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Climate Effects on Phytoplankton Biomass and Functional Groups

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Abstract

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Future climate in temperate regions is projected to get warmer and in many cases wetter. This poses questions about how phytoplankton in our lakes will respond. A dynamic modeling approach based on an allometric description of phytoplankton characteristics was used to investigate how the biomass of different functional groups of phytoplankton will respond to a changed future climate.

Simulations based on a warmer future climate scenario suggest that we will experience an increase in phytoplankton biomass in northern temperate lakes. Moreover, phytoplankton groups are projected to shift towards a dominance of cyanobacteria at the expense of diatoms.

Climate may affect phytoplankton, either via in-lake changes in temperature and stratification, or due to altered processes at the watershed level, which influence rates of nutrient export and water discharge. This study found that changes in lake temperature and stratification are the major causes of the projected increase in phytoplankton biomass, but that changes in the timing of nutrient export did influence the succession of diatoms.

Variation in SPIM (suspended particulate inorganic matter) can have an important role in influencing the depth of the euphotic zone in a turbid lake, and hence the light climate experienced by phytoplankton. Wind and river discharge were found to regulate SPIM in this study, not only wind as in many other studies. Variations in SPIM could be adequately described by a few governing equations.

This thesis suggests that, as a result of climate change, lakes close to the limit of becoming eutrophied may be pushed past a threshold beyond which water quality problems will become more prevalent. Finally it is important to bear in mind that all models are simplifications of the reality as we understand it. Still, the use of models can often give a good indication as to what might be expected in the future.

Keywords: Climate change, phytoplankton, chlorophyll a, Lake Mälaren, Galten, PROTBAS, numerical modeling, water quality, succession, shallow lake

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Till Max och Love

Cover photos: Phytoplankton bloom from below and Galten,
by Henrik Jacobson

List of papers

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals

- I Markensten H. Climate effects on early phytoplankton biomass over three decades modified by the morphometry in connected lake basins. (*Accepted by Hydrobiologia*)
- II Markensten H. & Pierson D.C. (2003) A dynamic model for flow and wind driven sediment resuspension in a shallow basin. *Hydrobiologia*, **494**, 305-311.
- III Pierson D.C., Markensten H. & Strömbeck N. (2003) Long and short term variations in suspended particulate material: the influence on light available to the phytoplankton community. *Hydrobiologia*, **494**, 299-304.
- IV Markensten H. & Pierson D.C. Weather driven influences on phytoplankton succession in a shallow lake during contrasting years. Application of PROTBAS. (*Manuscript*)
- V Markensten H., Moore K. & Persson I. Lake phytoplankton response to a future climate scenario – a model approach. (*Manuscript*)

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Contents

Introduction.....	9
Phytoplankton growth in relation to climate	9
Future climate simulation studies.....	11
Overview of phytoplankton model approaches.....	11
Aims of the thesis.....	14
Methods	15
Study site and data collection	15
Data collection.....	16
Climate scenario	16
The SPIM model.....	18
The PROTBAS model.....	18
Results and discussion	21
Phytoplankton response to a future climate	21
Simulation of phytoplankton in a changing environment	24
Conclusions and perspectives	27
Den globala uppvärmningens påverkan på alger i sjöar (Swedish Summary).....	29
Mängd och alggrupp påverkar vattenkvalitén	29
Modeller för att förutspå hur klimatförändringar påverkar våra sjöar	29
Mer alger och cyanobakterier med varmare klimat	30
Orsaker till en förändrad alg tillväxt och algsammansättning	30
Betydelse av resultaten – framtidsscenarioer och möjligheter att påverka vår framtida miljö.....	31
Acknowledgements.....	32
References.....	34

Abbreviations

A2	Future climate scenario (OBS modified by delta change)
CO ₂	Carbon dioxide
GCM	General Circulation Model
GWLF	Watershed model (Generalized Watershed Loading Functions)
N	Nitrogen
OBS	Observed period 1970-1990
P	Phosphorus
PIM	Particulate inorganic matter
PROBE	Physical lake model (PROgram for Boundary layers in the Environment)
PROTBAS	Phytoplankton model (PROTech Based Algal Simulations)
PROTECH	Phytoplankton model (Phytoplankton RespOnses To Environmental CHange)
Q	Discharge (m ³ s ⁻¹)
r'	Growth rate exponent
RCM	Regional Climate Model
s	Surface area (μm ²)
Si	Silica
SPIM	Suspended particulate inorganic matter
v	Volume (μm ³)
α _r	Slope of light dependent growth
ε	Light extinction coefficient (m ⁻¹)
β	Factor for temperature dependent growth
1D	One dimension
3D	Three dimensions

Introduction

This thesis will elaborate on a model-based approach to answer questions about how future climate will affect phytoplankton in temperate lakes. It includes constructing, improving and finally applying a phytoplankton model to a future climate scenario.

Phytoplankton growth in relation to climate

Climate change is a topic which has been given much attention the last decades. A projected warmer future climate all over the globe (IPCC, 2001) will have implications for both terrestrial and aquatic environments (Firth & Fisher, 1992; IPCC, 2001). Not only is temperature expected to change, but precipitation is projected to deviate from the present situation in many areas e.g. increase in northern Europe (Räsänen et al., 2003a). Long term studies have shown that important factors for phytoplankton growth are water temperature, stratification, ice cover, discharge and nutrient loading (Fee et al., 1992).

As might be expected, higher air temperature has caused increased water temperatures in boreal lakes during all seasons of the past decades (Scheffer et al., 2001; Gerten & Adrian, 2002). Lake thermal structure determines the mixed depth that is important in influencing the light climate experienced by phytoplankton (Ramberg, 1979) as well as nutrient availability, which will influence the success and dynamics of different phytoplankton functional groups (Talling, 1971; Reynolds, 1987, 1992).

Increased air temperature will obviously influence ice break up positively. Many North American and North European lakes lose ice cover around 2 weeks earlier as a result of a 1 °C increase in winter air temperature (Gerten & Adrian, 2002). Early ice break-up has resulted in higher phytoplankton biomass in June-August (Blenckner, Pettersson & Padisák, 2003) and earlier spring bloom (Weyhenmeyer, Blenckner & Pettersson, 1999). Once the ice cover is gone, thermal stratification can develop earlier, which favors vertically migrating species (e.g. *Gloeotrichia echinulata* and *Microcystis* sp.) that often develop and dominate in summer.

