Modelling the impact of higher temperature on the phytoplankton of a boreal lake

Anita Pätynen[1)2)]*, J. Alex Elliott[3)], Petri Kiuru[1)], Jouko Sarvala[4)], Anne-Mari Ventelä[5)] and Roger I. Jones[2)]

[1)] Finnish Environment Institute, Modelling and Assessment Unit, Survontie 9, FI-40500 Jyväskylä, Finland (*corresponding author's e-mail: anita.patynen@ymparisto.fi)
[2)] Department of Biological and Environmental Science, PL 35, FI-40014 University of Jyväskylä, Finland
[3)] Centre for Ecology and Hydrology Lancaster, Algal Modelling Unit, Lake Ecosystem Group, Library Avenue, Bailrigg, Lancashire LA1 4AP, UK
[4)] Department of Biology, FI-20014 University of Turku, Finland
[5)] Pyhäjärvi Institute, Sepäntie 7, Ruukinpuisto, FI-27500 Kauttua, Finland

We linked the models PROTECH and MyLake to test potential impacts of climate-change-induced warming on the phytoplankton community of Pyhäjärvi, a lake in southwest Finland. First, we calibrated the models for the present conditions, which revealed an apparent high significance of internal nutrient loading for Pyhäjärvi. We then estimated the effect of two climate change scenarios on lake water temperatures and ice cover duration with MyLake. Finally, we used those outputs to drive PROTECH to predict the resultant phytoplankton community. It was evident that cyanobacteria will grow significantly better in warmer water, especially in the summer. Even if phosphorus and nitrogen loads to the lake remain the same and there is little change in the total chlorophyll *a* concentrations, a higher proportion of the phytoplankton community could be dominated by cyanobacteria. The model outputs provided no clear evidence that earlier ice break would advance the timing of the diatom spring bloom.

Introduction

Climate change can alter the present state of aquatic ecosystems, because the warming of waters is expected to change species composition and even lead to decreased biodiversity (Sala *et al*. 2000). In lakes, most attention is being paid to potential changes in phytoplankton communities, because these relate directly to water quality as well as representing the productive base of lake ecosystems. The phytoplankton group expected to benefit most from warming is the cyanobacteria (e.g. Jöhnk *et al*. 2008, Paerl and Huisman 2009), because the optimal growth temperature for cyanobacteria is generally higher than that for other species. Furthermore, due to their buoyancy properties, they more readily remain in the warmer, less viscose epilimnion and are able to form dense surface blooms, blocking light from competing species, if warming strengthens the stratification (Reynolds 2006, Paerl and Huisman 2008, Wagner and Adrian

2009). How cyanobacteria may respond to rises in temperature is an important question, because extended growth of cyanobacteria, and especially of toxic strains, will decrease the value of lake water resources and potentially be harmful to humans and other organisms (e.g. Codd *et al.* 2005, White *et al.* 2005). Moreover, cyanobacteria can alter lake ecosystems because they have structural features that make them inedible for most grazers, whilst cyanobacterial blooms can hinder the living conditions of other organisms by increasing water turbidity and creating night time oxygen depletion through respiration and increased bacterial decomposition (*see* Paerl and Paul 2012).

High-latitude regions are predicted to experience the greatest climate-change-related warming (IPCC 2007). Indeed, climate change is argued to be the single most important future stressor for freshwaters at high latitudes (Sala *et al.* 2000). Despite this, most studies of climate change effects on freshwaters are made for lower latitudes, and their findings cannot be directly extrapolated to e.g. boreal areas (Heino *et al.* 2009). One important difference arises from the fact that, besides problems caused by the direct warming of air and water, higher temperatures cause indirect phenomena for high latitude lakes, such as reduced winter ice cover (e.g. Magnuson *et al.* 2000). When the duration of winter ice cover in boreal lakes is shorter due to milder winters, it leads to a longer growing season for phytoplankton, while earlier ice break in spring can cause a shift in the timing of the spring phytoplankton bloom, which alters the phytoplankton growth pattern for the rest of the growing season (e.g. Gerten and Adrian 2000, Shatwell *et al.* 2008). Such drastic changes within the primary producers can be expected to affect the zooplankton and further, the higher trophic levels (Adrian *et al.* 1999, Straile 2000), but also the chemical properties of the lake. Therefore, studies of the likely responses of phytoplankton in boreal lakes to predicted climate change are urgently required.

To address these issues, we studied Pyhäjärvi, a lake in southwest Finland. The lake is socially and economically very important to the region, and many management actions have been taken to achieve good water-quality standards (Ventelä

et al. 2007). However, climate-change-induced changes in rainfall and nutrient loading could threaten these improvements in water quality (Ventelä *et al.* 2011). Here, we aimed to evaluate whether warming alone might promote earlier and/or greater cyanobacterial growth in this boreal lake. First, we predicted that a rise in temperature will selectively benefit the growth of cyanobacteria, and that this effect will be more distinct the greater the rise in temperature, even though total phytoplankton biomass does not increase if nutrient levels remain unchanged. Second, we predicted that earlier ice break affects the diatom spring bloom, which also leads to changes in the summer phytoplankton population. To test these predictions we linked two existing models. We used the PROTECH model (Phytoplankton response to environmental change, Reynolds *et al.* 2001, Elliott *et al.* 2010), to simulate the succession of phytoplankton communities in the lake, and the thermodynamic part of the MyLake model (Multi-year simulation model for Lake thermo- and phytoplankton dynamics, Saloranta and Andersen 2007) to provide the daily thermal profiles and the duration of ice cover required by PROTECH.

Material and methods

Site description

Pyhäjärvi is the largest lake in southwest Finland (61.00°N, 22.29°E, surface area 154 km^2, mean depth 5.4 m, maximum depth 26 m). However, it has a relatively small drainage area (615 km^2 including the lake), and a retention time of approximately three years (Malve *et al.* 1994). About half of the drainage area is forest and one fifth is in intensive agricultural use. Pyhäjärvi does not develop persistent summer stratification and it has a Secchi depth of 2.6 m and a colour of 20 mg Pt l^{-1} (both median values for 2000–2010).

