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A dynamic regulatory model of phytoplanktonic acclimation to light, nutrients, and temperature

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Abstract

A new regulatory model can describe acclimation of phytoplankton growth rate (μ), chlorophyll a:carbon ratio and nitrogen:carbon ratio to irradiance, temperature and nutrient availability. The model uses three indices of phytoplankton biomass—phytoplankton carbon (C), phytoplankton nitrogen (N), and chlorophyll a (Chl). The model links the light-saturated rate of photosynthesis to $N:C$, requires that Chl a synthesis be coupled to nitrogen assimilation, and includes several regulatory features. These include feedback inhibition of the nitrogen assimilation rate by increases in the $N:C$ ratio, as well as regulation of Chl a synthesis by the balance between light absorption and photosynthetic carbon fixation. The model treats respiration as the sum of the maintenance metabolic requirement and the cost of biosynthesis. In addition, the model can account for accumulation and mobilization of energy reserves (i.e. variability of $N:C$) and photoacclimation (i.e. variability of Chl:N and Chl:C) in response to variations in irradiance and nutrient availability. The assumptions of the model are shown to be in agreement with experimental observations and the model output compares favorably with data for cultures in balanced and unbalanced growth.

The light-, nutrient-, and temperature-dependencies of phytoplankton growth rate have often been modeled separately. Phytoplankton growth rate has been treated as a function of the dissolved nutrient concentration using the Monod equation or as a function of the cellular content (or quota) of limiting nutrient using the Droop equation (McCarthy 1980; Droop 1983; Morel 1987). Under conditions of balanced growth, the Droop and Monod equations are consistent with each other and with Michaelis–Menten nutrient uptake kinetics (Morel 1987). The temperature-dependence of growth rate has been treated as an exponential dependence or an Arrhenius equation, although other functions have also been used (Eppley 1972; Li 1980; Ahlgren 1987). The light-dependencies of growth and photosynthesis rates have been treated by a number of equations, including a modification of the Monod equation, a hyperbolic tangent, and a Poisson function (Jassby and Platt 1976). A large body of experimental work has proven the utility of these descriptions of the effect of a single environmental factor on a single physiological process.

Despite success in describing the individual resource-response relationships for light and nutrients, there is little consensus on how the relationships for different resources should be combined to describe growth as a function of multiple resources (Rodhe 1978; Droop 1983). Some researchers advocate a multiplicative interaction among light and nutrient limitation (Droop 1983), whereas others require that growth rate be either light-limited or nutrient-limited (Rodhe 1978). Moreover, the models are valid only under the restrictive conditions of balanced growth, which is achieved when the specific rates of change of all measures of biomass are equal (Eppley 1980). Balanced growth requires strict coupling of nutrient uptake, light harvesting, and carbon fixation. Thus, balanced-growth models cannot describe the uncoupled rates of nutrient assimilation or photosynthesis that occur during the transients arising from fluctuations in environmental conditions.

The chemical composition of cells changes in response to cues received from the environment. This adjustment of cellular physiology is termed acclimation. Its importance to phytoplankton growth rate in the sea is indicated by variations of pigment:biomass observed in vertical profiles (Cullen 1982; Campbell et al. 1994) and along horizontal transects (Buck et al. 1996). Variability of the Chl a-to-carbon ratio (Chl:C) owing to physiological acclimation and taxonomic composition (Geider 1987; Langdon 1988; Cloern et al. 1995) has long been recognized as a major source of uncertainty in investigations of phytoplankton growth (Eppley 1972; Banse 1977).

Typically, it is assumed that acclimation serves to increase growth rate under suboptimal conditions over the value that would be achieved if cellular chemical composition were static. The assumption that biochemical composition (i.e. Chl:C and the phytoplankton nitrogen:carbon ratio, or $N:C$) is actively adjusted to yield maximum growth rate under prescribed environmental conditions has been applied in the development of some phytoplankton growth models (Shuter 1989). However, acclimation may also serve to limit the damage that may be incurred as a consequence of exposure to adverse environmental conditions. Damage to the photo-

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Table 1. List of definitions of variables and parameters.