Besides the influence from the length of ice cover, the length of snow cover on the ground and lake ice has implications for phytoplankton growth through the influence on discharge, nutrient load, and light transmission

through ice cover. Increased air temperature and precipitation over three decades in Finland resulted in decreased snow cover and increased winter runoff (Bouraoui et al., 2004). A shift towards higher winter runoff and lower spring runoff caused a slight overall increase in the contribution of solutes, sediments and nutrients (nitrogen and phosphorus) from diffuse sources (Bouraoui et al., 2004). However, it is important to consider the timing of nutrient transport since high loads in winter may result in comparatively less phytoplankton growth due to the light and temperature constraints in winter. The effect on the phytoplankton varies from case to case since many counteracting factors may act simultaneously. I summarize the different factors influencing phytoplankton growth from a climate perspective in a conceptual model (Fig. 1).

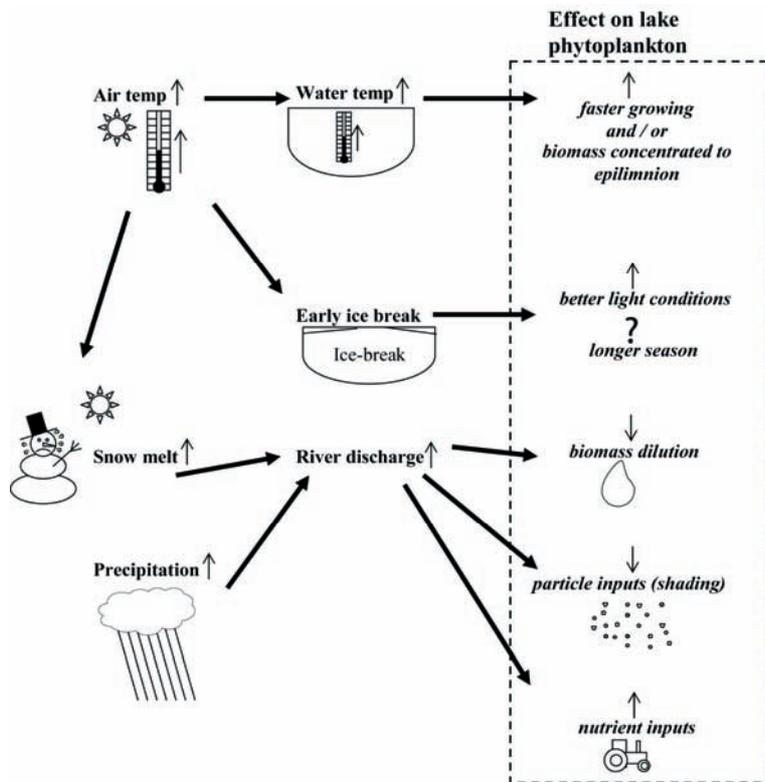


Fig. 1. A conceptual model summarizing effects of increasing air temperature and precipitation on water temperature, ice break-up, snowmelt, river discharge and how these factors can influence phytoplankton biomass.

Future climate simulation studies

The response of phytoplankton to climate change has been studied using general circulation models (GCM) to drive lake models predicting phytoplankton (Hassan, Hanaki & Matsuo, 1998; Frisk et al., 1999; Hamilton et al., 2002). Phytoplankton biomass are projected to stay unchanged (Hamilton et al., 2002) or increase slightly (Frisk et al., 1997; Hassan et al., 1998) on an annual basis (for details see discussion in **paper V**). However, it was difficult to interpret the results since simulations covered a short time period (3 years) (Frisk et al., 1997; Hamilton et al., 2002) which may not capture all the variability that could be expected from longer studies (>20 years). Furthermore, in the modeled oligotrophic lake (Hamilton et al., 2002) it can be expected that the phytoplankton will be limited by other factors e.g. nutrients, which could mask a response to climate change. To bridge the gap in time, trophic state, and resolution in phytoplankton groups, I will use 21 years in a eutrophic lake focusing on three functional phytoplankton groups (See Methods, and **paper V**).

Overview of phytoplankton model approaches

Water authorities have long understood that the reduction of nutrients can lead to improved water quality. To better predict the effects of nutrient management programs, different water quality models targeting phytoplankton biomass have been created and used. Statistical steady-state empirical models have been widely used (Vollenweider, 1968; Dillon & Rigler, 1974; Schindler, Fee & Ruscynski, 1978; OECD, 1982). These empirical models make use of a regression between phytoplankton and total phosphorus in lakes. The strength is that they are easy to use. However, there is a high degree of uncertainty in the prediction of phytoplankton biomass, since data used for the regressions are log transformed. No estimate on the biomass of specific functional groups or species is given from the prediction.

Neural network models are another type of empirical model that is dynamic in the sense that it calculates phytoplankton biomass depending on the conditions of the preceding time step. They make use of a flexible algorithm that changes to best fit the calibration data and have been used to predict phytoplankton primary production (Scardi & Harding Jr, 1999), cyanobacteria concentration (Recknagel, 1997), and phytoplankton succession (Olden, 2000). The advantage of the neural network models is that, given a sufficient training data set, they may predict phytoplankton biomass very well. The drawback is that the results are not based on any underlying process governing phytoplankton growth, which means that the results need to be interpreted carefully (Whitehead, Howard & Arulmani, 1997). The lack of underlying process is a problem if the environment is changing, e.g. due to in-

creasing global temperature. In such cases, the training data set may not be valid for the new conditions. Moreover, this type of computationally intensive model tends to be managed and evaluated by experts in these algorithms.

