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The effect of irradiance, vertical mixing and temperature on spring phytoplankton dynamics under climate change: long-term observations and model analysis

Katrin Tirok · Ursula Gaedke

Abstract Spring algal development in deep temperate lakes is thought to be strongly influenced by surface irradiance, vertical mixing and temperature, all of which are expected to be altered by climate change. Based on long-term data from Lake Constance, we investigated the individual and combined effects of these variables on algal dynamics using descriptive statistics, multiple regression models and a process-oriented dynamic simulation model. The latter considered edible and less-edible algae and was forced by observed or anticipated irradiance, temperature and vertical mixing intensity. Unexpectedly, irradiance often dominated algal net growth rather than vertical mixing for the following reason: algal dynamics depended on algal net losses from the euphotic layer to larger depth due to vertical mixing. These losses strongly depended on the vertical algal gradient which, in turn, was determined by the mixing intensity during the previous days, thereby introducing a memory effect. This observation implied that during intense mixing that had already reduced the vertical algal gradient, net losses due to mixing were small. Consequently, even in deep Lake Constance, the reduction in primary production due to low light was often more influential than the net losses due to mixing. In the regression model, the dynamics of small, fast-growing algae was best explained by vertical mixing intensity and global irradiance, whereas those of larger algae were best explained by their biomass 1 week earlier. The simulation model additionally revealed that even in late winter grazing may represent an important loss factor during calm periods when losses due to mixing are small. The importance of losses by mixing and grazing changed rapidly as it depended on the variable mixing intensity. Higher temperature, lower global irradiance and enhanced mixing generated lower algal biomass and primary production in the dynamic simulation model. This suggests that potential consequences of climate change may partly counteract each other.

Keywords Deep lake · Functional algal groups · Multiple statistics · Simulation model · Turbulence

K. Tirok (✉) · U. Gaedke
Department of Ecology and Ecosystem Modelling, Institute of Biochemistry and Biology, University of Potsdam, Maulbeerallee 2, 14415 Potsdam, Germany
e-mail: tirok@rz.uni-potsdam.de

Introduction

We anticipate that climate change will have far-reaching – but currently poorly understood – consequences for the functioning of planktonic food webs. Climate models predict substantial warming during the winter and spring (1–5.5°C), increases in storm activity and decreasing cloudiness during the years 2070–2100 as compared to 1960–1990 in Western and Central Europe (IPCC 2001; Giorgi et al. 2004; Leckebusch and Ulbrich 2004). Higher air temperatures imply higher water temperatures (George and Hewitt 1999; Straile 2000), which will directly enhance heterotrophic processes such as zooplankton activity and algal respiration, but may leave others undisturbed (e.g.

primary production is primarily regarded as light limited in spring; Tilzer et al. 1986). In addition, higher water temperatures will typically increase thermal stratification and thus water column stability (Straile et al. 2003). This, in turn, influences the underwater light climate experienced by individual algal cells of non-ice-covered lakes. The temperature-related reduction in vertical mixing intensity may be counteracted by an increase in storm activity, which complicates predictions for the direction and magnitude of changes in mixing intensity due to climate change. The effect of potential changes in mixing on the underwater light climate may interact with changes in cloudiness, which also affects the light availability for algal growth. Global irradiance is known as a driving variable for net phytoplankton growth in spring in shallow waters (e.g. Neale et al. 1991), but it is rarely considered in relation with deep waters. Hence, predicting the response of phytoplankton to climate change requires untangling the effects of surface irradiance, vertical mixing and temperature.

Vertical mixing is of particular importance in deep waters where light does not penetrate to the bottom, as phytoplankton may be permanently transported from the euphotic to the aphotic depth. Assuming that vertical mixing intensity depends on stratification it has been suggested that in deep waters the mixing depth must be less than the "critical mixing depth" sensu Sverdrup (1953) to provide a light climate sufficient for positive net phytoplankton growth. The critical depth is the depth at which the depth-integrated daily gross primary production equals respiration, yielding zero net daily primary production. This leads to the assumption that the temperature and light climate are linked in deep waters. However, a large mixing depth does not necessarily imply intense vertical mixing (high turbulence) because during periods of low wind vertical mixing may be low in the absence of any stratification (Bäuerle et al. 1998). That is, a relaxation of vertical mixing allows positive net algal growth irrespective of the thickness of the upper water column (Huisman et al. 1999a). This hypothesis has seldom been applied to lakes but is supported by studies from marine systems (Eilertsen 1993; Ragueneau et al. 1996) and a demonstrated inverse relationship between algal net growth and vertical mixing intensity during the spring for large, deep Lake Constance (Gaedke et al. 1998a). Here, phytoplankton formed small blooms prior to stratification during calm periods which were, however, quickly terminated when wind enhanced vertical mixing. This suggests that short-term weather effects such as individual wind events may play a major role in spring phytoplankton develop-

ment. Numerous studies have analyzed the potential impacts of climate change, but most considered only changes in temperature and neglected short-term weather effects (Müller-Navarra et al. 1997; Scheffer et al. 2001).

Beyond its impact on total biomass, mixing may also affect the composition of phytoplankton due to species-specific adaptive strategies to light, nutrients and sedimentation (Reynolds 1997; Huisman et al. 1999b; Ptacnik et al. 2003). Consequently, we tested for potential differences in the susceptibility of different algal groups to climate change. We treated small edible algae, mostly typical C-strategists ("competitors", Reynolds 1988), which grow fast during periods of high light and high nutrient availability, and larger less-edible forms separately in our analyses. The latter were dominated by large diatoms in Lake Constance, which perform relatively well at low light and which represent R-strategists ("ruderals", Reynolds 1988).

Our study is based on long-term observations of plankton biomasses and abiotic factors in Lake Constance which are analyzed using four different approaches, whereas vertical mixing intensity is inferred from a detailed hydrodynamic model (Bäuerle et al. 1998; Gaedke et al. 1998a). These four approaches are: (1) the effects of global irradiance and deep vertical mixing intensity on phytoplankton development in spring are first visualized by comparing the respective time series; (2) potential relationships between observed algal biomass and driving factors are then tested using multiple regression analysis; (3) the effects of irradiance and mixing on algal net growth are compared, and the losses by deep mixing and the reduction of maximum primary production by light limitation are estimated from the data; (4) ongoing effects of climate-related factors on biotic variables are identified and this knowledge is assimilated into a simulation model for the spring period in Lake Constance. Sensitivity studies of the model allowed us to estimate the potential impact of climate change on spring phytoplankton development.

Using all approaches, we tested the following hypotheses in particular:

H1. Spring phytoplankton dynamics in deep Lake Constance is dominated by abiotic forcing and, in particular, by vertical mixing intensity (turbulence), which is unrelated to mixing depth.

H2. Edible algae are more responsive to abiotic forcing than less-edible algae.

H3. Anticipated climate change will have substantial effects on the phytoplankton community and its consumers. In particular,

(a) Enhanced global irradiance will increase algal biomass especially during the winter and early spring.

(b) Increasing water temperature will decrease algal biomass, since enhanced respiration and zooplankton grazing will not be fully compensated for by higher production due to light limitation.

(c) Decreasing vertical mixing will increase euphotic algal biomass due to a reduction in losses to the aphotic, non-productive water layer and vice versa.

(d) Under natural conditions, the driving factors may not vary independently. Thus, the direct effect of an increase in water temperature on algal biomass will be counteracted by decreasing mixing intensity.

Methods

Study site and long-term time series

Upper Lake Constance is a large (area = 472 km^2, volume = 48 km^3), deep ($z_{mean} = 101$ m, $z_{max} = 252$ m), mesotrophic lake north of the European Alps (9°18′E, 47°39′N). It is warm-monomictic and was never covered by ice during the study period. Due to large, co-operative programs conducted at Lake Constance from 1979 to 1998, unusually comprehensive data sets were available for model calibration and validation (Bäuerle and Gaedke 1998). Plankton sampling was carried out weekly in the spring and approximately every 2 weeks in the winter at the point of maximal water depth in Überlinger See (147 m), the north-western part of the lake. The abundance of planktonic organisms was assessed using standard microscopy techniques (Müller 1989; Straile and Geller 1998; Gaedke et al. 2002, and literature cited therein). Phytoplankton (Gaedke 1998a) and crustaceans (Straile and Geller 1998) were sampled from 1979 to 1998 (except 1983), ciliates (Weisse and Müller 1998) from 1987 to 1998. For conversion of cell numbers to biomass, see Weisse and Müller (1998) and Gaedke et al. (2002). Chlorophyll a concentrations were measured by means of hot ethanol extraction in the uppermost 20 m from 1980 to 1998 (with the exception of 1984/1985) and also down to a depth of 140 m from 1980 to 1983 and in 1986 (Häse et al. 1998), providing a second independent measure of algal biomass. Primary production was measured using a modified radiocarbon method in 1980–1997 (with the exception of 1984/1985; Häse et al. 1998; Tilzer and Beese 1988). We considered the average values of the uppermost 0–20 m and of the 20–100 m water layers separately, which roughly correspond to the maximal euphotic and epilimnetic zone and to the mean aphotic, hypolimnetic zone, respectively (Tilzer and Beese 1988).

