROBE lake modelling has earlier been applied in several studies (e.g., Svensson, 1978; Sahlberg, 1988; Omstedt, 1984; Elo, 1994). In RCA1 (Rummukainen et al., 2001) the lakes are parameterised based on the averaged lake surface area in each atmospheric grid cell and the lake size distribution. In order to analyse an individual lake we need to consider the specific lake characteristics. The actual Erken characteristics (location, depth-area distribution) are therefore applied in the present study.

To model Lake Erken, a 1-dimensional (vertically-resolved) approach is used including a buoyancy extended turbulent model. Here we only concentrate on temperature and ice equations. The lake temperature T_l is given as:

$$\frac{\partial T_l}{\partial t} = \frac{\partial}{\partial z}\left[\frac{\nu_T}{\sigma_T}\frac{\partial T}{\partial z}\right] + \Gamma_{sun} \qquad (1)$$

where z is the vertical coordinate (positive upwards), ν_T is the kinematic eddy viscosity, σ_T is the turbulent Prandtl number (the ratio of kinematic eddy viscosity to thermal diffusion) and Γ_{sun} is the source term for solar radiation. The boundary condition is the net heat exchange with the atmosphere. Γ_{sun} is given by:

$$\Gamma_{sun} = \frac{1}{\rho c_p}\{\Phi_{sun}(1-\delta)(1-A_i) + \Phi^i_{sun} A_i\}\beta e^{-\beta(D-z)} \qquad (2)$$

where Φ_{sun} and Φ^i_{sun} are the short wave fluxes to the water and through the ice, respectively, c_p is the specific heat of water, ρ is the density of water, A_i is the ice concentration, $1-\delta$ is the fraction of solar radiation into the deeper layers, β is the absorption coefficient and D the water depth.

Ice thermodynamics and some ice dynamics are also modelled. During the initial ice formation, ice thickness grows linearly with time:

$$\frac{dh_i}{dt} = \frac{\Phi_{np}}{L_i \rho_i} \qquad (3)$$

where Φ_{np} equals the net heat flux from the surface ($\Phi_{np} = \Phi_h + \Phi_e + \Phi_{lu} + \Phi_{ld}$) when positive. A negative Φ_{np} is replaced by zero. Φ_h is the sensible heat flux, Φ_e is the latent heat flux, $\Phi_{lu} + \Phi_{ld}$ the net long-wave radiation, h_i is the ice thickness, L_i is the latent heat of freezing/melting and ρ_i is the ice density.

The ice thickness grows later according to:

$$L_i \rho_i \frac{dh_i}{dt} = \frac{k_s k_i}{(k_i h_s + k_s h_i)}(T_f - T_a) - \Phi_w + \Phi_{it} - \Phi_{ib} \qquad (4)$$

where h_s is the thickness of snow on ice, T_f is the freezing temperature of the water, T_a is the air temperature, k_s and k_i are the thermal conductivity of snow and ice, Φ_w is the heat flux from water to ice, Φ_{it} is the solar radiation to ice surface, and Φ_{ib} is the solar radiation that penetrates the ice and goes into the water. If the air temperature is greater than the freezing temperature the ice growth part in (4) is put to zero.

Ice ridging is modelled by introducing an ice front model according to:

$$\frac{dX_f}{dt} = U_i - \frac{X_f}{h_i}\frac{\Phi_{np} - \Phi_w}{L_i \rho_i} \tag{5}$$

where X_f is the horizontal position of the ice edge and U_i is the ice drift. With an off-shore wind, the ice drift is taken as 2% of the surface wind speed (which gives U_i^{free}). With on-shore winds, ice drift reads:

$$U_i = U_i^{free} - \frac{P_i}{X_{dim} - X_f} \tag{6a}$$

and with off shore winds, ice drift is calculated as:

$$U_i = U_i^{free} \tag{6b}$$

where X_{dim} is the horizontal dimension of the lake and P_i is the ice strength parameterised according to Hibler (1979):

$$P_i = P_* h_i e^{-c_i(1-A_i)} \tag{7}$$

where P_* and c_i are constants. So, ice is deformed by wind blowing towards the shore but drifts freely with off-shore winds. With the ice edge, the ice concentration can be calculated, and the heat fluxes are calculated separately for the fraction of the lake that is ice-free $(1-A_i)$ and for the ice-covered fraction (A_i). In this application, ridging is assumed to occur only when the ice moves towards the northern lake-shore (southerly winds). Ice ridging is important particularly during ice break-up when winds may drastically reduce the ice cover, which is also often observed at Lake Erken due to the fact that the lake is so exposed to the dominant westerly wind.

Statistics and data treatment

Seven variables denoting water characteristics are defined to analyse the potential biological response (Table 1). Linear correlation analysis was used to establish relationships between two variables of interest. All data were checked for normal distribution with the Shapiro-Wilks' W test. If they were normal, the Pearson correlation coefficient (r) was applied. Data distributed non-normally were correlated with the non-parametric Spearman rank correlation (r_s). The non-parametric Mann Whitney test (U-test) was applied to compare the control with scenario simulations.

Results

The meteorology in STD, CTRL and SCEN

The mean annual course of the meteorological variables used to drive the PROBE-model is shown in Figure 1. The 10-year long RCA1-results appear somewhat jagged compared with the 30-year database, which is to be expected due to the difference in the length of the periods.

In general, the CTRL compares reasonably with the observed meteorology. The CTRL is slightly colder than the STD. The CTRL monthly mean temperature bias is around 1 °C during the summer months. Somewhat larger biases occur during the other seasons, especially in the

Table 1. Parameters used to define water temperature characteristics (modified from Fang and Stefan, 1999).

Parameter	Description
Maximum surface temperature	Maximum daily temperature at the lake surface
Surface temperature above 20 °C	Number of days with a daily temperature at the surface above 20 °C; cyanobacteria are favoured by high water temperature (Reynolds, 1997; Robarts and Zohary, 1987)
Bottom temperature in May above 10 °C	Number of days in May with a daily bottom temperature above 10 °C; enhances bacterial mineralisation (Törnblom and Rydin, 1998) from the decay of the spring phytoplankton bloom
Bottom temperature above 10 °C	Number of days during the year of a bottom temperature above 10 °C; enhances bacterial mineralisation (Törnblom and Rydin, 1998)
Onset of stratification	Bottom-surface temperature differences above 3 °C; based on long-term data experiences
End of stratification	First day without differences between bottom and surface temperature after the onset of stratification
Mixing period	Days between the ice break-up and onset of stratification as well as days between end of stratification and onset of ice cover

