

Photosynthetic and growth responses of three freshwater algae to phosphorus limitation and daylength

ELENA LITCHMAN, DANIEL STEINER AND PETER BOSSARD

Limnological Research Centre, EAWAG, Kastanienbaum, Switzerland

SUMMARY

1. Three common species of freshwater phytoplankton, the diatom *Nitzschia* sp., green alga *Sphaerocystis Schroeteri* and cyanobacterium *Phormidium luridum*, were grown under contrasting daylengths [18 : 6 h light : dark cycles (LD) versus 6 : 18 h LD] and phosphorus (P) regimes (P-sufficient versus 1 μM P). The rates of growth and photosynthesis, as well as growth efficiencies and pigment concentrations, were compared among treatments.
2. The growth and photosynthetic parameters of the three species depended on both P status and daylength in a species-specific way. The responses to P limitation depended on daylength and, conversely, the responses to daylength depended on P status.
3. Growth rates and the maximum rates of photosynthesis (P_{max}) of all species decreased under P limitation under both light regimes. However, the decrease of P_{max} because of P limitation was greater under long daylength. The P_{max} of the green alga *S. Schroeteri* decreased the most (ca. sixfold) under P limitation compared with the other two species. The photosynthesis saturation parameter I_k also decreased under P limitation; the decline was significant in *Nitzschia* and *Sphaerocystis*. P-limitation significantly increased photo-inhibition (β) in *Nitzschia* and *Sphaerocystis*, but not in *Phormidium*. The excess photochemical capacity (the ratio of the maximum photosynthesis rate to the photosynthesis rate at the growth irradiance), characterising the ability to utilise fluctuating light, was significantly lower under P limitation.
4. The growth efficiency (growth rate normalised to daylength) declined with increasing daylength in all species. Under short daylength the cyanobacterium *Phormidium* had the lowest growth efficiency of the three species.
5. The cellular chlorophyll *a* concentration in both *Nitzschia* and *Sphaerocystis* was significantly higher under short daylength, but only under P-sufficient conditions. In *Nitzschia*, under short daylength, P-limitation significantly decreased cellular chlorophyll concentration. In contrast, P-limitation increased cellular chlorophyll concentration in *Sphaerocystis*, but under long daylength only. The ratio of chlorophyll *a* to *b* in the green alga also declined under short daylength and under P-limited conditions.

Keywords: daylength, growth rate, phosphorus limitation, photosynthesis, phytoplankton

Introduction

Phytoplankton in most natural environments experience significant seasonal changes in daylength.

Experimental studies show that daylength affects growth and photosynthesis of many groups of algae and these effects may be species-specific. Shorter daylength decreased growth rates of cyanobacteria and diatoms, and the decrease was greater in cyanobacteria (Foy & Gibson, 1993). The cyanobacterium *Oscillatoria agardhii* had higher maximum rates of photosynthesis under shorter daylengths and its growth rate was a

Correspondence: Elena Litchman, School of Biology, 310 Ferst Dr., Georgia Institute of Technology, Atlanta, GA 30332, U.S.A.
E-mail: elena.litchman@biology.gatech.edu

saturation function of daylength (Post, Loogman & Mur, 1986). Growth rates normalised to daylength decreased with increasing daylength (Tang & Vincent, 2000).

The responses of phytoplankton to daylength may also depend on various environmental factors. For example, Tang & Vincent (2000) showed that growth and photosynthetic responses of an Arctic cyanobacterium to daylength depended on temperature. In many temperate lakes phytoplankton are phosphorus-limited during at least part of the year (Hecky & Kilham, 1988). P limitation may modify growth and photosynthetic responses to daylength. Such influence of P limitation may be species-specific. At the same time, daylength may influence algal responses to P limitation. The differential physiological responses of species to P limitation under different daylengths may then affect community composition. Our model investigations indicate that daylength may affect competition for P among phytoplankton (Litchman & Klausmeier, 2001; Litchman, Klausmeier & Bossard, in press), in part because P uptake is light-dependent. Sommer (1994) found that the dynamics and outcome of competition for nutrients among marine phytoplankton depended on daylength. Moreover, the interactions between light regime and nutrient status determine the nutritional quality of phytoplankton for zooplankton (Sterner & Elser, 2002). Therefore it is important to assess simultaneous influence of different daylengths and P status on phytoplankton.

