

An empirical model of the phytoplankton chlorophyll: carbon ratio --the conversion factor between productivity and growth rate

Abstract— We present an empirical model that describes the ratio of phytoplankton chlorophyll a to carbon, Chl: C, as a function of temperature, daily irradiance, and nutrient-limited growth rate. Our model is based on 219 published measurements of algal cultures exposed to light-limited or nutrient-limited growth conditions. We illustrate an approach for using this estimator of Chl : C to calculate phytoplankton population growth rate from measured primary productivity. This adaptive Chl : C model gives rise to interactive light-nutrient effects in which growth efficiency increases with nutrient availability under low-light conditions. One implication of this interaction is the enhancement of phytoplankton growth efficiency, in addition to enhancement of biomass yield, as a response to eutrophication.

We have not yet found a **satisfactory** method for routinely measuring or calculating the intrinsic growth rate of phytoplankton populations in their natural habitat. However, the consensus is that we can measure primary productivity, phytoplankton biomass, and environmental variables thought to control growth rate, such as nutrient concentrations, light, and temperature. How can we use these measurable quantities to reliably estimate phytoplankton growth rates in nature? Modeling approaches to address this question have followed two somewhat separate paths: development of mechanistic physiological models to explain phytoplankton chemical composition and growth rates measured under defined culture conditions (Laws and Bannister 1980; Kiefer and Mitchell 1983; Sakshaug et al. 1989); and development of simpler empirical formulations to estimate phy-

toplankton growth rates in numerical models of ecosystem dynamics (e.g. Winter et al. 1975). Although the second approach is largely based on results of laboratory experimentation, the two approaches have not yet been synthesized into a universally accepted equation set for calculating the growth rate of natural phytoplankton populations as a function of light, temperature, nutrients, and photosynthetic capacity.

The growth rate problem has been a challenge because phytoplankton productivity is usually measured as carbon assimilation rate, and biomass is often measured as chlorophyll a concentration. Transformation of productivity and biomass into population growth rate requires a conversion factor between these different units of measurement—the cellular ratio of chlorophyll a to carbon, Chl : C. Measurements with phytoplankton grown in culture show that Chl : C is highly variable, ranging from -0.003 (Falkowski et al. 1985) to >0.1 mg Chl a (mg C)⁻¹ (Geider 1987). This variability includes adaptive responses to ambient light, temperature, and nutrient conditions. Although Chl : C is a sensitive indicator of algal physiological condition and growth rate in the laboratory, there is no unique relation between growth rate and Chl : C. For example, Laws and Bannister (1980) demonstrated that different functional relations exist between Chl : C and growth rate y , depending on whether phytoplankton are grown under conditions of nutrient limitation (Chl : C increases with y) or light limitation (Chl : C decreases with y).

Here, we present an empirical equation that describes much of the variability in Chl : C ratios expressed by phytoplankton grown in culture. Then we suggest an approach

Table 1. Data sources for the empirical Chl : C model. Laboratory experiments included measurements of Chl : C and growth rate of unialgal cultures exposed to nutrient (*N*)-limited or light (*I*)-limited growth. Taxonomic identification follows that used in the original publication. Codes identify the species and sources of data in Figs. 1 and 2, *n* is the number of distinct growth conditions (daily irradiance, temperature, nutrient-limited growth rate) for which each investigator reported Chl : C.

Code	Limitation		<i>n</i>	Reference
1	<i>N</i> & <i>I</i>	<i>Skeletonema costatum</i>	53	Sakshaug et al. 1989*
2	<i>I</i>	<i>Leptocylindricus danicus</i>	49	Verity 1981, 1982
3	<i>I</i>	<i>Skeletonema costatum</i>	24	Yoder 1979
4	<i>N</i> & <i>I</i>	<i>Thalassiosira fluviatilis</i>	21	Laws and Bannister 1980
5	<i>I</i>	<i>Skeletonema costatum</i>	11	Langdon 1987
6	<i>N</i> & <i>I</i>	<i>Pavlova lutheri</i>	10	Chalup and Laws 1990
7	<i>I</i>	<i>Fragilaria crotonensis</i>	9	Rhee and Gotham 1981
8	<i>N</i>	<i>Cyclotella nana</i>	6	Caperon and Meyer 1972
9	<i>N</i>	<i>Dunaliella tertiolecta</i>	5	Caperon and Meyer 1972
10	<i>N</i>	<i>Monochrysis lutheri</i>	9	Caperon and Meyer 1972
11	<i>I</i>	<i>Thalassiosira weissflogii</i>	5	Falkowski et al. 1985
12	<i>I</i>	<i>Isochrysis galbana</i>	5	Falkowski et al. 1985
13	<i>N</i>	<i>Thalassiosira pseudonana</i>	3	Eppley and Renger 1974
14	<i>I</i>	<i>Cylindrotheca fusiformis</i>	1	Chan 1980
15	<i>I</i>	<i>Thalassiosira eccentrica</i>	1	Chan 1980
16	<i>I</i>	<i>Olisthodiscus luteus</i>	7	Langdon 1987

* Excludes measurements for cultures grown under very high light ($I > 30$ mol quanta $m^{-2} d^{-1}$).

for using this estimator of Chl : C to calculate growth rates of phytoplankton populations from measurable quantities—carbon assimilation rate, chlorophyll biomass, nutrient concentrations, light, and temperature. Our approach differs from that of Geider (1987) by including an explicit connection between nutrient-limited growth rate and Chl : C. Our model is built from theoretical guidelines provided by the mechanistic models describing the links between algal growth and biochemical composition (e.g. Laws and Bannister 1980; Kiefer and Mitchell 1983; Laws and Chalup 1990).

