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Long time series from the English Lake District: Irradiance-dependent phytoplankton dynamics during the spring maximum

Abstract—We analyzed rates of phytoplankton increase and decline during the spring maximum via long-term (25 yr) records of biomass (Chl *a*) and abundance of the dominant diatom, *Asterionella formosa*, sampled from the surface waters of Windermere (English Lake District). Average rates of net increase in early spring (i.e. up until the end of March) are best correlated with the logarithm of surface irradiance ($r^2 = 0.71-0.87$). Average spring growth rates in late February and March (weeks 6–13 of the year) defined by this analysis significantly exceed rates predicted from calculations of integrated production with existing physiological data for *A. formosa* but are similar to the predicted growth rates at the mean irradiance in the mixed layer. In late spring (April–May), stratification becomes well established and the rate of population increase lessens. This decrease occurs before dissolved silicate is depleted to growth-limiting concentrations during increasing average irradiance in the surface layer. Near exhaustion of dissolved silicate and rapid loss of *A. formosa* from the surface layer follow. P limitation, enhanced sedimentation, and photoinhibition are factors that may slow net diatom accumulation before the onset of silicate limitation.

The prediction of phytoplankton growth and production as a function of surface irradiance is a fundamental goal of much work in limnology and oceanography. There is a long history of studies (see Cullen 1990) that translate descriptions of the photosynthetic conversion of light energy into predictions of irradiance-dependent phytoplankton growth rates. Experimental techniques for such work have usually been limited to measuring growth rates and photosynthesis under constant irradiance or, at best, in incubations held at a fixed proportion of sur-

face irradiance. On the other hand, there are several time-dependent variations of photosynthetic physiology that are known to occur in the environment but are difficult to incorporate into laboratory or incubation protocols. Two examples are short-term variations in photosynthetic capacity in response to like-scaled irradiance variations (Marra 1978; Neale and Marra 1985) and photoinhibition (see Neale 1987). Thus, a relevant question given the current attention to model development (Sakshaug et al. 1989; Cullen 1990) is whether there is evidence that photophysiological processes in natural populations significantly modify the predictions of general models of the growth-irradiance relationship. In situ observations of phytoplankton dynamics may provide such evidence.

A unique time series of measurements of phytoplankton biomass has been compiled for various lakes in the English Lake District from 1945 to the present for cell counts and from 1964 to present for Chl *a* measurements. Of particular interest is the record of the diatom growth maximum in spring—a period when the lakes are initially well mixed and no significant grazing of larger algae occurs. Under these conditions, cell-specific rates of production (K) will be closely approximated by successive differences in time series of biomass estimates. Therefore, the spring pulse of phytoplankton growth can be estimated directly without estimating all biomass gains or losses (e.g. Welschmeyer and Lorenzen 1985) or extrapolating production rates measured during incubations to the whole mixed layer.

One of the most studied of these lakes is Windermere, for which a large set of historical data on biological, physical, and

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chemical factors is available (e.g. Talling and Heaney 1988). The spring diatom increase in Windermere is dominated by *Asterionella formosa* Hass. (see Lund 1964). Previous studies have demonstrated the exponential character of *A. formosa* growth in spring (e.g. Lund 1949), the sensitivity of the specific rate of increase to major environmental change (e.g. thermal stratification), and the correlation of the final abrupt decline in abundance with depletion of silicate to $<0.5 \text{ mg SiO}_2 \text{ liter}^{-1}$ (Lund 1949, 1950). Cell sedimentation increases greatly during the late phase as indicated by a silicon budget (Lund et al. 1963). Talling (1957*a,b*, 1966) showed that some photosynthetic activity persisted beyond the exponential phase and that the denser populations exert appreciable self-shading (Talling 1960). He deduced that the integral column production rate was broadly related to the logarithm of surface-penetrating irradiance and applied (Talling 1971) a corresponding light function to analyze differences in timing of the diatom spring growth in the basins of Windermere and adjacent lakes over 1964–1970.