A third type of model is the process based mass balance model, which attempts to describe the processes underlying the growth of e.g. phytoplankton. Examples of early versions of process based models describing nutrient and phytoplankton interaction and cycling in a lake are the Glumsø-model (Jørgensen, Mejer & Friis, 1978; Jørgensen et al., 1986a), EAWAG-model (Imboden & Gächter, 1978), SALMO-model (Benndorf & Recknagel, 1982; Recknagel, 1985) and more recent LakeWeb-model and LEEDS-model (Boulion & Håkanson, 2003; Malmaeus & Håkanson, 2004). The strength of these models is that their mechanistic description of processes makes it easier to understand the coupling of climate to processes and to adapt the models to changes in environmental conditions e.g. temperature regime. These models use a time resolution of weeks or months, which makes them useful to predict trends over years or even seasons. An additional advantage is that it is relatively easy to get access to validation data from monitoring programs that often run at similar time scales. With a vertical representation that is often restricted to epilimnion, hypolimnion, and sediment they may sufficiently describe many processes in a lake. However, these models may not capture events occurring on the scale of days such as sedimentation of heavy diatoms, effects from sudden rainstorms, etc.

For studies of the timing of phytoplankton blooms and succession of functional groups more detailed models with high temporal resolution (≤ 1 day) and vertical resolution (≤ 1 m) have been used, e.g. the DYRESM Water Quality-model (Hamilton & Schladow, 1997) and the DyLEM-1D-model (Bonnet & Poulin, 2004). At the extreme end of the spectrum are models using 3D representation of lakes, producing very detailed results e.g. the ELMO-model (Bonnet & Wessen, 2001). The obvious advantages with these models are that more details can be predicted and short time dynamics can be studied. However there are also disadvantages such as the expense of, and need for experts running them, that many parameters needs to be determined, and finally that a high temporal and spatial resolution is required in the validation data sets.

One way to reduce the number of model parameters in phytoplankton modeling is to adopt an allometric approach, in which key processes can be linked to phytoplankton size and shape that describes functions for temperature dependence, nutrient uptake, light absorption, settling and grazing rates. Allometric determined growth functions have been used to model phytoplankton in size ranges 0.4-25 μm (Gin, Guo & Cheong, 1998) and with a dynamically changed model that allowed for both phytoplankton and zooplankton succession (Jørgensen et al., 2002). The PROTECH model uses a 1D lake representation (0.1 m layers) combined with an allometric approach

for predicting the daily concentration of phytoplankton (Reynolds, Irish & Elliott, 2001). The PROTBAS model used in this thesis is derived from the description of PROTECH. It shares the allometric approach and uses the same behavioral characteristics of some phytoplankton groups, which define their means of moving in the water column, and acquiring nutrients.

Aims of the thesis

The aims of the thesis are:

1. To elucidate how phytoplankton functional groups and biomass respond to a future climate.
 - Will the total yearly biomass change?
 - Will the timing of phytoplankton growth and succession change?
 - Will the extent of growing season in lakes change?
 - Will the abundance of potential nuisance groups such as cyanobacteria change?
 - What are the mechanisms behind changes in phytoplankton biomass and composition?
 - Will the changes in water temperature or river discharge be most important for the future pattern of phytoplankton abundance?
2. To resolve what is needed from a phytoplankton model to satisfactorily simulate phytoplankton biomass and composition in a changing environment.
 - How can we in modeling handle lakes having a highly variable light climate?
 - Do we really need a model capable of describing phytoplankton vertical movements in a frequently mixed lake?
 - Do we need to care about nutrient regeneration in a flushed lake?
3. To reconstruct and adapt the phytoplankton model PROTECH, which uses an allometric approach, to a northern temperate lake.

Methods

Study site and data collection

This study was conducted in the temperate Lake Mälaren in Sweden (**paper I**) (Fig. 2), which can be divided into different subbasins. The basins covered in this work are characterized in Table 1. The primary focus has been on Galten, the western basin of Lake Mälaren (59°27'N, 16°11'E) (**paper II, III, IV and V**) that is polymictic, and eutrophic (Willén, 2001b). The Galten basin is flushed, shallow, and wind exposed due to the low topography of the surrounding land. Galten is fed by four rivers draining an area of 8508 km² primarily covered with forest (55%) dominated by coniferous species, lakes and watercourses (10-15%) and to a lesser extent farmland (10%).



Fig. 2. Map over Lake Mälaren in Sweden showing selected subbasins. Filled circles denote sampling locations.

Table 1. Selected subbasins of Lake Mälaren. Modified from Håkanson (1979), Wallin (2000), Lemming, Lindell & Kvarnäs (1971) and Willén (2001b)

	Galten	Blacken	Björkfjärden- Prästfjärden	Ekoln	Skarven	Görvåln
Volume (km ³)	0.210	0.953	6.678	0.458	0.409	1.716
Lake Area (km ²)	61.2	96.7	339	29.8	43.4	134.8
Average depth (m)	3.4	9.9	19.7	15.4	9.4	12.7
Retention time (year)	0.07	0.2	1.4	0.56	0.46	0.4
Total phosphorus (µg l ⁻¹)	50	—	22	55	—	—
Total nitrogen (µg l ⁻¹)	870	—	625	1920	—	—
Phytoplankton (mm ³ l ⁻¹)	3.9	—	0.6	1.3	—	—

Data collection

Water samples were collected weekly or biweekly during two years (1999-2000) to be used for model calibration and validation. Standard chemical analyses and phytoplankton biovolume counts (**paper II, III and IV**) were performed together with analyses of suspended particulate inorganic matter (SPIM) (**paper II and III**) and the light extinction coefficient (ϵ) of PAR (Photosynthetically Active Radiation) (**paper III**). On site wind speed, water temperature (**paper II, III and IV**) and under water beam attenuation at 660 nm were recorded within the lake basin (**paper II and III**). Water quality data for rivers and lake basins were available from an online database (<http://info1.ma.slu.se/db.html>) provided by Department of Environmental Assessment, Swedish University of Agricultural Sciences and Mälarens vattenvårdsförbund (**paper I and IV**). Stream discharge and meteorological data were acquired from the Swedish Meteorological and Hydrological Institute (SMHI) (**paper I, IV and V**).

