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# Growth rates of phytoplankton under fluctuating light

ELENA LITCHMAN
*University of Minnesota, 1987 Upper Buford Circle, St. Paul, MN 55108, U.S.A.*

**SUMMARY**

1. The effect of light fluctuations on the growth rates of four species of freshwater phytoplankton was investigated. Experimental light regimes included constant irradiance and fluctuations of a step function form, with equal proportion of high (maximum of 240 μmol photons $m^{-2}$ $s^{-1}$) and low light (minimum of 5 μmol photons $m^{-2}$ $s^{-1}$) (or dark) in a period. Fluctuations of 1, 8 and 24-h periods were imposed over several average irradiances (25, 50, 100 and 120 μmol photons $m^{-2}$ $s^{-1}$).
2. Growth rate responses to fluctuations were species-specific and depended on both the average irradiance and the period of fluctuations. Fluctuations at low average irradiances slightly increased growth rate of the diatom *Nitzschia* sp. and depressed growth of the cyanobacterium *Phormidium luridum* and the green alga *Sphaerocystis schroeteri* compared to a constant irradiance.
3. Fluctuations at higher average irradiance did not have a significant effect on the growth rates of *Nitzschia* sp. and *Sphaerocystis schroeteri* (fluctuations around saturating irradiances) and slightly increased the growth rates of the cyanobacteria *Anabaena flos-aquae* and *Phormidium luridum* (when irradiance fluctuated between limiting and inhibiting levels).
4. In general, the effect of fluctuations tended to be greater when irradiance fluctuated between limiting and saturating or inhibiting levels of a species growth-irradiance curve compared to fluctuations within a single region of the curve.
5. The growth rates of species under fluctuating light could not always be predicted from their growth-irradiance curves obtained under constant irradiance. When fluctuations occur between limiting and saturating or inhibiting irradiances for the alga and when the period of fluctuations is long (greater than 8 h), steady-state growth-irradiance curves may be insufficient to predict growth rates adequately. Consequently, additional data on physiological acclimation, such as changes in photosynthetic parameters, may be required for predictions under non-constant light supply in comparison to constant conditions.

*Keywords:* growth rate, phytoplankton, fluctuating light

## Introduction

Environmental variability is an important structuring force in ecological communities (Nisbet & Gurney, 1982; Chesson, 1994). Fluctuations in physical factors and resources should have an especially strong effect on community structure and dynamics in aquatic ecosystems, due to the tight coupling between physical forcing and biota (Steele, 1985). Light is a major resource for phytoplankton and has a complex pattern of spatial and temporal variability. Temporal frequencies of light variation range from fast fluctuations caused by surface waves (on the order of 10 Hz) to seasonal changes of irradiance ($10^{-7}$ Hz). The light levels experienced by phytoplankton cells can extend from the complete darkness in the aphotic zone to irradiances greater than 1500 μmol photons $m^{-2}$ $s^{-1}$ at the surface. A number of studies demonstrated that fluctuations in irradiance can affect major physiological processes such as photosynthesis and respiration (Marra, 1978; Quéguiner & Legendre, 1986; Ferris & Christian, 1991; Kroon *et al.*, 1992; Kromkamp &

Correspondence and present address: Elena Litchman, Smithsonian Environmental Research Center, PO Box 28, Edgewater, MD 21037, U.S.A. E-mail: litchman@serc.si.edu

Limbeek, 1993; Ibelings *et al*., 1994). A variety of responses has been documented: rates of photosynthesis and productivity could be enhanced (e.g. Marra, 1978; Mallin & Paerl, 1992), depressed (Kroon *et al*., 1992) or not changed (Yoder & Bishop, 1985) by fluctuations, compared to light regimes without fluctuations. Fewer studies have looked at the effects of fluctuations in irradiance on growth rates. Growth rate responses to fluctuations also appear to be species-specific (Gibson, 1985; Ibelings *et al*., 1994; Nicklisch, 1998) and highly variable: growth rates can increase (Gibson, 1985), decrease (Nicklisch, 1998) or remain the same (Cosper, 1982) compared to the growth rates under constant light. Different regimes of temporal variability in light supply may stimulate different species or taxonomic groups, which can lead to changes in phytoplankton community composition (Litchman, 1998).

Changes in phytoplankton species composition strongly influence the biomass and community structure of higher trophic levels, as well as various ecosystem processes such as the carbon, nitrogen, phosphorus and silica cycles (Falkowski, 1994; Smith & Gilbert, 1995). Therefore, it is necessary to understand and be able to predict the effects of dynamic light regimes on phytoplankton growth. Previous studies on the effects of fluctuating light report a wide variation of growth rate responses, both in direction and magnitude. Quéguiner & Legendre (1986) showed that growth rates of a green alga were similar under constant light and a fluctuating light of high frequency (10 Hz), but were depressed by lower frequency fluctuations (1 and 0.1 Hz). Other studies have shown growth enhancement of some species of algae by a rapidly fluctuating light (e.g. Greene & Gerard, 1990). Gibson & Fitzsimons (1992) found that the growth rates of two diatoms grown under light–dark cycle were depressed by an interruption of a dark period. Nicklisch (1998) found that fluctuating light depressed growth rates of several species from different taxonomic groups, with cyanobacteria experiencing the greatest and diatoms the smallest decrease, compared to their growth rates under constant light. The depression of growth rates was smaller under a fluctuating light with a longer time period.