Our objective here was to obtain an overall picture of diatom dynamics during the spring increase by analyzing mean abundances over a 25-yr period (1964–1988) when weekly samples (with a few gaps) were taken of Chl concentration, abundance of *A. formosa*, light, and temperature-density structure. A 7-m integrating tube was used to sample at stations in the deepest parts of two largely independent basins: the larger, deeper north basin (area, 8.05 km^2 ; maximal depth, 64 m; mean depth, 25.1 m) and the smaller, shallower south basin (area, 6.72 km^2 ; maximal depth, 42 m; mean depth, 16.8 m). Algal cell numbers were determined with the Utermöhl inverted microscope technique after sedimentation in Lugol's iodine solution (Lund et al. 1958); Chl *a* was measured based on absorbance of methanol extracts at 665 nm, uncorrected for the presence of pigment degradation products (Talling 1974). Measurement of dissolved inorganic nutrients, including historical variation in methods, has been discussed by Talling and Heaney (1988).

Surface irradiance (total shortwave, cal

Notation

α	Initial slope of the photosynthesis-irradiance curve, $\text{mg O}_2 (10^9 \text{ cells cal cm}^{-2} \text{ h}^{-1} \text{ PAR})^{-1}$
Chl	Chlorophyll <i>a</i> concentration, $\mu\text{g liter}^{-1}$
<i>D</i>	Daylength, h
ϵ_{min}	Minimum vertical attenuation coefficient for scalar irradiance, m^{-1}
ϵ	Vertical scalar attenuation coefficient for PAR (mean value over mixed layer), m^{-1}
<i>G/P</i>	Ratio of specific rate of growth to photosynthesis rate per cell, ln units $10^9 \text{ cells (mg O}_2)^{-1}$
I_{sml}	Mean daytime irradiance (PAR) in the surface layer, $\text{cal cm}^{-2} \text{ h}^{-1}$
I_k	Characteristic irradiance for photosynthesis saturation, $\text{cal cm}^{-2} \text{ h}^{-1}$
I'_0	Mean daytime surface-penetrating PAR, $\text{cal cm}^{-2} \text{ h}^{-1}$
I''_0	Week-integrated surface-penetrating PAR, $\text{cal cm}^{-2} \text{ week}^{-1}$
K_{Ast}	Net rate of change of <i>A. formosa</i> abundance, ln units week^{-1}
K_{Chl}	Net rate of change of Chl, ln units week^{-1}
<i>N</i>	Brunt-Väisälä buoyancy frequency, s^{-1}
PAR	Photosynthetically active radiation, cal
P_{max}	Light-saturated rate of photosynthesis, $\text{mg O}_2 (10^9 \text{ cells})^{-1} \text{ h}^{-1}$
<i>R</i>	Respiration rate, $\text{mg O}_2 (10^9 \text{ cells})^{-1} \text{ h}^{-1}$
μ	Growth rate, week^{-1} or h^{-1}
z_{mix}	Mixed-layer depth, m

cm^{-2}) was measured continuously by a thermopile solarimeter (Kipp), on the roof of the Windermere Laboratory of the Institute of Freshwater Ecology (formerly the Freshwater Biological Association). Surface-penetrating, photosynthetically active radiation (PAR, see notation), was calculated as 0.46 of total irradiance less 10% to correct for surface reflection (Talling 1971). Irradiance was integrated over each week previous to the sampling date. This integral was also used to compute a daytime hourly average irradiance with daylength from the Smithsonian Meteorological Tables (List 1968). Vertical profiles of water temperature ($\pm 0.1^\circ\text{C}$) were measured with a thermistor sensor and used to derive characteristic vertical mixing lengths.

The average hourly daytime irradiance available to the surface phytoplankton community was calculated with the data described above and an equation based on integrated irradiance over the water column:

$$I_{\text{sml}} = [I'_0 / (\epsilon z_{\text{mix}})] [1 - \exp(-\epsilon z_{\text{mix}})] \quad (1)$$

where I_{smi} is the mean hourly daytime irradiance over the surface mixed layer, z_{mix} the surface mixing layer depth, I'_0 the mean hourly daytime surface irradiance, and ϵ the effective quantum attenuation coefficient over the euphotic zone for PAR. The attenuation coefficient is defined as a function of Chl concentration via an empirical relation for Windermere in spring (Talling 1960):

$$\epsilon = 0.432 + 0.027 \text{ Chl}. \quad (2)$$

Here a factor of 1.33 has been used for the ratio between ϵ and the minimum attenuation coefficient (ϵ_{min}) for the most penetrating green waveband (Talling 1971). During isothermal conditions the surface mixed-layer depth was set equal to the mean depth of the basin, corrected from overrepresentation of the littoral zone as described by Talling (1971). When stratification was present, the depth of the mixed layer was estimated as the depth at which temperature decreased to 0.5°C cooler than that at 2 m (Talling 1971). An alternate approach based on the Monin-Obukhov mixing length (Denman and Gargett 1983) gave essentially equivalent depths.