Here we report an investigation of how photosynthesis and growth of three species of freshwater phytoplankton respond to contrasting daylength and P conditions.

Materials and methods

Algae and growth conditions

Three species of freshwater phytoplankton from three major taxa were used in the experiments. The diatom *Nitzschia* sp. and the green alga *Sphaerocystis Schroeteri* Chodat were obtained from the Plant Biology Department, University of Minnesota and the cyanobacterium *Phormidium luridum* var. *olivace* Borech (UTEX 426) was obtained from the University of Texas Culture Collection. All these species can be quite common in temperate lakes. The genus *Phormidium* is similar to the genus *Oscillatoria* in its ecological niche and can be either planktonic or benthic (Whitford & Schumacher, 1984).

Cultures were grown in a temperature-controlled room at 20 °C on shaker tables (100 r.p.m.). Two daylengths were used: 18 : 6 and 6 : 18 h LD. Light was provided by cool-white fluorescent lamps (Osram, Munich, Germany). In both light regimes the irradiance (400–700 nm) was 100 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ measured with a quantum scalar sensor (Biospherical Instruments, QSL-100, San Diego, CA, U.S.A.) inside the bottles with the medium. Cultures were grown in the WC medium (Guillard, 1975) in semicontinuous regime (daily dilutions of 0.2 day⁻¹). The WC medium for P-limited cultures had 1 μM phosphate concentration. The cultures were grown under experimental conditions for at least 4 days (nutrient-replete conditions) or 8 days (P-limited conditions) before photosynthetic and other parameters were measured.

Growth rates were determined as the slope of the linear regression of the natural logarithm of cell density versus time adjusted for dilution rate. To compare growth efficiency (light utilisation efficiency) between daylengths, growth rates were normalised to daylength.

Photosynthesis–irradiance curves

Photosynthesis–irradiance (P–I) curves were determined by ¹⁴C incorporation in the incubator which is a custom modification of the small volume photosynthetron (Lewis & Smith, 1983). Samples (7 mL) were incubated in 20-mL scintillation vials placed in metal holders through which water circulated to maintain the desired temperature. Light was provided from the bottom by four 250 or 400 W high intensity discharge lamps (Osram HQI-D) with the spectrum close to natural sunlight. The UV portion of the spectrum was blocked by a sheet of UV-opaque plexiglas (395 nm cutoff). The platform holding the metal racks was shaken constantly so that the samples were shaken as well. Irradiance was adjusted with layers of neutral density screen. The irradiance was determined as the average of several measurements made over 1–2 min and recorded with a LICOR Inc. data logger (Lincoln, NE, U.S.A.) to take into account changes because of shaking.

The samples were incubated for 2 h. After the incubation, 50 μL of 1 N HNO₃ was added and samples were bubbled with air for 1 h (Gächter & Mares, 1979). Dark uptake measured in triplicate was subtracted from the light uptake.

Dissolved inorganic carbon concentration was determined from pH and alkalinity measurements. Alkalinity was determined by titration with HCl. Chlorophyll *a* (and *b* for *S. Schroeteri*) was determined after filtering a sample onto a GF/F filter (Whatman International Ltd, Kent, UK) and extracting chlorophyll in 90% methanol 10 min at 75 °C. Chlorophyll *c* in the diatom was not determined because the high performance liquid chromatography (HPLC) system was not calibrated for chlorophyll *c*. Pigment concentrations were determined using an HPLC system with a LichroSpher 100 RP-18 column (Merck & Co. Inc., White House Station, NJ, USA) connected to a Jasco AS-950 autosampler and PU-980 liquid chromatography system. The system was calibrated with the chlorophyll *a* and *b* standards (Fluka).

We modelled the P-I data using the hyperbolic tangent equation (Jassby & Platt, 1976) modified to include photoinhibition:

$$P = P_{\max} \tanh(\alpha I / P_{\max}) \left(\frac{1}{1 + \beta I} \right) \quad (1)$$

where P is the rate of photosynthesis at irradiance I , P_{\max} is the maximum potential light-saturated photosynthetic rate (with no photoinhibition), α is the initial slope of the P-I curve and β characterises inhibition of photosynthesis at high irradiance. We also determined I_k , the saturation parameter, as the ratio of P_{\max} to α .