Functional classification of algae

Phytoplankton morphotypes were functionally grouped into two categories called "edible" and "less-edible" based upon their shape, size, defense tactics and susceptibility to grazing pressure, mainly by cladocerans (Knisely and Geller 1986). This classification also accounts for differences in adaptive strategies to light, temperature and sedimentation. Edible phytoplankton was typically represented by fast-growing, small unicellular nanoplankters (e.g. small phytoflagellates) and small centric diatoms, and less-edible algae by large unicells, colony-forming species, filamentous algae and pennate diatoms. Cyanobacteria are of minor importance in Lake Constance, particularly in the winter and spring (Gaedke 1998a).

Vertical mixing intensity

The vertical mixing intensity was inferred from a one-dimensional, numerical, hydrodynamic k-ε model simulating the turbulent transports of momentum, heat and mass in the water column, which provided estimates of the vertical mixing intensity based on ambient (1979–1995) and moderately changed meteorological conditions (Bäuerle et al. 1998; Gaedke et al. 1998b; Ollinger and Bäuerle 1998). The model computed three vertical exchange rates, $mix_{0–20}$, $mix_{0–100}$ and $mix_{8–100}$ (Gaedke et al. 1998b; Ollinger and Bäuerle 1998), which reflect mean residence times in distinct water layers. $mix_{0–20}$ represents mixing within the uppermost 0–20 m and is defined as the proportion of a passive tracer that is transported from the layer at 0–8 m depth to that at 8–20 m within 24 h. mix_{deep} represents deep vertical mixing and is calculated from $mix_{0–100}$ and $mix_{8–100}$ (Appendix, Eq. 3), which are defined as the proportion of a tracer that is transported from the layer 0–8 m depth to that at 20–100 m and from the layer at 8–20 m depth to that at 20–100 m, respectively. $mix_{0–100}$ and $mix_{8–100}$ are highly correlated. Given the large mixing depth we assume that phytoplankton is passively transported.

Analysis of the impact of deep vertical mixing and global irradiance on algal growth

The relative importance of global irradiance and vertical mixing for algal net growth in the euphotic layer was estimated by calculating algal production (*prod*)

and net losses due to deep vertical mixing (*loss*). Production was estimated from a P–I curve, with light integrated over the euphotic layer (0–20 m; Appendix Eqs. 1–13; Häse et al. 1998; Kotzur 2003). The maximum daily production rate $\tilde{r}$ was set to 1, a typical value for Lake Constance phytoplankton in spring (Häse et al. 1998). Light inhibition of production was disregarded as this effect is known to be irrelevant for Lake Constance phytoplankton (Häse et al. 1998). For estimating in situ production, we used weekly to bi-weekly values of epilimnetic algal biomass and the corresponding measured values of surface irradiance. In situ losses by mixing were calculated from the vertical algal gradients (Eq. 4) and the corresponding deep vertical mixing intensities (Eq. 3). The former were obtained from weekly to bi-weekly depth profiles of chlorophyll *a*. Loss (Eq. 2) represents the net export of algal biomass from the euphotic to the aphotic layer. In situ production and losses were calculated for the years 1980–1983 and 1986.

Dynamic simulation model

A two-box dynamic simulation model was driven by time-series of water temperature, vertical mixing intensity and global irradiance, and incorporated the state variables edible and less-edible algae in the euphotic (0–20 m) and aphotic layer (20–100 m). The equations for edible and less-edible algae differed only in their parameterization (Appendix, Eqs. 14–21). Primary production depended on light and temperature. Their combined effect was calculated by a Liebig formulation (Eq. 16) based on the well-known temperature independence of light-limited photosynthetic rates at temperatures $>2°C$ (Tilzer et al. 1986). We neglected nutrients in our model as we focused on the spring period during which we have no indication of nutrient limitation for the observational period (1979–1998) (Gaedke 1998a; Tirok and Gaedke 2006). Both algal groups experienced a dynamic mortality rate that depended on previous algal densities (Appendix, Eq. 20). By these means, predator dynamics and, thus, their grazing pressure followed their prey with a time lag of 7–15 days (Müller et al. 1991). This mortality rate predominantly represented grazing by fast-growing small ciliates for edible algae and grazing by copepods for less-edible algae. We assumed a stronger temperature dependence of heterotrophic than of autotrophic processes (compare Table 2, Hancke and Glud 2004).

Parameter values were chosen according to existing knowledge if available and adjusted otherwise. Parameter adjustment was made by visualizing the fit

of the model to the data using 6 years (1980, 1981, 1987, 1988, 1992 and 1994) of the data set, which were chosen to represent a range of different abiotic conditions. The other 9 years (1979, 1984–1986, 1989–1991, 1993 and 1995) were available for model validation.

Sensitivity to the individual forcing factors and scenarios

To better understand the potential impacts of climate change on phytoplankton dynamics, we tested the reaction of algal biomass to the individually altered forcing factors. Observed deviations from the long-term mean mixing intensity (1979–1995) within individual years ranged from – 72 to +28% when averaged from January to mid-May. This interannual variability in mean mixing intensity was larger than that in mean global irradiance, for which corresponding values fell between – 9 and +13%, and than that in mean temperature, which deviated by –1.3 and +1.7°C from the long-term mean. Consequently, we altered the observed daily values of mixing intensity by ±30 and 60%, and of irradiance by 10 and 30%. We use the lower values (±30 and 10%) to represent the observed interannual variability as observed deviations fell below these values in most years, and the higher ones (±60 and 30%) to reflect potential climate change. Observed temperature values were decreased by 2°C and increased by 2°, 4° and 6°C according to climate change scenarios (IPCC 2001).

In addition to these proportional alterations in the mixing intensity throughout the entire spring period we used vertical mixing rates derived from the hydrodynamic model which was run with altered weather conditions in 1989. (1) The wind speed during 3 days (March 7–9, 1989), including a strong wind event (up to 19 m s^{-1}), was replaced by a constant wind speed of 2.5 m s^{-1}, which corresponds to typical wind speeds in March, in order to assess the impact of a strong individual wind event. (2) The hydrodynamic model was run with a 2°C increase in air temperature above the observed one from January 1 onwards. To account for the interplay of forcing factors, we assumed in addition in our simulation model an increase in water temperature by 2°C and a decrease in global irradiance by 10% to reflect increased cyclone activity with more cloudiness (Leckebusch and Ulbrich 2004).

Calculations and graphics were performed with SAS ver. 9 (SAS Institute, Heidelberg, Germany) and Matlab ver. 6.5 (The MathWorks, Munich, Germany). Unless otherwise noted, all computations were carried out for the period January to mid-May as we focused on

the climate sensitive winter–spring transition in this study. We defined "late winter" as January (day 1) to mid-March (day 74), with data mostly available from mid-January onwards, and "spring" as mid-March (day 75) to mid-May (day 135). Multiple regression analysis was performed with the SAS procedure "reg" using the method "stepwise selection", which selected the explanation variables one-by-one and retained them when they significantly increased the model R^2 ($p<0.15$) (SAS OnlineDoc 1999).

Results

Field data

Visual inspection of the observed time-series revealed a highly variable onset of net spring algal growth, which occurred between February (e.g. 1986) and April (e.g. 1988) (Fig. 1). This variability was related to the high intra- and interannual variability in the vertical mixing intensity, leading to an alteration between almost complete and little mixing of the unstratified water column. For example, in 1988, values of mix_{0-100} typically surpassed 0.6 from January until the end of March – i.e. often >60% of the water in the 0–8 m layer was transported to that in 20–100 m depth per day, entailing a well-mixed water column (Fig. 1). In contrast, in 1986, deep vertical mixing was low in February, facilitating phytoplankton net growth,

although water temperature did not reach more than 6°C and the water column was not stratified. This covariation in algal biomass and vertical mixing rates was also found for the other 15 years under consideration, with few exceptions ($r=0.61$, $p<0.001$, $n=209$; 1979–1995).

Despite a high day-to-day variability, global irradiance generally increases throughout the spring in contrast to mixing which tends to decrease (Fig. 1). This covariation of both variables with time yielded a scattered, but significant, negative correlation between irradiance and mixing when all days from January until mid-May were considered ($r = -0.5$, $p<0.001$, $n=2035$; 1979–1995). Nevertheless, during individual years and periods the opposite pattern could be found. For example, during April 1986 high global irradiance (>150 W m^{-2} on many days) and high vertical mixing rates ($mix_{0-100}>0.6$) coincided, potentially explaining the rather high algal biomass despite intense mixing (Fig. 1). The covariation of both forcing factors complicates the identification of their individual effects on phytoplankton growth from the observational data, which will thus be performed by multiple statistics and dynamic model studies.