Variable	Definition	Typical units
a^{Chl}	Chl-specific light absorption coefficient	m^2 (g Chl a)$^{-1}$
A_E	Slope of the linear region of the Arrhenius plot	Dimensionless
Chl	Chl a	g Chl a m^{-3}
E_0	Incident scalar irradiance	μmol photons m^{-2} s^{-1}
K_{nit}	Half-saturation constant for nitrate uptake	μM
n	Shape-factor describing dependence of V^C_{max} on Q	Dimensionless
N_i	Inorganic nitrogen concentration	μM
C	Phytoplankton carbon	g C m^{-3}
N	Phytoplankton nitrogen	g N m^{-3}
P^C_{phot}	C-specific rate of photosynthesis	d^{-1}
P^C_{max}	Maximum value of P^C_{phot} at temperature T	d^{-1}
P^C_{ref}	Value of P^C_{max} at temperature T_{ref}	d^{-1}
Q	The cell quota of nitrogen ($N:C$)	g N (g C)$^{-1}$
Q_{min}	Minimum value of Q	g N (g C)$^{-1}$
Q_{max}	Maximum value of Q	g N (g C)$^{-1}$
R^C	Maintenance respiration rate constant	d^{-1}
R^{Chl}	Chl a degradation rate constant	d^{-1}
R^N	N remineralization rate constant	d^{-1}
R_{ref}	Degradation rate constant at the reference temperature	d^{-1}
T	Temperature	K
$T_{function}$	Temperature-response function	Dimensionless
T_{ref}	Reference temperature	K
V^C_{nit}	Phytoplankton carbon-specific nitrate uptake rate	g N (g C)$^{-1}$ d^{-1}
V^C_{max}	Maximum value of V^C_N at temperature T	g N (g C)$^{-1}$ d^{-1}
V^C_{ref}	Value of V^C_{max} at temperature T_{ref}	g N (g C)$^{-1}$ d^{-1}
α^{Chl}	Chl a-specific initial slope of the photosynthesis-light curve	g C m^2 (μmol photons g Chl a)$^{-1}$
ϕ_{max}	Maximum photon efficiency of photosynthesis	mol C (mol photons)$^{-1}$
θ^C	Chl a:phytoplankton carbon ratio	g Chl a (g C)$^{-1}$
θ^N	Chl a:phytoplankton nitrogen ratio	g Chl a (g N)$^{-1}$
θ^N_{max}	Maximum value of θ^N	g Chl a (g N)$^{-1}$
ρ^{Chl}	Chl a synthesis regulation term	Dimensionless
ζ	Cost of biosynthesis	g C (g N)$^{-1}$

synthetic apparatus can occur when the excitation energy in absorbed photons exceeds the ability of cells to dissipate excess energy as heat. The excess of light absorption over photosynthesis will be more pronounced when nutrients are scarce or temperature is lowered. Thus, acclimation may include a tradeoff between maximizing growth at low irradiance vs. minimizing the potential for photooxidative damage at high irradiance (Raven 1980).

New, dynamic models of phytoplankton growth (Baumert 1996; Geider et al. 1996) allow explicit mechanistic treatment of photoacclimation of Chl:C and growth rate in variable light environments such as would be experienced by cells in nature. These models describe phytoplankton growth as a function of both environmental variables and cellular chemical composition. Light history is reflected in changes of Chl:C in these models. Chl:C in turn affects the instantaneous photosynthesis–light response. Here we extend the Geider et al. (1996) treatment of acclimation of Chl:C to include nitrogen limitation and variability of the $N:C$ ratio.