The long-term averages (as geometric means) of Chl concentration and abundance of *A. formosa* in the surface-layer sampling tube were calculated for each week from January through June (weeks 1–26) (Fig. 1). The increase in Chl closely parallels the increase in abundance of *A. formosa*. The main increase in the south basin (after week 11) precedes by several weeks the corresponding stage in the north basin (after week 14). The sequence of log abundance in spring has a clearly sigmoidal profile that is also apparent in several previously published sequences of *A. formosa* abundance in individual years (Lund 1950, 1964). We used the time series to estimate specific net rates of change of phytoplankton biomass (K) as indicated by both Chl (K_{Chl}) and *A. formosa* (K_{Ast}) cell counts. In each case, the logarithm of the raw data was taken and specific rates of change were calculated from weekly differences. The resulting differenced data series is inherently noisy; e.g. the C.V. of K_{Chl} over the sampling period in the north basin is 485%. Sufficient data were available, however, to make accurate estimates

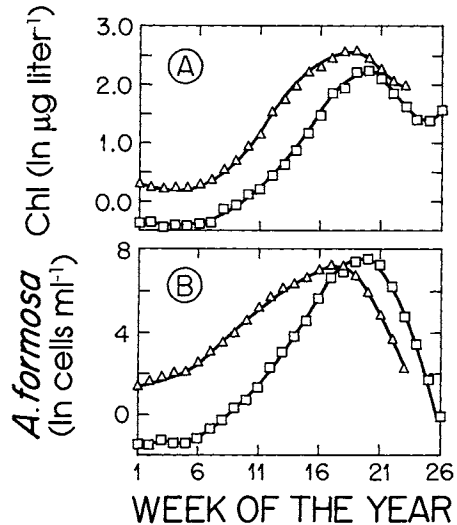


Fig. 1. Variation with time in phytoplankton biomass as Chl *a* and *Asterionella formosa* cell concentration in winter–spring based on weekly surface samples taken from midbasin stations in Windermere, 1964–1988. Results shown are long-term averages over each week of \ln Chl and \ln *A. formosa* counts for the north (\square) and south basins (Δ).

of long-term mean K for each week of the year (Fig. 2).

Best accuracy was obtained in the early-spring period of net biomass accumulation. The pooled standard error (SE) for this period ($n = 25$) in the north basin (weeks 1–17) was 0.05 week⁻¹ for mean K_{Chl} and 0.19 week⁻¹ for mean K_{Ast} . During the corresponding period in the south basin (weeks 1–15) the SE ($n = 25$) was 0.04 week⁻¹ for mean K_{Chl} and 0.11 week⁻¹ for mean K_{Ast} . Thus, differences between weeks were highly significant ($P < 0.005$, ANOVA). After the early spring period of increasing rates, biomass accumulation slows and then rapidly yields to net population decline (Fig. 2). We analyzed these two phases of positive and negative trends in K separately.

We analyzed rates of increase during the biomass accumulation phase in relation to light—the primary resource limiting growth rate. These long time series of K present a unique opportunity to accurately define the relationship between in situ diatom growth and irradiance with sufficient accuracy to test the explanatory power of mathematical formulations for the dependence of growth on irradiance. Several formulations already