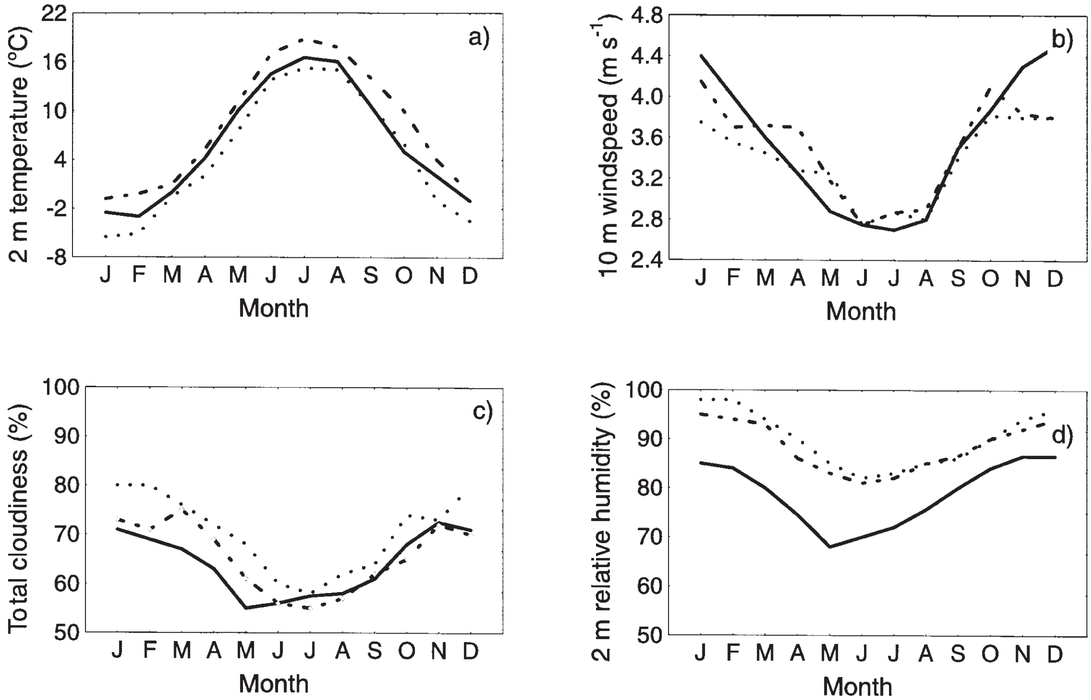

Figure 1. The meteorological data 2 m air temperature (a), wind at 10 m height (b), total cloudiness (c) and 2 m relative humidity (d), used to drive PROBE in the STD (solid), CTRL (dashed) and SCEN (dashdotted). All data are monthly mean values over the 30-year database period and the 10-year RCA1-runs, respectively.

winter when, however, the lake evolution is decoupled from the air temperature due to the establishment of ice cover. (Note that STD includes much of the warm 1990s whereas RCA1-CTRL more resembles the 1961–90 climatology (not shown)). The 10 m winds in STD and CTRL are very comparable in the mean outside the coldest months. The wind speed frequency distribution is shown in Figure 2.

The constant reduction factor applied to the geostrophic wind in STD probably overestimates the wind at 10 m in winter when stable stratification conditions are likely. Furthermore, there is some tendency for the CTRL to underestimate the occurrence of the lowest and the highest winds. The total cloudiness is quite similar during the second half of the year in STD and CTRL, but there is some overestimate of cloudiness in CTRL during the first half of the year. The largest difference between STD and CTRL appears to be in the 2 m relative humidity.

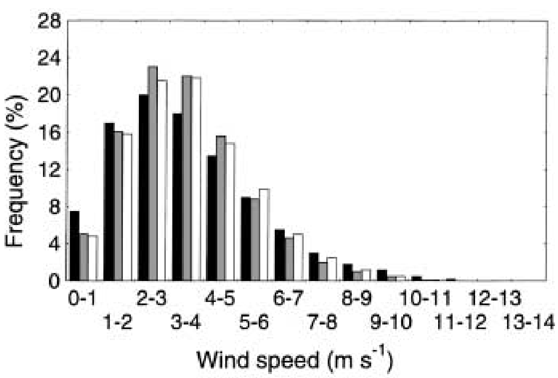

Figure 2. Occurrence of different wind speeds at 10 m height in STD (black), CTRL (grey) and SCEN (white). The highest wind speeds in the data exceed over 20 m s^{-1} but are very infrequent.

The change in the regional climate between the CTRL and the SCEN includes about a 4 °C annual mean temperature increase (more than double the annual mean difference between STD and CTRL). The change is somewhat larger (~ 5 °C) in winter but somewhat smaller (~ 3 °C) in summer. There is a small increase in the mean 10 m wind (3 % in the annual mean) and, accordingly, a slight increase in the frequency of the higher wind speeds.

The lake model performance in STD

The STD-forced lake simulation produces results that exhibit a strong correlation with all of the manually measured surface temperature data ($r = 0.98$, $n = 319$, $p < 0.0001$). In addition, for the 1990s, when an automatic station in Lake Erken was installed for the measurement of the water temperature, it is possible to compare even the day-to-day variation in surface lake water which is reasonably simulated (all years $r > 0.90$) (see for example Fig. 3).

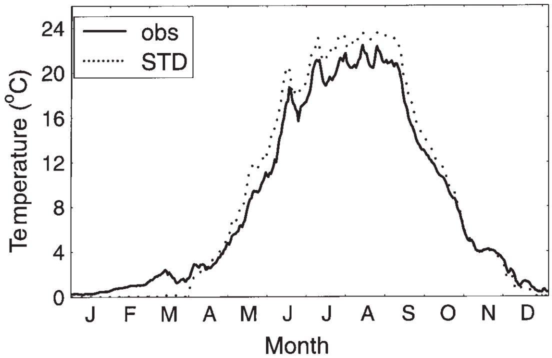

Figure 3. Daily surface temperature in Lake Erken according to observation (obs) and the standard run (STD) in 1997.

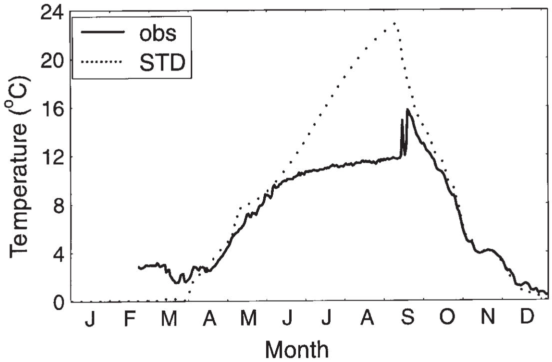

Figure 4. Daily bottom temperature in Lake Erken according to observation (obs) and the standard run (STD) in 1997.

The manually measured bottom temperature is also strongly correlated to the STD ($r = 0.92$, $n = 352$, $p < 0.0001$). In the beginning of the year the lake model predicts mixing even under ice. Here, bottom water temperatures are low but still above zero. Especially in summer, the modelled day-to-day variation was characterised by higher water temperatures than those observed (as an example, see Fig. 4).