Municipal waste waters were discharged into the lake for a short period during the 1960s but the water quality remained good through the 1970s. Increasing phosphorus levels since the early 1980s, and the more prominent role of cyanobacteria in the 1990s (*see* e.g. Ventelä *et*

al. 2011), aroused concerns about the gradual eutrophication of the lake. An intensive restoration program started in 1995 when the Pyhäjärvi Protection Fund (PPF) was created. Today, actions continue to maintain the good condition of Pyhäjärvi. These include implementing protection measures like wetlands and filtering systems in the catchment area, and biomanipulation through fish removal from the lake. Besides PPF, several research institutes and universities are involved in monitoring (since the 1960s) and research of Pyhäjärvi and its catchment. The information gathered about the lake and, by Finnish standards, comprehensive monitoring data make the lake particularly suitable for modelling.

MyLake modelling

As PROTECH does not currently include a routine for ice, the thermodynamic part of the MyLake model was employed to create daily thermal profiles and ice-break and ice-formation dates for Pyhäjärvi within the period 2001–2009. MyLake is a one-dimensional process-based model code for predicting daily vertical distribution of lake water temperature, and thus stratification. The model layer thickness was set to 1 m, but for PROTECH the data were interpolated to 0.1 m thickness. Daily meteorological forcing data from the Jokioinen observatory of the Finnish Meteorological Institute (FMI), less than 100 km E from Pyhäjärvi, including air temperature, relative humidity, air pressure, wind speed and precipitation, were used in setting up the MyLake model application. In addition, daily time series of global radiation from Jokioinen were used until September 2008, after which the incoming solar radiation at the water or ice surface was calculated in the model from cloudiness measured at the Pirkkala station of FMI (about 100 km NE from Pyhäjärvi). A more detailed description of the model code and equations is given in Saloranta and Andersen (2007).

The model was calibrated manually against lake water temperatures measured monthly from the deepest site of Pyhäjärvi in 2006–2007. Calibration was mostly done using the parameter for the wind sheltering effect of surrounding terrain.

In addition, the melting snow albedo, that is constant in MyLake, was adjusted to force the simulated ice-on and ice-off dates to agree with the observations. This resulted in slightly thinner snow cover in wintertime, but had scarcely any effect on the water temperature. The other thermodynamic parameters in the simulation were the same as those presented by Saloranta and Andersen (2007).

PROTECH modelling

PROTECH is a one dimensional, vertically layered model (0.1 m layers) that has the ability to simulate the simultaneous growth of eight different phytoplankton species, or functional groups (e.g. *Oscillatoria* representing also *Planktothrix*), at daily resolution. From the available phytoplankton data for Pyhäjärvi, eight taxa selected for modelling based on their recorded prevalences were: three cyanobacteria (*Anabaena*, *Oscillatoria* and *Gloeotrichia*), two diatoms (*Asterionella* and *Aulacoseira*), a chrysophyte (*Mallomonas*), a dinophyte (*Gymnodinium*), and a cryptophyte (*Cryptomonas*) (*see* Apendix). In PROTECH, the growth of phytoplankton is regulated by the availability of nutrients and light, and adjusted to the ambient water temperature. In addition, each modelled phytoplankton taxon has a specific description inside the model which includes information about the cell/colony size, motility, ability to fix nitrogen, requirement for silica and whether the taxon is grazed or not. These qualities additionally determine the fate of the taxa through possible loss processes or increased opportunities to utilize available resources. It is also important to stress that Cyanobacteria are given no specific growth advantage in higher temperatures. A more complete description of the base formulas and a more detailed introduction to PROTECH is given in Reynolds *et al*. (2001) and Elliott *et al*. (2010).

Simulations for Pyhäjärvi were done for 2001, 2005 and 2008 because the most complete input and validation data were available for these years. These years also differed in their seasonal temperatures and nutrient loadings (Table 1), which gave three contrasting initial settings for

the models when exploring the development of phytoplankton growth in the lake during the year. The main inflow rivers, Yläneenjoki and Pyhäjoki cover 68% of the drainage area and are frequently monitored: discharge daily, PO_4-P and NO_3-N concentrations weekly in summer and about once per month in winter (HERTTA database of Finnish Environmental Administration). Daily discharge values from the outflow river, Eurajoki, are also available. PROTECH runs require daily figures for every variable, so missing nutrient concentrations were linearly interpolated. Silica concentrations are measured only once or twice per year, so for the modelling these were fixed at the average value (ca. 12 mg l^{-1}). This was considered adequate as measured silica concentrations in the lake have been consistently high (average of eight spring samples 2002–2009 from 15 meters, 2.9 mg l^{-1}), and hence silica is probably not a growth-limiting nutrient for phytoplankton in Pyhäjärvi. As the monitoring sites in Yläneenjoki and Pyhäjoki do not represent the whole drainage area, discharges from the rivers Yläneenjoki and Pyhäjoki were multiplied by coefficients (1.2 and 1.06 respectively) taken from a loading study by Malve *et al.* (1994), that would add the impact of the rest of the drainage area to the nutrient loading. This addition was separated to represent a third

inflow. The meteorological variables required for PROTECH simulations (wind speed, cloud cover, air temperature and air humidity) were obtained from the Jokioinen observatory (FMI). Occasional missing values were either interpolated, or values from other nearby observatories were used if regression correspondence between the locations had been shown at other times.

Model validation used the approximately fortnightly measured chlorophyll-*a* concentrations (HERTTA) and phytoplankton counts from May to October. The total chlorophyll-*a* concentration was divided among different phytoplankton groups based on their fresh weight biomass proportions (g m^{-3}) in the sample. PROTECH outputs were expressed as total, cyanobacterial and diatom chlorophyll concentrations, representing the upper 5 metres of the lake water column. Visual comparison and regression analysis were used to achieve the best congruity between measured and PROTECH output results. In the calibration process, the composition of the phytoplankton community, proportion of different species at the beginning and the base chlorophyll-*a* level (input from inflow etc.) in different seasons was slightly tuned. This means that we gave the model the composition of the starting population, and expected the model otherwise to work through the rest of the

Table 1. Soluble reactive phosphorus (SRP) and nitrate-nitrogen (NO_3-N) loadings in 2001, 2005 and 2008, average water temperatures, ice break dates and duration of ice free period for Pyhäjärvi. Change in water temperature (ΔT) according to climate scenario A1B for years 2040–2069 (S1) and 2070–2099 (S2) and new ice break dates are also given beside the original (orig) values. Note that to be more comparable, all temperature and ice values are from model results.