Climate scenario

To drive the lake and watershed models during the observation period (1970-1990) two different sets of meteorological data were used both provided by (SMHI). A high resolution grid (4x4 km²) was used for the GWLF model (Johansson & Chen, 2003) and a more coarse resolution grid (110x110 km²) was used for the lake models (PROBE and PROTBAS) (http://www.smhi.se/sgn0102/bhdc/metdata_3h_grid.htm) (**paper V**).

Modeled present and future climate were taken from regional climate model output (RCAO-H) forced by the general circulation model HadAM3H (Räisänen et al., 2003b). For the future climate I used scenario A2 assuming

a doubling of the present carbon dioxide concentration in the atmosphere in approximately 100 years (IPCC, 2001). The "delta change approach" was used to create the driving data for scenario A2 (Hay, Wilby & Leavesley, 2000; Andréasson et al., 2004). From now on I refer to the observed period (1970-1990) as OBS and scenario A2 as A2 (OBS modified by delta change) (**paper V**).

In **paper V** I use the forcing data from OBS and A2 scenarios to project biomass of phytoplankton functional groups from using three models in a sequence: PROBE, GWLF and PROTBAS (Fig. 3).

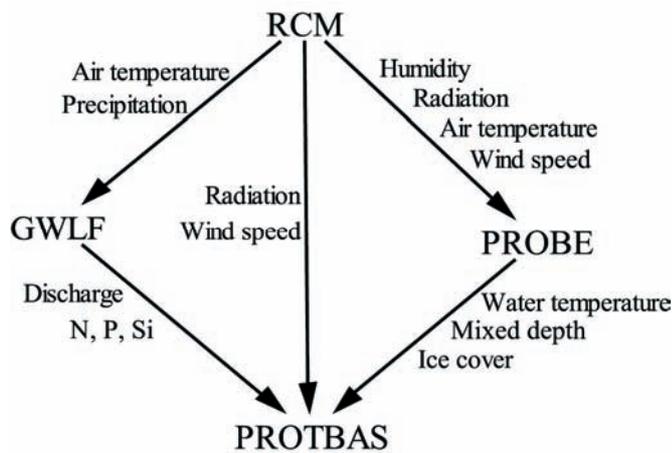


Fig. 3. Flow-chart showing the sequential use of RCM (regional climate model), watershed model (GWLF), physical lake model (PROBE) and biological lake model (PROTBAS) and their driving data requirements.

To further separate the direct effect of climate change on phytoplankton through lake physical properties, and the indirect effects acting through watershed processes regulating nutrient loads, two additional sets of simulations were run (Table 2) (**paper V**).

Table 2. Combinations of driving data used for simulations with the phytoplankton model PROTBAS.

Simulation	Lake model (PROBE) driving data	Watershed model (GWLF) driving data
OBS	OBS	OBS
A2	A2	A2
OBS+A2 nutrients	OBS	A2
A2+OBS nutrients	A2	OBS

The SPIM model

The model presented in **paper II** to determine SPIM concentration (g m^{-3}) consists of three state variables that conserve mass between each time step: particulate inorganic matter (PIM) from the catchment forced by discharge (Q), PIM available for resuspension by wind, and the suspended PIM (SPIM) (Fig. 4). PIM moves between the different state variables in a rate determined by optimization of the two rates "Resusp" (ton day^{-1}) and "PIM in" (ton day^{-1}) against high frequency (10 minute) data from the lake (**paper II**). The model is used as a submodel to PROTBAS to determine the light extinction coefficient (ϵ) (**paper IV**). In **paper III** the modeled SPIM concentration was used in a model that predicts the spectral variations in subsurface light and to estimate PAR.

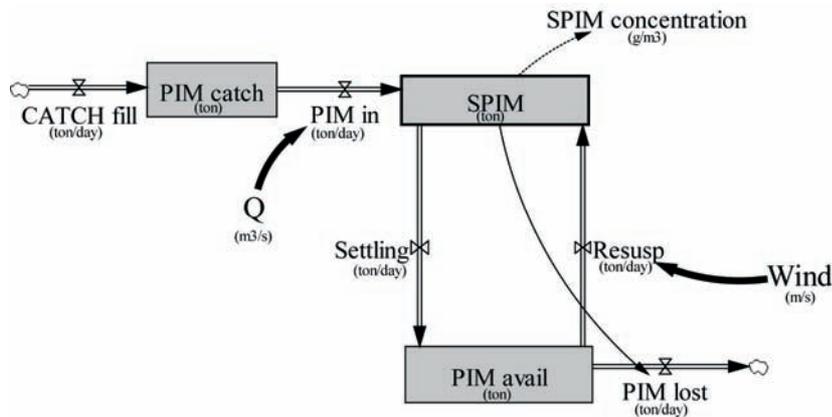


Fig. 4. A sketch of the SPIM model applied in the Galten basin of Lake Mälaren.

The PROTBAS model

PROTBAS (PROTech Based Algal Simulations) is a model, which is used in **paper IV and V**, and is based on the PROTECH model (Reynolds et al., 2001). The PROTBAS model calculates the daily increase in biomass of each phytoplankton species, measured as chlorophyll a . The growth rate for phytoplankton (A) is given by:

$$A_t = A_0 \times e^{r't} \quad (\text{g}) \quad (1)$$

where A_0 is the initial biomass, A_t is biomass after time t , r' is the growth rate (day^{-1}), and t is the time interval between A_0 and A_t . Since the PROTBAS model has a time step of 1 day, the model calculated change in A is in the units of g day^{-1} .

Including losses the daily change in biomass measured as chlorophyll *a*, ΔB (g), is given by:

$$\frac{\Delta B}{\Delta t} = A - \text{SETTLING} - \text{GRAZING} - \text{RESPIRATION} \quad (\text{g day}^{-1}) \quad (2)$$

where SETTLING is the loss due to settling out of the water column (g day^{-1}), GRAZING the loss due to grazing (g day^{-1}), and RESPIRATION the loss due to respiration (g day^{-1}).