Most previous studies used widely different fluctuation regimes (different average irradiances, amplitudes and frequencies of fluctuations) on different species, which complicates comparisons between species or fluctuation regimes. Also, there was little attempt to predict growth rates under dynamic light regimes from the available physiological data. The goal of this study was to examine the effects of the same fluctuation regimes on species from different major taxa and assess how well such effects can be predicted based on species growth under constant light. The approach for predicting growth rates under fluctuating light used in this paper is similar to that proposed by Thornley (1974) and Dromgoole (1988) to predict rates of photosynthesis. They suggested that photosynthetic rates under fluctuating light could be predicted from steady state photosynthesis-irradiance curves. Two methods can be applied, depending on the frequency of fluctuations. When fluctuations are fast compared to the physiological response times, algae may integrate the irradiance. In this case photosynthesis (or growth) rate under fluctuating light would be equal to the rate under constant light of the same total irradiance. When fluctuations are slow, algae are able to adjust their photosynthesis (or growth) rates to the new irradiance, so that the photosynthetic (or growth) rate under fluctuating light would be the average of the rates under high and low light levels. Because it is unknown whether the chosen fluctuations are fast or slow compared to the response times of growth rates, both methods were used to predict growth rates under different dynamic light conditions.

Although in nature many fluctuation regimes of different amplitude and period are superimposed, this study used only square-wave fluctuations. The main intent was to compare fluctuating and constant light regimes, rather than mimic natural light fluctuations. Nevertheless, as previous studies with phytoplankton suggest, valuable insights can be gained from experiments even with simple laboratory systems (Sommer, 1990).

To reveal the effects of fluctuations *per se*, treatments had the same daily irradiance, but differed in the degree of temporal variability of light supply. Because the effect of fluctuations might depend on the absolute irradiance levels (Dromgoole, 1988; Stramski *et al*., 1993), fluctuations were applied at several average irradiances, from limiting to saturating or inhibiting levels. Within each average irradiance fluctuations of several periods were used, from 1 h to 24 h. As fluctuations matching characteristic

response times of a process should have a strong effect on the process (Abbott, 1993), periods comparable with important photophysiological time scales of phytoplankton were chosen: less than 2 h, associated with changes in the electron transport of photosynthesis and greater than 5 h, associated with pigment turnover (Neale & Marra, 1985). In nature, fluctuations of similar frequencies may result from vertical mixing processes in the epilimnion and metalimnion (Denman & Gargett, 1983; Imberger, 1985; Imboden, 1990).

## Methods

The effects of fluctuating light on growth rates of four common species of freshwater phytoplankton were investigated in two types of experiments. First, growth-irradiance curves were determined for each species under constant light. Second, growth rates of each species were determined under different fluctuation regimes. The following species were used: cyanobacteria *Anabaena flos-aquae* (Lyng.) Brébisson, obtained from the American Type Culture Collection (clone 22664) and *Phormidium luridum* var. *olivace* Boresch (UTEX 426) from the University of Texas Culture collection; diatom *Nitzschia* sp., obtained from the Plant Biology Department of the University of Minnesota; and green alga *Sphaerocystis schroeteri* Chodat (Plant Biology Department, University of Minnesota). These species can be quite common in many temperate lakes. For convenience, each species will be referred to by its genus name. Growth rates of each species in all experiments were determined in batch monocultures (Kilham, 1978; Langdon, 1987). Each culture was preconditioned to a given experimental irradiance (or the average irradiance for fluctuating light treatments) for two weeks, which corresponded to several generation times, even under the lowest irradiances used (e.g. for a growth rate of 0.2 $day^{-1}$ generation time is 3.5 days). Cultures were grown in WC freshwater medium (Guillard, 1975) in 1 L Erlenmeyer flasks (750 mL culture volume) at 20 °C. Cultures were shaken several times a day; no continuous stirring was applied. The initial cell or filament densities were low (10–50 cells (or filaments)/mL) to minimize cell interactions due to competition for nutrients and light. Irradiance was provided by 'cool white' fluorescent lamps (Philips) and measured with a quantum scalar ($4\pi$) sensor (Biospherical Instruments, QSL-100, San Diego, CA). Irradiance was adjusted with neutral density screens, so that light levels in the center of the flask were within 1–1.5 μmol photons $m^{-2}$ $s^{-1}$ of the assigned irradiance.

Experiments were run for 6 or 7 days, and 25–50 mL samples were taken every day or every two days and preserved with Lugol's solution (Wetzel & Likens, 1991). Due to low cell density, especially in the beginning of experiments, samples were concentrated before counting by allowing cell settling in graduated cylinders for at least 24 h and by aspirating 50–80% of the sample volume, depending on the cell density. Concentrated samples were counted in 5-mL settling chambers using the inverted microscope technique (Lund *et al*., 1958). At least 200 cells or colonies were counted in each sample.

The growth rates of species were calculated by fitting a least-squares linear regression to the natural logarithm-transformed cell concentrations from individual replicates plotted against time. The mean of all replicates for each light regime was then calculated. The linear part of the curve corresponding to exponential growth was used, so that the effects of shading or decreasing nutrient concentrations were minimal (density-independent growth). Each growth rate regression was fitted to at least 4–5 data points.

### *Growth-irradiance curves*

In this set of experiments, growth rates of each species were determined under different constant irradiances as described in the previous section. There were three replicates at each irradiance. For *Nitzschia* and *Sphaerocystis* a Monod function was fit to the data (Marquardt–Levenburg least squares minimization method) using TableCurve2D software package (Jandel Scientific, 1992):

$$\mu = \mu_{max}\frac{I}{I+k} - r \qquad (1)$$

where $\mu$ is the growth rate ($day^{-1}$), $\mu_{max}$ is the maximum growth rate ($day^{-1}$), $I$ is the irradiance (μmol $m^{-2}$ $s^{-1}$), $k$ is a half-saturation constant (μmol $m^{-2}$ $s^{-1}$), and $r$ is the metabolic loss rate (respiration) ($day^{-1}$). The lower limit for parameter estimates was set to 0 and the upper limit to 2, 1000 and 1 for $\mu$, $k$ and $r$, respectively.