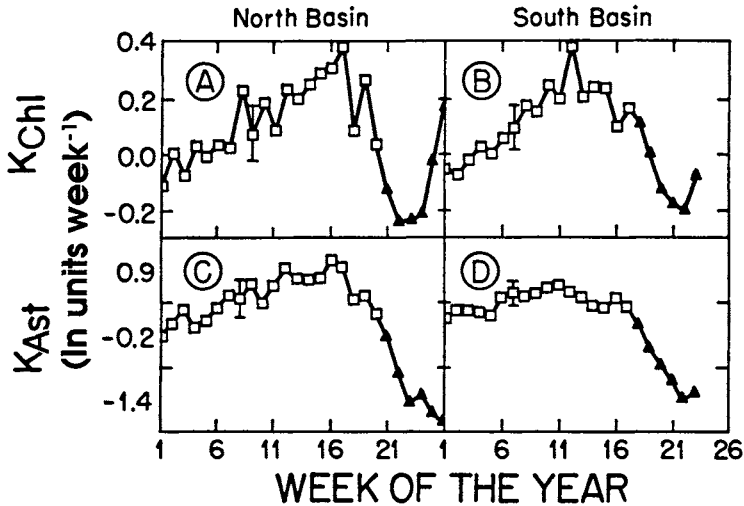


Fig. 2. Average net specific rates of change of Chl (K_{ChI}) and *Asterionella formosa* cell counts (K_{Ast}), 1964–1988, based on variations in Chl or counts of *A. formosa* in surface samples from the north or south basins of Windermere. Rates computed from samples and average silicate concentration >0.5 mg SiO_2 liter $^{-1}$ —□; when <0.5 mg SiO_2 liter $^{-1}$ —▲. Vertical bars indicate 95% C.I. for mean K .

exist that relate phytoplankton production to surface irradiance based on both empirical (Platt et al. 1988 and references cited therein) and theoretical (e.g. Talling 1957*b*; Platt et al. 1977) analyses. Growth models of diatoms in nutrient-sufficient conditions assume a tight coupling of gross growth and photosynthetic assimilation (Sakshaug et al. 1989). Theoretical models predict a logarithmic relationship between integral productivity and surface-penetrating irradiance (Talling 1957*b*; Platt et al. 1977; Cullen 1990). Empirically, a simple linear relationship is a fair approximation. Inherent non-linearity, however, forces an unrealistic positive intercept, i.e. production in the dark (Platt et al. 1988). Hitchcock and Smayda (1977) reported a linear correlation between K for a marine diatom and I_{sml} , but did not attempt a logarithmic analysis.

The logarithmic week-integrated irradiance was a more successful predictor of K in Windermere than arithmetic week-integrated irradiance (Table 1). Arithmetic irradiance accounted for 57–79% of the variance in K_{Ast} , whereas 71–87% of variance is explained by a logarithmic formulation. The improvement in fit is statistically significant (Table 1). The improvement due to using a logarithmic term was less, but still evident, for K_{ChI} . The lack of fit for the linear

formulae was due to a positive bias at low irradiance (data not shown), consistent with other theoretical and empirical analyses (Talling 1957*b*; Platt et al. 1988). Week-integrated I'_0 , mean daytime hourly I'_0 , and I_{sml} were all highly correlated (Table 2). Thus, separate regressions are not presented for each irradiance variable. For convenience in comparisons, week-integrated I'_0 was chosen as the main independent variable. The equations in Table 2 can be used to convert to other irradiance units.

The overall fit of the logarithmic equation is illustrated with week-integrated I'_0 as the independent variable in Fig. 3, which also compares north and south basin data. In the south basin, the linearly increasing portion of the relationship is a smaller proportion of the whole data set (Fig. 3). Generally, higher absolute growth rates are exhibited in the count data than in the Chl data. Chl is an integrative variable that includes responses by all species of the phytoplankton. Nevertheless, the main contributor to Chl increase in spring will be growth of *A. formosa*. Additional factors for Chl-based rates of change are that a portion of the measured pigment will derive from nongrowing or detrital material and that *A. formosa* Chl content per cell will tend to decrease as irradiance increases during early spring, unless

Table 1. Least-squares regression analysis of mean specific growth rate of phytoplankton in the north and south basins of Windermere based on average net rates of change of Chl (K_{Chl}) and cell counts of *Asterionella formosa* (K_{Ast}) for each week of the year and on mean week-integrated surface irradiance (I'_0 or $\ln I'_0$) over weeks 1–17 (north basin) or weeks 1–13 (south basin). Equations logarithmic in I'_0 (a) or linear in I'_0 (b) were analyzed; also linear regressions for both $\ln I'_0$ and the square of the maximum Brunt-Väisälä frequency (N^2) in the water column over weeks 1–23 in both basins (c). Asterisks indicate statistical significance of the difference in goodness-of-fit between I'_0 and $\ln I'_0$ regressions: *— $P < 0.05$; **— $P < 0.01$.