The hyperbolic tangent equation (eqn 1) gave slightly higher R^2 for most P-I curves than the equation by Platt, Gallegos & Harrison (1980); therefore, here we report and compare parameters for this equation only. Previous studies noted that photosynthetic parameters such as α can only be compared when the same equation is used (Frenette *et al.*, 1993).

At least two, and in most cases three or four, replicate cultures were grown under each combination of daylength and P concentration and the P-I curves were determined for each culture. We also determined the excess photochemical capacity as the ratio of the maximum photosynthetic rate, P_{\max} to the photosynthetic rate under growth irradiance, P_g (Cullen & MacIntyre, 1998). High excess photochemical capacity indicates good capability to utilise fluctuating light.

Statistical analyses

The effects of daylength, P concentration and their interaction on various parameters were analysed

using two-way ANOVA. In some cases, to meet the assumptions of ANOVA, the data were log-transformed. Student-Neuman-Keuls test was used for multiple pairwise comparisons. Within each factor (daylength or P status) treatments were compared using a *t*-test.

Results

Photosynthetic parameters

Both daylength and P status influenced photosynthetic parameters of all three species (Fig. 1; Table 1). The maximum rates of photosynthesis (P_{\max}) normalised to chlorophyll *a* ($P_{\max}/\text{Chl } a = \text{Assimilation}$

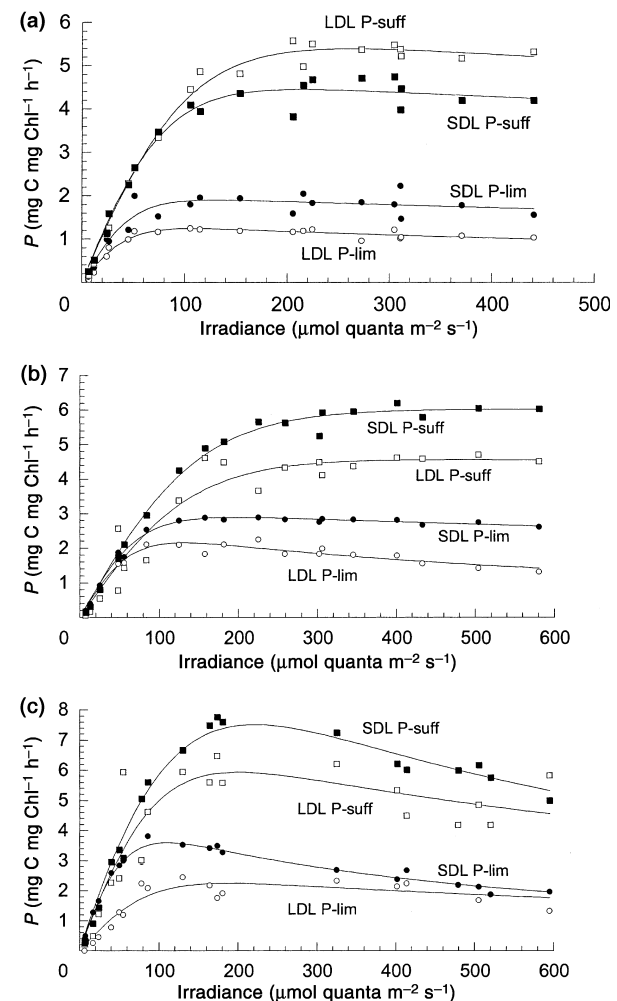


Fig. 1. Representative P-I curves for the three species. (a) *Nitzschia*; (b) *Sphaerocystis*; (c) *Phormidium*. LDL, long daylength; SDL, short daylength; P-lim, P-limited; P-suff, P-sufficient cultures.