The growth rate exponent, r' is adjusted for temperature and light limitation and will be zero (no growth) if any of the nutrients required by the specific phytoplankton are absent in the water column (Fig. 5). To calculate phytoplankton growth rate exponent I used a standard replication rate at 20 °C (r'_{20}) for each phytoplankton “species” determined from the surface area to volume ratio (s/v) of the phytoplankton. The r'_{20} is temperature corrected by a factor (β), which also depend on s/v , and becomes $r'_{(t)}$. If phytoplankton is light limited I make use of the calculations in the shaded area of Fig. 5 where the central calculation is the experimentally derived slope of light dependent growth (α_r). The α_r is obtained from phytoplankton s/v and the longest dimension of the phytoplankton measured in μm (M). The central concept in the PROTECH and PROTBAS model is the use of phytoplankton length, surface area and volume to obtain the two parameters, α_r and β for each of the modeled phytoplankton “species” (**paper IV**) (Reynolds et al., 2001).

The calculation of the temperature and light corrected growth rate exponent ($r'_{(t,l)}$) differs in PROTBAS from that used in PROTECH. In the new formulation the light limited growth rate will not be limited by temperature at all. This is a result of my assumption that when phytoplankton are not light saturated, pigment content, pigment packaging size, and shape of the phytoplankton will be of greater importance than e.g. temperature dependent enzyme activities. The assumption is important especially in turbid water where a significant share of the phytoplankton growth is occurring at low light levels. Another important adaptation of PROTBAS to the turbid lake basin is that the light extinction is calculated from a combination of the SPIM submodel and the chlorophyll *a* concentration (Fig. 5) (**paper IV**).

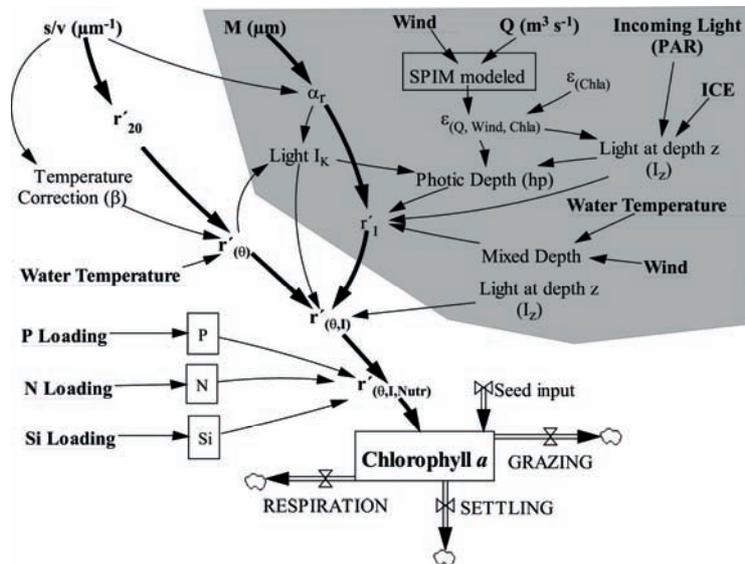


Fig 5. A conceptual outline of how each phytoplankton group at each depth in the lake is calculated through the modification of the replication rate (r'). The shaded grey area concerns light dependent growth. Boxes are state variables in the models which conserve the mass between time steps.

Results and discussion

Phytoplankton response to a future climate

The main results from this work suggest that the phytoplankton biomass in northern temperate flushed shallow lakes will increase in response to a warmer future climate (2xCO₂, A2 scenario) (Fig. 6) (**paper V**). Future projections show that the phytoplankton growing season will start earlier, which is consistent with historical observations (Weyhenmeyer et al., 1999), and end later (**paper V**). As a consequence the growing season is expected to increase by approximately three weeks. The projected increase in phytoplankton biomass was supported by results from other future climate simulation studies (Frisk et al., 1997; Hassan et al., 1998), which is discussed in **paper V**. The increased phytoplankton biomass was a result of the projected shorter ice cover period and increased lake stability, a modeling result supported by observations from many lakes in America and Europe (Schindler et al., 1990; Gerten & Adrian, 2002) and simulation studies (Frisk et al., 1997). A sensitivity test of the parameter describing the temperature dependence (β) in the phytoplankton growth function did not change the direction of the results (**paper V**).

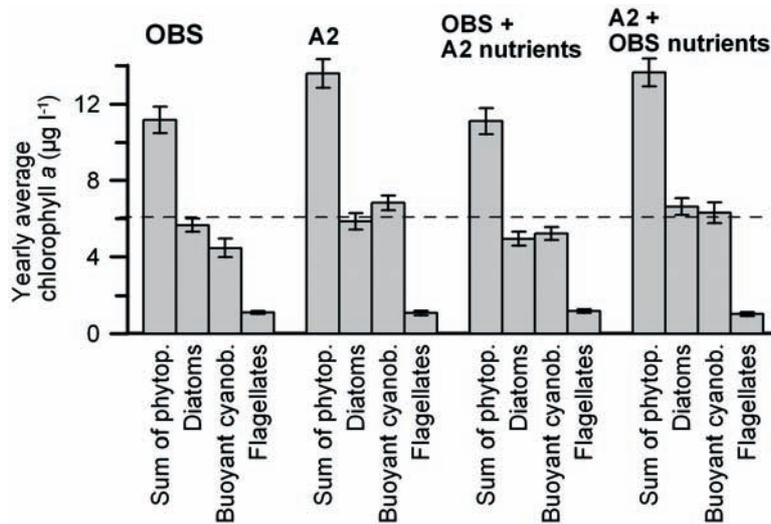


Fig. 6. Simulated yearly average chlorophyll *a* from four combinations of input data in Galten basin, Lake Mälaren. OBS=observed data, A2=future projections, OBS+A2 nutrients=OBS weather with discharge and nutrient load from A2, A2+OBS=A2 weather with discharge and nutrient load from OBS. The 95% confidence interval from 21 years as error bars. Dashed horizontal lines are help lines for comparing overlapping of error bars.

The projected change in phytoplankton biomass was divided into three functional groups based on their nutrient requirements and characteristic movements in response to light and nutrient concentrations (Elliott, Irish & Reynolds, 2002) that form a successional strategy (**paper IV**). The first group is dominated by buoyant cyanobacteria with the ability to fix nitrogen (N) and regulate their vertical position in the water column i.e. these can only be nutrient limited by phosphorus (P). The second group, diatoms, tends to sink and require silica (Si) in addition to N and P for growth. The third group is composed of flagellates capable of moving up and down in the water column, and is potentially growth limited by N and P.