Multiple linear regression models including the independent variables mix_{0-100}, global irradiance, temperature, biomass of ciliates and of copepods and algal biomass at the previous sampling date confirmed the impact of mixing on spring phytoplankton biomass (Table 1). Deep vertical mixing intensity and the algal

Fig. 1 Phytoplankton biomass (*solid line*), chlorophyll *a* concentration (*triangles*, displayed as 20×Chla), deep vertical mixing intensity mix_{0-100} (*shaded area*), global irradiance (*needles from top to bottom*) and temperature in the 0–20 m water layer (*dashed line*, displayed as 1/10×T) in the spring for 1980, 1986, 1988 and 1992
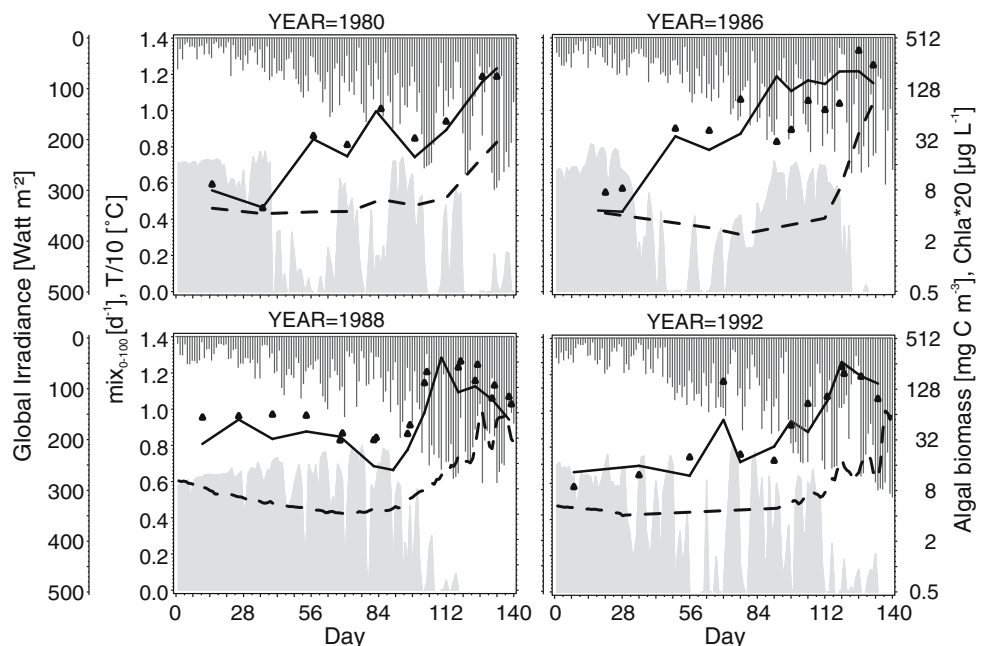
biomass 1 week earlier explained 62% of the variability in total algal biomass. Considering edible and less-edible phytoplankton separately revealed different sensitivities of the two functional groups to abiotic forcing factors. The biomass of both groups was related to their own biomass at the previous sampling date. In addition, biomass of edible algae depended strongly on deep vertical mixing intensity and weakly on global irradiance (Table 1). In contrast, biomass of less-edible algae depended only weakly on deep vertical mixing intensity (Table 1). This implies that the biomass at the previous sampling date was by far the best predictor for the ambient biomass of less-edible algae and that the sensitivity to altered growth conditions was low on a time scale of 7–14 days. No algal group correlated with water temperature of the upper 20 m and no negative correlations were found with the biomass of ciliates and copepods representing the most important grazers.

Impact of deep vertical mixing and global irradiance on phytoplankton

The previous data analysis suggests that spring phytoplankton biomass was related to both vertical mixing and global irradiance, which may be attributed to the effect of vertical mixing on algal losses from the euphotic layer and of irradiance on light-dependent production. However, these processes explained only a part of the variability in algal biomass, indicating that an influential factor was not yet identified.

Phytoplankton was not homogenously distributed over the water column in Lake Constance. Rather, a more-or-less pronounced and temporally highly vari-
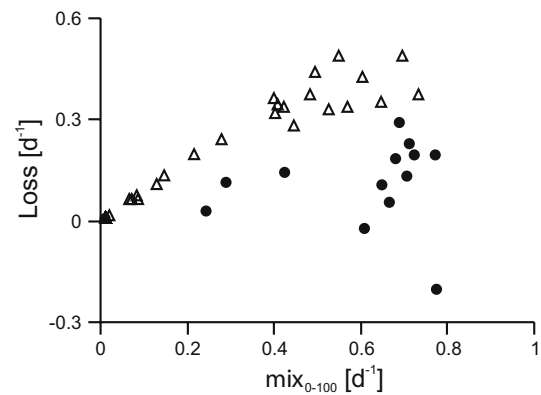

Fig. 2 Relationship between the proportion of algae lost from the euphotic (0–20 m) to the aphotic layer (20–100 m) (*Loss*) and deep vertical mixing intensity (mix_{0-100}) in 1980–1983 and 1986. Loss was estimated from the mixing intensity and the measured vertical algal gradient (vag_{meas}, $n=52$; for details see Eqs. 3, 4). *Dots* vag_{meas} <2, *triangles* vag_{meas} ≥2. Losses to the aphotic layer were maximal when high vertical gradients and intense mixing coincided. Losses were low or even negative when the chlorophyll *a* concentration in the aphotic layer was similar or higher than that in the euphotic layer

able vertical gradient in algal biomass was observed from January to mid-May. The ratio between mean chlorophyll concentrations in the layers at 0–20 m and 20–100 m depth was generally low (approx. 1) from January until mid-February, highly variable until the end of April (approx. 1–10) and high afterwards (approx. 10–38). This ratio strongly influenced the algal net losses from the euphotic layer. A strong positive relationship between algal losses from the surface layer and mixing intensity was only found if a strong vertical gradient in algal biomass existed (Fig. 2). If the algae

Table 1 Results of linear stepwise regression models for total, edible and less-edible phytoplankton biomass

Dependent variable	Independent variables[a]	Parameter estimates[b]	Type II SS	df Model	df Error	Model R^2
Total algae	Lagtot	0.56***	82.84	2	135	0.62***
	mix_{0-100}_7	–2.18***	26.59			
Edible algae	mix_{0-100}_7	–3.22***	40.42	3	134	0.65***
	Laged	0.36***	31.31			
	I_0_7	0.004*	3.06			
Less-edible algae	Lagled	0.77***	262.7	2	135	0.66***
	mix_{0-100}_7	–0.72*	3.45			

* $p<0.1$, *** $p<0.001$

[a] Models with the independent variables biomass at the previous sampling date of total algae (lagtot), edible algae (laged) and less-edible algae (lagled), average irradiance (I_0_7), deep vertical mixing intensity (mix_{0-100}_7), and temperature (temp_7) during the previous 7 days and biomass of ciliates (cil) and copepods (cop) were computed for January to mid-May in 1987–1995. As temp_7, cil and cop were removed by the models ($p≥0.15$), subsequent models with the remaining independent variables were run for 1979–1995 to use the maximal number of observations available

[b] The Type II Sum of Squares (SS) indicates the amount of variability explained by the respective variable. It is adjusted for all other independent variables included into the model. Algal, ciliate and copepod biomasses were log-transformed

were fairly homogenously distributed over the water column due to intense previous mixing, net losses were low, even at high mixing intensity because the export from the surface to deep layers and the import from deep into surface layers approximately compensated each other. Similarly, a high vertical gradient only led to high losses if vertical mixing was intense and vice versa (Fig. 2). Consequently, the impact of vertical mixing on algal net growth was highly variable. Mixing only influenced algal net growth if the algal distribution was not homogenous across the water column. Otherwise, losses by vertical mixing were marginal, and light availability for production was the dominant factor determining net growth since primary production was not yet light-saturated and self-shading was low during late winter. Low irradiance limited production at numerous sampling dates in the spring (Fig. 3). Daily primary production typically reached only approximately 30–60% of its maximum value (Fig. 3) – i.e. the
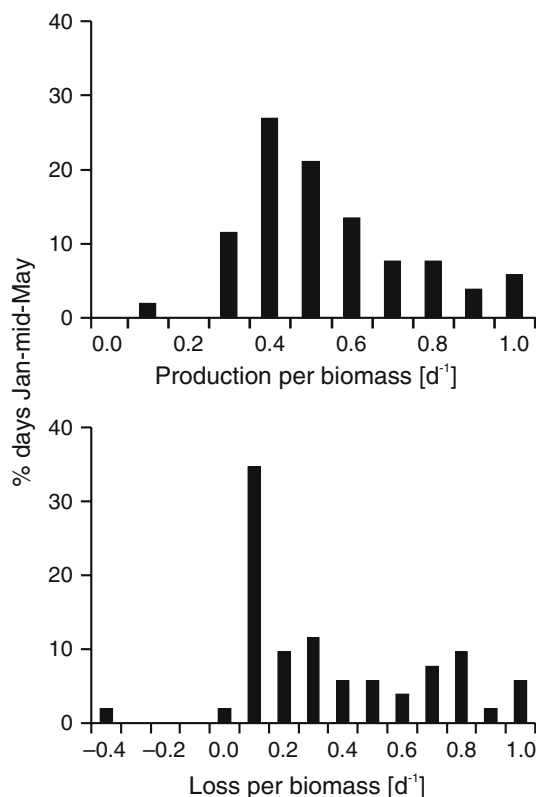