Table 1. Various physiological parameters of the three species under different light regimes and P conditions

| Light regime | P conditions | <i>Nitzschia</i> | | <i>Sphaerocystis</i> | | <i>Phormidium</i> | |
|---|--------------|------------------|-------------------|----------------------|------------------|-------------------|------------------|
| | | LDL | SDL | LDL | SDL | LDL | SDL |
| α , $\times 10^{-2}$, mg C mg Chlorophyll h^{-1} | P-sufficient | 4.2 \pm 1.2 | 4.9 \pm 0.8 | 5.4 \pm 1.0 | 4.6 \pm 0.5 | 7.4 \pm 2.0 | 6.8 \pm 0.4 |
| | P-limited | 2.7 \pm 0.2 | 5.2 \pm 0.2 | 3.0 \pm 0.8 | 3.8 \pm 0.3 | 2.6 \pm 0.1 | 6.4 \pm 0.7 |
| I_k , $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ | P-sufficient | 91.5 \pm 15.3 | 106.7 \pm 12.24 | 127.8 \pm 36.5 | 132.4 \pm 10.8 | 138.5 \pm 15.3 | 104.7 \pm 15.7 |
| | P-limited | 52.8 \pm 4.2 | 65.8 \pm 13.0 | 59.6 \pm 15.6 | 71.4 \pm 4.6 | 93.5 \pm 13.9 | 70.8 \pm 10.8 |
| β , $\times 10^{-4}$ | P-sufficient | 1.0 \pm 3.5 | -4.5 \pm 1.7 | -3.1 \pm 0.6 | -1.4 \pm 0.3 | -8.7 \pm 0.3 | -8.1 \pm 0.5 |
| | P-limited | -7.6 \pm 1.4 | -4.8 \pm 0.7 | -6.1 \pm 1.4 | -3.2 \pm 1.1 | -8.4 \pm 1.5 | -7.9 \pm 1.0 |
| Chlorophyll <i>a</i> , pg cell $^{-1}$ | P-sufficient | 4.4 \pm 1.6 | 13.4 \pm 0.7 | 12.7 \pm 3.6 | 28.6 \pm 2.6 | nd | nd |
| | P-limited | 3.4 \pm 1.0 | 8.9 \pm 3.3 | 35.7 \pm 7.0 | 34.6 \pm 10.0 | nd | nd |
| Chlorophyll <i>a</i> : <i>b</i> | P-sufficient | na | na | 3.31 \pm 0.01 | 2.9 \pm 0.08 | nd | nd |
| | P-limited | na | na | 2.61 \pm 0.07 | 2.76 \pm 0.12 | nd | nd |
| Growth rate, day $^{-1}$ | P-sufficient | 0.87 \pm 0.09 | 0.32 \pm 0.04 | 0.62 \pm 0.07 | 0.32 \pm 0.08 | 0.54 \pm 0.10 | 0.23 \pm 0.07 |
| | P-limited | 0.16 \pm 0.05 | 0.09 \pm 0.04 | 0.16 \pm 0.05 | 0.10 \pm 0.03 | 0.13 \pm n.d. | 0.07 \pm 0.04 |
| Excess photochemical capacity | P-sufficient | 1.26 \pm 0.06 | 1.31 \pm 0.08 | 1.52 \pm 0.16 | 1.55 \pm 0.09 | 1.48 \pm 0.12 | 1.25 \pm 0.11 |
| | P-limited | 1.00 \pm 0.03 | 1.06 \pm 0.06 | 1.03 \pm 0.03 | 1.10 \pm 0.02 | 1.34 \pm 0.19 | 1.05 \pm 0.06 |

LDL, long daylength (18 : 6 h LD); SDL, short daylength (6 : 18 h LD); na, not applicable; nd, not determined.

Excess photochemical capacity was determined as the ratio of P_{max} , maximum rate of photosynthesis to the P_g , the photosynthetic rate at the growth irradiance (Cullen & MacIntyre, 1998).

number) in all species were significantly lower under P-limited conditions (Fig. 2). The decrease of P_{max} due to P limitation ($\Delta P_{\text{max}} = P_{\text{suff}} - P_{\text{lim}}$) was greater under long daylength (LDL) than under short daylength (SDL). The decline of P_{max} under P-limitation was the most pronounced in *Sphaerocystis* under LDL (more than sixfold, $p < 0.01$), in *Nitzschia* it was threefold ($p < 0.05$) and in *Phormidium* it was 2.6-fold ($p < 0.05$) (Fig. 2). Also, the difference in the P_{max} decrease because of P-limitation between LDL and SDL {difference = [(P-suff_{LDL} - P-lim_{LDL}) - (P-suff_{SDL} - P-lim_{SDL})]} was the greatest in *Sphaerocystis*. Under P limitation the daylength had a strong effect on P_{max} : it was significantly higher under SDL than under LDL (Fig. 2). The saturation parameter I_k also decreased under P limitation under both SDL and LDL (see Table 1). The decrease was significant in *Nitzschia* ($p = 0.018$) and *Sphaerocystis* ($p < 0.001$).