The greatest increase in biomass for the future scenario was found for buoyant cyanobacteria which increased in all months of the year (**paper V**). These findings are in line with results from historical studies (Adrian et al., 1995; Adrian & Deneke, 1996) and future projections (Hassan et al., 1998). In **paper V** it is suggested that one reason for the cyanobacteria success is a projected longer growing season and higher stability, which leads to an increase in the number of days when the lake is thermally stratified. A stratified lake allows the cyanobacteria to move to favorable light intensities and cross the thermocline to areas of higher nutrient concentrations (Reynolds et al., 2001). Another important factor that favors the cyanobacteria group is the ability to fix nitrogen. As the growing season increases, N, P and Si con-

centrations fall to low levels and cyanobacteria are comparatively better off since only P may be limiting (**paper V**).

The diatom group showed an opposite pattern in that it decreased in the future scenario for the months June through September (**paper V**). In the model, diatoms are characterized by good ability to survive low light conditions, but are dependent on external physical forcing (wind) to stay in the water column (Reynolds et al., 2001). The higher frequency of stratification in the future scenario was unfavorable for the heavy diatoms that sunk out of the euphotic zone. This was shown, both in model simulations and by phytoplankton counts, during two weekly stratification events during 1999 (**paper IV**). Another important constraint for the diatoms is their dependency on silica, which in future climate simulations can be depleted earlier due to an earlier start of phytoplankton growth. One may argue that phosphorus would be depleted as quickly as silica, which may be true over short time scales (hours-days). But the regeneration time for phosphorus is two orders of magnitude higher than for silica in the model, as used by other modeling studies for silica (Bowie, Mills & Porcella, 1985; Krivtsov, Sigee & Bellinger, 2001) and phosphorus (Jørgensen, Kamp-Nielsen & Jørgensen, 1986b), leading to a greater shortage of silica over longer time periods (months) (**paper IV**).

The last simulated group of phytoplankton was flagellates. They displayed a low biomass through all simulations and did not show much change in the future projection (**paper V**). The main reason for the low biomass was probably due to the small size of the flagellates ($< 50 \mu\text{m}$) making them susceptible to grazing, and the fact that the lake was frequently mixed, which lowered the comparative advantage of vertical migration. In contrast, flagellates increased in abundance in a less mixed environment subjected to a raised temperature (Strecker, Cobb & Vinebrooke, 2004).

In the projected future scenario I could see a shift in the yearly dominance of diatoms to dominance by buoyant cyanobacteria (**paper V**) in line with earlier findings (Adrian et al., 1995; Adrian & Deneke, 1996) and assumptions (Blenckner, Omstedt & Rummukainen, 2002). From simulations which selectively manipulated input data from the watershed model and the physical lake model, it was shown that future climate effects on lake physical properties such as lake temperature, stratification and growing season were the major reason for the increased future phytoplankton biomass. My suggested in-lake causes for the projected increase in future phytoplankton biomass differs from watershed related causes assumed by e.g. Schindler et al. (1990) based on historical data. It was difficult to see any effect from the modest projected increase in nutrient loading, which may be due to changes in the seasonal pattern of nutrient loading with lower summer discharge followed by higher discharge in the less productive winter months. Among the different functional groups, the cyanobacteria were most favored by changes in lake mixing and temperature, but the lower nutrient load during summer

also favored the cyanobacteria that can continue to grow when lack of nitrogen limits the other phytoplankton groups (Fig. 6).

As shown in other studies (Gerten & Adrian, 2000), increased temperature in winter and spring was followed by an increase in spring phytoplankton biomass (**paper I**). In **paper I** I suggest that increasing temperature will enhance the May chlorophyll *a* concentration not only in the flushed shallow basin, but also in deeper basins with longer retention time.

Simulation of phytoplankton in a changing environment

When modeling phytoplankton in turbid lakes with high light extinction, getting a good estimate of the light available for growth is very important. In **paper III** it was shown that the effect of suspended inorganic matter (SPIM) on the light climate may be significant. Many studies have modeled sediment resuspension in lakes from wind (Teeter et al., 2001). However, I have not found any model using both river inflow and wind to predict suspended matter, even if the mechanism has been suggested (Hawley & Lesht, 1992; Bloesch, 1994). I show in **paper II** that the SPIM concentration in a flushed shallow lake basin could be successfully simulated from wind speed together with river discharge (Fig. 7). The topic of underwater light was also one of the targets in **paper IV**. I improved rules and equations for phytoplankton utilization of light to better capture the factors that regulate light-limited growth in response to the turbid water of the modeled lake basin (**paper IV**).