Our new model of phytoplankton growth and physiological acclimation to irradiance (E_0), nutrient concentration (N_i), and temperature (T) treats nutrient uptake and photosynthesis rates as functions of both environmental factors and cellular chemical composition (Chl:C and $N:C$); *see* Table 1 for list of symbols). The environmental variables (E_0, N_i, T) determine the instantaneous rates of light utilization, carbon assimilation, Chl a synthesis, and nutrient assimilation. We allow modulation of these instantaneous rates due to the effects of past environmental conditions by including the intracellular variables Chl:C and $N:C$. The model is based on three features of phytoplankton acclimation. First, it includes downregulation of pigment content at high irradiance and(or) when growth rate is limited by nutrient availability or temperature (Falkowski and La Roche 1991; Geider et al. 1996). Second, it includes the accumulation of energy-storage polymers when growth rate is light saturated and(or) nutrient limited, as well as the subsequent mobilization of these polymers when light is limiting or nutrients are resupplied (Foy and Smith 1980). Third, it includes feedback between nitrogen and carbon metabolism. The model differs from previous steady-state models of balanced growth (Bannister 1979; Shuter 1979; Kiefer and Mitchell 1983; Laws et al. 1983; Geider et al. 1997) by explicit consideration of the time-dependence of biomass and pigment accumulation under non-steady-state conditions of unbalanced growth. It extends the treatment of our dynamic model of light limitation (Geider et al. 1996) to include nitrogen limitation and variability of the N:C ratio.

The model

The model (Table 2) is based on mass balances for phytoplankton carbon (C), phytoplankton nitrogen (N), and chlorophyll a (Chl) (Eq. 1, 2, 3). We assume that photosynthesis is a Poisson function of irradiance (Eq. 4), that nutrient uptake is a Michaelis–Menten function of nutrient concentration (Eq. 6), and that temperature affects light-saturated photosynthesis, maximum nutrient-uptake rates, and maintenance respiration rates by an Arrhenius relation (Eq. 10). We assume that the maintenance metabolic rate constants describing respiration of C, remineralization of N, and degradation of Chl are equal. The model includes the following regulatory features: (1) The carbon-specific, light-saturated photosynthetic rate depends on the internal nitrogen status

Table 2. The model equations.

$$\frac{1}{C}\frac{dC}{dt} = C_{phot} - R^C - \zeta V_N^C \quad (1)$$

$$\frac{1}{N}\frac{dN}{dt} = \frac{V^N}{Q} - R^N \quad (2)$$

$$\frac{1}{Chl}\frac{dChl}{dt} = \frac{\rho_{Chl} V_N^C}{\theta^C} - R^{Chl} \quad (3)$$

$$P_{phot}^C = P_{max}^C\left[1 - \exp\left(\frac{-\alpha^{Chl}\theta^C E_0}{P_{max}^C}\right)\right] \quad (4)$$

$$P_{max}^C = P_{ref}^C\left[\frac{Q - Q_{min}}{Q_{max} - Q_{min}}\right]T_{function} \quad (5)$$

$$V_N^C = V_{max}^C\left(\frac{N_i}{N_i + K_{nit}}\right) \quad (6)$$

$$V_{max}^C = V_{ref}^C\left[\frac{Q_{max} - Q}{Q_{max} - Q_{min}}\right]^n T_{function} \quad (7)$$

$$\rho_{ChL} = \theta_{max}^N \frac{C}{\alpha^{Chl}\theta^C E_0} \quad (8)$$

$$R^C = R^N = R^{Chl} = R_{ref} T_{function} \quad (9)$$

$$T_{function} = \exp\left[A_E\left(\frac{1}{T} - \frac{1}{T_{ref}}\right)\right] \quad (10)$$

of the cells (Eq. 5). (2) The carbon-specific, light-limited photosynthetic rate depends on the Chl : C ratio (Eq. 4). (3) Chl *a* synthesis requires nitrogen assimilation (Eq. 3). (4) Chl *a* synthesis is downregulated when the rate of light absorption exceeds the rate of utilization of photons for carbon fixation (Eq. 3), with the extent of downregulation being governed by the imbalance between rates of light absorption and photosynthesis (Eq. 8). (5) The maximum rate of nitrogen assimilation is regulated by the internal nitrogen status of the cells (Eq. 7). (6) The respiration rate is coupled to the rate of nitrogen assimilation through the cost of biosynthesis (Eq. 1). The essential features of the feedbacks among carbon and nitrogen metabolism included in the model are summarized in Fig. 1. In addition to predicting the growth rate (μ), the model predicts the Chl *a*-to-carbon (Chl : *C*), chlorophyll *a*-to-nitrogen (Chl : *N*), and nitrogen-to-carbon (*N* : *C*) ratios under both balanced and unbalanced growth.