Fig. 3 Frequency distribution of light-dependent production (*upper graph*) and losses by vertical mixing (*lower graph*) in Lake Constance for January until mid-May in 1980–1983 and 1986 (*n*=52). Production was estimated from observed surface irradiance and algal biomass influencing self-shading. Losses were derived from the deep vertical mixing intensity and the observed vertical gradient in chlorophyll concentration. For details, see Methods. Data were standardized to the observed maximum production and mixing loss, respectively

potential production was reduced by 40–70% due to light limitation. In contrast, the daily losses through mixing were ≤30% of the algal biomass in the surface layer on most days during the spring, although losses were >60% on about 25% of the days during this same period (Fig. 3). We conclude that global irradiance may have an important effect on net phytoplankton growth even in deep well-mixed waters. When a strong vertical algal gradient exists, light limitation and losses by mixing may be of similar importance for algal net growth.

Simulation model

The simulation model satisfactorily reproduced the observed dynamics during the spring in Lake Constance following the calibration of a few model parameters (Table 2). Despite some inevitable deviations, overall patterns, such as the timing and the height of the algal spring bloom (Fig. 4a) and the ratio between primary production and algal biomass (P:B ratio) (Fig. 4c), fitted well during most of the years investigated. Furthermore, the simulated vertical gradient fell mostly within the observed range (compare Fig. 5). This result indicates that the exchange between the two water layers and the mortality in the aphotic zone were reasonably reproduced. As expected from the weak dependence on known driving factors established by the previous data analysis, the dynamics of less-edible algae was less well reproduced than those of the edible ones (Fig. 4b). The autocorrelation in the biomass of less-edible algae was even more pronounced in the model than in the data (Fig. 4b).

The relative importance of losses by vertical mixing and grazing exhibited a high-temporal variability in late winter, whereas grazing losses dominated in the spring (Fig. 5). A high proportion of algal biomass was lost by mixing at the onset of a strong vertical mixing event due to the initially large vertical gradient. With decreasing differences in algal biomass between the surface and deep layers, mixing-induced losses per unit biomass declined without a reduction in mixing intensity. If mixing intensity was high throughout late winter, the loss rates by mixing surpassed those by grazing (Fig. 5, 1994). If turbulent periods alternated with calm ones, the loss rates by mixing and by grazing alternated in their relative importance as well (Fig. 5; 1980). That is, grazing mortality may play an important role as early as February and is already present prior to the onset of stratification. To conclude, the dynamics of edible algae was well predicted by irradiance, vertical mixing and a density-dependent mortality representing grazing.

The satisfying fit of the model is supported by comparing observed and modeled algal biomasses for all study years which had a similar median for both edible and less-edible algae in late winter and spring (Fig. 6). The variability of algal biomass in the model and in the observed data was similar during late winter and smaller in the model later on for both algal groups (Fig. 6). The observed variability in chlorophyll concentrations, which were measured with a higher vertical resolution than algal biomass, was

Table 2 Full list of model parameters

Parameter	Symbol[a]	Value	Unit	Source
Proportion of photosynthetic active radiation (PAR) of global irradiance directly below water surface	$\widetilde{q}_{PAR}$	0.414	–	Tilzer and Beese (1988)
Depth of euphotic water layer	$\widetilde{d}$	20	m	Tilzer and Beese (1988)
Minimal PAR of saturated photosynthesis	$I\_\widetilde{opt}\_min$	40	W m^{-2}	Baretta et al.(1995), Kotzur (2003)
Background turbidity	$\widetilde{turb}$	0.2	m^{-1}	Tilzer and Beese (1988)
Self-shading coefficient	$\widetilde{selfsh}$	0.002	(mg C m^{-2})$^{-1}$	Calibrated and validated with primary production measurements of Lake Constance (Häse et al. 1998)
Q_{10} value for autotrophic processes	$\widetilde{Q}_{10,A}$	1.5	–	We assumed a stronger temperature dependence of heterotrophic processes than of autotrophic processes (Hancke and Glud 2004)
Q_{10} value for heterotrophic values	$\widetilde{Q}_{10,H}$	2.0	–	
Dilution constant for algae imported into aphotic zone	$\widetilde{c}$	1/3	–	The aphotic layer is three times as thick as the euphotic one when assuming a mean mixing depth of 80 m
Potential growth rate of edible algae in the upper 20 m	$\widetilde{r}_{we}$	2.9	d^{-1}	Calibrated and validated with primary production measurements of Lake Constance (Häse et al. 1998)
Potential growth rate of less-edible algae in the upper 20 m	$\widetilde{r}_{le}$	1.6	d^{-1}	Calibrated and validated with primary production measurements of Lake Constance (Häse et al. 1998)
Activity exudation rate	$\widetilde{puea}$	0.1	d^{-1}	Baretta et al. (1995), Gaedke et al. (2002)
Activity respiration rate	$\widetilde{pura}$	0.25	d^{-1}	Geider (1992)
Basal respiration rate of edible algae	$\widetilde{srs}_{we}$	0.1	d^{-1}	Baretta et al. (1995), Gaedke et al. (2002)
Basal respiration rate of less-edible algae	$\widetilde{srs}_{le}$	0.05	d^{-1}	Baretta et al. (1995), Gaedke et al. (2002)
Sedimentation parameter of edible algae	$\widetilde{ssed}_{we}$	0	d^{-1}	For small, edible algae sedimentation is assumed to be 0 (Reynolds 1988)
Sedimentation parameter of less-edible algae	$\widetilde{ssed}_{le}$	0.02	d^{-1}	Corresponds to a maximum sedimentation rate of 20% (Tilzer 1984; Güde and Gries 1998)
Exponent for density dependent mortality	$\widetilde{a}$	0.25	–	Calibrated
Time delay in density-dependent mortality for edible algae	$\widetilde{\tau}_{we}$	7	d	Ciliate spring growth lags approx. 1 week behind that of edible algae (Müller et al. 1991)
Time delay in density-dependent mortality for less-edible algae	$\widetilde{\tau}_{le}$	15	d	Calibrated, copepods, being the main grazers of less-edible algae, have longer response times than ciliates
Mortality parameter of edible algae	$\widetilde{m}_{we}$	0.13	$(\mathrm{mg\,C\,m^{-3}})^{-\widetilde{a}}\,\mathrm{d}^{-1}$	Calibrated
Mortality parameter of less-edible algae	$\widetilde{m}_{le}$	0.04	$(\mathrm{mg\,C\,m^{-3}})^{-\widetilde{a}}\,\mathrm{d}^{-1}$	Calibrated