The modelled ice extent is reasonably simulated compared with the observed data in terms of the onset of ice cover ($r_s = 0.80$, $n = 20$, $p < 0.0001$), the ice cover period ($r_s = 0.83$, $n = 19$, $p < 0.0001$) and the ice break-up ($r_s = 0.89$, $n = 21$, $p < 0.0001$). In general, in the STD a slightly earlier ice break-up and in most cases a slightly later onset of ice cover is simulated compared with the observations. However, the calculated mean ice cover period only differs by 12 days from the mean of the observation data (an underestimate of ~ 12%). To calculate the stratification period in the standard run, the temperature difference between bottom and surface is used. A significant correlation exists between the STD and the observed onset of stratification ($r_s = 0.59$, $n = 20$, $p < 0.01$). However, no correlation was found with the observations of the length or the end of the stratification period.

Lake water temperature in the CTRL and the SCEN

The monthly-mean lake surface temperature is reasonably simulated in the CTRL in terms of the seasonal cycle and the winter lake temperature compared with the STD (Fig. 5). However, the CTRL is slightly colder than the standard run, particularly in April and May.

The monthly-mean lake surface temperature simulated in the SCEN is significantly higher (U-test, $p < 0.0001$) from March until December (Fig. 5) compared with the CTRL. The highest monthly-mean differences between the SCEN and the CTRL (Δ) are found in April ($\Delta = 3.4$ °C), May ($\Delta = 3.5$ °C) and in November ($\Delta = 4.8$ °C). Obviously, no differences are found during January and February, considering the ice-covered years in the SCEN, but the surface temperature at the two ice-free years is distinctly higher in the first three months. After that period no difference in surface temperature between ice-free and ice covered years can be found (Fig. 6).

The maximum lake surface temperature is clearly higher in the SCEN (25.9 °C) compared with the CTRL

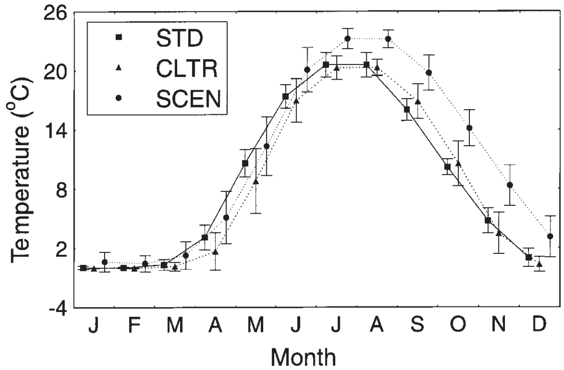

Figure 5. Calculations of monthly mean surface temperature according to the standard run (STD), the control run (CLTR) and the scenario run (SCEN). Error bars are standard deviations.

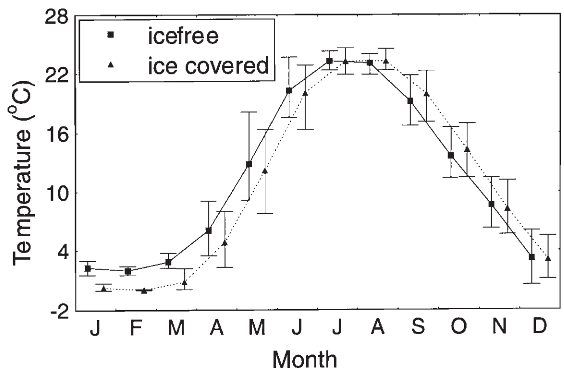

Figure 6. Comparison of the surface water temperature between the two ice-free years and the ice-covered years of the scenario run ($2 \times CO_2$). Error bars are standard deviations.

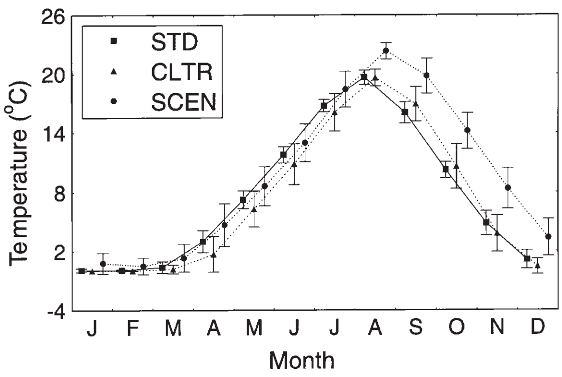

Figure 7. Calculations of monthly mean bottom temperature according to the standard run (STD), the control run (CLTR) and the scenario run (SCEN). Error bars are standard deviations.

(23.8 °C). Additionally, the period with a surface water temperature above 20 °C is, on average, 52 days longer per year in the SCEN than in the CTRL.

The monthly-mean lake bottom temperature in the CTRL is slightly colder from May to July, but warmer in September-October compared with the STD (Fig. 7). In general, the CTRL seems reasonable.

The monthly-mean lake bottom temperature in the scenario run was significantly higher (U-test, $p < 0.0001$) from March to December compared with the CTRL (Fig. 7). The greatest changes between the SCEN and the CTRL occurs in October ($\Delta = 3.6$ °C) and in November ($\Delta = 4.6$ °C) (see also Fig. 7). In May, the days with a bottom temperature above 10 °C increased in the scenario run to, on average, 10 days per year in the SCEN. Considering the whole year, the period above 10 °C increased in the SCEN to, on average, 36 days per year compared with the CTRL.

Duration of lake ice in the CTRL and the SCEN

In Figure 8 a–c, the interannual variation of the ice cover period is shown. In the CTRL, the onset of ice cover and ice break-up are earlier and the duration of ice cover is longer compared with the STD (Table 2).

In the SCEN, the ice season shortens on the average by two months. Two years out of 10 appear as completely ice-free. This gives a variation from no ice days to 102 days of ice cover. In addition, the difference between the SCEN and the CTRL indicates a delay by about one month in the onset of ice formation and about 40 days earlier ice break-up (Table 2).

Stratification and mixing patterns in the CTRL and the SCEN

The stratification period (see Table 1), as well as the onset and the end of stratification, is reasonably simulated in the CTRL compared with the STD concerning the averages, even though interannual variation of the stratification pattern and the simulated bottom water temperature are too high in the CTRL. The comparison between the CTRL and the SCEN can still be motivated under an assumption that any simulation errors in the RCA1-driven lake modelling are present in both the CTRL and the SCEN.

In the SCEN, the stratification period becomes ~ 10 days longer compared with the CTRL (Fig. 9) due to an earlier onset in the SCEN. The maximum difference between surface and bottom temperature increased from 9.7 °C to 11.2 °C and the period with a difference above 5 °C between the two layers increased, on average, to 14 days per year, i.e., the SCEN exhibits a two-week longer period of strong stratification.