Photosynthesis.—Changes in phytoplankton carbon content arise from imbalances between photosynthesis and respiration (Eq. 1). As in our previous models (Geider and Platt 1986; Geider et al. 1996, 1997), photosynthesis is expressed as a carbon-specific rate with units of inverse time. Carbon-specific photosynthesis is a saturating function of irradiance (Eq. 4; Fig. 1A). The carbon-specific, light-saturated rate of photosynthesis (P_{max}^C) is assumed to be a linear function of *N* : *C* (*see Eq. 5*) consistent with observations (Fig. 2A). This assumption regarding P_{max}^C provides a significant link between carbon metabolism and the nitrogen nutritional state of the phytoplankton. This differs from our previous treatment of P_{max}^C as constant under nutrient-replete conditions

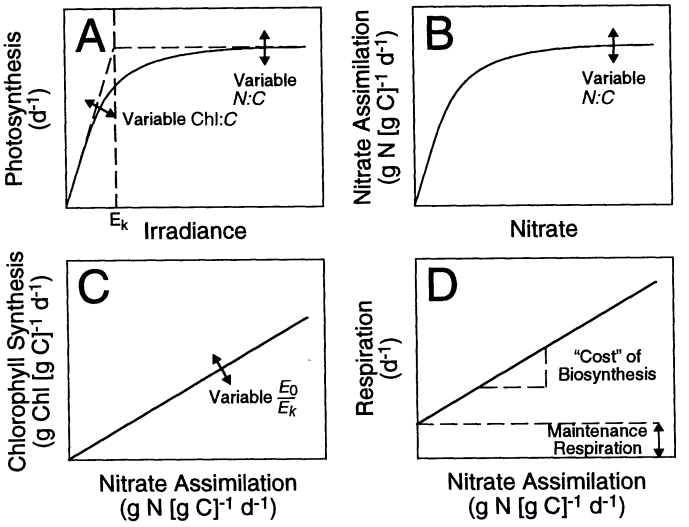

Fig. 1. Graphical summary of the model showing the dependencies of photosynthesis, nitrate assimilation, Chl *a* synthesis, and respiration on environmental and physiological variables (*see* Table 2 for mathematical details and the text for a fuller explanation). A. Photosynthesis is a saturating function of irradiance where the initial slope increases with increasing Chl : *C* and the light-saturated rate increases with increasing *N* : *C*. The light-saturation parameter (E_k) is given by the irradiance at which the initial slope intercepts the light-saturated rate. B. The carbon-specific nitrate assimilation rate is a saturating function of nitrate concentration where the maximum uptake rate is downregulated at high values of *N* : *C*. C. The rate of Chl *a* synthesis is obligately coupled to protein synthesis and thus to nitrate assimilation. However, the magnitude of the coupling depends on the ratio of irradiance to the light-saturation parameter (E_0/E_k). At a given rate of nitrate assimilation the carbon-specific rate of Chl *a* synthesis declines as E_0/E_k increases. D. The carbon-specific respiration rate is a linear function of the rate of nitrate assimilation. We assume that there is no lag between nitrate assimilation and protein synthesis. Major respiratory costs are associated with reduction of nitrate to ammonium, incorporation of ammonium into amino acids, and polymerization of amino acids into proteins. Other respiratory costs are assumed to scale with the rate of protein synthesis.

(Geider et al. 1996), or as a Monod function of external nutrient concentration under steady-state nutrient-limiting conditions (Geider et al. 1997). However, our previous models did not consider variability of *N* : *C* with growth irradiance or nutrient limitation. When used as a variable in the model, we designate the *N* : *C* ratio as *Q* (*Q* denotes the carbon-specific quota of limiting nutrient).

We assume that the light-limited photosynthesis rate is proportional to Chl : *C*, designated θ^C in the model equations. This assumption is based on two simplifications—first, that the rate of light absorption is proportional to the Chl *a* content of the cells; and second, that the maximum quantum efficiency of photosynthesis is invariant. Together, these two requirements are reflected in a constant value for the Chl *a*-specific initial slope of the *P*–E_0 curve (α^{Chl}) (*see Fig. 2B*).