[a] we, Edible algae; le, less-edible algae

Fig. 4 Biomass of edible (**a**) and less-edible algae (**b**) and the P:B ratio (**c**) in the seven (of nine) validation years for which comprehensive measurements are available. *Solid lines* Simulation results, *dots* measured values from Lake Constance for the corresponding year
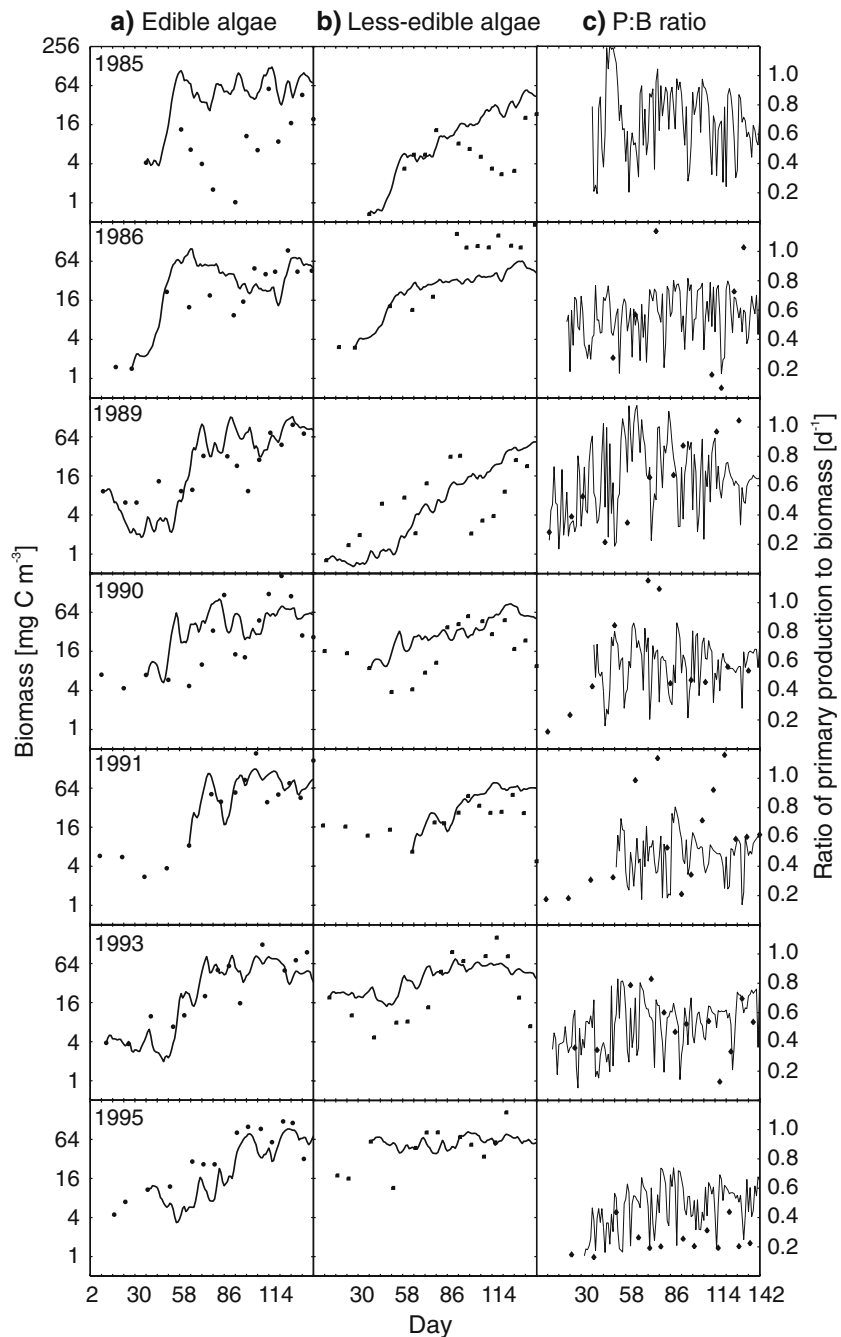
similar to that of algal biomass determined by microscopy (Fig. 6).

Sensitivity to the individual forcing factors and scenarios

To better understand the potential impacts of climate change on phytoplankton dynamics, we tested the response of modeled algal biomass to the individually altered forcing factors. As expected, reduced mixing on its own led to the computation of higher algal bio-

masses in the surface layer due to lower losses to the aphotic layer, whereas increased mixing had the opposite effect – although to a lesser extent (Fig. 7a for 1993). Increasing or decreasing global irradiance enhanced or repressed primary production and thus algal biomass, respectively (Fig. 7b). Higher temperatures resulted in lower algal biomass due to increased losses by respiration and grazing which were not balanced by enhanced production due to light limitation (Fig. 7c). The effects of altered mixing and global irradiance were most pronounced during late winter, prior to the
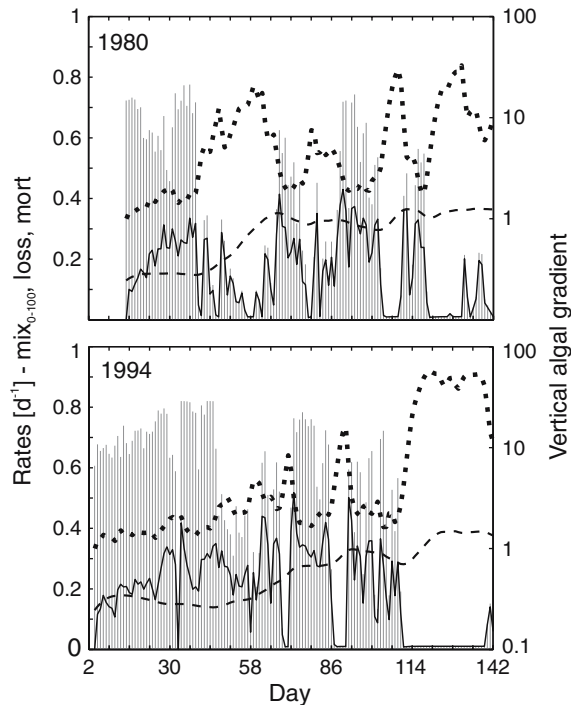
Fig. 5 Vertical mixing intensity (*mix*, *needles*), algal loss rate due to mixing (*loss*, *solid line*), mortality rate representing grazing (*mort*, *dashed line*) and vertical algal gradient (*vag_mod*, *dotted line*) in 1980 and 1994, 2 years with a high-temporal variability in mixing intensity. Vertical mixing intensity was given as forcing data; the other three variables were simulated by the model

start of stratification and during the most light-limited period, whereas a temperature increase had a lasting effect throughout winter and spring. The proportional alterations in all three forcing factors had little impact on the timing of the onset of pronounced algal growth and of the algal bloom. The latter was attributable to a
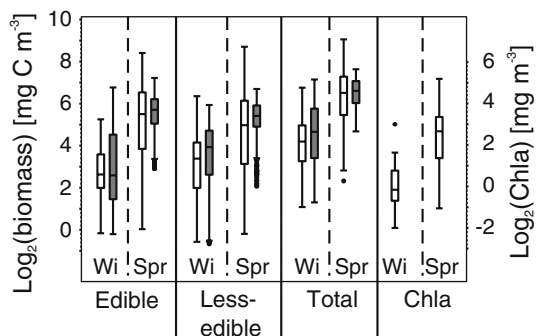

Fig. 6 Variability of measured (*unfilled boxes*) and simulated (*filled boxes*) biomasses of edible, less-edible and total algae and of measured chlorophyll *a* concentration in Lake Constance in late winter (*Wi*; January to mid-March) and spring (*Spr*; mid-March to mid-May). *Boxes* represent 25 and 75 percentile, *dots* outliers (>1.5 interquartile distance)

higher reduction of algal net growth by density-dependent processes as soon as algal biomass reached a higher level. To test the impact of individual weather conditions, we used vertical mixing intensities, which were obtained by smoothing an individual wind event in March 1989 (for details see methods). Reducing the wind speed for a 3-day period resulted in a lower vertical mixing intensity during the following 3 weeks which, in turn, affected algal biomass during this period, but not afterwards (Fig. 7d).

To obtain a more realistic scenario we accounted for the interplay between the forcing factors using the year 1989 as an example. The changes in mix_{0-100} that resulted from an increase in the air temperature by 2°C above the observed one from January 1 onwards, were small in January, increased slowly in February and were large in March when vertical mixing rates were considerably reduced (Fig. 8a). Changing mixing and temperature individually in 1989 (Fig. 8a, b) had similar effects on phytoplankton, as described for 1993. The combined effects of lower mixing intensity and higher water temperature on algal biomass almost compensated for each other in this scenario and were so low that they would be hard to detect in the field (Fig. 8c). In addition, decreasing global irradiance by 10% resulted in a substantial reduction in computed edible algal biomass during late winter, but not during the spring algal bloom (Fig. 8d).