*Anabaena* and *Phormidium* had decreased growth rates at irradiances above 50 and 100 μmol $m^{-2}$ $s^{-1}$,

respectively, possibly due to photoinhibition, and a Monod function with a photoinhibition term (Megard *et al*., 1984) was used instead:

$$\mu = \mu_{max} \frac{I}{I + k + \frac{I^2}{k_{inh}}} - r \quad (2)$$

where $\mu$, $I$, and $r$ are as in eqn 1, $\mu'_{max}$ is the theoretical maximum growth rate ($day^{-1}$), $k_1$ is the constant characterizing growth response to low irradiances ($\mu$mol photons $m^{-2}$ $s^{-1}$) and $k_{inh}$ is the photoinhibition constant ($\mu$mol photons $m^{-2}$ $s^{-1}$). Note that when $k_{inh}$ approaches infinity (i.e. no photoinhibition), eqn 2 becomes equivalent to eqn 1.

Eqn 2 was also fitted to the data for *Nitzschia* and *Sphaerocystis*, the species that did not exhibit noticeable depression of growth at the high irradiances used in these experiments. The inhibition constant was very large and had a less than 0.0001 relative contribution to explaining the total variance, so that eqn 1 was used for these two species. The parameter values for $\mu'_{max}$, $k$ and $r$ obtained by fitting eqn 1 were similar to the corresponding parameters obtained by fitting eqn 2.

### *Growth rates under different fluctuation regimes*

In this set of experiments, the effect of temporal variability in light supply on the growth rate of each species was investigated. To examine the effects of light fluctuations over different parts of growth-irradiance curves, fluctuations around several average irradiances were tested. At chosen irradiances, species were grown in monocultures under light regimes with the same total daily irradiance, but differing temporal distributions, including constant light (Table 1). Fluctuations of a square-wave form were achieved by periodically turning on and off additional light sources. The periods of high and low irradiance were of equal duration. Fluctuation treatments were assigned randomly to environmental chambers. There were two flasks for each treatment for each species. Flasks within a treatment were rotated every day to minimize effects of spatial heterogeneity in other environmental factors. There were two runs for each experiment, except for *Phormidium* at 25 $\mu$mol photons $m^{-2}$ $s^{-1}$. Growth rates of each species were determined as described above and compared among treatments within each average irradiance using a one-way ANOVA (Wilkinson, 1989). Data from both runs were pooled. Growth rates of *Sphaerocystis*, *Nitzschia* and *Phormidium* were determined for all experimental light regimes; *Anabaena*'s growth rate responses were determined with adequate replication only for fluctuations at two average irradiances, 50 and 120 $\mu$mol photons $m^{-2}$ $s^{-1}$ (Table 1).

**Table 1** Light regimes used in the experiments. Irradiances are expressed in $\mu$mol photons $m^{-2}$ $s^{-1}$. T is the fluctuation period of the square-wave fluctuations with equal duration of high and low light or darkness

| Treatment | Irradiance | | | |
|---|---|---|---|---|
| Average irradiance | 25 | 50 | 100 | 120 |
| Constant light | 25 | 50 | 100 | 120 |
| Fluctuating light, $T$ = 1 h | 15–35 | – | 65–135 | – |
| Fluctuating light, $T$ = 8 h | 15–35 | 15–85 | 65–135 | 35–205 |
| Fluctuating light, $T$ = 24 h | – | 15–85 | – | 35–205 |
| Light–dark, T = 24 h | – | 0–100 | – | 0–240 |

The fitted growth-irradiance curves were used to predict growth rates under different fluctuation regimes used in an independent set of experiments. Growth rates for the fluctuating light treatments were calculated (a) as growth rates at the average irradiance, assuming integration of irradiances: ($\mu(I_{fluct}) = [\mu[(I_{high} + I_{low})/2]$), and (b) as the averages of growth rates at high and low levels of fluctuation, assuming integration of growth rates ($\mu(I_{fluct}) = [\mu(I_{high}) + \mu(I_{low})]/2$. These are referred to as IA and GRA method, respectively.

To assess how the period of fluctuations affects the predictions, predicted growth rates were plotted against observed growth rates and linear regressions were fitted to the data, separately for each fluctuation regime. Within each fluctuation regime, data for all species and average irradiances were combined.

## Results

### *Growth-irradiance curves*

The growth rates of *Anabaena* and *Phormidium* decreased at higher irradiances, possibly due to photoinhibition, while the growth of *Nitzschia* and *Sphaerocystis* was not inhibited at those irradiances (Fig. 1). Of the four species, *Anabaena* was inhibited at the lowest irradiance and had the lowest realized maximum growth rate (Fig. 1, Table 2). For each species, $I_k$, the irradiance at the onset of saturation