Respiration.—Respiration of *C* is treated as the sum of a maintenance metabolic rate (R^C) and the cost associated with biosynthesis (Penning de Vries et al. 1974; Geider 1992)

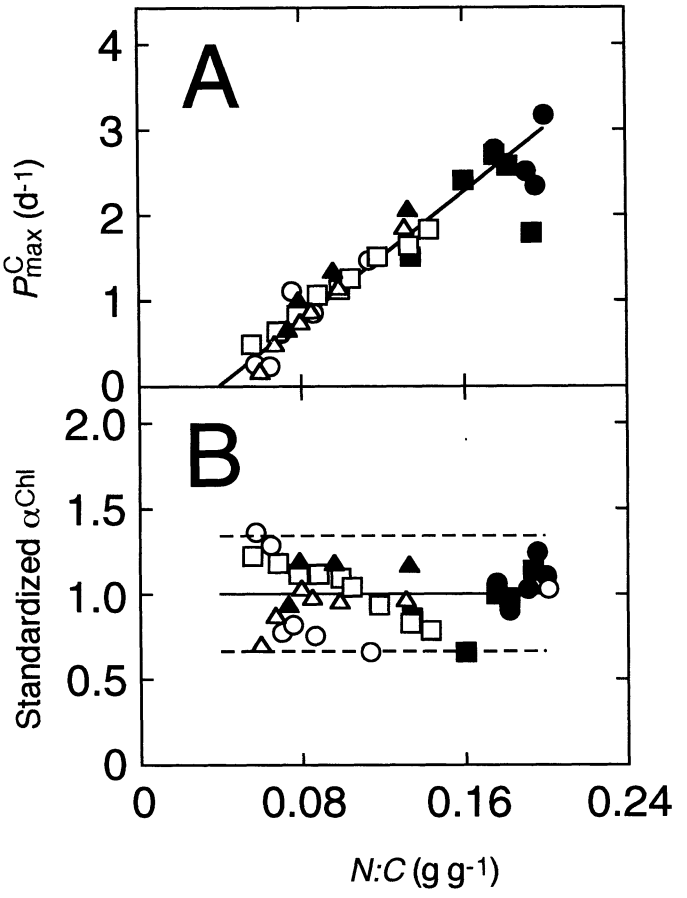

Fig. 2. The dependencies of (A) the carbon-specific, light-saturated photosynthetic rate (P^C_{max}) and (B) the Chl *a*-specific initial slope (α^{Chl}) of the photosynthesis–irradiance curve on $N:C$. Observations are for *Phaeodactylum tricornutum* (circles) (Osborne and Geider 1986; Geider et al. 1985), *Isochrysis galbana* (squares) (Falkowski et al. 1985; Dubinsky et al. 1986; Herzig and Falkowski 1988), and *Pavlova lutheri* (triangles) (Chalup and Laws 1990). Data for the initial slope are presented relative to the mean values observed for each species (7.9×10^{-6}, 1.4×10^{-5}, and 4.6×10^{-6} g C m^{-2} [g Chl *a* μmol photons]$^{-1}$ for *P. tricornutum, I. galbana,* and *P. lutheri,* respectively). For *P. tricornutum* and *I. galbana,* open and closed symbols indicate nutrient-limited and nutrient-replete cultures, respectively. For *P. lutheri,* open symbols represent high-light nutrient-limited conditions and closed symbols represent low-light, nutrient-limited conditions. The solid and dashed lines represent the mean ± 2 SD. The coefficient of variation of the standardized values was 17%.

(Fig. 1D). We neglect excretion of dissolved organic carbon, although this could be treated as another carbon-specific loss term in Eq. 1. Biosynthesis is assumed to be strictly coupled to nitrogen assimilation, and thus the cost of biosynthesis is given by the product of the rate of nitrogen uptake (V^C_N) and the biosynthetic efficiency (ζ) (Fig. 3). We note that ζ is expected to depend on the nitrogen source: it will be greater for oxidized forms of nitrogen such as nitrate than for reduced forms such as ammonium or urea. This link between respiration and nitrogen assimilation recognizes that nitrate reduction, amino acid synthesis, and peptide bond formation are major metabolic costs (Penning de Vries et al. 1974).