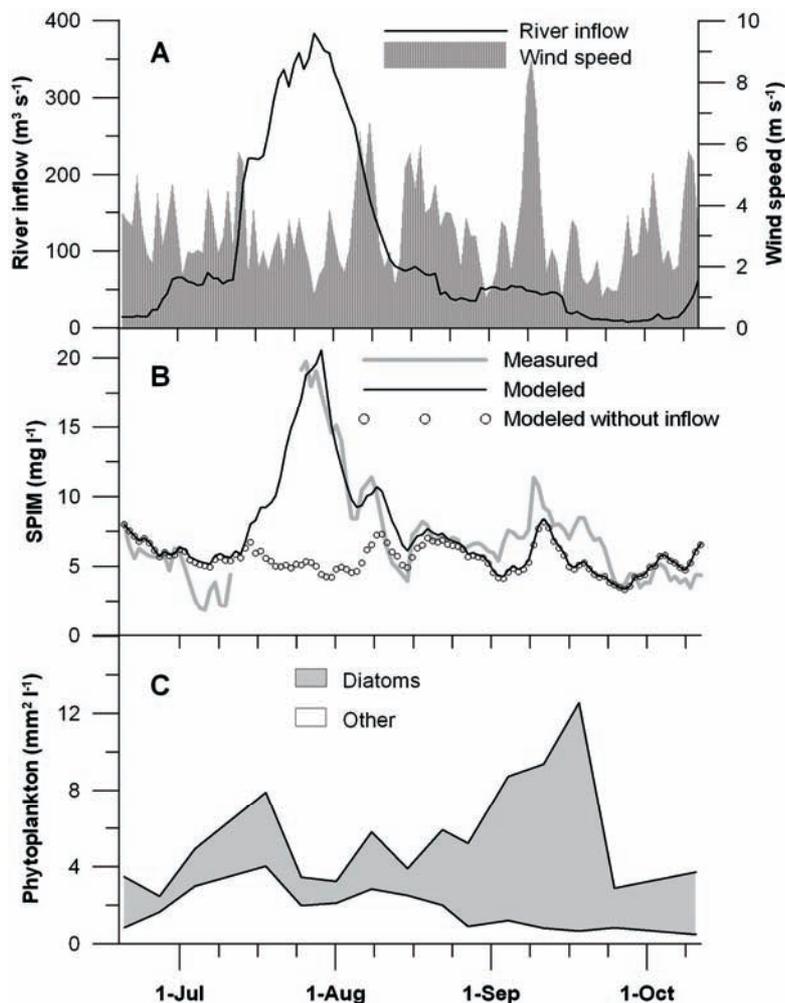


Fig. 7. A. Wind speed (at 13 m) and river inflow in western Lake Mälaren during year 2000. 7 B. Measured and modeled suspended particulate inorganic matter (SPIM). Circles indicate a simulation where river inflow was not included. 7 C. Biomass of phytoplankton calculated from weekly microscope counts.

A lake basin that is frequently mixed may for modeling purposes be viewed as a mixed reactor (no vertical dimension) which will simplify model formulation and calculations. This is appropriate if the aim is to estimate the bulk chlorophyll *a* in the lake, such as the approach used by Vollenweider (1968), but it is not enough to describe the succession of phytoplankton functional groups over the season. Results from **paper IV** and **V** clearly show that even if stratification events were scattered over the season they significantly influenced the phytoplankton succession in favor of buoyant cyanobacteria. Heavy diatoms sink out of the euphotic zone and will consequently grow slower than the buoyant cyanobacteria close to the water surface. This dem-

onstrates the need for a vertical dimension when simulating functional groups of phytoplankton, even in a frequently mixed basin.

In a flushed lake that continuously receives nutrients from river discharge it was important to describe nutrient regeneration to balance phytoplankton growth adequately (**paper IV**). I added algorithms for regeneration of N, P and Si to the model in order to balance the nutrient budget during long periods of low discharge.

Conclusions and perspectives

The main results of the papers presented in this thesis can be summarized as follows:

1. A simulations based on a warmer future climate scenario suggest that we will experience an increase in phytoplankton biomass in northern temperate lakes. Moreover, the phytoplankton groups are projected to shift towards a dominance of cyanobacteria at the expense of diatoms.
2. Climate may affect phytoplankton, either via in-lake changes in temperature and stratification, or due to altered processes at the watershed level, such as precipitation and temperature driven rate of nutrient export and water discharge. This thesis demonstrates that the changes in lake temperature and stratification are causing the projected increase in phytoplankton biomass. However, projected changes in the timing of nutrient export from the catchment did influence the succession of diatoms.
3. Variation in SPIM can have an important role in influencing the depth of the euphotic zone in a turbid lake, and hence the light climate experienced by phytoplankton. In this study wind and river discharge are of significant importance for the suspended sediment concentration, not only wind as in many other studies. The variation in SPIM can adequately be described by a few governing equations.

This study suggests that lakes which are already close to the limit of becoming eutrophied may be pushed past a threshold beyond which the water authorities and public will experience increased water quality problems. In addition great amounts of phytoplankton decomposing will increase the risk of anoxia in lakes, further enhancing eutrophication by phosphorus leakage from sediments. Toxins, but also foul taste and odor caused by high concentrations of algae can also affect the quality of drinking water and the cost of producing it (Wnorowski, 1992; Chorous & Bartram, 1999).

This study projects that buoyant cyanobacteria including potential toxin producing species will become more abundant. The presence of toxin producing species in Lake Mälaren, which was investigated in this thesis, has already been confirmed (Willén, 2001b). The knowledge that phytoplankton

and especially cyanobacteria biomass are expected to increase in the future is one of many factors that managers need to consider when planning for the need of future drinking water purification. With increased biomass of buoyant cyanobacteria there is also a greater risk for water blooms that will negatively affect the recreational value of lakes. In Lake Mälaren many remedial measures have already been taken, which has greatly improved the present water quality compared with three decades ago (Willén, 2001a). The projected eutrophication effect from climate change will need to be counteracted, e.g. by reduction of nutrient loading, if the lake water quality is to remain at present levels.

An interesting continuation of this research would be to use the regional gradient in the future projected climate (Räisänen et al., 2003b) to assess the local effect on the lake phytoplankton community. This could range from north to south in Scandinavia and Europe. Such an approach opens new possibilities to adapt water management strategies and remedial measures for the local authorities, since sometimes catchments processes may dominate over in-lake processes and vice versa.

Another modeling application could be as a tool in planning the management of water reservoir systems such as: when to empty or fill a reservoir, what water level should be maintained to avoid unwanted phytoplankton groups, and at what frequency should it be artificially de-stratified (Lewis et al., 2002).

A future task would be to test the climate effect over different gradients, e.g. the retention time or length and strength of summer stratification. It would then be easier to generalize and interpret the results on different types of lakes. Such a modeling attempt was made to compare lakes with varying retention times in the context of climate change and phosphorus internal loading (Malmaeus et al., in press).

Finally, there are a number of technical improvements from which the PROTBAS model would benefit. One possible improvement is to integrate the model into a hydrodynamic model such as PROBE that could get feedback on light extinction derived from chlorophyll *a*. Another improvement might be incorporating a description of nutrient cycling between different states in oxic and anoxic environments. Additionally, revision of the temperature dependence and respiration in the model might improve the timing of phytoplankton spring burst and autumn decline.