	2001			2005			2008		
SRP load (kg)		2772			2674			3388	
NO_3-N load (kg)		103 089			184 994			231 864	
Mean water T (°C)	orig	ΔT_{S1}	ΔT_{S2}	orig	ΔT_{S1}	ΔT_{S2}	orig	ΔT_{S1}	ΔT_{S2}
whole year	7.5	+1.0	+1.7	8.0	+0.5	+1.1	7.2	+0.8	+1.4
April	0.6	+3.2	+5.1	2.5	+1.9	+3.8	1.8	+0.0	+1.1
May	8.7	+2.5	+3.4	9.8	+1.6	+2.5	8.6	+0.4	+1.8
June	14.4	+3.2	+3.9	15.7	+2.0	+2.7	14.3	+1.6	+2.4
July	20.5	+0.1	+0.8	20.5	+1.1	+1.8	17.2	+2.2	+3.0
August	18.8	+0.8	+1.5	18.5	+1.2	+1.9	17.6	+1.9	+2.6
September	14.7	-0.2	+0.6	12.6	+0.2	+1.0	12.1	+2.4	+3.2
Ice break date	orig	S1	S2	orig	S1	S2	orig	S1	S2
	27.IV	8.IV	20.III	18.IV	7.IV	10.III	24.IV	24.IV	15.IV
Ice free period (days)	229	259	315	235	278	308	248	249	262

year itself without parameterisation or changes in the base formulas or assumptions about the properties of different species. Also the nutrient levels measured from the lake at the beginning of the year were entered in the model to initialize the simulation. When calibrating the model, it became evident that the phosphorus entering from inflows was insufficient to maintain phytoplankton growth after the spring peak, even if the amounts were artificially doubled. The grazing function of PROTECH already assumes that all chlorophyll *a* that is consumed is returned to the water as nutrients (zooplankton exretion is shown to be very important in the phosphorus cycling of Pyhäjärvi, Helminen and Sarvala 1997), in the same ratio as it is supposed to be anabolised: 8.2 g nitrogen:1.2 g phosphorus:1 g chlorophyll (Reynolds *et al.* 2001). Therefore, an internal nutrient loading from sediments was added to the model by slightly increasing the in-lake phosphorus concentration (by 0.08–0.2 μg l^{-1}) for some period during late summer. In fact, the existence of an internal loading in Pyhäjärvi has previously been calculated from mass balance equations (Ekholm *et al.* 1997, Nürnberg *et al.* 2012) and demonstrated in laboratory experiments (Lehtoranta and Gran 2002), and elevated phosphorus concentrations near the bottom were also evident in the monitoring data. Therefore the incorporation of a simple internal loading factor in the PROTECH modelling was considered justified.

Changes in temperature and wind

After PROTECH had been calibrated according to the conditions of the three selected study years, the effect of altered air temperature on the conditions represented by each year was in turn examined by creating new thermal profiles with MyLake while retaining the original values for that year of the other model parameters. The higher daily air temperatures applied were the averages from estimations of 19 global models (sub group of the 23 models used in the IPCC (2007) fourth assessment report) with emission scenario A1B (FMI). As compared with other possible scenarios, the A1B leads to estimated temperatures running in between

the two extremes. First, we took an average for each day from the period 2040–2069, and then from 2070–2099 and used those as new daily temperatures for one year. We also wanted to take into account one possible indirect effect of higher temperatures, a change in windiness. According to some estimations by the FMI, the windiness in southwestern Finland could increase by as much as 2%–4% by the end of the century, mostly during the windiest period in September–April (Finnish Wind Atlas, http://www.tuuliatlas.fi). Wind-induced changes to the mixing and water column stability of Pyhäjärvi could have significant impact on the phytoplankton community. Therefore, after first making the simulations with higher air temperatures alone, the values for wind speed were also changed. The original wind data were modified by adding first 2% then 4% to the values, which would be an extreme change but provides a test of whether wind should be taken into account as a potential impacting factor in this lake.