Furthermore, the average 40-days earlier ice break-up and only 9 days earlier onset of stratification in the SCEN implies that the spring mixing period is lengthened by a month compared with the CTRL. The end of stratification was simulated to be one week longer, but on average the 30-day delay of ice onset implies a three-week longer mixing period in autumn as well. Thus, the SCEN has an almost two-month longer annual mixing period.

Table 2. Calculated averages (mean) and standard deviations (std) of annual ice and stratification patterns of observations (obs), standard run (STD), control run (CTRL) and the scenario run (SCEN). Number of samples are given in brackets.

	Ice onset (days since 1 Nov)		Ice cover (days)		Ice break-up (days since 1 Jan)		Stratification onset (days since 1 Jan)		Stratification period (days)		Stratification end (days since 1 Jan)	
	mean	std	mean	std	mean	std	mean	std	mean	std	mean	std
Obs (n = 20)	53	23.3	103	36.0	156	22.1	153	14.8	88	22.4	241	13.4
STD (n = 28)	54	17.8	90	24.9	145	18.0	137	12.9	94	14.9	231	9.9
CTRL (n = 10)	37	10.9	119	27.0	98	14.6	138	7.1	90	8.7	228	4.1
SCEN (n = 10)	69	21.3	54	40.0	58	39.2	132	10.0	103	10.0	235	5.8

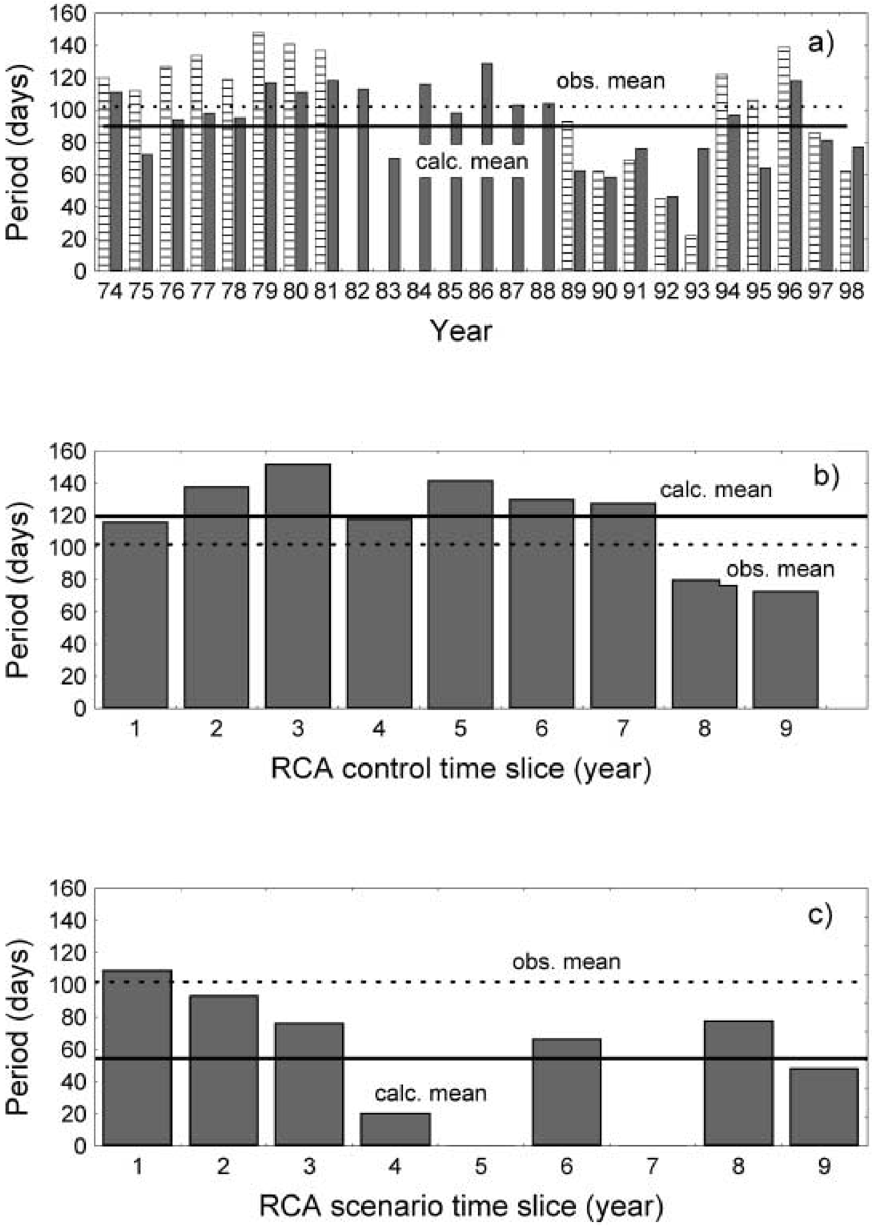

Figure 8. Annual maximum ice cover period of a) the observation (striped columns) and calculation (black columns) of the PROBE lake model and observed forcing field, b) the control run and c) the scenario run. Average lines from the observations (obs. mean) and the calculated mean (calc. mean) are included.

Discussion

The applicability of the physical lake modelling

Physical lake modelling is used in this work to obtain the setting of discussing the impact of climate variability and climate change on lake ecology. To study the validity of the approach, the PROBE-lake model was first run using observed meteorology for a ~30-year period (STD). The 10 m wind observation data were not available for the long period at the site and had to be derived from geostrophic winds as direct wind. The higher bottom water temperature in summer (in the STD, Fig. 4) indicates that the wind driving used might be too strong, resulting in too strong surface layer mixing in the lake and an increase of bottom water temperature. A constant reduction of the geostrophic wind has many limitations and may likely explain some of the lake results as seen in the comparison with in situ lake observations. The main limitation is that high winds should not be reduced in the same way as low winds. However, as the meteorological database does not include actual winds, we feel that the existing verification possibilities do not justify a further