The initial slope of the P-I curves α appeared to be higher in P-sufficient cultures, the difference was not, however, significant in *Nitzschia* and *Sphaerocystis*. In *Phormidium*, both P status and the interaction term (daylength by P status) significantly influenced α ($p = 0.016$ and 0.033 , respectively, two-way ANOVA). P-sufficient *Phormidium* cultures had significantly higher α compared with P-limited cultures, but only under LDL. Under P-limited conditions, the LDL cultures had significantly lower α than the SDL cultures of *Phormidium*.

Under P-sufficient conditions, the cyanobacterium *Phormidium* was significantly more inhibited (greater β) than the diatom *Nitzschia* and the chlorophyte *Sphaerocystis* (one-way ANOVA, $p = 0.005$). P-limitation significantly increased photoinhibition in *Nitzschia* (two-way ANOVA, $p = 0.034$) and *Sphaerocystis* ($p = 0.048$), but not in *Phormidium*. In *Nitzschia*, photoinhibition was different between P-limited and P-sufficient cultures only under LDL.

The excess photochemical capacity (EPC) decreased under P limitation; the difference was highly significant for both *Nitzschia* and *Sphaerocystis* ($p = 0.002$ and < 0.001 , respectively). The daylength did not have a significant impact on the EPC ($p > 0.05$).

Growth rates

Growth rates of all species decreased significantly under P limitation under both light regimes. The decline due to P limitation was more pronounced under LDL (Table 1). The growth rate of *Nitzschia* declined more than fivefold under this light regime versus 3.6-fold under the short daylength.

Under P-sufficient conditions, the growth rates were the lowest under the shortest daylength and increased linearly with daylength in *Sphaerocystis* [growth rate = (0.0217 \times daylength) + 0.2; $R^2 = 0.98$] and *Phormidium* [growth rate = (0.0308 \times daylength) + 0.03; $R^2 = 0.98$] (Fig. 3a). The growth rates under

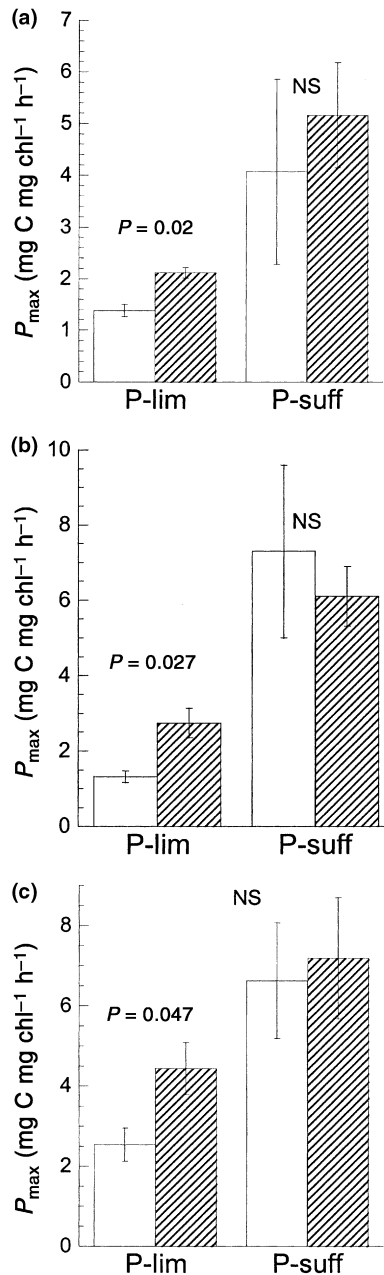


Fig. 2. Chlorophyll-normalised maximum rates of photosynthesis of the three species under P-limited and nutrient-sufficient conditions. (a) *Nitzschia*; (b) *Sphaerocystis*; (c) *Phormidium*. Open bars are long daylength treatments and hatched bars are short daylength treatments.

continuous irradiance of $100 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ were taken from Litchman (2000). In *Nitzschia*, the growth rate dependence on daylength was better described by a saturating curve (Fig. 3a) [growth rate = $[-0.0036 \times (\text{daylength})^2] + (0.1314 \times \text{daylength}) - 0.34$; $R^2 = 1$] (Fig. 3a).