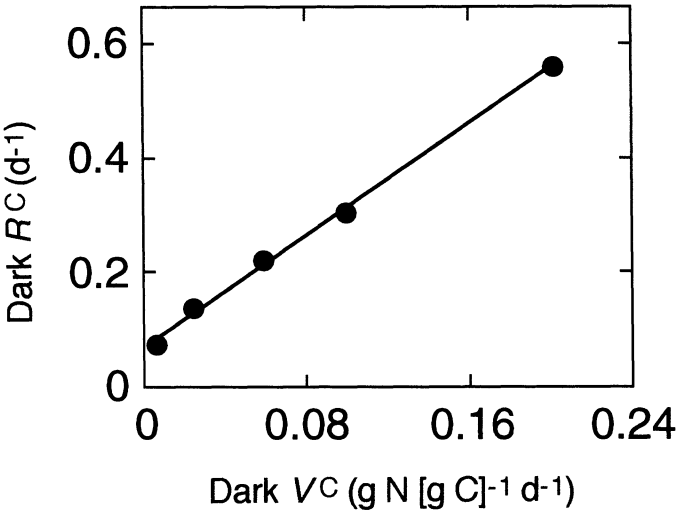

Fig. 3. The dependence of the dark respiration rate on the dark nitrate assimilation rate for *Thalassiosira allenii* (data of Laws and Wong 1978). The rate of nitrate assimilation was calculated as the product of $N:C$ and growth rate.

This link is consistent with the commonly observed covariability of respiration and growth rates (Geider 1992).

Inorganic nitrogen assimilation.—The rate of change of (N) is described as the difference between nitrogen assimilation and remineralization (Eq. 2). Nitrogen assimilation is treated as a Michaelis–Menten function of the dissolved inorganic nitrogen concentration (Eq. 6; Fig. 1B). We assume that the maximum carbon-specific, nitrogen-uptake rate (V^C_{max}) is a function of $N:C$ ($=Q$), providing a significant link between cellular carbon metabolism and nitrogen metabolism. Specifically, V^C_{max} is required to decline nonlinearly as Q increases (Eq. 7), consistent with observations (Fig. 4A). This assumption is necessary to prevent unrealistically high ratios of $N:C$ in low light and in darkness. Maximal, cell-specific nitrate-uptake and ammonium-uptake rates have been found to be largely independent of cellular nitrogen content in nitrogen-limited chemostat cultures of microalgae (McCarthy 1980), although increases of V^C_{max} for ammonium-uptake rate with ammonium-limited growth rate have been reported (Wantanabe and Miyazaki 1996). The relationship between maximum uptake velocities and cell quota for limiting nutrient may need to be modified if phosphate or iron are limiting factors because of the greater potential for luxury uptake of phosphorus and iron relative to nitrogen (McCarthy 1980; Morel 1987).

We do not differentiate among uptake of nitrate, ammonium, or dissolved organic nitrogen, although this could be done (Fasham et al. 1990). We also make the simplifying assumption that nitrate uptake is tightly coupled to protein synthesis, and thus neglect accumulation and mobilization of intracellular nitrate, ammonium, and amino acid pools (Dortch 1982; Villareal and Lipshultz 1995; Flynn et al. 1997). Remineralization of nitrogen is assumed to be proportional to N concentration through a rate constant R^N. More comprehensive treatments of nitrogen metabolism are available (Flynn et al. 1997), but there are few experimental