Results

With very little calibration the MyLake model simulated the measured seasonal lake water temperature changes very well (Fig. 1), indicating that the model outputs provided appropriate thermal input for PROTECH. PROTECH outputs also matched the measured phytoplankton values well (Fig. 2). For cyanobacteria, the regression r^2 values between measured and output values were high for each study year, and with two exceptions this was also true for the total chlorophyll *a* and diatoms (Table 2). The most problematic year for the calibration was 2001, when the lack of concordance between the modelled and measured autumn diatom growth weakened the r^2 value. The same was true for total chlorophyll *a* in 2005, when the high measured value at the beginning of November was not reflected in the model simulation. When these outliers were excluded from the regression, the r^2 values improved appreciably (Table 2), which indicated good model performance at other times of the year. Overall, and given the sensitivity of regression to any temporal mismatch between PROTECH outputs *vs.* observation, the model performed satisfactorily
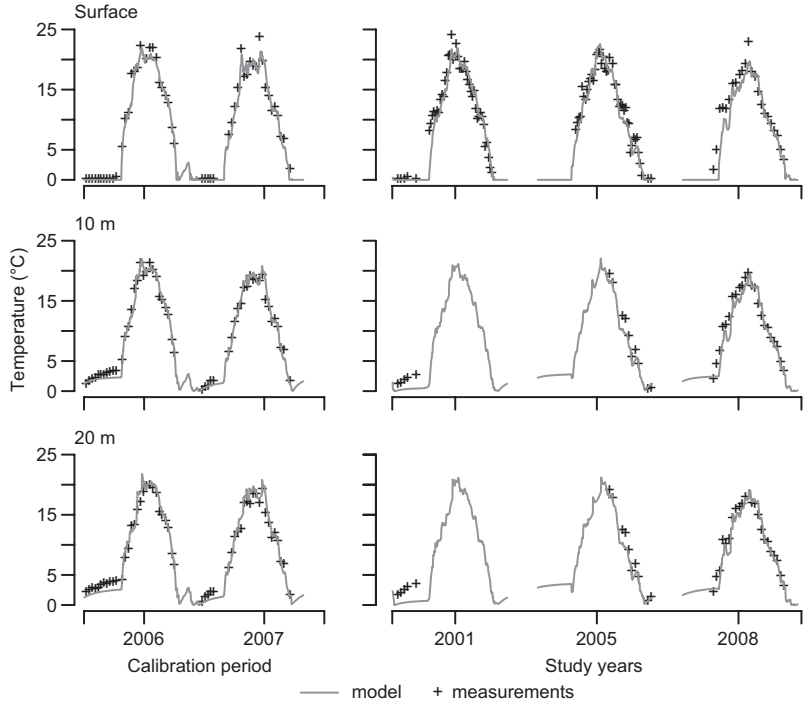
Fig. 1. Measured (crosses) and MyLake-simulated (line) temperatures at different water depths for Pyhäjärvi. Years 2006 and 2007 were used for calibration of the model.
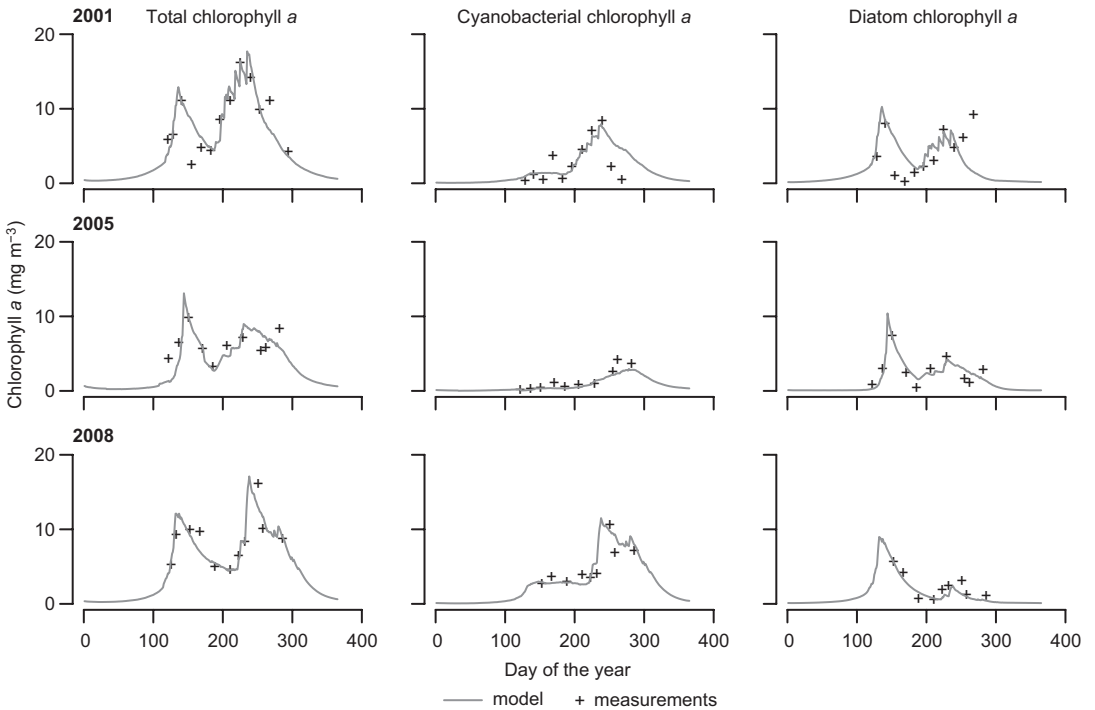
Fig. 2. Measured (crosses) and PROTECH-simulated (solid line) chlorophyll-*a* concentrations for Pyhäjärvi in 2001, 2005 and 2008.
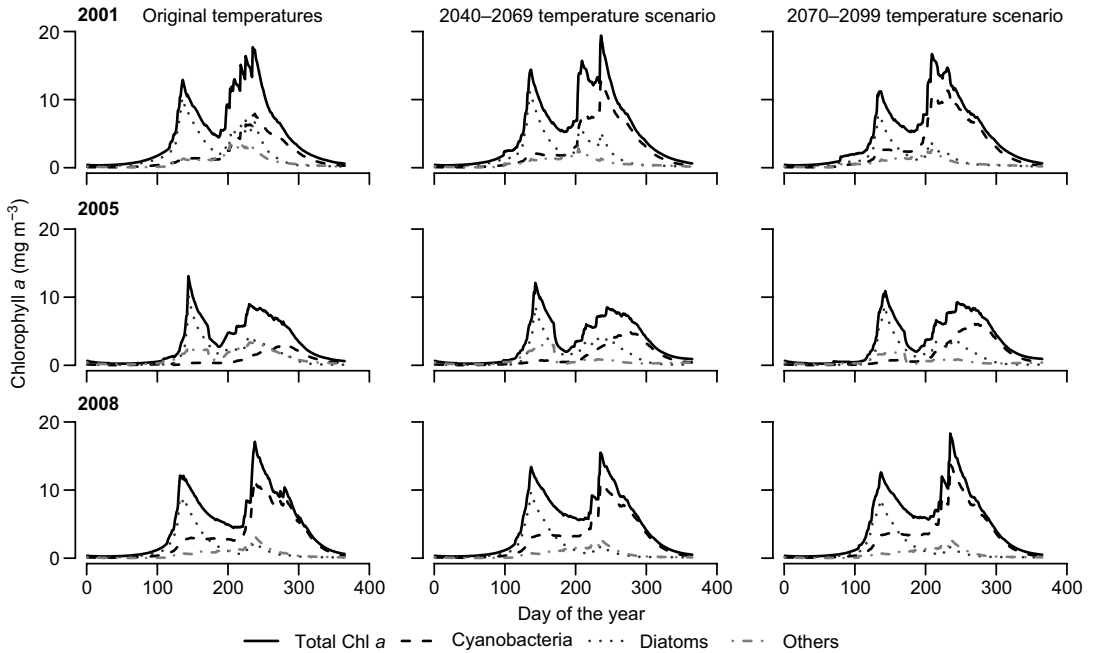
Fig. 3. Total chlorophyll-*a* concentrations (mg m⁻³) and its proportions for different phytoplankton groups simulated with PROTECH. Left-hand-side column: plots with the original data for 2001, 2005 and 2008; middle column: plots for the respective years with the A1B scenario of higher 2040–2069 temperatures applied; right-hand-side column: plots for the respective years with the A1B scenario of even higher 2070–2099 temperatures applied.

at simulating the observed succession of the phytoplankton community.