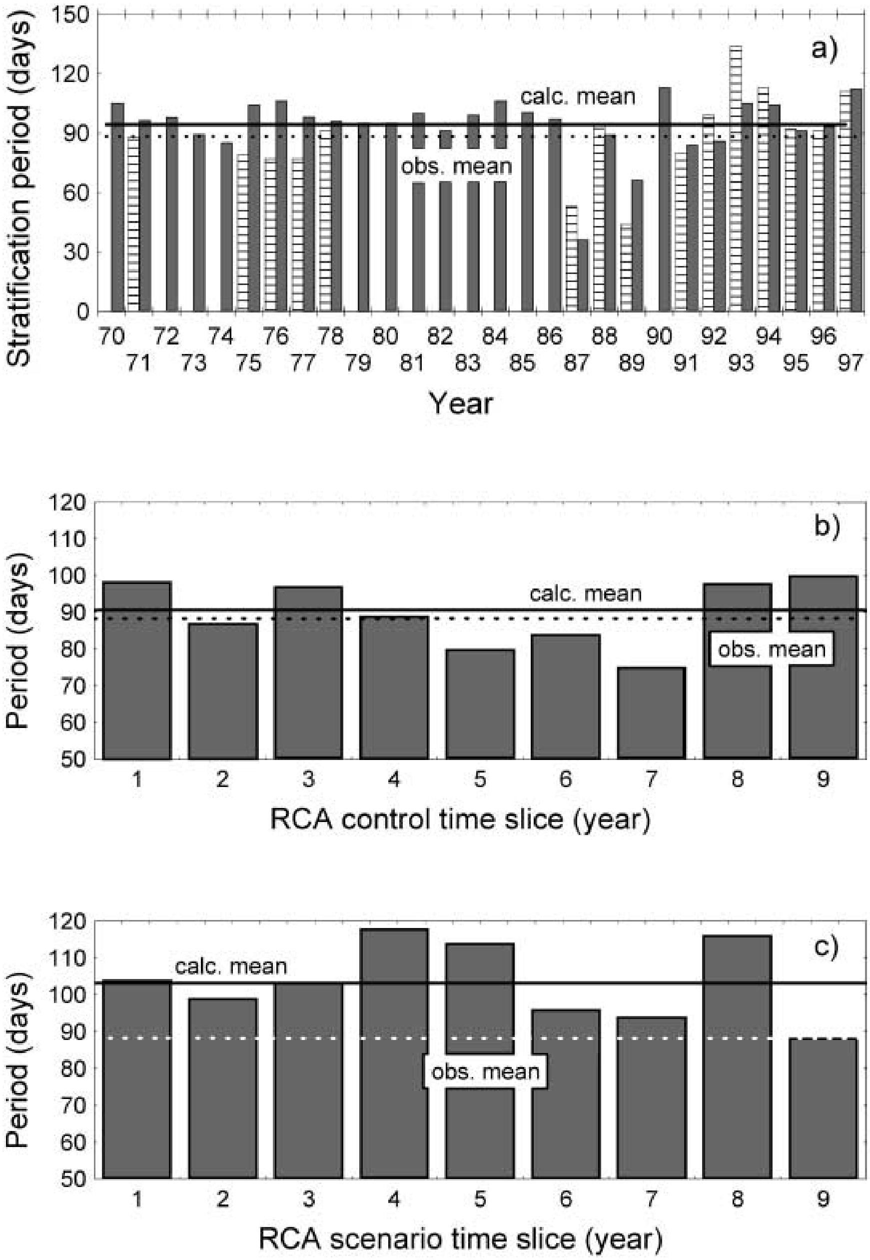

Figure 9. Annual maximum stratification period of a) the observation (striped columns) and calculation (black columns) of the PROBE lake model and observed forcing field, b) the control run and c) the scenario run. Average lines from the observations (obs. mean) and the calculated mean (calc. mean) are included.

modification of the reduction of geostrophic wind used in the present study.

The ice cover period was underestimated by 12% (by comparing STD with observations), which could be caused by errors in the meteorological data and in the lake modelling and by errors in the ice observations. We consider the results satisfactory and will not make any corrections of the forcing data.

In general, however, the lake model behaved quite reasonably. Further improvements could be gained if actual 10 m wind data could be derived for the Erken location.

The differences of relative humidity between the STD and the two other simulations are relatively large (see Fig. 1d). However, one of the features between the version of the RCA-model used to provide the meteorological forcing data for the CTRL and SCEN was a wintertime cold and moist bias at the lowest model level due to a too high latent heat flux at the expense of sensible heat flux. The reason for this has been attributed to the aerodynamic resistance for snow-covered surfaces (Patrick Samuelsson, SMHI, personal communication). The PROBE-lake model is not sensitive to the possible bias in relative humidity. To check this, the CTRL was run with an artificially reduced relative humidity data, which showed no differences (data not shown). It should also be noted that whereas the meteorological forcing for STD has been derived from land-based meteorological observations, the RCA-model always calculates subgrid surface-atmospheric interaction separately for the land and the water fractions in each grid box. In the summer, for example, the surface moisture over the water-fraction contributing to the meteorological data derived from RCA and used to force CTRL and SCEN would not limit local evaporation and thus the near-surface relative humidity.

The differences between the RCA-simulated cloud cover (CTRL and SCEN, Fig. 1 c) are smallish and communicate the fact that these regional climate simulations suggest that the local changes in total cloudiness would be small.

It is also noteworthy that the CTRL and SCEN periods are short in the climatological sense – only 10 years each – and thus likely to deviate more or less from the observed climate. The difference in the local physiography (land-based observations in STD and direct influence from the lake itself in CTRL and SCEN) may introduce further discrepancies in the meteorological forcing derived for the PROBE-lake.

Using the same RCM in climate scenario mode then leads to establishing one climate change scenario for the lake system. The physical changes in the lake system include significantly higher temperatures and less extensive ice cover, leading to changes in stratification and mixing period, for example. These results help focus the discussion of the ecological consequences of climate change on the lake system.

Ecological consequences in a warmer climate

Phytoplankton processes in winter. The physical lake model response to the "$2 \times CO_2$" climate scenario is distinct. For example, that the two years out of ten become totally ice-free would likely lead to substantial changes in the lake ecosystem. In the following, possible chemical and biological responses to a warming are discussed. For the winter and spring period, large changes in temperature are simulated. The one-month reduced duration of ice-cover would induce earlier spring phytoplankton blooms, following a trend which already is apparent today in Lake Erken (Weyhenmeyer et al., 1999). In the two ice-free years, in particular, distinct changes in the winter and spring phytoplankton dynamics are likely. It has been found that either large diatom species like *Asterionella formosa* and *Aulacoseira* spp. (Reynolds, 1984) or small centric diatoms and flagellates (Sommer et al., 1986) dominate temperate lakes with no ice cover. Water column mixing, which is less intensive but occurs during ice-cover (Kelley, 1997), might change the successional sequence of phytoplankton, with diatoms likely to dominate in the period before the spring bloom (Adrian et al., 1999), perhaps displacing the current dominance of dinoflagellates during ice-covered winters.

Furthermore, the phytoplankton biomass in the warming case (SCEN) is expected to be higher during the winter period of nutrient sufficiency, due to reduced light limitation from ice and snow cover, as well as increased temperatures.

Consequently, spring phytoplankton biomass in ice-free years can be 3–4 times higher than in ice-covered years (Müller-Navarra et al., 1997; Adrian et al., 1999). Additionally, the open-water nutrient concentration may be lowered due to the increase in phytoplankton biomass. Therefore, the phytoplankton community is likely to be pushed from a light-limited to a potentially nutrient-limited phase in a warmer climate.

Processes related to lake bottoms. The spring phytoplankton bloom can substantially influence the benthic macro- and meiofauna (Goedkoop and Johnson, 1996). A change in spring bloom timing, biomass and phytoplankton composition is likely to affect benthic invertebrate abundance in terms of food quality and period of food availability, depending on when sedimented cells reach the lake bottom.