To increase the level of generality, we calculated the response of edible algal biomass and primary production to altered forcing factors for all days of all study years (Fig. 9). The results confirmed the findings represented above for individual years – that changes in global irradiance and vertical mixing intensity mostly acted in late winter, whereas effects of temperature changes lasted throughout the winter and spring. In addition, the intra- and interannual variability of the algal response was higher in late winter than in the spring (Fig. 9). Changes in the forcing factors within the mean variability observed in 1979–1995 resulted in small deviations – i.e. less than a factor of 1.5 on average – of algal biomass and primary production from the original runs, and alterations in the three forcing factors had effects of similar magnitude (white areas in Fig. 9); that is, decreasing irradiance by 10% had a similar effect on edible algal biomass as increasing mixing by 30% or temperature by 2°C. In most, but not all, scenarios edible algal biomass and primary production responded more strongly to alterations beyond the observed variability in the forcing factors (gray areas in Fig. 9). In late winter, a decrease in mixing intensity by 60% had a similar effect as an increase in
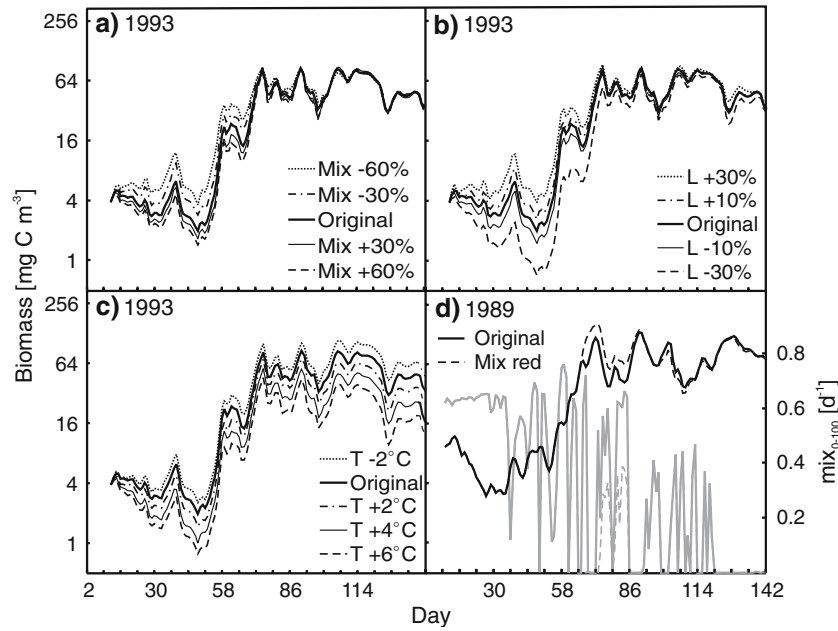
Fig. 7 Simulation runs of edible algal biomass with altered mixing intensity (**a**), global irradiance (**b**) and temperature (**c**) in 1993 and reduced mixing intensity in 1989 (**d**). In 1993, mixing intensity and global irradiance were altered relative to original values by 10, 30 and 60%, and temperature was altered by 2, 4 and 6°C. In 1989, altered mixing intensity was inferred from the hydrodynamic model after replacing a strong wind event on March 7–9 (days 66–68) with the average wind speed. This run represents the effect of a short-term alteration in weather conditions. mix_{0-100} at observed (*solid gray line*) and changed (*dashed gray line*) wind speed is drawn in graph **d** (compare Gaedke et al. 1998a)

irradiance by 30%, whereas the algae were less responsive to enhanced mixing intensity. Decreasing global irradiance by 30% and enhancing temperature by 6°C had the most pronounced effect of all scenarios, i.e. a decrease in both algal biomass and primary production by a factor of 2–3 on average. That is, a reduction in irradiance affected algal biomass more strongly than an equivalent increase. The extent of a temperature increase was reflected in the amount of algal biomass reduction. Primary production and

Fig. 8 Simulated biomass of edible algae from model runs with individually altered mixing intensity (**a**) and temperature (**b**), and combined alteration of both factors (**c**) in 1989. In a fourth run, global irradiance was also changed (**d**). Altered mixing intensity was inferred from the hydrodynamic model after increasing the air temperature by 2°C above the observed one from January 1, 1989 onwards. mix_{0-100} at observed (*solid gray line*) and increased (*dashed gray line*) air temperature is drawn in graph **a** (compare Gaedke et al. 1998a). Water temperature was increased by 2°C, and global irradiance was decreased by 10%
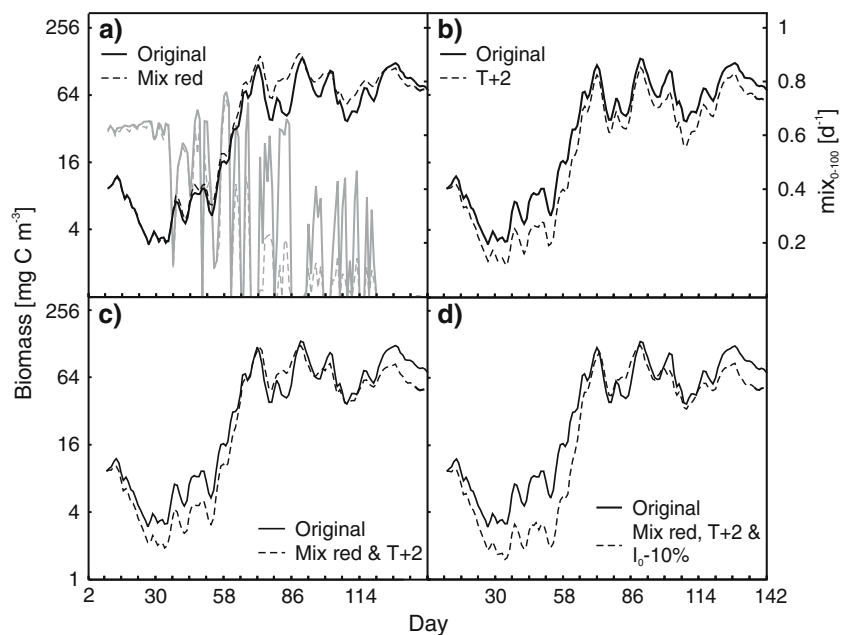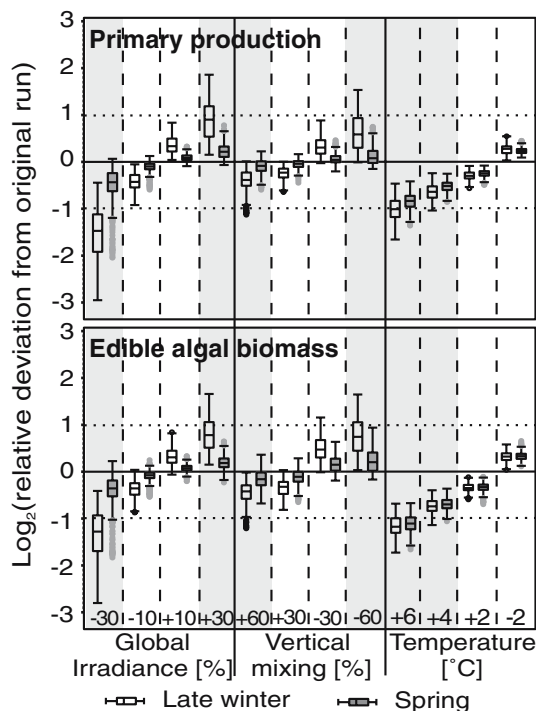
Fig. 9 Relative deviations between the standard run and scenario calculations for primary production (*upper graph*) and edible algal biomass (*lower graph*) during late winter (January to mid-March, *unfilled boxes*) and spring (mid-March to mid-May, *filled boxes*) in 1979–1995, with the exception of 1982 and 1983. The first 14 days of each simulation were omitted to exclude too small deviations resulting from the start value. Scenarios are defined according to alterations in global irradiance, vertical mixing intensity and temperature. *White areas* Alterations in the forcing factors within their mean variability observed in 1979–1995, *gray areas* alterations beyond the observed variability. *Boxes* represent 25 and 75 percentile, *dots* outliers (>1.5 interquartile distance)

biomass were similarly responsive when the three forcing factors were altered independently within their observed range of variability (Fig. 9).

Discussion

Potential limitation of the simulation model

The simulation model satisfactorily reproduced the observed absolute values and dynamics of primary production, the vertical algal gradient and the biomass of edible algae and, to a lesser extent, the biomass of less-edible algae. From these results we conclude that the model accounted for the relevant factors that drive the fast-growing edible algae which dominate primary production. The inevitably remaining deviations between that data and model results may arise partly from simplifying model assumptions but also from

measurement errors and uncertainties in the estimates of vertical mixing intensity.

The relatively simple primary production module that neglects light acclimation may be one reason for model artifacts. When surface irradiance changed suddenly from low to high values, the modeled growth rate increased immediately, which resulted in an earlier increase of biomass in the model than observed in the data. This recurrent pattern may be explained by the fact that algae need up to 3 days to modulate their protein pool in order to adapt to high-light intensity after a low-light period (Quigg and Beardall 2003).

The spring algal dynamics was well reproduced by the model in 10 of the 15 years studied, including years with low and high mixing and light intensity. The 5 years with larger deviations between observations and model results included some of the colder years (1979 and 1985–1987) but also a year with a very mild spring (1990). Deviations were lowered by reducing algal growth at very low temperatures. However, this had to be done to an extent which was in conflict with the measurements. Increasing the vertical resolution of the primary production module and using an appropriate co-operative function of light and temperature limitation might improve the model fit. For example, a temperature sensitivity of maximum algal growth has been observed in laboratory studies (Hawes 1990; Montagnes and Franklin 2001). Otherwise, deviations between observed and modeled values did not vary systematically with the forcing data. That is, the different climate conditions were almost equally well represented by the model, indicating its suitability to explore consequences of increased temperature and altered light and mixing conditions.

The observed variability in algal biomass, measured by microscopy, and in chlorophyll *a* concentrations was similar although chlorophyll *a* was measured with a higher vertical resolution. This suggests that algal dynamics inferred from algal biomass was not strongly influenced by errors in the measurements. The variability in observed and modeled algal biomass was similar during late winter, when abiotic forcing prevailed, whereas during spring, the observed variability exceeded the modeled one. This result indicates that the observed algal biomass responded more strongly to vertical mixing or that mixing intensity was underestimated by the hydrodynamic model in the spring. In addition, the lower number of high values in the model points to a rather strong dampening of algal dynamics by the mortality term despite its time-lagged dependence on algal biomass, which will therefore be replaced by an explicit consideration of herbivores in a future model version.