With the application of the climate change scenarios, there was a clear rise in the lake water temperatures with higher air temperatures (Table 1), which changed the phytoplankton community (Fig. 3). However, a change in windiness had no effect either on the mixing of the Pyhäjärvi water column (poorest regression $y = 0.99x + 0.61$, $r^2 = 0.99$ between mixing during original windiness and increased windiness, in 2005), or on the phytoplankton community. Regardless of the slightly different starting points between the study years, the impact of a temperature rise was always similar, with increased cyanobacterial growth (mostly *Oscillatoria*), especially in summer (sign test: $n = 92$, $p < 0.001$; Figs. 3 and 4). The growth also increased significantly in spring for 2001 (sign test: $n = 92$, $p < 0.001$) and in autumn for 2001 and 2005 ($n = 91$, $p < 0.001$), whereas in autumn for 2008 there was a clear drop in cyanobacterial growth with higher temperatures (Fig. 4) because, according to PROTECH out-

puts, phosphorus became limiting. Decreased diatom growth was noticeable with the higher 2070–2099 temperature rise throughout 2001 and in summer and autumn for 2005 and 2008 (sign test: $n_{summer} = 92$, $n_{autumn} = 91$, $p < 0.001$). A drop in diatom abundance occurred with 2040–2069 temperatures during summer for 2001 and autumn for 2001 and 2008 (sign test: $n_{summer} = 92$, $n_{autumn} = 91$, $p < 0.001$). However, this shift between different phytoplankton groups produced little change in the total chlorophyll-*a* levels, as the decreased diatom growth was offset
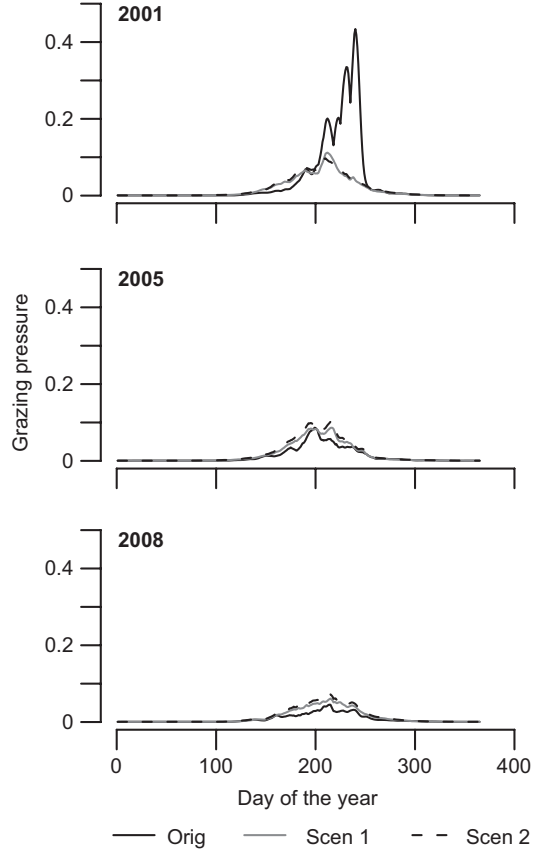
Table 2. Coefficients of determination r^2 for the regression between measured chlorophyll *a* and PROTECH outputs. In parentheses are the values for regressions excluding one most extreme difference between measured and modelled values in late autumn. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	2001	2005	2008
Total chlorophyll *a*	0.71***	0.14 (0.51*)	0.66**
Cyanobacteria	0.60**	0.87***	0.77**
Diatoms	0.02 (0.33)	0.79**	0.81**
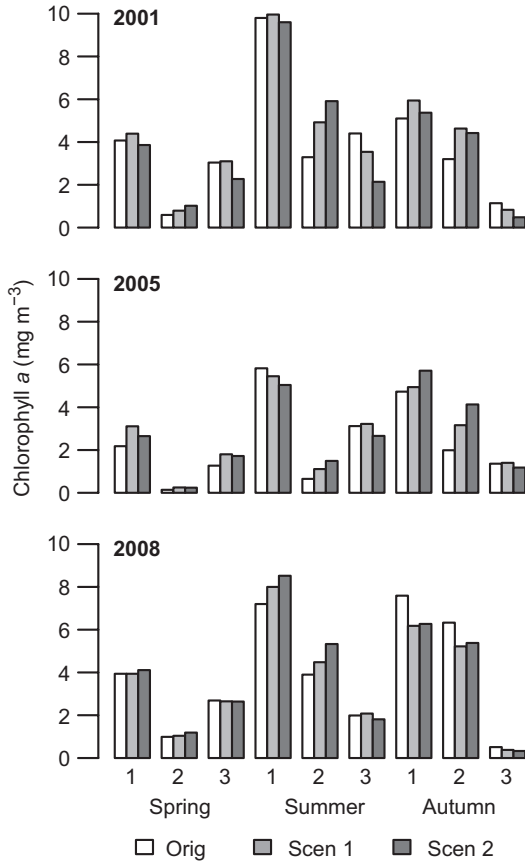
Fig. 4. PROTECH-simulated seasonal means for total chlorophyll *a* (1), cyanobacteria (2) and diatoms (3). White bars (Orig) are with original data, light-grey bars (Scen 1) with A1B scenario temperatures for years 2040–2069, and dark-grey bars (Scen 2) with A1B scenario temperatures for years 2070–2099.

Fig. 5. PROTECH-simulated grazing pressure in original situation (Orig), with A1B scenario temperatures for years 2040–2069 (Scen 1) and with A1B scenario temperatures for years 2070–2099 (Scen 2).

by the increased cyanobacterial growth. Besides phosphorus limitation, PROTECH showed some higher values for grazing after the diatom spring peak at higher temperatures for 2005 and 2008 (Fig. 5) that could partly account for the disappearance of non-cyanobacterial taxa (cyanobacteria are classified as inedible in PROTECH) and the decline in total chlorophyll *a*. The clear drop in the grazing with higher temperatures in 2001 is a bottom-up effect resulting from the lack of suitable edible phytoplankton taxa as food. In the 2070–2099 higher temperature scenario, which can be considered the worst-case scenario of our study, the average proportion of cyanobacteria in the summer total chlorophyll *a* was ca. 30% for 2005 and ca. 60% for 2001 and 2008 (Fig. 4), the

original proportions being ca. 10% in 2005, ca. 30% in 2001, and ca. 50% in 2008.

The ice-break dates obtained from the MyLake outputs advanced with higher air temperatures (Table 1). The ice-free period also lasted longer in autumn (Table 1), with ice formation usually delayed until January the following year. However, except for 2005, the earlier ice break had no clear effect on the timing of the diatom spring bloom. Even for 2005 the time of the highest peak did not move, but the growth preceding it advanced by about four days with 2040–2069 temperatures and by about eight days with 2070–2099 temperatures. There was, of course, some rise in the total chlorophyll *a* concentration after earlier ice break for 2001 and 2008, but this was due to a slight increase in the growth of many taxa and the "early start" quite

quickly returned to fall in line with the original concentrations.

Discussion

PROTECH simulated well the growth of different phytoplankton groups in Pyhäjärvi, although exactly the same taxa were retained in the model each year, and the model calibration was done solely by slightly tuning the initial proportions of different species and the base chlorophyll-*a* levels as described in the methods. Using outputs from MyLake for daily thermal profiles and for dates of ice break and formation as inputs to PROTECH worked well and enhanced the description of these physical processes for Pyhäjärvi. A similar model connection was applied previously between PROTECH and PROBE for modelling Lake Erken, Sweden (Elliott *et al.* 2007).