Basin	Variable	(a) $K = A + B \ln I'_0$			(b) $K = A + B \times 10^{-3} I'_0$			(c) $K = A + B \ln I'_0 + C N^2$			
		A	B	r^2	A	B	r^2	A	B	C	r^2
North	K_{Ast}	-2.66	0.536	0.87**	-0.105	1.35	0.79	-2.14	0.441	-0.721	0.88
South	K_{Ast}	-1.27	0.295	0.71*	-0.086	0.935	0.57	-1.14	0.241	-0.738	0.73
North	K_{Chl}	-0.964	0.187	0.85	-0.081	0.491	0.84				
South	K_{Chl}	-1.10	0.217	0.85	-0.116	0.748	0.81				

sinking is predominant (cf. Talling 1966, figure 6d). These factors will result in an underestimate of the true specific rates of population change. Overall, the coefficients for the fitted equations for Chl are less than the analogous coefficients for counts of *A. formosa* (Table 1).

The logarithmic irradiance regression seems to be a good empirical representation of how the growth of *A. formosa* in a surface mixed layer responds to variations in surface irradiance. These results can be compared to predictions made for the same conditions with models based on incubation measurements of cultures or samples from natural populations. This approach has been previously applied to the growth of another diatom, *Fragilaria crotonensis*, in large, limnetic enclosures under summer conditions (Reynolds 1983). Here, irradiance-dependent growth is estimated via a formulation for integral water-column production

derived from Talling (1957b, equations 3 and 5)

$$\begin{aligned} \mu &= (G/P)\bar{P} \\ &= f \ln(2I'_0/I_k) - 24R; \\ f &= [0.9 D P_{\text{max}}(T)]/\epsilon z_{\text{mix}}. \end{aligned} \quad (3)$$

Here (G/P) is the ratio that converts net photosynthetic rates per cell (P) to growth rates (μ), R the hourly respiration rate per cell, D the daylength, I'_0 (PAR) the mean hourly, daytime, surface-penetrating PAR, and $P_{\text{max}}(T)$ the light-saturated rate of photosynthesis as a function of temperature. The equivalence between photosynthesis and growth is based on observations of *A. formosa* cultured over a range of temperature and irradiance (Talling 1955; Heaney unpubl.).

The model (Eq. 3) was used to estimate K_{Ast} during the spring period, using published data on the photosynthetic and growth characteristics of *A. formosa* and correcting for sinking loss (Table 3). The growth rates based on this model underestimate observed K_{Ast} in the north basin during the late-winter to early-spring (week 6–13) period when the water column is usually completely mixed (Fig. 4). For example, in week 12 (i.e. late March) the integrated production model predicts a growth rate of 0.10 \ln units week^{-1} . By contrast, the long-term average K_{Ast} is 0.94 week^{-1} and the regression equation (Table 2) predicts 0.60 week^{-1} , consistent with the qualitative assessment (Lund et al. 1963) that (by the end of March) the crop about doubles each week (i.e. 0.69 \ln units week^{-1}). Thus, the relative growth rate of Windermere populations of *A. for-*

Table 2. Correlation between week-integrated I'_0 , hourly daytime I'_0 , and I_{sml} in the north and south basins of Windermere based on means for each week of the year in late winter to early spring (i.e. weeks 1–17 in the north basin and weeks 1–13 in the south basin). Statistics are for the linear regression between the logarithm of each irradiance variable with the logarithm of week-integrated I'_0 (i.e. the independent irradiance variable used in Table 1).

Dependent variable	Coefficients for regression $\ln(I) = A + B \ln(I'_0)$		
	A	B	r^2
Hourly daytime I'_0	-2.87	0.727	0.998
I_{sml} —north basin	-4.40	1.273	0.949
I_{sml} —south basin	-2.35	0.957	0.996