Our analysis is of results from 12 published studies that included measurements of growth rate and chemical composition of unialgal cultures grown under defined conditions of light, temperature, and nutrient delivery (Table 1). These studies were designed to address different questions and they used different methods, but the general experimental approach was to measure algal responses under different conditions of light limitation (exponential growth in nutrient-rich batch cultures) or nutrient limitation with continuous cultures. In each study the investigators reported measurements of temperature, irradiance, photoperiod, nutrient-limited growth rate μ' (growth rate normalized to the maximum rate at nonlimiting nutrient concentrations, and assumed here to equal 1 for cultures grown in nutrient-rich media), and cellular concentrations of chlorophyll *a* and carbon (or Chl : C). We calculated total daily irradiance and standardized the units to (PAR) mol quanta $m^{-2} d^{-1}$, using these conversions: $1 ly h^{-1} \approx 0.19$ mol quanta $m^{-2} d^{-1}$, and continuous light of $1 W m^{-2} \approx 0.4$ mol quanta $m^{-2} d^{-1}$. The pooled data set includes results from 219 different growth conditions and is heavily weighted by results from experiments with coastal diatoms. This data set is not compre-

hensive; for example we excluded results from experiments with dinoflagellates, which systematically have smaller Chl : C ratios than diatoms (Chan 1980). Our analysis, therefore, is representative of physiological adaptations expressed by species that have the potential for rapid growth; most of these species are commonly found in temperate coastal waters.

From this data set we sought the simplest empirical equation consistent with several observations central to other models relating Chl : C to growth rate. First, there seems to be a lower limit to the Chl : C ratio, on the order of $0.003 \text{ mg Chl } a (\text{mg C})^{-1}$. Second, for fixed combinations of light and temperature, Chl : C is positively and linearly related to μ' (Laws and Bannister 1980; Sakshaug et al. 1989; Chalup and Laws 1990). Third, the linear relation between Chl : C and μ' varies as a function of the light condition under which cultures are grown; the comprehensive experiments of Sakshaug et al. (1989) with *Skeletonema costatum* suggest that the slope of the relation between Chl : C and μ' decreases nonlinearly with daily light exposure. This adaptation to the light climate is included also in Geider's (1987) model of Chl : C for nutrient-saturated growth. Finally, from the systematic investigations of Yoder (1979) with *S. costatum* and Verity (1982) with *Leptocylindricus danicus*, Chl : C appears to increase exponentially with temperature (Geider 1987).

These responses can be described with a function of the form:

$$\text{Chl : C} = 0.003 + A \exp(BT) \exp(-CI) \mu' \quad (1)$$

Chl : C is the ratio of Chl *a* to C in phytoplankton grown at steady state under defined temperature T ($^{\circ}\text{C}$), daily irradiance I (mol quanta $m^{-2} d^{-1}$), and at nutrient-limited growth rate μ' . We fit the 219 measured values of Chl : C

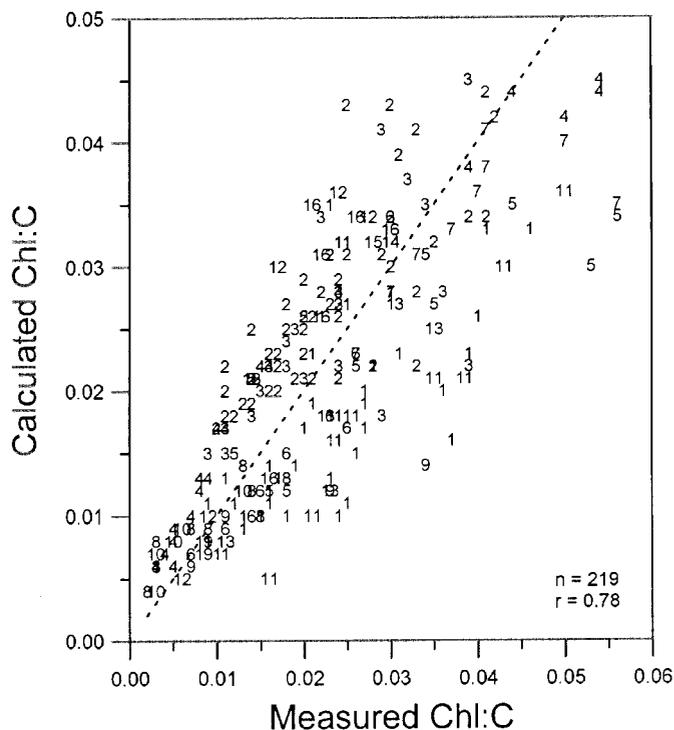


Fig. 1. Relationship between calculated Chl:C from Eq. 2 and measured Chl:C from the 219 determinations summarized in Table 1. Units for both are mg Chl *a* (mg C)⁻¹. The dashed line shows a 1:1 relation. Numbers identify the species and references listed in Table 1.