However, PROTECH had some problems simulating growth peaks in early spring and late autumn. One reason could be that the eight selected taxa did not adequately represent the actual species growing at those times. Unfortunately no phytoplankton count data from Pyhäjärvi for validation exist outside the May–October period, which makes deeper evaluation of PROTECH's performance for the colder and darker periods impossible within this study. This would be an important future development, because better understanding is needed of the causes for occasional under-ice cyanobacterial blooms in some boreal lakes, for example as reported from the Lake Pien-Saimaa area, SE Finland in 2009 (Kauppi and Saukkonen 2010).

These problems may relate to the unchanged diatom spring bloom timing in the model results. Although the ice breaks advanced by little over one month with the highest temperature scenarios for 2070–2099, there was only a slight change in the diatom spring bloom timing when higher temperatures were applied to 2005 conditions. In their study of Lake Mälaren, Sweden, with the PROTECH-based model PROTBAS, Markensten and Pierson (2007) also found a later start of phytoplankton growth after ice break in the modelled results than in reality. They concluded that phytoplankton growth was possibly limited in the model by light and/or temperature, given that the nutrient levels in the early spring were high and grazing pressure low. In our study, the temperature in Pyhäjärvi was rising, but quite slowly, as it took 10–20 days after ice break (2070–2099) to reach ca. 4.0 °C. That temperature is equivalent to the one Eloranta (1980) measured in a pond in central Finland warmed by power station cooling waters, in which chlorophyll-*a* concentrations as high as 20 mg m^{-3} were measured already in February, directly after the short ice-cover period. Hence, his finding also contrasts with the idea that phytoplankton growth would be severely light-limited in early spring if the lake is ice free. However, Huber and Adrian (2008) observed a "delayed" spring bloom after ice break in some years in Müggelsee, a lake in Germany, and suggested that lower phosphorus availability in eutrophic conditions in some years as compared with that in hypertrophic conditions in other years can counteract any warming effect. Despite mesotrophic Pyhäjärvi being at a higher latitude, these kinds of interactions may take place under altered conditions, even if just one factor is changed.

Nevertheless, good simulations for the open-water growing season are often sufficient for addressing the most high profile cyanobacteria-induced problems in lakes. The years we selected to provide the starting conditions for the modelling carried out in this study exhibited contrasting weather conditions that were reflected by differences in the original phytoplankton community compositions, but despite these differences the predicted rise in temperature always created a clear pattern of increased cyanobacterial growth. Thus, we can be sure that the starting point makes no fundamental difference to the main concern about harmful cyanobacterial concentrations in Pyhäjärvi. Furthermore, the simulated results for the three different years did not differ dramatically from the original 2008 observations. The year 2008 appears to be a useful point of reference, because in that year the proportion of cyanobacteria was originally high and the phytoplankton community did not change markedly with the seasonally increasing temperature. The weather conditions for 2008 reveal an unusually warm spring and

early summer, while the preceding winter had been mild and the ice-cover period on Pyhäjärvi was exceptionally short at only 55 days (mean duration in 1958–2009 141 days, Ventelä *et al.* 2011). Hence, 2008 shows a striking congruity to weather conditions expected more frequently on average under future climate scenarios. It is therefore striking that under 2008 conditions the phytoplankton counts from July showed high abundance of a species normally rare in the lake, the potentially toxic cyanobacterium *Planktothrix agardhii*. In PROTECH, the taxon *Oscillatoria* also represents *Planktothrix*, so the model outputs suggest that nuisance cyanobacterial blooms may indeed be expected to occur more frequently in the future.

Our model outputs showed no changes in lake stratification due to higher temperatures or increased windiness, because Pyhäjärvi is very easily mixed due to the lack of wind shelter. Therefore, a rise in temperature alone, and in some cases even quite a mild increase (scenario for years 2040–2069, Table 1), can offer a significant advantage for cyanobacteria. This is consistent with previous measured (Jöhnk *et al.* 2008) and modelled (Elliott *et al.* 2006, Malve *et al.* 2007) stronger cyanobacterial growth at higher temperatures. In addition, stronger growth did not require any nutrient addition. Instead, when the nutrient resources become limited, the proportion of cyanobacteria increased at the expense of other taxa, and there were only minor changes in the total phytoplankton biomass (expressed as chlorophyll *a*). A similar rise in the proportion of cyanobacteria in the phytoplankton community, regardless of weak effects of climatic conditions on total phytoplankton biomass, has been reported in other studies (e.g. Kosten *et al.* 2012). Furthermore, some modelling studies (Mooij *et al.* 2007, Trolle *et al.* 2011) have shown that warming will actually decrease critical nutrient loads from present values, thus possibly shifting mesotrophic lakes nearer the boundary to eutrophic. Thus, it is important to take into account the likely temperature change as a significant stressor for lake ecosystems when planning management actions and evaluating their effectiveness. Also, predictions for total chlorophyll *a* alone may not be sufficient; if a principal concern is with cyanobacteria, their response needs to be modelled separately.

The model simulations suggest that warming poses a similar risk of higher cyanobacteria abundances in summer for boreal lakes as for the more widely studied temperate lakes. If in addition to this general result we aim for more detailed or even multiyear modelling of boreal lakes and their ecosystems in the future, the true reason for the unchanging spring bloom timing and the weak predictability of spring and autumn growth require further study. Phytoplankton time series from winter ice-covered central European lakes show that mild winters and shorter ice cover can benefit Oscillatoriales (Shatwell *et al.* 2008). After early ice break the water may be too cold for zooplankton growth, offering a longer unrestricted growing period for the early spring phytoplankton, which can have an impact on the nutrient availability in the summer. In addition, the uncoupling of phytoplankton and zooplankton peaks and possible decrease of the zooplankton population can eventually affect the higher trophic levels (Adrian *et al.* 1999, Straile 2000, Shatwell *et al.* 2008). Because the mean ice cover period for Pyhäjärvi (141 days) and other boreal lakes is clearly longer than, for instance, for Müggelsee (*see* Adrian *et al.* 1999), and because in boreal areas a mild winter and short ice cover actually leads to very cool lake water (Keller 2007), these changes in different trophic levels can be more drastic.