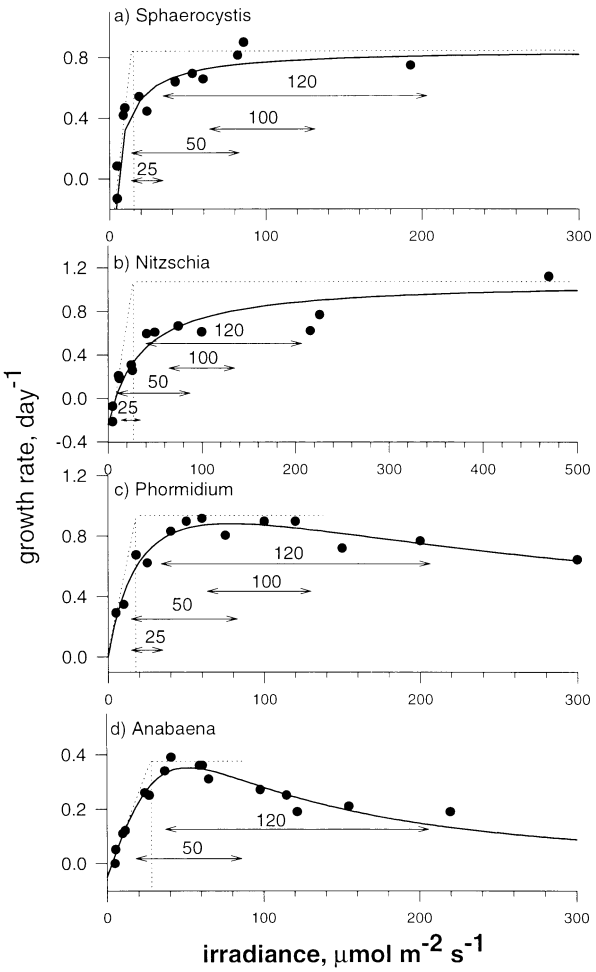


**Fig. 1** Growth–irradiance curves based on the continuous light data: (a) *Sphaerocystis* (b) *Nitzschia* (c) *Phormidium* (d) *Anabaena*. Each data point is a mean of the slopes of the three replicate regressions. Solid curve in each graph represents a model fit. Dashed lines show how $I_k$, the irradiance at the onset of saturation, was determined. Horizontal arrows show fluctuation amplitudes used in experiments, and the numbers above the arrows are average irradiance levels.

of growth, was determined as the intercept of the linear part of the growth-irradiance curve and the maximum growth rate or its asymptote. *Nitzschia* had the highest $I_k$ among the four species, and *Phormidium* had the lowest $I_k$ (Table 2).

### *Effects of fluctuating light on growth rates*

The temporal regime of light supply (constant light vs. fluctuating light of different fluctuation periods) in some cases had a significant effect on the growth rates of species. Growth rate responses were species-specific and depended on the average irradiance and the period of fluctuations (Fig. 2). All species tested were sensitive to fluctuations at low average irradiances. Fluctuations tended to have a greater effect on the growth rates of *Sphaerocystis* and *Nitzschia* when they occurred around the transition from the limiting to the saturating part of their growth-irradiance curves, around their $I_k$ values (at 25 μmol photons $m^{-2}$ $s^{-1}$ for *Sphaerocystis* and 25, 50 and 100 μmol photons $m^{-2}$ $s^{-1}$ average irradiances for *Nitzschia*). At low average irradiances, fluctuations tended to decrease growth rate of *Sphaerocystis* (except for the light:dark treatment at 50 μmol photons $m^{-2}$ $s^{-1}$) and slightly increase the growth rate of *Nitzschia*. The growth rate responses were sensitive to the period of fluctuations (Fig. 2). At higher average irradiances (100 and 120 μmol photons $m^{-2}$ $s^{-1}$ for *Sphaerocystis* and 120 μmol photons $m^{-2}$ $s^{-1}$ for *Nitzschia*), fluctuations did not significantly change growth rate compared to constant light (Fig. 2), even though the absolute fluctuation amplitudes were the same or even greater than at lower average irradiances.

The growth rate of *Phormidium* was sensitive to the regime of light supply at the lowest irradiance used (25 μmol photons $m^{-2}$ $s^{-1}$) and at the highest irradiance (120 μmol photons $m^{-2}$ $s^{-1}$) (Fig. 2c). The lowest average irradiance was close to the $I_k$ of the species, and the highest irradiance level was in the region where photoinhibition of growth may have occurred.

**Table 2** Best-fit values for the parameters of eqn 1 for *Nitzschia* and *Sphaerocystis* and of eqn 2 for *Anabaena* and *Phormidium*. $I_k$, the irradiance at the onset of saturation, determined as the intercept of the linear part of the growth-irradiance curve and the maximum growth rate or its asymptote

| Alga | $\mu_{max}$ ($day^{-1}$) | $k$ (μmol photons $m^{-2}$ $s^{-1}$) | $k_1$ (μmol photons $m^{-2}$ $s^{-1}$) | $k_{inh}$ (μmol photons $m^{-2}$ $s^{-1}$) | $r$ ($day^{-1}$) | $R^2$ | $I_k$ (μmol photons $m^{-2}$ $s^{-1}$) |
|---|---|---|---|---|---|---|---|
| *Anabaena* | 1.19 | – | 42 | 61 | 0.1 | 0.93 | 25 |
| *Nitzschia* | 1.31 | 34.5 | – | – | 0.24 | 0.89 | 35 |
| *Sphaerocystis* | 1.44 | 6 | – | – | 0.6 | 0.87 | 19 |
| *Phormidium* | 1.4 | | 22 | 267 | 0.001 | 0.92 | 17 |

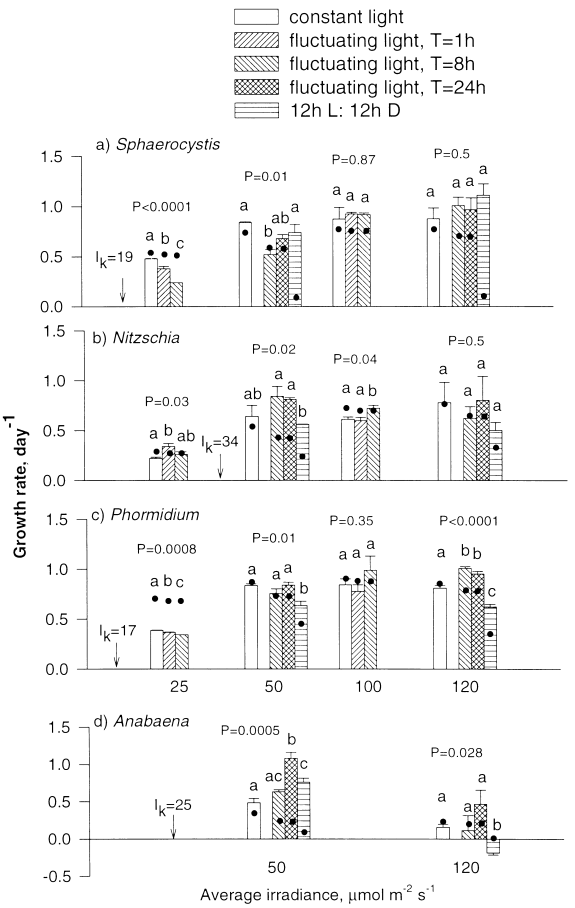


**Fig. 2** Growth rates (mean ± SE) of four species under different light regimes. Within each average irradiance, treatments differing in the temporal distribution of light supply were compared by one-way ANOVA. Values with no common letters were significantly different (pairwise comparisons using Student-Newman–Keuls test, $P < 0.05$). Black dots represent growth rates predicted based on irradiance averaging for constant light treatments and growth rate averaging for fluctuating light treatments. For fluctuating light treatments, irradiance averaging method predicts same growth rates as for constant light treatments.