described above to Eq. 1 by nonlinear least-squares, giving

$$\text{Chl:C} = 0.003 + 0.0154 \exp(0.050T) \exp(-0.059I) \mu'. \quad (2)$$

The correspondence between calculated and measured Chl:C is shown in Fig. 1. The correlation coefficient between calculated and measured values is 0.78, so 60% of the variance contained in this data set is accounted for by a three-parameter function of *T*, *I*, and μ' (other, more complex functions can be found to explain a larger proportion of the variance; we selected this function because of its relative simplicity). Much of the residual around this regression could be the result of errors in the conversion of light units, interspecific differences in adaptive Chl:C, or differences in experimental protocols (e.g. sample collection at different phases of the light-dark cycle; different methods for measuring growth rate, Chl *a* and C concentrations, or light exposure of algal cells grown in culture vessels; Laws and Bannister 1980).

One criterion for judging the utility of Eq. 2 is the accuracy with which it describes the conversion between phytoplankton growth rate and photosynthetic rate in cultures. For this analysis we begin with the energy balance representation of phytoplankton growth, following Cullen (1990) and others:

$$\mu = P^B(\text{Chl:C}) - r. \quad (3)$$

This equation describes the daily specific growth rate μ

(d⁻¹) as a function of the biomass-specific photosynthetic rate P^B [mg C (mg Chl *a* d)⁻¹], the ratio Chl:C [mg Chl *a* (mg C)⁻¹], and respiration losses *r* (d⁻¹). A simplistic interpretation of this equation is that phytoplankton growth has three components: photosynthetic C assimilation (at rate P^B), synthesis of new cellular biomass (at a rate proportional to Chl:C), and metabolic costs of biosynthesis and cell maintenance.

Expressions similar to Eq. 3 have been used to describe growth rates of unialgal cultures from measured photosynthesis, Chl:C, and respiration (e.g. Laws and Bannister 1980). Our objective here is to extend this approach to estimate growth rates of multispecies communities from measured photosynthesis and calculated Chl:C. The approach requires an estimate of the respiratory loss *r*, which is extremely variable, ranging from 0.01 to 1.2 d⁻¹ in the laboratory (Geider 1992). All models of phytoplankton population growth have inherent large uncertainty because the underlying mechanisms of this variability are not well understood. The approach used here is simple and based on the assumption that the algal respiration rate *r* has two components—a basal rate r_0 and an additional component associated with cell synthetic activities and proportional to μ (this approach and its limitations are discussed by Geider 1992):

$$r = r_0 + r_1\mu. \quad (4)$$

Substitution of the respiration equation into Eq. 3 gives

$$\mu = P^B(\text{Chl:C}) - (r_0 + r_1\mu); \quad (5)$$

so,

$$\mu = [1/(1 + r_1)]P^B(\text{Chl:C}) - [1/(1 + r_1)]r_0. \quad (6)$$

We presume here that the maintenance respiration rate $[1/(1 + r_1)]r_0$ is 0.015 d⁻¹, consistent with Langdon's (1987) measurements of dark oxygen consumption by *S. costatum* maintained at zero growth rate. Selection of the parameter r_1 is more tenuous because of the enormous scatter observed in measured respiration rates expressed as a function of growth rate (Geider 1992). We estimated r_1 from least-squares fits of μ and $P^B(\text{Chl:C})$ to Eq. 6, using measurements described below.

In six of the studies referenced in Table 1, the investigators measured and reported photosynthetic rate of algal cultures in a form that could be used to calculate the daily carbon assimilation rate P^B . In some cases photosynthesis was reported as a photosynthetic "index" (Laws and Bannister 1980) or "performance" (Langdon 1987), measured as oxygen evolution or ¹⁴C uptake. These data were converted to units [mg C (mg Chl *a* d)⁻¹] using reported values of the photosynthetic quotient where necessary. In other cases the investigators reported parameters of photosynthesis-irradiance functions based on either ¹⁴C uptake rates (Chalup and Laws 1990) or least-squares fit of growth rates to a model similar to Eq. 3 (Sakshaug et al. 1989). We estimated photosynthetic parameters from Verity's (1981) data by nonlinear least-squares fits to the photosynthesis-irradiance function:

$$p^B = p_m^B [1 - \exp(-I\alpha/p_m^B)]. \quad (7)$$

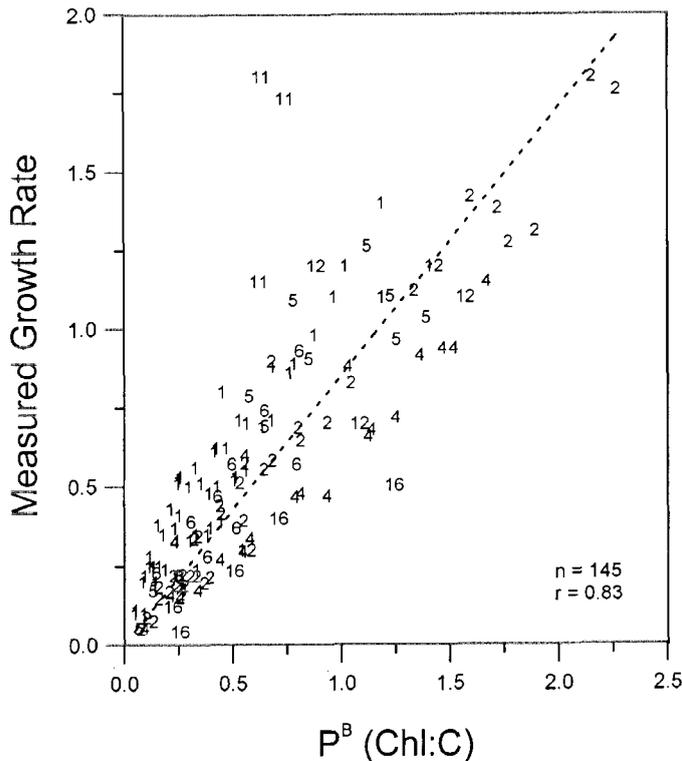


Fig. 2. Relationship between measured growth rate μ and the product of measured P^B times calculated Chl:C from Eq. 2. Numbers identify the species and references listed in Table 1. Dashed line is the least-squares fit to Eq. 6, with the y intercept fixed at -0.015 . This data set excludes Verity's (1981) measurements at 20°C , which did not yield reliable estimates of photosynthetic parameters.

Here p_m^B is the maximum hourly rate of photosynthesis normalized to chlorophyll biomass [$\text{mg C} (\text{mg Chl } a \text{ h})^{-1}$]. α defines photosynthetic efficiency at low irradiance, and I_t is instantaneous irradiance (PAR, $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$). From the photosynthetic parameters p_m^B and α we estimated the daily C assimilation rate of cultures as

$$P^B = D p_m^B [1 - \exp(-I_t / p_m^B)]. \quad (8)$$

D is the photoperiod (h) and I_t the constant irradiance under which cultures were grown.

From these sources we compiled results of 145 experiments in which phytoplankton growth rate and gross photosynthesis were measured. We fit these data to Eq. 6 using measured μ and P^B and calculated Chl:C from Eq. 2, giving

$$\mu = 0.85 P^B (\text{Chl:C}) - 0.015. \quad (9)$$

Residuals around this regression (Fig. 2) reflect errors arising from the assumption of a universal growth-photosynthesis relationship, the nonuniformity of experimental protocols, the assumption of constant respiration coefficients, and errors in the estimated Chl:C ratio. The correlation coefficient between μ and $P^B(\text{Chl:C})$ is 0.83, so almost 70% of the variance in this diverse set of growth rate measurements is associated with the product $P^B(\text{Chl:C})$.

C). When Eq. 9 is used to estimate growth rate ($\hat{\mu}$), the mean error $[100|(\hat{\mu} - \mu)|/\mu]$ is 35% of the measured growth rate μ . This is one estimator of the best precision we can expect when calculating the growth rate of diverse phytoplankton assemblages from measured photosynthesis.

We note that the respiration coefficient r_1 is treated here as a fitting parameter. From the slope of Eq. 9 (0.85) we calculate that $r_1 = 0.18$. This value of r_1 implies that respiratory loss is 30% of gross photosynthesis at low growth rate ($\mu = 0.1$) and 17% of gross photosynthesis at high growth rate ($\mu = 1$). These respiratory losses are near the low end of the broad range of the direct measurements summarized by Geider (1992). However this range is consistent with the calculations of Laws and Bannister (1980) that dark respiration typically does not remove more than 10–30% of daytime C production.

If Eq. 2 and 9 describe the general adaptive responses of phytoplankton species capable of rapid cell division, then they can be used to estimate growth rates in population dynamics models. We suggest here one approach and illustrate its application to the simple case of a homogeneous surface layer in which the rate of turbulent mixing is faster than the rate of physiological adaptation to the vertical light gradient. The examples use quantities representative of shallow, nutrient-rich coastal systems, such as estuaries and bays influenced by river runoff.

The growth rate equation requires an estimate of daily gross photosynthesis per unit biomass—the C assimilation rate P^B . Laboratory experiments designed to identify responses of phytoplankton photosynthesis to changing nutrient concentrations have yielded equivocal and sometimes contradictory results. In their review, Cullen et al. (1992, p. 69) concluded that “when it comes to nutrient limitation of marine photosynthesis, a good paradigm is hard to find.” So, our approach does not include explicit influence of nutrient availability on photosynthesis; gross photosynthesis is treated as a function only of light availability (Cullen 1990). The relation between photosynthesis and irradiance can be described with empirical functions such as Eq. 7 (Platt et al. 1990). The P – I parameters p_m^B and α can be measured in natural populations using short-term incubations with ^{14}C (e.g. Lewis and Smith 1983), and any effects of nutrient availability, temperature, or light adaptation on photosynthetic performance will be included implicitly if the growth rate calculation is based on measured p_m^B and α .