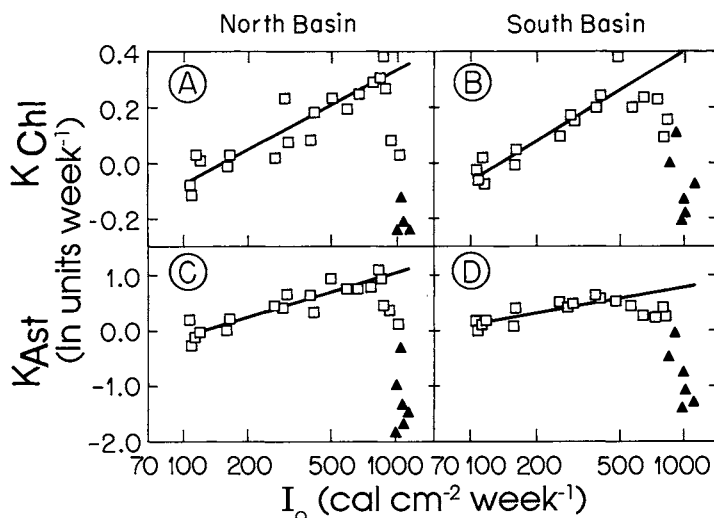


Fig. 3. Correlation of average net specific rates of change in abundance (K_{Ch1} , K_{Ast}) with mean time-integrated surface irradiance (I_0) based on irradiance recorded at the Windermere Laboratory (1964–1988). Shown is the relationship based on variations in Chl or counts of *Asterionella formosa* in surface samples from the north or south basins of Windermere. The solid line in each plot shows the regression line fitted to points from weeks 1–17 (north basin) or weeks 1–13 (south basin) (see also Table 1). Symbols same as for Fig. 2. Note logarithmic scale for irradiance.

mosa in early spring is 20–25% of the maximal growth rate at the indicated temperature (Talling 1955), but higher than would be predicted with Eq. 3 and existing data on physiological characteristics under these irradiances and temperatures.

Another approach to modeling the growth of diatom populations in the late-winter to early-spring period when the water column is well mixed is to consider light-dependent growth to be a function of the average light intensity in the mixed layer (I_{sml}). It has already been noted that logarithmic I_{sml} can

be an effective predictor of K in Windermere via the irradiance interconversion regressions in Table 2. A simple model of mixed-layer growth dependent on mean irradiance can be based on the growth-irradiance function

$$\mu = 7\{D \mu_{\max} [1 - \exp(-\alpha_g I_{sml}/\mu_{\max})] - 24\mu_0\}. \quad (4)$$

Here μ is the specific growth rate (week^{-1}), μ_{\max} the maximal specific growth rate per hour of daylength (D), α_g the slope of the growth-irradiance curve at zero irradiance,

Table 3. Parameters used to calculate the light-dependent growth rates of *Asterionella formosa* during spring in the north basin of Windermere via Eq. 3.

Parameter	Description	Value	Source
$P_{\max}(T)$	Light-saturated rate of photosynthesis as a function of temperature	$P_{\max}(10) \times (0.925)^{10-T} \text{ mg O}_2 (10^9 \text{ cells})^{-1} \text{ h}^{-1}$	Talling 1957a, 1966
$P_{\max}(10)$	P_{\max} at 10°C	8.0 mg O ₂ (10 ⁹ cells) ⁻¹ h ⁻¹	Talling 1966
α	Initial slope of the photosynthesis-irradiance function	7.95 mg O ₂ (10 ⁹ cells cal cm ⁻² PAR) ⁻¹	Talling 1966
I_k	Geometric measure of the irradiance at which photosynthesis begins to saturate	P_{\max}/α (e.g. 0.50 cal cm ⁻² h ⁻¹ PAR at 5°C)	
R	Respiration rate per cell	$P_{\max}(T) \times 0.055$	Talling 1957a
G/P	Growth/photosynthesis ratio	0.0046 ln units 10 ⁹ cells (mg O ₂) ⁻¹	Talling 1955
ν	Sinking rate	0.2 m d ⁻¹	Davey 1988

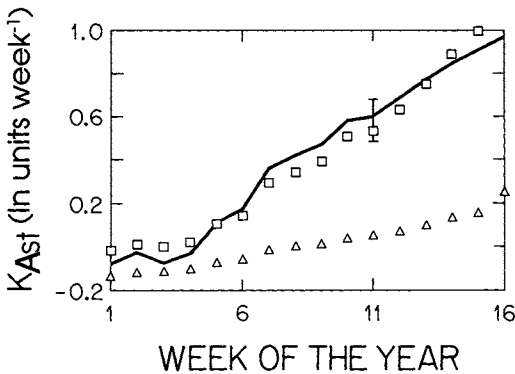


Fig. 4. Progression with time of specific net growth rates of *Asterionella formosa* in the north basin of Windermere in early spring estimated from Eq. 3 via daytime mean surface irradiance and water temperature recorded for each week in the period 1964–1988 (Δ) and for growth rates computed with the mean irradiance in the mixed layer via Eq. 4 (\square). Rates computed with the same irradiance data with the regression relationship defined for north basin *A. formosa* (Fig. 3B) are shown for comparison (solid line). Vertical bar indicates 95% C.I. for the regression estimate of K_{Ast} .