Impact of deep vertical mixing and global irradiance on algal growth

The analysis of time-series, regression models as well as the simulation model led to the conclusion that spring phytoplankton growth is mainly driven by vertical mixing intensity and global irradiance during the spring in Lake Constance. In addition, the simulation model suggested a direct temperature effect of a magnitude similar to that of mixing and irradiance.

In deep temperate lakes the beginning of spring phytoplankton growth depends on the extent of vertical mixing and, hence, on the meteorological and hydrodynamic conditions (Sverdrup 1953; Erga and Heimdal 1984). Suitable conditions for algal net growth may be achieved by two fundamentally different mechanisms: (1) when the mixing depth falls below the ''critical depth'' sensu Sverdrup (1953) or (2) when the mixing intensity becomes lower than a ''critical turbulence'' (Huisman et al. 1999a). Previous studies on spring algal development in lakes mostly considered only the extension of the mixing depth or the onset of stratification – i.e. the ''critical depth'' but not the intensity of mixing or ''critical turbulence'' (Diehl 2002; Lehman 2002; Winder and Schindler 2004). In Lake Constance, a spring algal bloom developed when vertical mixing intensity was low, either by thermal stratification or during calm periods. Thus, both mechanisms were involved and differed in their relative importance between study years. The latter is comparable with studies from marine systems, where algal blooms occur despite large mixing depth. As observed for Lake Constance, the blooms may have several peaks, periodically interrupted by intermittent strong wind mixing or convective cooling, and can last over an extended period of time' both of these factors have lasting effects on zooplankton (Townsend et al. 1992; Tian et al. 2003; Waniek 2003).

Previous explanations of the correlation between vertical mixing and phytoplankton net growth were implicitly based on the assumption that high mixing intensity results in high algal losses from the euphotic layer (Gaedke et al. 1998a, 1998b). However, we have been able to show that vertical mixing is a necessary –but not a sufficient – factor for substantial net losses of algae from the euphotic layer, since the vertical gradient in algal biomass plays a crucial role as well. Given its dependency on the previous mixing intensity, there is no trivial relationship between ambient vertical mixing and the resulting algal losses, but the mixing history has to be considered for short-term predictions. As indicated by vertical profiles of chlorophyll concentrations, algae were often almost homogenously distributed in Lake Constance during periods of intense vertical mixing.

Consequently, high net losses occurred on fewer days than expected, and losses were often less important for algal growth than light limitation. An analysis of the interacting effects of global irradiance and deep vertical mixing revealed that on many days during the winter and spring net phytoplankton production was lowered by 40–80% due to light limitation but biomass decreased by only 10–30% due to losses by vertical mixing. This result is confirmed by other studies showing a decisive impact of PAR/global irradiance on spring algal development (Neale et al. 1991; Tian et al. 2003). We conclude that global irradiance may have an important effect on spring net phytoplankton growth, not only in shallow but also in deep, well-mixed waters.

Response of functional algal groups to abiotic and biotic forcing factors

The biomass of small, fast-growing and edible algae fluctuated more strongly than that of the less-edible algae during spring in Lake Constance. Small algae reacted immediately to alterations in mixing and light conditions due to their short generation times, high grazing susceptibility and presumed higher mortality at large depth. This explains their correlation with vertical mixing intensity and global irradiance found in the regression analysis. The lower variability of the larger, less-edible algae led to a stronger autocorrelation at the given sampling interval and may be attributed to lower growth and loss rates by grazing and respiration (Sicko-Goad et al. 1986; Reynolds 1988). Their lower responsiveness reduced our potential to predict their dynamics from the abiotic forcing factors and suggests that factors determining the dynamics of these algae are not yet well understood.

The model indicated rapid changes in the relative importance of losses of edible algae by deep mixing and grazing which depended on the variability in the mixing intensity. The latter may explain why grazing was not included into the regression model. Ciliates are the dominant herbivores in Lake Constance during spring (Gaedke et al. 2002; Tirok and Gaedke 2006). During calm periods, these fast growing protozoans with generation times similar to their prey almost immediately react to increased food concentrations (Müller et al. 1991; Tirok and Gaedke 2006). If wind induces strong vertical mixing again, this top-down effect on edible algae is immediately interrupted as ciliate biomass in the euphotic layer is strongly reduced due to losses to larger depths. Thus, in contrast to expectation (Sommer et al. 1986), a complex interplay of abiotic and biotic regulation of algal dynamics has to be assumed during late winter and early spring even in deep waters.

Sensitivity to the individual forcing factors
and scenarios

The assimilated insights into the factors controlling
spring phytoplankton dynamics provide a basis to
forecast algal responses to anticipated climate change.
Moderate proportional alterations in observed irradi-
ance, mixing intensity and temperature had little impact
on the timing of the onset of net algal growth and algal
bloom. This was due to a smaller reduction in algal net
growth by density-dependent self-shading and mortality
when algal growth started from a lower absolute level.
The responses of algal biomass and primary production
were similar. Changes amounted typically to approxi-
mately ±10–20% of the long-term mean when the
forcing factors were altered within the range observed
during the investigation period. They increased to ±20–
60% by doubling or tripling the observed range of
fluctuations in the forcing factors. An alteration of algal
biomass by 60% is low compared to the large seasonal
amplitude with two orders of magnitude between the
winter minimum and the spring maximum (Gaedke
1998a). However, from the consumer perspective a
change in prey availability by 20 or 60% at a given date
may substantially influence their growth rates. By using
proportional alterations in forcing factors we preserved
their general temporal patterns; that is, we did not shift
the timing of stratification in our scenarios, which
exhibits a high interannual variability and has far-
reaching consequences. Our model does not consider
any effects of potential adaptation processes (e.g.
genetic or species shifts), which may dampen the
responsiveness or consequences of a further reduction
in phosphorus concentrations.

The overall significance of the predicted responses
to anticipated climate change can be rated by com-
paring the former to the observed responses to
re-oligotrophication. From 1980 to 1997 mean algal
biomass and primary production declined by approx-
imately 50 and 25%, respectively, during the summer
in Lake Constance (Gaedke 1998a; Häse et al. 1998).
These changes were of a magnitude similar to those
found in this model study and had lasting effects on
the next trophic levels (Gaedke 1998b). In addition,
mixing-related interannual variability in the algal
biomass and species composition during the late
winter effectively influenced the structure of the
zooplankton community for the subsequent 3 months
and the extent of the clear-water phase in Lake
Constance (Tirok and Gaedke 2006).

The effects of proportional alterations in mixing and
global irradiance on algal biomass and production varied
seasonally. They were most pronounced during late

winter since mixing and global irradiance were the most
decisive factors influencing algal dynamics prior to
stratification, which coincided with the period of the
most severe light limitation. In contrast, modeled tem-
perature increases had a lasting and negative effect
throughout winter and spring due to an ongoing
enhancement of respiration and grazing. The potential
ability to counteract these increased losses by enhanced
primary production was strongly reduced by the light-
limited primary production. Primary production under
conditions of low light is generally assumed not be
greatly affected by temperature (Tilzer et al. 1986), as
was also assumed in our model. Assuming a stronger
temperature dependence enhances production in addi-
tion to respiration and grazing at higher temperatures.
This leads to a dampening – but not to a removal – of the
negative effect of temperature on algal biomass, which is
in line with more theoretical considerations of con-
sumer-resource dynamics (Vasseur and McCann 2005).

In addition to the direct temperature effect on phys-
iological processes, temperature may indirectly have a
lasting effect on algal dynamics by altering water column
stability, which may lead to an extension of the stratifi-
cation period (Lehman 2002; Winder and Schindler
2004). An individual storm event of a few days influ-
enced the vertical mixing intensity and thus simulated
algal dynamics during the following approximately
3 weeks, but not considerably longer. That is, an increase
in storm frequency by about once per month would have
pronounced effects on algal development. An increased
frequency of cyclones may additionally lead to more
cloudy weather and thus decreased global irradiance.
Our results suggest that this, in turn, may affect algal
growth during late winter and that we have to consider
changes in cloud cover in addition to temperature
and wind when making assumptions about the effects of
climate change on phytoplankton dynamics.

Overall, hypothesis 1 was confirmed in the sense
that mixing intensity (turbulence) rather than mixing
depth played a dominant role. However, the vertical
algal gradient strongly modified the impact of vertical
mixing, and irradiance was important during periods
with a small net export of algae from the euphotic
zone, i.e., during calm periods and when strong mixing
yielded a homogenous algal distribution. Unexpect-
edly, we found an alternation between abiotic and
biotic algal control even in late winter as grazing was
the dominant loss factor during calm periods.
Hypothesis 2 was confirmed as was hypothesis 3 in a
qualitative manner. However, in contrast to expecta-
tions, a further increase or prolongation of an already
high mixing intensity hardly decreased algal biomass,
whereas an increase of mixing from a low level strongly

influenced algal losses. This means that additional storm events following calm periods may substantially alter algal dynamics.