The quantity of interest here is the daily, depth-averaged value of μ in a mixing water column of depth H (m), so the appropriate value for P^B is the daily rate of gross photosynthesis per unit biomass, averaged over depth H :

$$\begin{aligned} P^B &= (1/H) \int_0^{24} \int_0^H p^B dz dt \\ &= (1/H) \int_0^{24} \int_0^H p_m^B [1 - \exp(-I_{z,t} \alpha / p_m^B)] dz dt. \end{aligned} \quad (10)$$

$I_{z,t}$ is the instantaneous irradiance at depth z . This equa-

tion can be evaluated numerically once the time and depth variations of $I_{z,t}$ are prescribed. We used a standard approach, prescribing uniform exponential light attenuation in the water column:

$$I_{z,t} = I_{0,t} \exp(-kz). \quad (11)$$

k is the spectrally averaged light attenuation coefficient (m^{-1}). We used a simple sinusoidal light curve (see Platt et al. 1990) to describe diurnal surface irradiance $I_{0,t}$:

$$I_{0,t} = I^* \sin[\pi(t - t_{am})/D]. \quad (12)$$

I^* is surface irradiance ($\mu\text{mol quanta } m^{-2} s^{-1}$) at solar noon, t is time of day (h), t_{am} is hour of sunrise, and D is photoperiod (h).

The second quantity in Eq. 9 is Chl:C, which can be calculated from Eq. 2 after appropriate values for I and μ' are identified. For an actively mixing water column, a candidate measure of I is the daily irradiance averaged over the depth of the mixing layer H because algal growth rate is determined largely by total daily light exposure (Cullen 1990):

$$\begin{aligned} I &= (1/H) \int_0^H I_\phi \exp(-kz) dz \\ &= (I_\phi/kH) [1 - \exp(-kH)]. \end{aligned} \quad (13)$$

I_ϕ is daily irradiance ($\text{mol quanta } m^{-2} d^{-1}$) just below the surface ($I_\phi = \int_0^{24} I_{0,t} dt$).

Prescription of the nutrient-limited growth rate μ' is more problematic because of the great uncertainty about how fluctuations in nutrient availability translate into fluctuations in phytoplankton growth rate. One traditional modeling approach is to assume balanced growth and then define nutrient-limited growth rate with the Monod equation,

$$\mu' = N/(K_N + N). \quad (14)$$

N is the concentration of the most limiting nutrient and K_N the half-saturation constant that defines sensitivity of μ' to changes in nutrient concentration. We follow this approach here because of its simplicity; an alternative is to describe μ' as a function of cell nutrient quota calculated from a separate equation for nutrient uptake (Tett and Droop 1988). For this example we specify the limiting nutrient as nitrogen, measured as the sum of all dissolved inorganic species (DIN); we prescribe $K_N = 1 \mu\text{M DIN}$; and we define N as the depth-averaged DIN concentration in the mixing layer. Substitution of the Monod expression (Eq. 14) for μ' into Eq. 2 gives a formulation to estimate the Chl:C ratio expected in a phytoplankton population having adaptive capabilities similar to those shown in Fig. 1:

$$\begin{aligned} \text{Chl:C} &= 0.003 + 0.0154[\exp(0.050T)] \\ &\times \langle \exp\{-0.059(I_\phi/kH) [1 - \exp(-kH)]\} \rangle \\ &\times [N/(K_N + N)]. \end{aligned} \quad (15)$$

Daily, depth-averaged μ can now be calculated from

Eq. 9, using Eq. 10–12 to solve for P^B and Eq. 15 to solve for Chl:C. This approach requires six quantities that describe the growth environment and can be measured: I_ϕ , D , k , H , T , and N . Two parameters (p_m^B and α) define the population-specific photosynthesis-irradiance function, and these also can be measured. The remaining six parameters (A , B , C , K_N , r_0 , r_1) define the adaptive Chl:C ratio and respiration rate; these cannot be routinely measured in natural populations and we suggest values for each based on measurements with unialgal cultures under defined growth conditions.