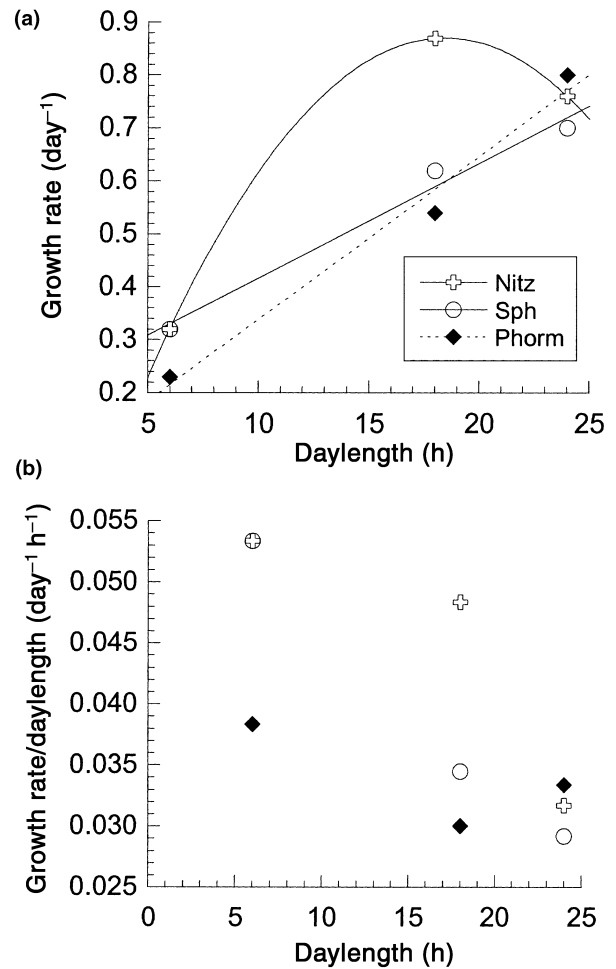


Fig. 3. (a) Growth rates of the three species and (b) daylength-normalised growth rates (growth efficiencies) under different light regimes and nutrient-sufficient conditions for *Nitzschia* (cross), *Sphaerocystis* (circle) and *Phormidium* (diamond). Growth rates at the 24 h daylight were taken from Litchman (2000).

Under P-sufficient conditions growth rates normalised to light dose (growth efficiency) were the greatest under the shortest daylength (Fig. 3b). The growth (light utilisation) efficiency increased with decreasing daylength in all species. The pattern of increase was, however, species-specific: the increase was less pronounced in *Phormidium* compared with *Nitzschia* and *Sphaerocystis* (Fig. 3b).

Cellular chlorophyll concentrations

Chlorophyll concentration (measured in *Sphaerocystis* and *Nitzschia*, no data for *Phormidium*) tended to be higher under SDL (Table 1). Under P-sufficient conditions, the effect of daylength on cellular chlorophyll

concentration was much more pronounced than under P-limited conditions. In *Nitzschia*, the effect of both P-status and daylength on cellular chlorophyll concentration were highly significant, as well as their interaction term ($p = 0.003, 0.002$ and 0.01). In both *Nitzschia* and *Sphaerocystis*, the LDL treatments had significantly lower chlorophyll *a* concentrations than the SDL treatments, but only under P-sufficient conditions (Table 1). P-limitation significantly decreased chlorophyll concentration in *Nitzschia*, but under SDL only. In *Sphaerocystis*, under LDL only, P-limited cultures had higher cellular chlorophyll concentration than P-sufficient cultures ($p = 0.035$).

The ratio of chlorophyll *a* to *b* in *Sphaerocystis* under LDL was significantly higher ($p < 0.001$) in nutrient-sufficient cultures compared with its P-limited cultures (3.3 versus 2.6, respectively). The interaction term of daylength and P limitation (daylength \times P status) was also significant ($p = 0.038$). Under P-sufficient conditions, the chlorophyll *a* : *b* ratio also significantly depended on daylength: it was 3.3 under LDL versus 2.9 under SDL, $p < 0.01$).