At 25 μmol photons $m^{-2}$ $s^{-1}$ fluctuations had a negative effect on growth rates, while fluctuations around 120 μmol photons $m^{-2}$ $s^{-1}$ enhanced growth rate compared to constant light (Fig. 2c). Also, at 50 μmol $m^{-2}$ $s^{-1}$ average irradiance, the light–dark treatment was significantly different from the other treatments (Fig. 2c).

At 50 μmol photons $m^{-2}$ $s^{-1}$ average irradiance, *Anabaena* had significantly higher growth rates under fluctuating light of a 24-h period as well as the light–dark regime (Fig. 2d). At the average irradiance level of 120 μmol photons $m^{-2}$ $s^{-1}$ fluctuations of a 24-h period led to a significantly higher growth rate compared to other treatments (Fig. 2d).

*Comparison of predicted and observed growth rates*

To determine whether steady-state growth-irradiance curves can be used to predict growth rates under dynamic light regimes, the observed growth rates of each species were compared to predicted growth rates. For each species, growth rates under fluctuating light were estimated from its growth-irradiance curve in two ways: based on the assumption of (a) averaging of irradiance (IA), and (b) averaging of growth rates (GRA) (see Methods section). In the case of perfect agreement between predicted and observed growth rates, a regression line would have an intercept of 0, a slope coefficient of 1 and $R^2$ of 1. For the constant light treatments, the observed growth rates agreed well with the growth rates predicted from individual growth-irradiance curves: the regression line was not significantly different from a 1:1 line of a perfect prediction (as tested by ANCOVA, Table 3). Under fluctuating light, the agreement between the predicted and observed growth rates was poorer than under constant light. For the fluctuating regimes of 1 and 8-h periods the regression line did not differ significantly from a 1:1 line, but the $R^2$ was lower than for the constant light regression line (Table 3). The agreement between predicted and observed growth rates for 8 h fluctuating period was similar to the 1-h period fluctuation regime (similar $R^2$). However, when fluctuation period increased further, to 24 h, the discrepancy between the observed growth rates and the growth rates predicted either by averaging irradiance or growth rates, was much greater than for fluctuating regimes with shorter periods (Table 3). The agreement between the observed and predicted growth rates (IA method) was better for the light–dark fluctuations than for the high light: low light fluctuations of the same period. Also, for light–dark regime the GRA method gave much poorer estimates compared to IA method (Table 3), often underestimating growth rates (Fig. 2); for all other fluctuation regimes the two methods gave very similar results.

The GRA method assumes that $\mu(I_{high})$ and $\mu(I_{low})$ contribute equally to estimating the average growth rate under fluctuating light, $\mu(I_{fluct})$; or that it takes equal time for the growth rate to adjust to low and high irradiance. To determine whether relaxing this

**Table 3** Linear regression of observed vs. predicted growth rates of all four species for five light regimes differing in the temporal distribution of light supply. Predicted growth rates under fluctuating light were calculated from the growth-irradiance curves based on the assumption of (a) averaging of irradiance (IA): $\mu(I_{fluct}) = \mu[(I_{high} + I_{low})/2]$ and (b) averaging of growth rates (GRA): $\mu(I_{fluct}) = [\mu(I_{high}) + \mu(I_{low})]/2$. SE of the mean for each parameter estimate is given in parentheses. Regression lines that are significantly different from 1 : 1 line (as compared by ANCOVA) are marked with an asterisk (both the slope and the intercept were tested, $P < 0.05$)

| Light regime | Prediction method | Intercept | Slope | $R^2$ | *P*-value of regression |
|---|---|---|---|---|---|
| Constant light | IA | 0.03 (0.09) | 0.95 (0.14) | 0.6 | < 0.0001 |
| Fluctuating light, | IA | 0.0009 (0.19) | 0.85 (0.28) | 0.48 | 0.012 |
| $T$ = 1 h | GRA | 0.018 (0.18) | 0.86 (0.26) | 0.52 | 0.008 |
| Fluctuating light, | IA | 0.041(0.13) | 0.93 (0.18) | 0.44 | < 0.0001 |
| $T$ = 8 h | GRA | 0.11 (0.12) | 0.92 (0.20) | 0.39 | < 0.0001 |
| Fluctuating light, | IA | 0.62 (0.17)* | 0.27 (0.26)* | 0.06 | 0.3 |
| $T$ = 24 h | GRA | 0.65 (0.17)* | 0.27 (0.28)* | 0.04 | 0.35 |
| Light–dark, | IA | 0.06 (0.19) | 0.83 (0.27) | 0.29 | 0.007 |
| $T$ = 24 h | GRA | >0.52 (0.13)* | 0.31 (0.5)* | 0.02 | 0.54 |

assumption and allowing unequal contribution of $\mu(I_{high})$ and $\mu(I_{low})$ to $\mu(I_{fluct})$ could lead to better prediction, I used a stepwise linear regression model, with $\mu(I_{high})$ and $\mu(I_{low})$, estimated from the growth-irradiance curves of each species, as raw predictors. Predictors (independent variables) with low significance do not contribute significantly to predicting the dependent variable. For the shortest fluctuation period (1 h), only the growth rate at the low irradiance was a significant predictor ($P < 0.001$, coefficient of 0.97). For the intermediate fluctuation period (8 h), both $\mu(I_{high})$ and $\mu(I_{low})$ were significant predictors ($P = 0.001$ and 0.06 with coefficients of 0.61 and 0.42, respectively). For the longest fluctuation period (24 h), the high light growth rate was a significant predictor ($P < 0.001$, coefficient of 1.1). The less restrictive model also predicted growth rates under light–dark fluctuations significantly better than the GRA model (with $\mu(I_{high})$ as a significant predictor, $P < 0.001$ and coefficient of 0.71).