In years with a high spring phytoplankton biomass, especially when dominated by diatoms that have a relatively high fatty acid content (Phillips, 1984), the abundance of benthic invertebrates will be enhanced (Ahlgren et al., 1997). The utilization of deposited phytoplankton cells by benthic meiofauna will, in turn, influence bacterial decomposition and mineralization rates of the algae (Goedkoop and Johnson, 1996). In a warmer climate, it is likely that there will be a greater supply of detritus to the lake bed, which would probably result in an increase in sediment respiration, together with the increase in temperature. This might be highly important under a longer summer stratification regime.

In the SCEN case, bottom water temperatures exceed 10 °C for an additional 36 days in a year. This allows for a substantial increase in bacterial activity in the sediment (Goedkoop and Johnson, 1996), which enhances nutrient mineralization turnover rates (Hamilton et al., 2002). Consequently, more nutrients will be available for phytoplankton in late spring and early summer, leading to an increase in primary productivity during that period.

Already now an increasing trend in the nutrient turnover rates is detectable in Lake Erken: earlier spring blooms in the 1990s combined with higher water temperatures in May have enhanced nutrient turnover rates and led to increases in summer phytoplankton biomass compared with the 1970s (Blenckner et al., 2002). It can be assumed that an additional increase in the number of days in May with a bottom temperature above 10 °C would lead to an amplification of such a trend.

Pelagic processes in summer. In summer, phosphorus and ammonium are released from the sediments and accumulate in the hypolimnion of Lake Erken (Pettersson, 1998; Pettersson and Grust, 2002). This process is strongly related to stability and duration of the water column stratification: a weak stratification increases the possibility of nutrient entrainment from the nutrient-rich hypolimnion to the nutrient-poor epilimnion, the environment with the most favourable light conditions. Furthermore, it increases the probability that mixing processes could at least temporarily remove stratification to effect nutrient transfers to the mixed layer. In contrast, a stronger stratification increased the water column stability associated with an enhanced sedimentation and a low oxygen concentration in the hypolimnion (Schindler, 1996), which will increase the nutrient release from the sediment to the overlying water (hypolimnion) and a depletion in the epilimnion. Simultaneously, a longer stratification period combined with a higher bottom temperature, both simulated in the SCEN, would presumably also increase the phosphorus and ammonium release from the sediment. The resulting elevated concentrations will be mixed in the whole water column after the stratification period and will increase the exposure of nutrients to phytoplankton cells and, therefore, increase the phytoplankton production in autumn.

This trend occurs in Lake Erken at present: elevated nutrient concentrations during autumn turnover (after summer stratification) in the 1990s led to larger autumn phytoplankton blooms (Pettersson and Grust, 2002). Today, low oxygen periods in the hypolimnion are very rare in Lake Erken during summer, but they might increase under a warmer climate due to temperature-stimulated respiration of organisms (Törnblom and Rydin, 1998) and a stronger and more prolonged stratification (Schindler, 1996).

Consequences for the planktonic food web. Today, the summer phytoplankton species composition is dominated mostly by cyanobacteria, in particular the filamentous, nitrogen-fixing species *Gloeotrichia echinulata*, which has a bloom period varying between two and eight weeks in Lake Erken (Istvanovics et al., 1993). *Gloeotrichia* forms 2 mm colonies that are too large to be grazed by zooplankton and therefore constitute a "dead end" for the trophic chain in the ecosystem. The bloom starts when these cells migrate (start to become buoyant) from the sediment, where the cells take up phosphorus to store as poly-phosphate for their survival in the epilimnion. The possibility of higher nutrient concentrations in spring and early summer for *Gloeotrichia* or potentially other cyanobacteria might either increase the occurrence of this "dead end" or alter the species composition. In general, the dominance of potentially toxic cyanobacteria is likely to increase because this group is favoured by elevated water temperatures (Robarts and Zohary, 1987) and longer periods of stable stratification (George et al., 1990), both of which occur in the SCEN. Especially, the longer stratification period will either favour buoyant species like *Microcystis* (Wallace and Hamilton, 1999) and/or *Gloeotrichia* or flagellated phytoplankton species like *Ceratium* sp. (Sommer et al., 1986).

The long-term database of Lake Erken provides examples of the consequences of climatic variability on summer phytoplankton blooms. For example, in 1989, ice break-up in early February was followed by a warm and windy spring and resulted in a high hypolimnetic water temperature under a weak thermal stratification (Pierson et al., 1992). By contrast, in 1996, the ice break-up was two months later and a warm period in the beginning of June led to an early stratification with a much colder hypolimnion temperature and therefore a stronger and longer stratification period (unpublished data) compared with 1989.

The weaker stratification combined with a higher bottom water temperature and a deeper thermocline in 1989 seems to lead to a much higher entrainment of phosphorus into the epilimnion (Pierson et al., 1992) and it is likely that this causes the twofold higher summer and autumn phytoplankton biomass compared with 1996.

In a future climate, the thermal characteristic of Lake Erken, as simulated in the SCEN, resembles a combination of observed years, such as 1996 with a long stratification period and 1989 with rather warm water temperatures. Of course, even in the future, rather large interannual variations are more than likely, superimposed on the evolution of climate change.

Consequences for zooplankton and fish. In general, no long-term data of zooplankton are available from Lake Erken, which makes it very difficult to discuss possible responses to a warmer climate. In general, zooplankton growth rate largely depends on temperature elevation (Vijverberg, 1980) and the timing of its occurrence (Kratz et al., 1987). The zooplankton found in lakes can tolerate quite high summer temperatures, but small increases in the winter temperature may have significant effects on their seasonal dynamics (George and Hewitt, 1999). For example, *Daphnia* biomass responded to the variability of ice break-up (Jassby et al., 1990), probably due to the water temperature variability, which is strongly related to the variability of ice break-up.

Additionally, a higher temperature as projected in SCEN might enhance the predation rate of fish on

Daphnia through a higher consumption rate and reduced fish mortality. If this stronger uptake cannot be compensated by *Daphnia*, this species could decline, as has been found in a German lake (Mehner, 2000).

The variety of fish species as well as survival and growth depends strongly on temperature (Magnuson et al., 1990; De Stasio et al., 1996; Magnuson, 1997). Changes in the growth rates of fish, in particular predatory fish, might largely affect the survival of their populations and may result in cascading effects through the entire trophic structure (Carpenter et al., 1985). However, the zooplankton and fish response to warmer climate in Lake Erken still needs to be answered.

Ecosystem level. We conclude that climate warming can lead to substantial changes in the Lake Erken ecosystem, especially due to changes in phytoplankton production and increased nutrient cycling which can be derived from the long-term database and the SCEN simulation. This will extend nutrient availability for phytoplankton and enhance lake productivity as a result of higher temperature and longer growing seasons. Additionally, the scenario of a warmer climate in the near future, in particular the warmer winter, is likely to alter the geographical range of species and might, therefore, result in an invasion of other species into the ecosystem (as discussed by Mulholland et al., 1997). Their effects on the food web, together with behavioural and physiological adaptations of organisms, will determine the ecosystem processes in a warmer climate in a lake like Erken.