The potentials and limitations of the different approaches used to analyze the data complemented each other. The simulation model resolved important memory effects and short-term fluctuations not considered by the other approaches.

Appendix: model equations

Parameters are indicated by $\sim$, e.g., $\tilde{r}$. Their values are provided in Table 2. Variables taken from the time-series are indicated by (t) and are the following: water temperature (°C), $T(t)$; global irradiance (W m^{-2}), Globirad(t); vertical mixing intensity (day^{-1}) in the upper 20 m, mix$(t)_{0-20}$; deep vertical mixing intensity (day^{-1}), mix$(t)_{0-100}$ and mix$(t)_{8-100}$; chlorophyll a concentration (μg Chla l^{-1}) in the euphotic layer, chla$(t)_{0-20}$, and in the aphotic layer, chla$(t)_{20-100}$.

The functional response of primary production to light and temperature is written as being dependent on regulating factors. As a general rule, the regulating factors are non-dimensional and are 1 under optimum conditions and tend toward 0 when phytoplankton is in a limiting situation. The following indices were used:

i: we, le, tot referring to edible (we), less-edible (le) and total phytoplankton (tot), respectively;

j: 20, 100 referring to the euphotic layer (0–20 m) and the aphotic layer (20–100 m), respectively;

k: A, H referring to autotrophic processes (A) and heterotrophic processes (H), respectively.

Equations referring to method section "Analysis of the impact of deep vertical mixing and global irradiance on algal growth"

Production rate (day^{-1}):

$$\text{prod} = \tilde{r} \times \text{eI} \qquad (1)$$

with light regulation factor (eI) (see below).

Net algal losses (day^{-1}):

$$\text{loss} = \text{mix}_{\text{deep}} \times \left(1 - \frac{1}{\text{vag}_{\text{meas}}}\right). \qquad (2)$$

Deep vertical mixing intensity (day^{-1}):

$$\text{mix}_{\text{deep}} = \text{mix}(t)_{0-100} \times \frac{8}{20} + \text{mix}(t)_{8-100} \times \frac{12}{20}. \qquad (3)$$

Vertical algal gradient (measured):

$$\text{vag}_{\text{meas}} = \text{chla}(t)_{0-20} : \text{chla}(t)_{20-100}. \qquad (4)$$

Equations of the primary production module providing eI, the light regulation factor [adopted from Baretta et al. (1995) and Kotzur (2003)]

Primary production of algal group i per day (prod$_i$), averaged over the water column, is calculated as:

$$\text{prod}_i = \frac{1}{\tilde{d}} \int_0^{\tilde{d}} p_i(I(z)) \, dz \qquad (5)$$

with

$p_i(I(z))$: production at depth z of algal group i;

$I(z)$: photosynthetic active irradiance at depth z;

$I(z) = I(0) \times e^{-\kappa \times z}$ κ: vertical extinction coefficient (m^{-1}).

Substitution results in

$$\text{prod}_i = \frac{1}{\kappa \times \tilde{d}} \int_{I(\tilde{d})}^{I(0)} \frac{p_i(I)}{I} \, dI. \qquad (6)$$

For $p_i(I)$ the formulation of Steele (1962) was chosen:

$$p_i(I) = \tilde{r}_i \times \frac{I}{I\_\text{opt}} \times e^{\left(1 - \frac{I}{I\_\text{opt}}\right)}. \qquad (7)$$

The resulting function of the primary production is:

$$\text{prod}_i = \frac{1}{\kappa \times \widetilde{d}} \int\limits_{I(\widetilde{d})}^{I(0)} \frac{1}{I} \widetilde{r}_i \times \frac{I}{I\_\text{opt}} \times e^{\left(1 - \frac{I}{I\_\text{opt}}\right)} dI. \qquad (8)$$

Integration results in:

$$\text{prod}_i = \widetilde{r}_i \times \underbrace{\frac{1}{\kappa \times \widetilde{d}} \times \left(e^{\left(1 - \frac{I(\widetilde{d})}{I\_\text{opt}}\right)} - e^{\left(1 - \frac{I(0)}{I\_\text{opt}}\right)} \right)}_{\text{eI}}. \qquad (9)$$

Photosynthetic active radiation at the surface (W m^{-2}):

$$I(0) = \widetilde{q}_{\text{PAR}} \times \text{Globirad}(t). \qquad (10)$$

Extinction coefficient (m^{-1}):

$$\kappa = \widetilde{\text{turb}} + \widetilde{\text{selfsh}} \times A_{\text{tot},20}. \qquad (11)$$

Radiation integrated over the water column (W m^{-2}):

$$I\_m = I(0) \times \frac{(1 - e^{(-\kappa \times \widetilde{d})})}{\kappa \times \widetilde{d}}. \qquad (12)$$

Optimum irradiance (W m^{-2}):

$$I\_\text{opt} = \max\left(I\_m, \widetilde{I\_\text{opt}\_\text{min}}\right). \qquad (13)$$

Equations to describe algal dynamics

Algae in the euphotic layer: $A_{i,20}$ (mg C m^{-3}):

$$\frac{dA_{i,20}}{dt} = \left(\text{prod}_{i,20} - \text{resa}_{i,20} - \text{exud}_{i,20} - \text{resb}_{i,20}\right)$$
$$\times A_{i,20} - \text{mix}_{\text{deep}} \times \left(A_{i,20} - A_{i,100}\right)$$
$$- M_{i,20} \times eT_{20,H} \times A_{i,20} - \text{sed}_i \times A_{i,20}. \qquad (14)$$

Algae in the aphotic layer: $A_{i,100}$ (mg C m^{-3}):

$$\frac{dA_{i,100}}{dt} = \left(-\text{resb}_{i,100}\right) \times A_{i,100} + \text{mix}_{\text{deep}}$$
$$\times \widetilde{c} \times \left(A_{i,20} - A_{i,100}\right) - M_{i,100} \times eT_{100,H}$$
$$\times A_{i,100} + \text{sed}_i \times \widetilde{c} \times A_{i,20} - \text{sed}_i \times \widetilde{c} \times A_{i,100}. \qquad (15)$$

Production rate (day^{-1}):

$$\text{prod}_{i,20} = \widetilde{r}_i \times \min\left(eT_{20,A}, \text{eI}\right). \qquad (16)$$

Activity dependent respiration rate (day^{-1}):

$$\text{resa}_{i,20} = \widetilde{\text{pura}} \times \left(\text{prod}_{i,20} - \text{exud}_{i,20}\right). \qquad (17)$$

Activity dependent exudation rate (day^{-1}):

$$\text{exud}_{i,20} = \widetilde{\text{puea}} \times \text{prod}_{i,20}. \qquad (18)$$

Basal respiration rate (d^{-1}):

$$\text{resb}_{i,j} = \widetilde{\text{srs}}_i \times eT_{j,H}. \qquad (19)$$

Dynamic mortality rate (day^{-1}):

$$\frac{dM_{i,j}}{dt} = \frac{1}{\widetilde{\tau}_i} \times \left(\widetilde{m}_i \times A_{i,j}^{\widetilde{a}} - M_{i,j}\right). \qquad (20)$$

Mimicking grazers with algal dependent growth and first order mortality.

Sedimentation rate (day^{-1}):

$$\text{sed}_i = \begin{cases} \dfrac{\widetilde{\text{ssed}}_i}{(\text{mix}(t)_{0-20} + 0.1)}, & \text{if } \text{mix}(t)_{0-100} \leqslant 0.1 \\ 0, & \text{if } \text{mix}(t)_{0-100} > 0.1 \end{cases}. \qquad (21)$$

It is assumed that sedimentation depends on the mixing intensity (turbulence) within the euphotic layer if the deep vertical mixing intensity is small. Otherwise sedimentation plays no role, as $\text{mix}(t)_{0-100} > 0.1$ implies high values of $\text{mix}(t)_{0-20}$. During the winter and spring, 50% of the values of $\text{mix}(t)_{0-20}$ fell into the range of 0.05 and 0.43, resulting in a sedimentation rate between 13 and 4% if $\text{mix}(t)_{0-100} \leq 0.1$. This is consistent with the sedimentation rates reported by Güde and Gries (1998) and Tilzer (1984) (maximum values 10 and 15%, respectively).

Temperature regulation factor:

$$eT_{j,k} = \widetilde{Q}_{10,k} \frac{(T_j(t) - 10)}{10}. \qquad (22)$$

Vertical algal gradient (modeled):

$$\text{vag}_{\text{mod}} = A_{\text{tot},20} : A_{\text{tot},100}. \qquad (23)$$

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