Discussion

Both P limitation and daylength had significant effects on major physiological parameters of the three species. The growth rates of all three species declined under short daylength and the decline was species-specific. Nicklisch (1998) also observed a species-specific decrease in growth rates under short daylength. The ratio of the growth rate under continuous light to the growth rate under the shortest photoperiod was the greatest in the cyanobacterium, indicating the greatest inhibition of growth from shortening the daylength. Foy & Gibson (1993) also found greater decline in growth with decreasing photoperiod in cyanobacteria compared with diatoms. A decline in growth rate efficiency (growth rate per light hour) with increasing daylength has also been observed for many other species in both freshwater and marine environments (Gilstad & Sakshaug, 1990; Foy & Gibson, 1993; Tang & Vincent, 2000). The cyanobacterium had a relatively low growth efficiency under short daylength compared with the diatom and the green alga. However, the growth efficiencies were similar for the three species under continuous light. This may contribute to the dominance of cyanobacteria in the summer, under long daylengths and to their

disadvantage in the spring and fall when the daylength is shorter.

The responses of photosynthetic parameters to shortening of daylength were similar to the low irradiance acclimation. The increase in cellular chlorophyll *a* concentration under shorter light periods appears to be similar to the increase under lower irradiance and has been observed in other species, such as the cyanobacterium *O. agardhii* (Post *et al.*, 1986). The ratio of chlorophyll *a* to *b* is also known to decline under low light (Maxwell *et al.*, 1994; Falkowski & Raven, 1997). In the present study under nutrient-sufficient conditions the chlorophyll *a* : *b* ratio was significantly lower under short daylength.

P limitation decreased the maximum rates of photosynthesis in all three species, but the decrease was species-specific: the green alga was the most sensitive to P limitation and the diatom was the least sensitive. Many other studies have reported lower rates of light-saturated photosynthesis under P limitation (Senft, 1978; Geider *et al.*, 1998). The susceptibility to photoinhibition also increased due to P-limitation in *Nitzschia* and *Sphaerocystis*. A greater photoinhibition of photosynthesis in nutrient-limited phytoplankton has been reported previously (Litchman, Neale & Banaszak, 2002). A decrease in cellular chlorophyll concentration under P-limitation has been observed for both marine and freshwater microalgae (Geider *et al.*, 1998; Wykoff *et al.*, 1998). An increase in cellular chlorophyll concentration under P-limitation in *Sphaerocystis* may possibly be explained by slower cellular division rates resulting in larger cells with higher chlorophyll content. The effect of nutrient limitation on photosynthetic apparatus in some respects is similar to the effect of low irradiance, with decreased maximum rate of photosynthesis and lower saturation parameter values. Lower chlorophyll-specific maximum rates of photosynthesis as well as lower chlorophyll *a* : *b* ratios are characteristic for low-light acclimated phytoplankton. In the present study we observed significantly lower chlorophyll *a* : *b* ratio under P-limited conditions. P limitation also decreased excess photochemical capacity (Cullen & MacIntyre, 1998), suggesting that nutrient-limited phytoplankton are less capable of utilising light fluctuations.

The effect of P limitation on the rates of photosynthesis and the degree of photoinhibition was more pronounced under long daylength. It is possible that

by allowing faster growth, longer daylength leads to a stronger P limitation and subsequently to a greater decrease in the light-saturated rates of photosynthesis and greater susceptibility to photoinhibition. Lower P_{\max} have been reported for algae grown under longer daylength under nutrient sufficient conditions (Nielsen, 1997). In our study this effect of daylength was significant only under P-limited conditions.

Under nutrient-sufficient conditions daylength had a significant effect on growth rates and chlorophyll concentrations. The results show that the growth and photosynthetic responses to P limitation also depend on daylength, with stronger effects of limitation under longer daylength. Both photosynthetic and growth rates declined more under LDL due to P limitation. It is thus important when in the season P limitation occurs: the effects of P limitation on photosynthesis would be less pronounced in the early spring and autumn.

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