Conclusion

The physical lake model could be validated sufficiently due to the long-term monitoring database from Lake Erken. The reasonable control simulation of the lake model compared with the observed data showed the extremely precise simulation of the meteorological variables, forcing the lake model, by the regional climate model (RCA1). This suggests that the simulation power of RCMs is relatively realistic compared with the observed climate and a wider application of these models in combination with ecological models seems to be reasonable. The scenario run (the "$2 \times CO_2$" simulation) resulted in a warmer climate with about a 4 °C higher annual air temperature compared with the situation today. Consequently, a shorter ice cover period by, on average, one month with two of 10 years being totally ice-free, was simulated. Additionally, the water temperature both on the surface and on the bottom was increased, resulting in a longer stratification period compared with the present observations. These changes are likely to have distinct consequences for the ecosystem. The most pronounced effect will be an increase in nutrient cycling and lake productivity as a result of higher water temperature and longer growing seasons. The lake model simulation and the derived biological consequences for the lake suggest an extended coupled-model application (like Hamilton et al., 2002), forced with regional climate models, in order to project future lake management of a possibly enhanced lake productivity in a warmer climate.

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References

Adrian, R., N. Walz, T. Hintze, S. Hoeg and R. Rusche, 1999. Effects of ice duration on plankton succession during spring in a shallow polymictic lake. Freshw. Biol. **41:** 621–632.

Ahlgren, G., W. Goedkoop, H. Markensten, L. Sonesten and M. Boberg, 1997. Seasonal variations in food quality for pelagic and benthic invertebrates in Lake Erken – the role of fatty acids. Freshw. Biol. **38:** 555–570.

Arai, T., 2000. Global warming and the temperature of inland waters. Jap. J. Limnol. **61:** 25–34.

Bergström, S., B. Carlsson, M. Gardelin, G. Lindström, A. Pettersson and M. Rummukainen, 2001. Climate change impacts on runoff in Sweden – assessments by global climate models, dynamical downscaling and hydrological modelling. Clim. Res. **16:** 101–112.

Blenckner, T., K. Pettersson and J. Padisak, 2002. Lake plankton as tracer to discover climate signals. Verh. Int. Verein. Limnol. **28:** in press.

Carpenter, S. R., J. F. Kitchell and J. R. Hodgson, 1985. Cascading trophic interactions and lake productivity. BioScience **35:** 634–639.

Christensen, J. H., B. Machenhauer, R. G. Jones, C. Schär, P. M. Ruti, M. Castro and G. Visconti, 1997. Validation of present-day regional climate simulations over Europe: LAM simulations with observed boundary conditions. Clim. Dyn. **13:** 489–506.

Christensen, O. B., J. H. Christensen, B. Machenhauer and M. Botzet, 1998. Very high-resolution regional climate simulations over Scandinavia – present climate. J. Climate **11:** 3204–3229.

Christensen, J. H., J. Räisänen, T. Iversen, D. Bjørge, O. B. Christensen and M. Rummukainen, 2001. A synthesis of regional climate change simulations – A Scandinavian perspective. Geophys. Res. Lett. **28:** 1003–1006.

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

Eerola, K., D. Salmond, N. Gustafsson, J.-A. Garcia-Moja, P. Lönnberg and S. Järvenoja, 1997. A parallel version of the HIRLAM forecast model: Strategy and results. In: G. R. Hoffmann and N. Kreitz (eds.), Making its Mark. Proceedings of the seventh ECMWF Workshop of the use of Parallel Processors in Meterology. Reading, UK, pp. 134–143.

Elo, A.-R., 1994. A sensitivity analysis of a temperature model of a lake examining components of the heat balance. Geophysica **30:** 79–92.

Fang, X. and H. Stefan, 1999. Projections of climate change effects on water temperature characteristics of small lakes in the contiguous U.S. Climatic Change **42:** 377–412.

Felzer, B., S. L. Thompson, D. Pollard and J. C. Bergengren, 2000. GCM-simulated hydrology in the artic during the past 21,000 years. J. Paleolimnol. **24:** 15–28.

George, D. G., D. P. Hewitt, J. W. Lund and W. J. P. Smyly, 1990. The relative effects of enrichment and climate change on the long-term dynamics of daphnia in Eastwaite Water Cumbria. Freshw. Biol. **23:** 55–70.

George, D. G. and D. P. Hewitt, 1999. The influence of year-to-year variations in the winter weather on the dynamics of Daphnia and Eudiaptomus in Esthwaite Water, Cumbria. Functional Ecology **13:** 45–54.

Giorgi, F. and L. O. Mearns, 1991. Approaches to the simulation of regional climate change: A review. Rev. Geophys. **29:** 191–216.

Giorgi, F. and L. O. Mearns, 1999. Introduction to special section: Regional climate modelling revisted. J. Geophy. Res. **104:** 6335–6352.

Goedkoop, W. and R. Johnson, 1996. Pelagic-benthic coupling: Profundal benthic community response to spring diatom deposition in mesotrophic Lake Erken. Limnol. Oceanogr. **41:** 636–647.

Goedkoop, W. and E. Törnblom. 1996. Seasonal fluctuations in benthic bacterial production and abundance in Lake Erken: The significance of major abiotic factors and sedimentation events. Erg. d. Limnol. **48:** 197–205.

Hamilton, D. P., C. Spillman, K. L. Prescott, T. K. Kratz and J. J. Magnuson. 2002. Effects of atmospheric nutrient inputs on trophic status of Crystal Lake, Wisconsin. Verh. Int. Verein. Limnol. 28: in press.

Hibler, W. D. 1979. A dynamic thermodynamic sea ice model. J. Phys. Oceanogr. **9:** 815–846.

IPCC, 2001. Climate Change 2001. The Scientific Basis (Intergovernmental Panel on Climate Change). Cambridege University Press, Cambridge.

Istvanovics, V., K. Pettersson, M. A. Rodrigo, D. Pierson, J. Padisak and W. Colom, 1993. *Gloeotrichia echinulata*, a colonial cyanobacterium with a unique phosphorus uptake and life strategy. J. Plankton Res. **15:** 531–552.

Jassby, A. D., T. M. Powell and C. R. Goldman, 1990. Interannual fluctuations in primary production: Direct physical effects and the trophic cascade at Castle Lake, California. Limnol. Oceanogr. **35:** 1021–1038.

Källén, E., 1996. HIRLAM documentation manual. System 2.5. 178 pp. Swedish Meteorological and Hydrlogical Institute, Norrköping, Sweden.