and μ_0 the hourly maintenance rate. The theoretical basis for an exponential growth-irradiance curve has been discussed (Sakshaug et al. 1989). For comparison with the results of the integrated productivity model (Eq. 3), μ_{max} was taken as $(G/P)P_{max}$, α_g as $(G/P)\alpha$, and μ_0 as $0.055 \mu_{max}$ (cf. Table 3). During the period that I_{sml} was $\leq I_k$ (weeks 6–13), computed K at average irradiance and temperature (μ corrected for sinking loss) agrees remarkably well with the fitted logarithmic equation (Fig. 4). The net specific rate of increase estimated by Eq. 4 was on average only 0.06 week^{-1} less than the regression estimate. Over the same week 6–13 period, rates estimated with Eq. 3 were an average of 0.48 week^{-1} less than the regression equation (Fig. 4).

These results draw attention to the potential of the in situ growth data to serve as a benchmark for the application of models of irradiance-dependent growth to natural phytoplankton dynamics. The models discussed here illustrate two alternative approaches to modeling the *A. formosa* early-spring growth period in Windermere. The integrated production model assumes that rates measured in incubations are attained even during very short exposure times. The mean irradiance approach assumes that ir-

radiance exposure periods are short relative to saturation of photosynthesis. In reality, exposures to near-surface irradiances during which saturation behavior can be expected are probably on the order of 1–10 min (Denman and Gargett 1983). The better agreement with the mean irradiance model suggests that the high growth rates in the late-winter to early-spring period may be due to enhanced photosynthetic rates over short-term exposures to saturating near-surface irradiance. If so, this evidence would be the first that short-term variability in photosynthetic parameters significantly influences production and growth of phytoplankton in situ. Physiological evidence that such variations can occur in diatom cultures has already been presented (Marra 1978; Neale and Marra 1985).

We cannot wholly exclude that the low integrated rates in Fig. 4 are due to incorrect estimates of the parameters of irradiance-dependent growth. Our assumed proportionality between photosynthesis and growth has been found, however, to apply to cultures of *A. formosa* grown under a broad range of irradiances (Talling 1955; Heaney unpubl.). Another explanation for the low rates estimated by Eq. 3 is that *A. formosa* does not grow well in culture and existing experimental data reflects suboptimal performance. We also consider this possibility unlikely. The photosynthesis data used here came from both cultured and natural populations of *A. formosa*, and there are no systematic differences related to the origin of the material (Talling 1957a). Further, the irradiance-dependent growth rates of *A. formosa* are in the range of growth rates of other diatom species, such as *Thalassiosira weissflogii* (Falkowski et al. 1985), *Phaeodactylum tricornutum* (Geider et al. 1985), and *Skeletonema costatum* (Sakshaug et al. 1989) grown under similar conditions. Finally, nonlinear variation in cell-specific maintenance rates can lead to extremely low compensation irradiance for growth (Gibson 1987), although such nonlinearity was not displayed by *A. formosa* in previous studies (Talling 1955; Heaney unpubl.). Whether the discrepancies described here are due to short-term variations in photosynthetic performance or some other mech-

anism, it is clear that additional work is needed to improve our ability to predict light-limited phytoplankton growth in the mixed-layer environment.

After week 15 in the south basin and week 17 in the north basin, specific rates of change remain positive but cease to monotonically increase as a function of irradiance (Fig. 3). The falloff is not an effect of self-shading because I_{smi} continues to increase in spring even after including the effect of increased attenuation by Chl (data not shown). In late spring, thermal stratification becomes well established with several consequences. Best known is the eventual depletion of surface silicate. The decrease of silicate concentration below the equivalent of $0.5 \text{ mg SiO}_2 \text{ liter}^{-1}$ usually signals the start of the decline of diatom populations (Lund 1950, 1964). Additionally, under stable conditions of low turbulence intensity, net downward transport by sinking removes cells from the surface layer (Lund et al. 1963).