Does this approach yield growth rates that are fundamentally different from others? One traditional modeling approach is based on the threshold limitation hypothesis that instantaneous photosynthetic rate is limited by either light energy or a nutrient, and then the conversion of photosynthetic rate into growth rate with a constant Chl:C ratio. The procedure outlined above treats the Chl:C ratio as an adaptive variable such that phytoplankton growth can be limited simultaneously by light and nutrient availability. We explored the differences between these approaches by comparing the two procedures for calculating depth-averaged μ as a function of mean daily irradiance I over a range of N concentrations between 0.1 and 25 μM . For this comparison we fixed $H = 10$ m, $k = 1 m^{-1}$, $p_m^B = 8 \text{ mg C (mg Chl } a \text{ h)}^{-1}$, $\alpha = 0.05 [\text{mg C (mg Chl } a \text{ h)}^{-1} (\mu\text{mol quanta } m^{-2} s^{-1})^{-1}]$, $T = 20^\circ\text{C}$, and $D = 16$ h. Then we calculated μ for a range of I between 0 and 12 $\text{mol quanta } m^{-2} d^{-1}$. For the adaptive Chl:C model, we calculated μ from Eq. 9 and 15, using numerical solutions for P^B (trapezoidal integration of Eq. 10 with vertical grid spacing of 0.05 m and time step of 0.1 h). For the threshold limitation, fixed Chl:C model, we calculated μ with a constant Chl:C of 0.025 $\text{mg Chl } a (\text{mg C})^{-1}$. At every computation point in this numerical integration over time and depth, the instantaneous value of μ was taken as the minimum of light limitation,

$$\mu = 0.85p_m^B [1 - \exp(-I_{z,t}\alpha/p_m^B)] (\text{Chl:C}) - 0.015, \quad (16a)$$

or nutrient limitation,

$$\mu = 0.85p_m^B [N/(K_N + N)] (\text{Chl:C}) - 0.015. \quad (16b)$$

These two models are contrasted in Figs. 3 and 4. The adaptive Chl:C approach (Eq. 9 and 15) generates a series of unique μ - I curves for which the initial slope, x intercept, and maximum growth rate all vary with nutrient concentration (Fig. 3). The initial slope and x intercept change because for a given irradiance, Chl:C increases with increasing nutrient concentration (see Eq. 15). Both of these features can be interpreted as measures of growth efficiency. The initial slope of the μ - I curve measures the change in growth rate with incremental changes in irradiance; the x intercept defines the minimum (compensation) irradiance I_c required for growth. Both of these features vary with nutrient concentration (Table 2), so the results in Fig. 3 imply an interactive light-nutrient effect in which growth efficiency under low-light conditions is enhanced by nutrient enrichment. Rhee and Gotham (1981) observed this interactive effect in their

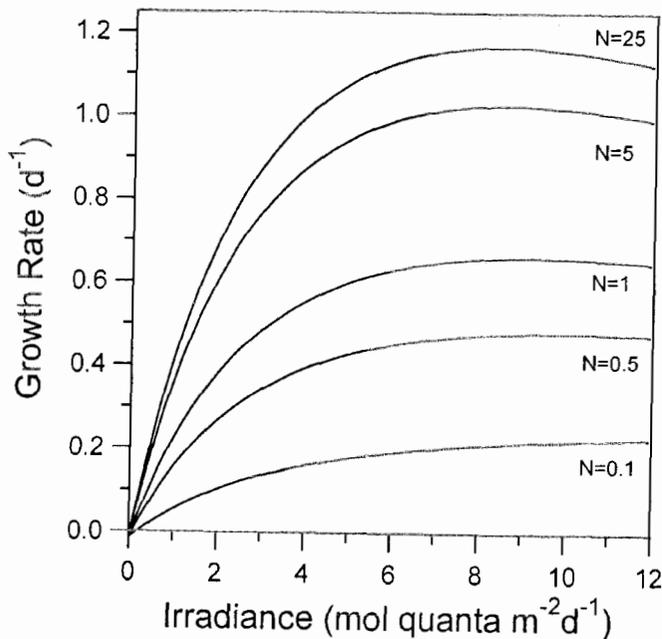


Fig. 3. Daily phytoplankton growth rate μ (Eq. 9 and 10) vs. daily irradiance I for nutrient (N) concentrations between 0.1 and 25 μM . This adaptive model expresses Chl : C as a function of T , I , and N (Eq. 15). Results are for a rapidly mixing water column where $H = 10$ m, $k = 1$ m⁻¹, $T = 20^\circ\text{C}$, $D = 16$ h, $p_m^b =$

column where $p_m^b = 8$ mg C (mg Chl a h)⁻¹, $\alpha = 0.05$ [mg C (mg Chl a h)⁻¹ ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$)⁻¹], and $K_N = 1$ μM .