The agreement between observed and predicted growth rates was also considered for each species separately. Three major aspects were analyzed: whether the agreement between predicted and observed growth rates depends on (a) the period of fluctuations (b) average irradiance, and (c) method of prediction (IA method or GRA method).

Under constant light, growth rates of each species agreed well with predictions, except for *Phormidium* under 25 μmol photons $m^{-2}$ $s^{-1}$ light level, where they were significantly lower. For *Sphaerocystis*, in the fluctuating light treatments, predictions based on irradiance averaging were similar to predictions based on growth rate averaging, except for the light–dark fluctuations, where the first method led to a much better agreement between the observed and predicted rates (Fig. 2), possibly because of the high loss rate, *r*. This suggests that fluctuations even of the 24-h period were relatively fast compared to the growth response time. For the estimates based on averaging irradiances, the discrepancy between observed and predicted growth rates was the greatest for fluctuations around 25 μmol photons $m^{-2}$ $s^{-1}$(close to its $I_k$) although at this average irradiance the amplitude of fluctuations was the smallest (Fig. 2). Growth rates were actually depressed more by fluctuations at this average irradiance than was predicted by either the IA or GRA method, and this depression was greater under the longer fluctuation period (Fig. 2).

Under fluctuating light regimes, the greatest discrepancy between observed and predicted growth rates of *Nitzschia* was for fluctuations around 50 μmol photons $m^{-2}$ $s^{-1}$, which is within the non-linear part of *Nitzschia*'s growth-irradiance curve (Fig. 1). At this light level, the irradiance averaging method gave better estimates than the growth rate averaging method, especially for the light–dark fluctuations (Fig. 2). At 120 μmol photons $m^{-2}$ $s^{-1}$ average irradiance, the growth rate under the light–dark cycle was in between the IA method estimate and the GRA estimate, which indicates that these fluctuations were of an intermediate time scale compared to the growth time scale.

For *Phormidium* under light–dark fluctuations at both 50 and 120 μmol photons $m^{-2}$ $s^{-1}$ average irradiances, the IA method overestimated and the GRA method underestimated growth rates, which

indicates that this fluctuation regime was of an intermediate period compared to the growth response time. For other fluctuation regimes, the estimates based on both methods were close to the observed growth rates, except for the 120 μmol photons $m^{-2}$ $s^{-1}$ average irradiance, where the GRA method significantly underestimated growth rates under both 8 h and 24 h fluctuation periods (Fig. 2).

For *Anabaena*, under fluctuating regimes, both the IA and GRA methods gave similar estimates; the difference between the two methods was the greatest for the light–dark fluctuation regime (Fig. 2). At 50 μmol photons $m^{-2}$ $s^{-1}$, fluctuations led to much higher growth rates than predicted from the growth-irradiance curve. At 120 μmol photons $m^{-2}$ $s^{-1}$ average irradiance, the agreement between observed and predicted growth rates was better than at 50 μmol photons $m^{-2}$ $s^{-1}$, even though the amplitude of fluctuations was greater (Fig. 2).

## Discussion

### *Growth rate responses to fluctuating light*

Temporal variability of light supply had a significant effect on the growth rates of four species tested. The dependence of growth rate responses to light fluctuations on the species, the average irradiance and the period of fluctuations observed in this study agrees with the results of previous studies on the effects of light fluctuations, which reported highly variable and species-specific effects (Table 4). Among four species tested in this study, the diatom was not negatively affected by fluctuations, which agrees with the results of Nicklisch (1998) who found that fluctuations had a least negative effect on growth rates of diatoms compared to other taxa (Table 4). In previously reported community experiments, relative abundance of diatoms, *Nitzschia* sp. in particular, was also increased by fluctuations (Litchman, 1998). Post *et al.* (1984) suggested that diatoms may be more capable than other algal groups of optimizing a relatively sudden exposure to high light by rapidly increasing their division rate.

Under constant light conditions, growth rates of both cyanobacteria were depressed at higher irradiances, while the green alga and the diatom did not exhibit growth inhibition. Greater sensitivity of cyanobacteria to high irradiances compared to other taxa might be a general feature of this taxon (Richardson *et al.*, 1983). The results of this study suggest that growth suppression under high irradiances (photoinhibition) may be reduced by fluctuations. These findings agree with previous studies that demonstrated enhancement of photosynthesis and productivity under fluctuating light due to reduced photoinhibition (Table 4). Inhibition of growth under high irradiances can be caused by inhibition of photosynthesis (Neale & Marra, 1985), increased respiration rates at high irradiances (Falkowski *et al.*, 1994) or increased allocation of resources to protection (avoidance) and repair mechanisms and thus a reduction in the allocation to growth (Raven, 1994). If there is a delay in the development of these processes, then fluctuations occurring on time scales shorter than times to reach steady states for the above mentioned processes may enhance growth rates.