Ice and snow normally create an efficient barrier for nutrient runoff and light penetration during the winter, and the loss of these due to warming can create further considerable changes in the physical and chemical properties of boreal aquatic environments (George 2010). Change in DOC concentration, which gives many boreal lakes their strong brown colouration, is an additional issue (*see* Keller 2007, Jennings *et al.* 2010). Thus impacts of climate warming on catchment conditions are expected to be important for in-lake processes. Arguably, even greater future focus should be put on the nutrient loading issues (external and internal) because if climate change proceeds towards warmer scenarios, it will not be possible to prevent lake temperatures rising. Hence the only measure to counter the contribution of rising temperature to undesirable water quality symptoms will be to further lower the in-lake nutrient concentrations. The

PROTECH modelling provided an unexpected but valuable demonstration of the importance of internal loading for the phytoplankton of Pyhäjärvi. Consistent with this, recent analyses of long-term phosphorus balance in Pyhäjärvi also indicate a high and increasing level of internal load (average about 60% of the external load, Nürnberg *et al.* 2012). As described, we needed to incorporate an internal phosphorus loading factor into PROTECH to obtain realistic phytoplankton growth in the summer. Our method was simple, and the adjustment covered only that period when the results showed a real lack of phosphorus. If, as is likely, more phosphorus is being released from the sediments at other times as well, it could further boost phytoplankton growth. Moreover, the evident internal nutrient loading from the sediment could be expected to increase at warmer temperatures (Jensen and Andersen 1992, Nürnberg *et al.* 2012), while the influence of fish (Tarvainen *et al.* 2010) on phosphorus cycling in the lake further compromises evaluations of nutrient issues based only on changes in external load. The model outputs thus highlight an important issue, and support the recent strategy of the Pyhäjärvi Protection Fund in which measures to combat external nutrient loading are accompanied by simultaneous attempts to reduce the internal loading.

Large, polymictic and mesotrophic Pyhäjärvi represents just part of the wide variation of high latitude lake types. Further modelling for different lakes, besides with better observation data, is required to highlight the most important potential different responses to warming, especially for lakes in even colder areas. For more oligotrophic lakes, the warming alone may not produce such distinct problems (Brookes and Carey 2011), but these could provide an opportunity to study the interaction between higher temperature and increased nutrient loading, without the uncertainties derived from internal loading. Moreover, oligotrophic lakes are the most valued water bodies for drinking water supply and recreational use, so all potential risks should be evaluated. Especially, modelling studies are needed for representatives of the many boreal lakes which exhibit summer stratification and stronger brown water colour, in which responses may be different. For example, our model results gave some suggestions of light limitation of phytoplankton growth (*see* also Markensten and Pierson 2007), which could be important for coloured high latitude lakes. Even if by the end of the century the Finnish climate might approach that in central Europe at present, the light climate will still be different given the more pronounced seasonality of solar radiation and the brown water colour of most boreal lakes. Unfortunately, the lack of detailed year-round and long-term monitoring data for such boreal lakes, is an obstacle to further modelling studies of these lakes.

References

Adrian R., Norbert W., Hintze T., Hoeg S. & Rusche R. 1999. Effects of ice duration on plankton succession during spring in a shallow polymictic lake. *Freshwater Biology* 41: 621–632.

Arvola L. & Rask M. 1984. Relations between phytoplankton and environmental factors in a small, spring-meromictic lake in southern Finland. *Aqua Fennica* 14: 129–138.

Brookes J.D. & Carey C.C. 2011. Resilience to blooms. *Science* 334: 46–47.

Codd G.A., Morrison L.F. & Metcalf J.S. 2005. Cyanobacterial toxins: risk management for health protection. *Toxicology and Applied Pharmacology* 203: 264–272.

Ekholm P., Malve O. & Kirkkala T. 1997. Internal and external loading as regulators of nutrient concentrations in the agriculturally loaded Lake Pyhäjärvi (southwest Finland). *Hydrobiologia* 345: 3–14.

Elliott J.A., Irish A.E. & Reynolds C.S. 2010. Modelling phytoplankton dynamics in fresh waters: affirmation of the PROTECH approach to simulation. *Freshwater Reviews* 3: 75–96.

Elliott J.A., Jones I.D. & Thackeray S.J. 2006. Testing the sensitivity of phytoplankton communities to changes in water temperature and nutrient load, in a temperate lake. *Hydrobiologia* 559: 401–411.

Elliott J.A., Persson I., Thackeray S.J. & Blenckner T. 2007. Phytoplankton modelling of lake Erken, Sweden by linking the models PROBE and PROTECH. *Ecological Modelling* 202: 421–426.

Eloranta P. 1980. Winter phytoplankton in a pond warmed by a thermal power station. *Annales Botanici Fennici* 17: 264–275.

Gerten D. & Adrian R. 2000. Climate-driven changes in spring plankton dynamics and the sensitivity of shallow polymictic lakes to the North Atlantic Oscillation. *Limnology and Oceanography* 45: 1058–1066.

George G. 2010. *The impact of climate change on European lakes*. Springer, Dordrecht.

Heino J., Virkkala R. & Toivonen H. 2009. Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biological Reviews* 84: 39–54.

Helminen H. & Sarvala J. 1997. Responses of Lake Pyhäjärvi (SW Finland) to variable recruitment of the major planktivorous fish, vendace (Coregonus albula). *Canadian Journal of Fisheries and Aquatic Sciences* 54: 32–40.

Huber V. & Adrian R. 2008. Phytoplankton response to climate warming modified by trophic state. *Limnology and Oceanography* 53: 1–13.

IPCC 2007. *Synthesis report*. *Contribution of working groups I, II and III to the fourth assessment report of the intergovernmental panel on climate change*. IPCC, Geneva, Switzerland.

Jennings E., Järvinen M., Allott N., Arvola L., Moore K., Naden P., Aonghusa C.N., Nõges T. & Weyhenmeyer G.A. 2010. Impacts of climate on the flux of dissolved organic carbon from catchments. In: George G. (ed.), *The impact of climate change on European lakes*, Springer, Dordrecht, pp. 199–252

Jensen H.S. & Andersen F.O. 1992. Importance of temperature, nitrate, and pH for phosphate release from aerobic sediments of four shallow, eutrophic lakes. *Limnology and Oceanography* 37: 577–589.

Jöhnk K., Huisman J., Sharples J., Sommeijer B., Visser P.M. & Stroom J.M. 2008. Summer heatwaves promote blooms of harmful cyanobacteria. *Global Change Biology* 14: 495–512.