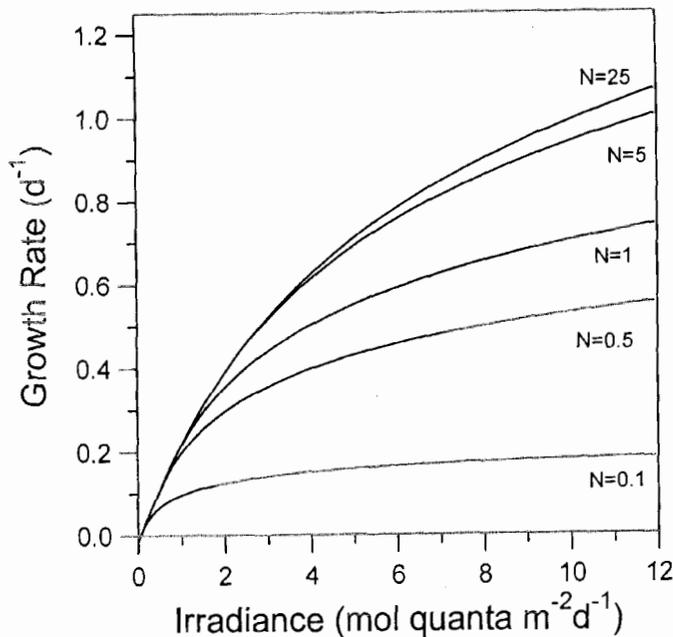


Fig. 4. Daily phytoplankton growth rate μ (Eq. 16 integrated over depth H and 24 h) vs. daily irradiance I for nutrient (N) concentrations between 0.1 and 25 μM . This model is based on fixed Chl : C of 0.025 mg Chl a (mg C)⁻¹ and instantaneous control of growth by either light or nutrient availability. Results are for a rapidly mixing water column where $H = 10$ m, $k = 1$ m⁻¹, $T = 20^\circ\text{C}$, $D = 16$ h, $p_m^b = 8$ mg C (mg Chl a h)⁻¹, $\alpha = 0.05$ [mg C (mg Chl a h)⁻¹ ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$)⁻¹], and $K_N =$

Table 2. Two measures of phytoplankton growth efficiency at low irradiance: the linear slope of μ - I curves (mol quanta m⁻²), and the compensation irradiance (I_c , mol quanta m⁻²d⁻¹) at which $\mu = 0$. These indices are listed for different N concentrations, comparing values derived from the adaptive Chl : C model (Fig. 3) and the fixed Chl : C model (Fig. 4).

N (μM)	Slope	I_c
Adaptive Chl : C		
0.1	0.078	0.192
0.5	0.193	0.078
1	0.270	0.056
5	0.430	0.035
25	0.490	0.031
Constant Chl : C		
0.1-25	0.255	0.059

chemostat experiments to characterize simultaneous growth limitation by light and nutrients. This interactive effect is absent from the fixed Chl : C threshold limitation model. Equation 16 generates a series of μ - I curves that are all bounded by one asymptotic function that defines the μ - I response under nutrient-saturated conditions (Fig.

intercept, so these measures of growth efficiency are sensitive to nutrient conditions (Table 2), only the maximum growth rate changes in response to nutrient concentration.

The two models describe very different functional responses of phytoplankton growth to light and nutrient availability, even though the P - I parameters, response rate, and defined growth environment were identical in these comparisons. The divergence of model calculations is greatest under high-nutrient ($N > K_N$) and low-irradiance (< 10 mol quanta m⁻² d⁻¹) conditions. For example, at $I = 3$ mol quanta m⁻² d⁻¹ and $N = 25$ μM , the calculated μ from Eq. 9 and 15 is 0.88 d⁻¹ and the calculated μ from Eq. 16 is only 0.52 d⁻¹. This difference is an example of the observations by Rhee and Gotham (1981), that algal requirements for light and nutrients "can compensate for each other to maintain the same growth rate under simultaneous limitations of N and light. This compensatory ability implies that one mechanism of coastal eutrophication might be the enhancement of growth efficiency. Phytoplankton populations in coastal or estuarine waters are often light limited by high seston concentrations (Cloern 1987). Calculated growth rates in Fig. 3 suggest that phytoplankton have the capacity to shift up their growth efficiency under low light conditions as a response to nutrient enrichment. Therefore, one mechanism of coastal eutrophication might be an enhancement of phytoplankton growth efficiency as well as biomass yield.

As a final example we show how the Chl : C model can be used to estimate μ directly from photosynthetic parameters, without the need for numerical integration. Platt et al. (1990, 1991) gave an accurate series

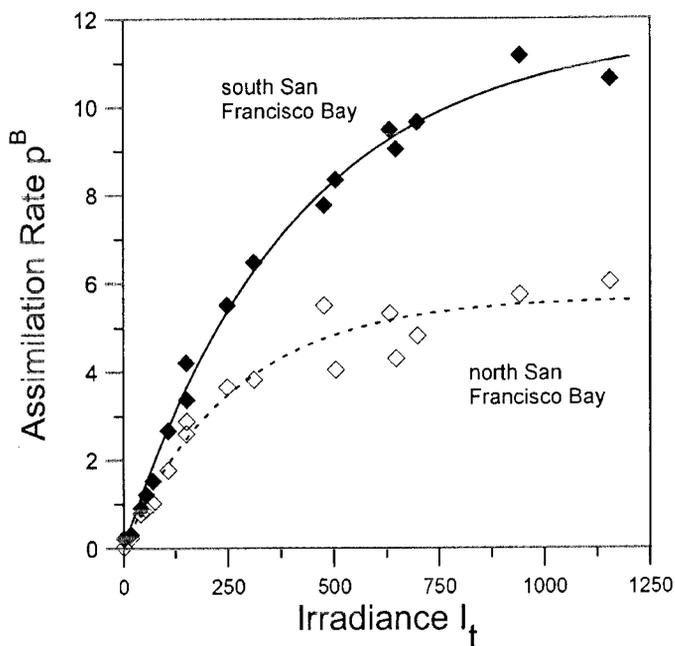


Fig. 5. P - I curves describing photosynthetic performance of phytoplankton collected in south San Francisco Bay (USGS station 32) and north San Francisco Bay (USGS station 6) on 14–15 June 1993. Assimilation rates p^B [mg C (mg Chl a h) $^{-1}$] are from 30-min incubations with ^{14}C at irradiances I_t between 2 and 1,160 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$. Curves are least-squares fits to Eq. 7; derived photosynthetic parameters are listed in Table 3.