### *Comparison of predicted and observed growth rates*

As expected from theoretical considerations (Thornley, 1974; Dromgoole, 1988), fluctuations had greater effect on growth rates of a species when they occurred around the non-linear part of their growth-irradiance curve: around the $I_k$, the irradiance at the onset of saturation, or around the transition from saturation to inhibition. The non-linear (hyperbolic) dependence of growth on irradiance can lead to altered growth rates under fluctuating light. If fluctuations occur in a non-linear part of the curve, the resulting average growth rate, at fluctuating irradiance can be lower than a growth rate at a constant irradiance level that equals the average of the two fluctuating irradiances. The depression can occur when fluctuations are relatively slow, so that an alga integrates the growth rate rather than the irradiance. In the case of fast fluctuations, growth rate under fluctuating light should be the same as under constant light of the same average irradiance. A similar steady-state explanation has been proposed for decreased rates of photosynthesis under slowly fluctuating light (Thornley, 1974; Dromgoole, 1988). The depression of the growth rates by fluctuations was, however, in some cases greater than predicted from its growth-irradiance curve by either method. In some cases growth rate changes due to fluctuations differed from those predicted by steady state irradiance curves not only in magnitude but also in direction.

According to the theoretical analysis by Thornley (1974) and Dromgoole (1988), if fluctuations are fast compared to growth response time, the irradiance averaging (IA) method should give better estimates of growth rates. The growth rate averaging (GRA) method should work better when fluctuations are slow compared to the growth response time, so that growth rates adjust to a change in irradiance. Also, the two methods should give similar predictions if fluctuation amplitude is small, or if fluctuations occur in the linear part of the growth-irradiance curve. Overall, the irradiance averaging method gave better estimates of growth rates under relatively fast fluctuating light regimes (< 8 h). The IA method also worked better than the GRA method for light–dark fluctuations, which suggests that applied fluctuations (from 1 to 24-h period) may be relatively fast compared to the response times of growth rates. A possible explanation for growth rates in the light–dark treatments being higher than predicted by the GRA method is that during the dark part of the cycle growth rate was not zero or negative as predicted by the steady state curve, but still positive (e.g. due to postillumination $CO_2$ fixation and/or use of stored carbohydrates for synthesis of protein in the dark (Falkowski & Raven, 1997)).

When the growth rates at low and high ends of the fluctuation amplitude, calculated from growth-irradiance curves, were used to predict resulting growth rate under fluctuating light, the significance of these two predictors depended on the period of fluctuations. Under fast fluctuations only the growth rate at low end was a significant predictor. Under slower fluctuations, growth rates at both low and high ends of a fluctuation amplitude were significant, which suggests that growth rate acclimation to high light may take longer than to low light. Some studies on photosynthetic acclimation to changing irradiance have also found that the low to high light acclimation takes longer than the high to low light acclimation (Prézelin *et al*., 1991).

The results of this study indicate that when fluctuations occur between limiting and saturating or inhibiting irradiances for the alga and when the period of fluctuations is long (greater than 8 h), steady-state growth-irradiance curves may be insufficient to predict growth rates adequately. In these cases, growth-irradiance data should be complemented with an investigation of the fluctuating light effects on photosynthesis, respiration and cellular pigment ratios, because growth rate of phytoplankton depends directly on these processes (Cullen, 1990; Cloern *et al*., 1995). Previous studies on the effects of fluctuating light showed that the number of photosynthetic units and the maximum rates of photosynthesis often increase in response to fluctuations (Table 4). Higher $P_{max}$ may be beneficial under intermittent exposure to high irradiances (Geider *et al*., 1985). Cullen & McIntyre (1998) suggested that phytoplankton with a high excess photochemical capacity (ratio of $P_{max}$ to photosynthesis rate at the growth irradiance) should do well under fluctuating light. It remains largely untested how important this characteristic is in determining growth rates under fluctuating light. In addition to changes in photosynthetic characteristics, changes in cellular biochemical composition may occur under non-continuous light (Sakshaug & Andresen, 1986; Ibelings *et al*., 1994) which may also influence the resulting growth rate. A survey of existing studies on the effects of fluctuations revealed a dichotomy in approaches, most often the effects of fluctuations are considered either on photosynthesis and pigments or on growth, but not on both processes simultaneously. However, the dynamic light affects phytoplankton on multiple scales (Vincent, 1990) and, as this study suggests, to predict growth rate responses under relatively slow fluctuations and fluctuations between growth-limiting and growth-saturating or growth-inhibiting irradiances it is necessary to consider simultaneously the photosynthesis and growth rate responses.

It is conceivable that temporal variability in light supply due to its differential effect on growth of different species may contribute to community changes during seasonal succession in lakes, in addition to other physical, chemical and biological factors. At low average irradiances, e.g. associated with the optically deep mixed layers (e.g. in spring and autumn), fluctuations due to turbulent mixing may stimulate growth of diatoms and have a negative effect on green algae and cyanobacteria. Later in the season, with increasing average irradiance (due to greater solar angle, increased daylength and the onset of summer stratification), fluctuations may increase cyanobacterial growth and have no effect on diatoms and green algae. Within each taxon the responses of species to light fluctuations may be different, however, and more studies are needed to determine the

**Table 4** The effects of fluctuating light regimes on photosynthesis and growth of phytoplankton. Table abbreviations: CL-constant light, FL-fluctuating light, PSU-photosynthetic unit, $P_{max}$-maximum rate of photosynthesis, TDLD-total daily light dose, LD-light:dark, $z_{mix}$-mixing depth, $z_{eu}$-depth of the euphotic zone, $T$-period of fluctuations, $I_{avg}$-average irradiance, $I_{max}$-maximum irradiance, sin-sinusoidal light regime