Kauppi M. & Saukkonen P. 2012. Pien-Saimaan poikkeuksellinen sinilevien massaesiintymä talvella [Exceptional cyanobacterial mass occurence in south-western Lake Saimaa during winter]. *Reports and studies in Forestry and Natural Sciences* 4: 131–140. [In Finnish with English summary].

Keller W. 2007. Implications of climate warming for Boreal Shield lakes: a review and synthesis. *Environmental Reviews* 15: 99–112.

Kosten S., Huszar V.L.M., Bécares E., Costa L.S., Van Donk E., Hansson L.-A., Jeppesen E., Kruk C., Lacerot G., Mazzeo N., De Meester L., Moss B., Lürling M., Nõges T., Romo S. & Scheffer M. 2012. Warmer climates boost cyanobacterial dominance in shallow lakes. *Global Change Biology* 18: 118–126.

Lehtoranta J. & Gran V. 2002. Sedimentistä veteen vapautuvat ravinteet Säkylän Pyhäjärvellä [Nutrient flux from sediment into water in Lake Säkylän Pyhäjärvi]. *Finnish Environment Institute Mimeographs* 247: 1–31. [In Finnish with English summary].

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

Malve O., Ekholm P., Kirkkala T., Huttula T. & Krogerus K. 1994. Säkylän Pyhäjärven ravinnekuormitus ja rehevyystaso. Tarkastelu vuosien 1980–1992 vedenlaatuaineiston sekä virtaus- ja vedenlaatumallien avulla. [Nutrient load and trophic level of Lake Pyhäjärvi (Säkylä). A study based on the water quality data for 1980–1992 using flow and water quality models]. *Publications of National Board of waters and the Environment—Series A* 181: 105 pp. [In Finnish with English summary].

Malve O., Laine M., Haario H., Kirkkala T. & Sarvala J. 2007 Bayesian modelling of algal mass occurrences — using adaptive MCMC methods with a lake water quality model. *Environmental Modelling and Software* 22: 966–977.

Markensten H. & Pierson D.C. 2007. Weather driven influences on phytoplankton succession in a shallow lake during contrasting years: Application of PROTBAS. *Ecological Modelling* 207: 128–136.

Mooij W.M., Janse J.H., De Senerpont Domis L.N., Hülsmann S. & Ibelings B.W. 2007. Predicting the effect of climate change on temperate shallow lakes with the ecosystem model PCLake. *Hydrobiologia* 584: 433–454.

Nürnberg G.K., Tarvainen M., Ventelä A.-M. & Sarvala, J. 2012. Internal phosphorus load estimation during biomanipulation in a large polymictic and mesotrophic lake. *Inland Waters* 2: 147–162.

Paerl H.W. & Huisman J. 2008. Blooms like it hot. *Science* 320: 57–58.

Paerl H.W. & Huisman J. 2009. Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. *Environmental Microbiology Reports* 1: 27–37.

Paerl H.W. & Paul J.V. 2012 Climate change: Links to global expansion of harmful cyanobacteria. *Water Research* 46: 1349–1363.

Reynolds C.S. 2006. *Ecology of phytoplankton*. Cambridge University Press, Cambridge.

Reynolds C.S., Irish A.E. & Elliott J.A. 2001. The ecological basis for simulating phytoplankton responses to environmental change (PROTECH). *Ecological Modelling* 140: 271–291.

Sala O.E., Chapin F.S.III, Armesto J.J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., Huenneke L.F., Jackson R.B., Kinzig A., Leemans R., Lodge D.M., Mooney H.A., Oesterheld M, Poff N.L., Sykes M.T., Walker B.H., Walker M. & Wall D.H. 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774.

Saloranta T.M., & Andersen T. 2007. MyLake — A multiyear lake simulation model code suitable for uncertainty and sensitivity analysis simulations. *Ecological Modelling* 207: 45–60.

Tarvainen M., Ventelä A.-M., Helminen H. & Sarvala J. 2010. Selective removal fishing — water quality and practical viewpoints. *International Association of Theoretical and Applied Limnology Proceedings* 30: 1653–1656.

Shatwell T., Köhler J. & Nicklisch A. 2008. Warming promotes cold-adapted phytoplankton in temperate lakes and opens a loophole for Oscillatoriales in spring.

Global Change Biology 14: 2194–2200.

Straile D. 2000. Meteorological forcing of plankton dynamics in a large and deep continental European lake. *Oecologia* 122: 44–50.

Trolle D., Hamilton D.P., Pilditch C.A., Duggan I.C. & Jeppesen E. 2011. Predicting the effects of climate change on trophic status of three morphologically varying lakes: Implications for lake restoration and management. *Environmental Modelling and Software* 26: 354–370.

Wagner C. & Adrian R. 2009. Cyanobacteria dominance: quantifying the effects of climate change. *Limnology and Oceanography* 54: 2460–2468.

Ventelä A.-M., Kirkkala T., Lendasse A., Tarvainen M., Helminen H. & Sarvala J. 2011. Climate-related challenges in long term management of Säkylän Pyhäjärvi (SW Finland). *Hydrobiologia* 660: 49–58.

Ventelä A.-M., Tarvainen M., Helminen H. & Sarvala J. 2007. Long-term management of Pyhäjärvi (southwest Finland): eutrophication, restoration — recovery? *Lake and Reservoir Management* 23: 428–438.

White S.H., Duivenvoorden L.J. & Fabbro L.D. 2005. Impacts of a toxic Microcystis bloom on the macroinvertebrate fauna in Lake Elphinstone, Central Queensland, Australia. *Hydrobiologia* 548: 117–126.

Appendix. Annual phytoplankton biomasses (μg l^{-1}) in each study year.

Species	2001	2005	2008
Anabaena flos-aquae	0.9		
Anabaena sp.			2.3
Aphanothece stagnina	2.0		
Asterionella formosa			0.9
Aulacoseira italica	3.1		
Cryptomonas sp.		0.5	
Cyclotella radiosa		2.6	
Fragilaria crotonensis			0.8
Gloeotrichia echinulata	3.6		
Gymnodinium fuscum	1.2	0.9	
Mallomonas caudata	0.7		
Melosira varians		1.4	
Pedinella sp.		0.6	
Planktothrix agardhii		1.7	
Planktothrix sp.			12.9
Snowella lacustris	1.5		
Surirella robusta		0.8	1.0
Synedra acus			1.1
Synura sp.			0.7
Tabellaria flocculosa	6.6	1.3	1.2
Others	13.5	7.2	7.6
Total	33.1	17.0	28.5