imation to the depth-, time-integral of photosynthesis in a homogeneous layer of depth H :

$$P = \frac{BDp_m^B}{\Pi k} \sum_{x=1}^5 w_x (I^* \alpha / p_m^B)^x - \frac{BDp_m^B}{\Pi k} \sum_{x=1}^5 w_x [\exp(-kH) I^* \alpha / p_m^B]^x. \quad (17)$$

P is integral photosynthesis [$\text{mg C (m}^2 \text{ d)}^{-1}$], B is chlorophyll concentration ($\text{mg Chl } a \text{ m}^{-3}$), w_x are coefficients (from table 2 of Platt et al. 1991), and instantaneous irradiance at noon can be calculated as $I^* = 438.4 I_\phi / D$. The mean daily assimilation rate is integral photosynthesis divided by integral biomass:

$$P^B = P / (HB), \quad (18)$$

and Eq. 17 and 18 can be used with Eq. 15 and 9 to estimate P^B , Chl:C, and then μ from measurable quantities.

Examples of P - I curves are shown in Fig. 5, which compares photosynthetic performance of populations sampled in south San Francisco Bay and north San Francisco Bay during summer. These results are from measured ^{14}C uptake during 30-min incubations in a photosynthetron (Lewis and Smith 1983). Derived P - I parameters are listed in Table 3 along with measures of those quantities required to calculate Chl:C, P^B , and μ .

Table 3. Example calculations of the phytoplankton Chl:C ratio (Eq. 15), mean carbon assimilation rate P^B (Eq. 17, 18), and population growth rate μ (Eq. 9) comparing growth conditions and population photosynthetic parameters from south (SB) and north (NB) San Francisco Bay on 14–15 June 1993. Measured quantities are from Caffrey et al. (1994) and Hager (1994). Calculations are based on the assumption of a homogeneous water column of depth $H = 10$ m.

	SB	NB
Measured quantities		
T ($^{\circ}\text{C}$)	19.6	19.6
k (m^{-1})	0.87	2.63
B ($\text{mg Chl } a \text{ m}^{-3}$)	2.55	5.58
N (μM)	24.4	11.0
D (h)	14.8	14.8
I_ϕ ($\text{mol quanta m}^{-2} \text{ d}^{-1}$)	57.0	57.0
p_m^B [$\text{mg C (mg Chl } a \text{ h)}^{-1}$]	11.74	5.67
α [$\text{mg C (mg Chl } a \text{ h)}^{-1} \times$ $[(\mu\text{mol quanta m}^{-2} \text{ s}^{-1})^{-1}]$]	0.029	0.022
Calculated quantities		
Chl:C [$\text{mg Chl } a \text{ (mg C)}^{-1}$]	0.030	0.036
P^B [$\text{mg C (mg Chl } a \text{ d)}^{-1}$]	29.3	5.9
μ (d^{-1})	0.73	0.17

Calculated growth rates in Table 3 correspond to population doubling times of ~ 1 d in the southern bay and 4 d in the more turbid northern bay. These rates are higher than previous estimates of summer growth rate from calculations based on constant Chl:C of 0.02 and the assumption that respiration loss r is a fixed fraction (0.1) of the maximum assimilation rate p_m^B (Cloern 1991). A second implication of the growth rate procedure developed here is that phytoplankton respiration losses may be considerably smaller than those estimated from models in which r scales with p_m^B . If the smaller respiration losses described here under low-light conditions are realistic, then this approach may help resolve the paradox between observed and calculated C balances of phytoplankton populations in turbid waters (e.g. Cole et al. 1992).

Our model is not the ultimate solution to the challenging problem of how we define population growth responses of phytoplankton to changing light and nutrient availability. For example, we do not consider diel variability of P - I parameters (Harding et al. 1981) or Chl:C (Eppley and Renger 1974), kinetics of photoadaptation (Lewis et al. 1984) and effects of changing turbulence distribution or mixed layer depth on Chl:C, differential adaptations among different phytoplankton taxa (Chan 1980), or variability in respiratory loss as a fraction of growth rate (Geider 1992). However, we do present an empirical function that describes much of the variability of Chl:C expressed by phytoplankton grown in the laboratory at steady state. This function can be incorporated into numerical models to describe phytoplankton growth rate as an interactive response to fluctuations in daily light and nutrient resources.

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