| Species | Comparable light regime parameter | ave. irradiance and fluctuation range, μmol $m^{-2}$ $s^{-1}$ | Contrasting light regimes | Response to fluctuations | Reference |
|---|---|---|---|---|---|
| *Lauderia borealis* | Similar TDLD (8–9; 10 or 5–6 mol $m^{-2}$, 12 : 12 h LD cycle | $I_{max}$ ≈ 500, 580 or 300 (CL) and 1000 or 1300 (FL) | Sinusoidal vs. fluctuating, $T$ = 3 h | Higher $P_{max}$, smaller afternoon depression of photosynthesis under FL | Marra, 1978 |
| *Scenedesmus protuberans* | Constant TDLD (1.83 mol $m^{-2}$) 10 : 14 h LD cycle | 0–80 ≈ 10–200 | Sinusoidal vs. fluctuating, $T$ = 1.25 or 2.5 h | Increased number of PSU per unit chl, decreased PSU size, increased $P_{max}$, similar to high light acclimation | Flameling & Kromkamp (1997) |
| *Senedesmus protuberans*, *Microcystis aeruginosa* | Constant $I_{max}$, 1100 μmol $m^{-2}$ $s^{-1}$ | 0–1100 | Sinusoidal vs. fluctuating $T$ = 1 h (a) $z_{mix}$ = 0.7 $z_{eu}$ (b) $z_{mix}$ = 2 $z_{eu}$ | Growth rates were lower under FL, but were higher if normalized to TDLD; $P_{max}$ per protein increased, was the highest for $z_{mix}$ = 2 $z_{eu}$ | Ibelings *et al.*, 1994 |
| *Skeletonema costatum* | Constant TDLD: 0.86 (LL) or 1.72 mol $m^{-2}$; 8 : 16 h LD cycle | LL: $I_{max}$ = 47 (sin) and 167 (FL) HL: $I_{max}$ = 100 (sin) and 320 (FL) | Sinusoidal vs. fluctuating, $T$ = 80 min | Number of PSU increased, size of PSU decreased at high FL | Kromkamp & Limbeek, 1993 |
| *Chlorella pyrenoidosa* | Comparable TDLD (mol $m^{-2}$ $d^{-1}$): 8.2 (CL), 10.73 (sinusoidal) and 11.83 (FL), 8 : 14 h LD cycle | $I_{avg}$ = 300 (CL), $I_{max}$ = 570 (sinus.) and 880 (FL) | Constant vs. sinusoidal vs. sinusoidal + fluctuations, 1 h cycle | Higher $I_k$, lower $P_{max}$ and respiration rate in FL | Kroon *et al.*, 1992 |
| Natural estuarine communities | Comparable $I_{ave}$ | $I_{avg}$ = 25–30% $I_{surface}$ | Static vs. rotating incubations, 25 min cycles | Increased productivity under FL due to lack of photoinhibition or decreased light limitation under FL | Mallin & Paerl, 1992 |
| Coastal assemblages | | 10–1000 | Static vs. rotating incubations, 10 min cycles | Similar productivities (mean photosynthesis under FL could be predicted from static incubations). There was no inhibition in static or FL samples | Yoder & Bishop, 1985 |

 

| | | | | | |
|---|---|---|---|---|---|
| Natural communities (waste ponds) dominated by *Euglena* and *Chlorella* | | $I_{max}$ = 588 | Static vs. rotating incubations | Higher productivity in rotating samples in the summer, but lower in the winter | Bosca & Dauta (1991) |
| *Anabaena flos-aquae*, *Oscillatoria agardhii*, *O. redekei* | Same *I* during light part of LD cycle | *I* = 100 at 15 °C; 37 at 10 °C and 22 at 6 °C | Varying light fraction in 1 h LD cycles | Increased growth rates under increasing light fraction, saturation at 0.5 light fraction, lower growth rate of *O. agardhii* under continuous light | Gibson, 1985 |
| *Skeletonema costatum* | Comparable TDLD (≈ 5.6 mol $m^{-2}$); 12 : 12 h LD cycle | $I_{avg}$ = 130, 10–500 | Constant vs. fluctuations, one cycle or 12 cycles in 12 h light period | Similar growth rates, even slightly higher under FL (1.0 $day^{-1}$ (CL) vs. 1.15 $day^{-1}$ under the 12 cycles $day^{-1}$; uncoupling of C production and other growth processes under high constant or FL | Cosper, 1982 |
| 22 sp. of marine coastal and oceanic phytoplankton | Same irradiance during light period | | Continuous vs. 14 : 10 h LD cycle | Coastal species grow better under continuous light, oceanic species – under LD cycle, due to possible adaptation of oceanic clones to a more predictable light regime. This trend was more characteristic in diatoms and coccolithophores, less pronounced in dinoflagellates | Brand & Guillard (1981) |
| *Scenedesmus acuminatus*, *S. armatus*, *Stephanodiscus minutulus*, *Synedra acus*, *Limnothrix redekei*, *Planktothrix agardhii* | Comparable TDLDs (≈ 3 mol $m^{-2}$ $day^{-1}$ or ≈ 7 mol $m^{-2}$ $day^{-1}$) | 1–1000 | Continuous vs. LD cycle (12 : 12 h, 8 : 16 h or 4 : 20 h) or LD cycle + fluctuations (30 or 60 min cycles) | Growth rate decreased under LD cycle and LD cycle + FL, the greatest decrease was in cyanobacteria and the smallest decrease in diatoms; shortening of photoperiod at saturating irradiances also decreased growth rates; growth suppression was smaller under longer period fluctuations | Nicklisch, 1998 |
| *Anabaena flos-aquae*, *Nitzschia* sp., *Phormidium luridum*, *Sphaerocystis shroeteri* | Same $I_{avg}$ | $I_{avg}$ = 25, 50, 100 or 120 μmol $m^{-2}$ $s^{-1}$ | Constant vs. square wave fluctuations, *T* = 1, 8 or 24 h | Growth rate was slightly higher under low FL for *Nitzschia*, under high FL for *Anabaena*; and lower under low FL for *Sphaerocystis* and *Phormidium*, greater effect of FL was when fluctuations were between limiting and saturating or inhibiting irradiances | This study |

generality of the observed trends.

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