Den globala uppvärmningens påverkan på alger i sjöar (Swedish Summary)

Denna avhandling handlar om hur framtida klimatförändringar kan komma att påverka mängden och vilka sorters alger som kommer att finnas i våra sjöar. I avhandlingen har jag konstruerat en datormodell som beskriver algers tillväxt i sjöar. Datormodellen har jag sedan använt för att förutspå effekter av framtida klimatförändringar.

Mängd och alggrupp påverkar vattenkvalitén

”Alg-soppa” i badvikar, vid båtplatser och i fiskevatten upplevs av de flesta som avskräckande och störande. Mängden alger i en sjö kan alltså göra sjöar mindre attraktiva för rekreation och turism, dessutom kan den orsaka problem för våra vattenverk. Efter många svarta rubriker med larm om blommande giftalger är de flesta väl införstådda med att vilken typ av alger (växtplankton) som växer påverkar vad vi kan använda sjövattnet till. Framför allt djur och barn, men också vuxna kan bli skadade av gifter (toxiner) från ”blågröna alger”, även kallade cyanobakterier. Dessa gifter kan också utgöra problem för vattenverken där ytvatten används för dricksvatten. Alger kan vidare göra att vattnet smakar och luktar illa. När stora mängder alger dör och bryts ned kan det bli syrebrist i sjön, vilket kan leda till fiskdöd.

Flera studier av alg tillväxt över längre perioder (20-30 år) visar att några grader varmare vatten ger både mer alger och påverkar vilka alger som växer mest och snabbast. Det innebär att den globala uppvärmning som förutspås kan förväntas påverka den framtida vattenkvalitén och vad vi kan använda vårt sjövattnet till.

Modeller för att förutspå hur klimatförändringar påverkar våra sjöar

Sedan länge har myndigheter med ansvar för vattenkvalitén känt till betydelsen av att försöka minska näringsutsläpp i våra sjöar. För att kunna hålla en god vattenkvalité har modeller som kan förutspå effekter av olika utsläpp och näringsläckage utvecklats. Men problemet hittills har varit att få tillräcklig säkerhet i vilka grupper av alger som växer till. Det är också svårt att få med snabba förändringar, till exempel plötslig och stark vind eller kraftiga regn

som kan ha stor betydelse för vilka alger som klarar sig bäst i sjön. I denna avhandling har jag använt en modell som kan ge goda förutsägelser både av olika grupper av alger, och hur de varierar över tid. Hänsyn tas också till framtida förutsägelser om klimatförändringar i just den studerade sjön. Datormodellen (PROTBAS) är en vidareutveckling av en brittisk algmodell (PROTECH). Jag har utvecklat och testat modellen i västra delen av Mälaren utifrån intensiva mätningar som pågått under två år. För att utvärdera om modellen fungerar har jag tagit vattenprover och mätt upp vilka näringsmängder det innehåller och samtidigt gjort vädermätningar. Jag har sedan använt SMHI:s klimatmodell som förutspår ett möjligt väder ca 100 år framåt i tiden. Klimatmodellen visar att medeltemperaturen och nederbörden kan förväntas stiga. Slutligen använder jag "framtidsvädet" för att göra förutsägelser om hur vår vattenkvalité kan tänkas se ut i framtiden.

Mer alger och cyanobakterier med varmare klimat

De flesta forskare är inställda på att vi kommer att få en global uppvärmning. Med detta som utgångspunkt har forskare gjort olika modeller för att se vilka konsekvenser en global uppvärmning kan leda till. Min modell förutspår att mängden alger i våra sjöar troligen ökar, vilket kan ge försämringar av kvalitén på vattnet i redan övergödda sjöar. Den visar också att det framförallt är blågröna alger (cyanobakterier) som förväntas öka, varav några kan vara giftproducerande. Också tillväxten av andra alger till exempel kiselalger förväntas öka, men inte lika mycket. Man måste dock vara medveten om att alla modeller är kraftiga förenklingar av verkligheten så som vi idag förstår den. Trots det kan användandet av modeller ofta ge en bra fingervisning om vilka problem som kan tänkas uppstå och utforska orsakssamband.

Orsaker till en förändrad alg tillväxt och algsammansättning

Det som verkar påverka hur mycket och vilka alger som dominerar i framtiden är förhöjd vattentemperatur som i sin tur leder till ökad skiktning, samt ett förändrat näringsinflöde till sjön från åar. Vissa cyanobakterier kan påverka hur nära de befinner sig ytan och därmed få bättre ljus att växa i. Därför gynnas de av skiktningen i sjöarna, på bekostnad av alger som sjunker till botten när sjöar skiktas.

Med varmare lufttemperatur blir vattnet varmare och isen ligger kortare tid på sjöarna eller till och med uteblir. Sjöar utan is eller där islossningen kommer tidigt ger bättre ljusförhållanden nere i vattnet och därmed en längre växtsäsong för algerna. Varmare klimat ger också minskade snötäcken, vilket tidigarelägger och minskar vårfloden. Detta tillsammans med en ökad nederbörd gör att mer av näring från åar kommer till sjön under vinterhalvåret, samtidigt som åflödet och medföljande näring minskar till sjöarna under det ännu varmare sommarhalvåret. Mindre inflöde av kisel till sjön under

sommaren gör att det tidigare under växtsäsongen blir kiselbrist i sjön och att de kiselberoende algerna (kiselalger) minskar och ger plats för till exempel blågröna alger (cyanobakterier).

Betydelse av resultaten – framtidsscenarier och möjligheter att påverka vår framtida miljö

Vi är beroende av god vatten kvalitet i våra sjöar ur rekreationssynpunkt, men också för ett tjänligt dricksvatten och för att bedriva yrkesfiske. Med modeller, som kan göra förutsägelser om hur mycket och vilka typer alger som kan komma att växa, samt där hänsyn tas till regionala klimatförändringar, kan politiker, naturvårdande myndigheter men också lokala vattenverk få redskap för att planera vilka insatser som behövs göras för att upprätthålla en god vattenkvalité i framtiden. Tillämpningen av min modell (PROTBAS) är en bra bit på vägen för att vi ska kunna klara av sådana uppgifter.

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