Although the most negative rates of change of both Chl and cell abundance occur during the period of silicate depletion, rates stop increasing monotonically as a function of irradiance well before silicate concentration is $<0.5 \text{ mg SiO}_2 \text{ liter}^{-1}$ (Fig. 3). Laboratory growth studies suggest that this value is an overestimate of the threshold for silicate limitation of *A. formosa* growth for spring temperatures in Windermere ($<20^\circ\text{C}$, Tilman et al. 1982). The divergence before silicate depletion is not accounted for by the sinking of healthy (i.e. not nutrient limited) *A. formosa* cells, which have a sinking rate of $\sim 0.2 \text{ m d}^{-1}$ (e.g. Neale et al. 1991 and references cited therein).

The highest sinking loss rates would occur during shallow ($<7 \text{ m}$) stratification. For the 0–7-m integrating tube samples from the north basin, the weekly loss rate before silicate depletion would then be 0.2 week^{-1} . This value is less than the divergence of observed from predicted growth rates, as indicated by the difference between the extrapolated regression lines and data points in Fig. 3. The sinking rate estimate applies only to the period before pronounced silicate depletion; higher sinking rates after silicate depletion are known to contribute to sedimentation out of the surface layer and

formation of a subsurface maximum of *A. formosa* (Heaney et al. 1989; Davey and Heaney 1989). On the other hand, mean net rates of change of *A. formosa* abundance over the entire spring (up to week 23 or the first week in June) are a positive function of $\ln I_0$ and a negative function of stability as indicated by the square of the Brunt-Väisälä frequency (N^2) ($r^2 = 0.73\text{--}0.88$, Table 2). Thus, consideration of loss factors should extend beyond sedimentation of healthy cells and silicate depletion to other processes correlated with increased stratification.

One factor to consider is P availability. Phosphate concentration drops to below detectable levels ($<1 \text{ } \mu\text{g PO}_4\text{-P liter}^{-1}$) during late spring (Talling and Heaney 1988), and the cell P quota of *A. formosa* falls, although growth can continue for some time on stored P (Mackereth 1953). Another factor that may have a negative influence on net rates of change before Si limitation becomes important is photoinhibition (reviewed by Neale 1987). Transient surface stratification occurs in Windermere (Neale et al. 1991), prolonging the residence time of cells in near-surface irradiance and increasing the probability of high-light damage to the photosynthetic apparatus of the diatom (Neale 1987). Transient stratification would also interrupt silicate supply to the surface layer and slow growth rates. Such mechanisms could explain why a significant proportion of the decrease in growth rates is statistically correlated with the depth-maximum N^2 (Table 1). Exposure of *A. formosa* from Windermere to near-surface irradiance during incubations in situ does depress photosynthetic rates (Talling 1957a, 1966). Growth rates of cultured cells in similar but week-long incubations, however, are little affected (Lund 1949; Talling 1955). The in situ occurrence of photoinhibition in late-spring populations of *A. formosa* is documented elsewhere via measurements of in vivo Chl fluorescence; prolonged exposure to near-surface irradiance both decreases photosynthetic capacity and increases the sinking rate of *A. formosa* (Neale et al. 1991).

Overall, data from several sources suggest that the latter period of the spring diatom peak is composed of two stages. In the first

stage, stratification has occurred and population increase slows. In this stage processes correlated with transient stratification, such as photoinhibition, could be important. In a second stage, nutrients are strongly depleted and very high losses start that may bring down population levels rapidly. In this stage nutrient exhaustion would be the primary factor, with a possible additional interaction between nutrient status and photoinhibition (Neale et al. 1991). Photoinhibition effects can be enhanced when metabolic performance is impaired (Neale 1987). The combined effect of high irradiance and nutrient depletion could also account for rapid decline of spring diatom populations in other systems.

In both the increasing and decreasing phases of the diatom maximum in Windermere, the overall pattern is broadly consistent with the present interpretation of environmental control of phytoplankton biomass accumulation and dissipation in spring. Clearly, positive increments result from increases in irradiance and negative increments are largely due to depletion of silicate. But the long-term means of surface irradiance, density structure, and phytoplankton abundance—in essence the climate of diatom growth in spring—indicate periods in late winter to early spring and after setup of stratification when presently available quantitative data are not sufficient to account for the observed phytoplankton dynamics. Hopefully, this climatological description will serve as an incentive for further appropriately designed physiological studies and incorporation of the results into improved dynamical models. In addition, having defined the climate of the spring maximum, analysis can also be made of when, and why, significant deviations from the average occur in particular years (Goldman et al. 1989).

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