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

Kelley, D. E., 1997. Convection in ice-covered lakes: effects on algal suspension. J. Plankton Res. **19:** 1859–1880.

Kratz, T. K., T. M. Frost and J. J. Magnuson, 1987. Inferences from spatial and temporal variability in ecosystems: long-term zooplankton data from lakes. American Naturalist **129:** 830–846.

Ljungemyr, P., N. Gustafsson and A. Omstedt, 1996. Parameterization of lake hydrodynamics in a high resolution weather forecasting model. Tellus **48 A:** 608–621.

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

Magnuson, J. J., K. E. Webster, R. A. Assel, C. J. Bowser, P. J. Dillon, J. G. Eaton, H. E. Evan, E. F. Fee, R. I. Hall, L. R. Mortsch, D. W. Schindler and F. H. Quinn, 1997. Potential effects of climate changes on aquatic systems: Laurentian great lakes and precambrian shield region. Hydrological Proc. **11:** 826–873.

Magnuson, J. J., D. M. Robertson, B. J. Benson, R. H. Wynne, D. M. Livingstone, T. Arai, R. A. Assel, R. G. Barry, V. Card, E. Kuusisto, N. G. Granin, T. D. Prowse, K. M. Stewart and V. S. Vuglinsky, 2000. Historical trends in lake and river ice cover in the Northern Hemisphere. Science **289:** 1743–1746.

Marsh, P. and L. F. W. Lesack, 1996. The hydrologic regime of perched lakes in the Mackenzie Delta: Potential responses to climate change. Limnol. Oceanogr. **41:** 849–856.

McGregor, J. L., 1997. Regional climate modelling. Meterol. Atmos. Phys. **63:** 105–117.

Mehner, T., 2000. Influence of spring warming on the predation rate of underyearling fish on Daphnia – a deterministic simulation approach. Freshw. Biology **45:** 253–263.

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

Mulholland, P. J., R. G. Best, C. C. Coutant, G. N. Hornberger, J. L. Meyer, P. J. Robinson, J. R. Stenberg, R. E. Turner, F. Vera-Herrera and R. G. Wetzel, 1997. Effects of climate change on freshwater ecosystems of the South-Eastern United States and the Gulf of Mexico. Hydrological Proc. **11:** 950–971.

Müller-Navarra, D. C., S. Güss and H. von Storch, 1997. Interannual variability of seasonal succession events in a temperate lake to its relation to temperature variability. Global Change Biology **3:** 429–438.

Omstedt, A., 1984. A forecast model for water cooling in the Gulf of Bothnia and Lake Vänern. SMHI, Stockholm, Sweden.

Omstedt, A., 1999. Forecasting ice on lakes, estuaries and shelf seas. In J. S. Wettlaufer, G. J. Dash and N. Untersteiner (eds.), Ice Physics and the Natural Environment, Springer, Berlin, Heidelberg, pp. 185–207.

Omstedt, A., B. Gustafsson, J. Rohde and G. Walin, 2000. Use of Baltic Sea modelling to investigate the water cycle and the heat balance in GCM and regional climate models. Clim. Res. **15:** 95–108.

Pettersson, K., 1998. Mechanisms for internal loading of phosphorus in lakes. Hydrobiologia **373/374:** 21–25.

Pettersson, K. and K. Grust, 2002. Seasonality of nutrients in Lake Erken – effects of weather conditions. Verh. Int. Limnol. 28: in press.

Phillips, N. W., 1984. Role of different microbes ans substrates as potential suppliers of specific, essential nutrients to marine detrivores. Bull. Mar Sci. **35:** 283–298.

Pierson, D. C., K. Pettersson and V. Istvanovics, 1992. Temporal changes in biomass specific photosynthesis during the summer regulation by enviromental factors and the importance of phytoplankton succession. Hydrobiologia **243/244:** 119–135.

Räisänen, J., M. Rummukainen and A. Ullerstig, 2001. Downscaling of greenhouse gas induced climate change in two GCMs with the Rossby Centre regional climate model for northern Europe. Tellus **53A:** 168–191.

Reynolds, C., 1984. The Ecology of Freshwater Phytoplankton. Cambridge University Press, Cambridge.

Reynolds, C. S., 1997. Vegetation Processes in the Pelagic: A Model for Ecosystem Theory. Ecology Institute, Oldendorf/Luhe.

Robarts, R. D. and T. Zohary, 1987. Temperature effects on photosynthetic capacity, respiration and growth rates of bloom-forming cyanobacteria. N. Z. J. Mar. Freshwat. Res. **21:** 391–399.

Roeckner, E., L. Bengtsson, J. Feichter, J. Lelieveld and H. Rohde. 1999. Transient climate change simulations with a coupled atmosphere-ocean GCM including the troposphere sulfur cycle. J. Climate **12:** 3004–3032.

Rummukainen, M., J. Raisänen, B. Bringfelt, A. Ullerstig, A. Omstedt, U. Willen, U. Hansson and C. Jones, 2001. A regional climate model for northern Europe: model description and results from the downscaling of two GCM control simulations. Clim. Dyn. **17:** 339–359.

Sahlberg, J., 1988. Modelling the thermal region of lake during the winter season. Cold Region Science and Technology **15:** 151–159.

Schindler, D. W., 1996. Widespread effects of climate warming on freshwater ecosystems in North America. Hydrological Proc. **11:** 1044–1069.

Schindler, D. W., S. E. Bayley, B. R. Parker, K. Beaty, G. D. R. Cruikshank, E. J. Fee, E. U. Schindler and M. P. Stainton, 1996. The effects of climate warming on the properties of boreal lakes and streams at the Experimental Lake Area, northwestern Ontario. Limnol. Oceanogr. **41:** 1004–1017.

Sommer, U., Z. M. Gliwicz, W. Lampert and A. Duncan, 1986. The Plankton Ecology Group model of seasonal succession of planktonic events in fresh waters. Archiv f. Hydrobiol. **106:** 433–472.

Svensson, U., 1978. A Mathematical Model of the Seasonal Thermocline, Lund Inst. of Technology, Dept. of Wat. Res., Lund, Sweden, 1002 pp.

Törnblom, E. and E. Rydin, 1998. Bacterial and phosphorus dynamics in profundal Lake Erken sediments following the deposition of diatoms: a laboratory study. Hydrobiologia **364:** 55–63.

Vijverberg, J., 1980. Effect of temperature in laboratory studies on development and growth of Cladocera and Copepoda from Tjeukemeer, The Netherlands. Freshw. Biol. **10:** 317–340.

Wallace, B. B. and D. P. Hamilton, 1999. The effect of variations in irradiance on buoyancy regulation in *Microcystis aeruginosa*. Limnol. Oceanogr. **44:** 273–281.

Weyhenmeyer, G., T. Blenckner and T. Pettersson, 1999. Changes of the plankton spring outburst related to the North Atlantic Oscillation. Limnol. Oceanogr. **44:** 1788–1792.