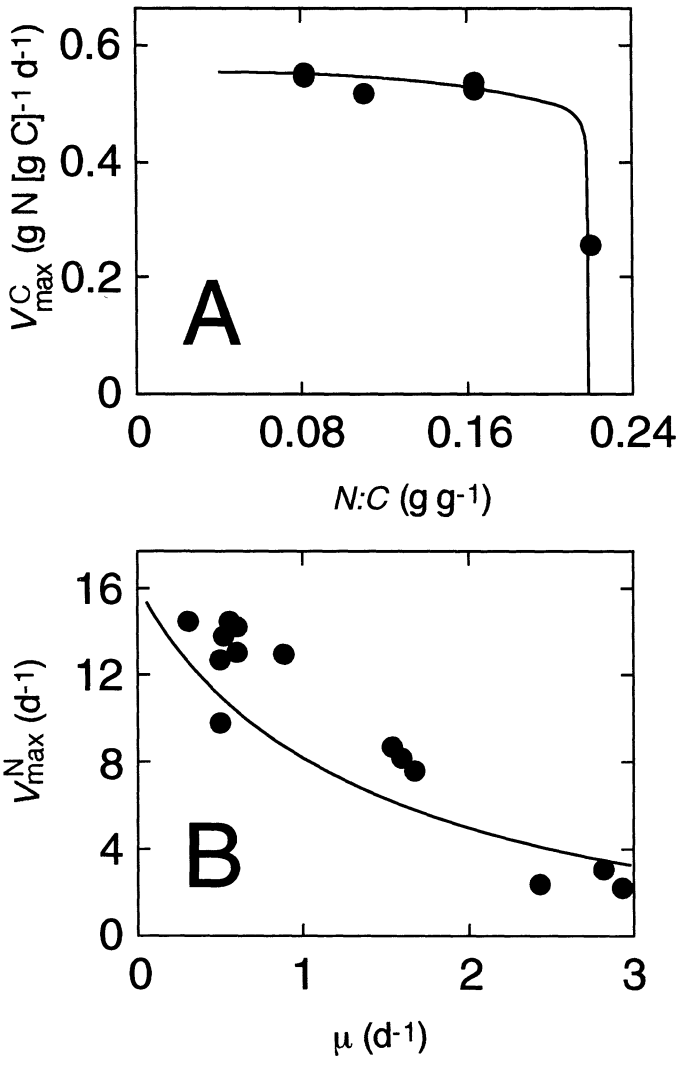

Fig. 4. A. The dependence of the carbon-specific, maximum nitrate uptake rate (V^C_{max}) on $N:C$ for the cyanobacterium *Oscillatoria agardhii* under nitrate-limited and nutrient-replete growth (Zevenboom and Mur 1978). Solid line shows relationship assumed in the model and closed circles are observations for *O. agardhii.* B. The dependence of the nitrogen-specific maximum nitrogen assimilation rate (V^N_{max} with units of d^{-1}) on the balanced growth rate (μ) for the diatom *Thalassiosira pseudonana* under ammonium-limited growth (McCarthy and Goldman 1979). Solid line shows the model output and closed circles show observations for *T. pseudonana.*

data available to judge the efficacy of these models. Our model treats the case where V^C_{max} for nitrogen assimilation does not vary between light and dark phases of an L/D cycle, as observed for organisms such as *Thalassiosira allenii* (Laws and Wong 1978). However, the model may need an additional term to account for light-dependence of V^C_{max} observed in organisms such as *Pavlova* (=*Monochrysis*) *lutheri* (Laws and Wong 1978).

Behavior of V^C_{max} *and* V^N_{max}—The model uses an arbitrary function to describe the relationship between V^C_{max} and $N:C$. The validity of this function rests on its ability to account for available data. V^C_{max} is assumed to be nearly constant at low values of $N:C$ (Eq. 7), but declines rapidly as $N:C$ approaches the maximum cell quota. This is consistent with the experimental data for *Oscillatoria agardhii* (Fig. 4A). Many estimates of nitrate and ammonium assimilation are reported as particulate nitrogen-specific rates (V^N_{max}) with units of inverse time (McCarthy 1980). It is commonly observed that V^N_{max} greatly exceeds the balanced growth rate under N-limiting conditions (McCarthy 1980). We obtained V^N_{max} by dividing V^C_{max} by $N:C$. The model prediction of an inverse dependence of V^N_{max} on growth rate compares favorably with observations (Fig. 4B).

Pigment synthesis—Chl *a* synthesis is assumed to be coupled to nitrogen assimilation (Eq. 3; Fig. 1C). This assumption is consistent with the obligate link of Chl *a* accumulation to synthesis of the apoproteins of pigment–protein complexes (Mortain-Bertrand et al. 1990) and the high ratio of protein to pigment in light-harvesting and other pigment-protein complexes of the photosynthetic apparatus (Raven 1984). It is also consistent with the observation that nitrogen-limited stationary-phase phytoplankton cultures lose the ability to photoacclimate to low light (Prezelin and Matlick 1983). Covariation of the rates of Chl *a* synthesis and nitrate assimilation have been observed in chemostat cultures in balanced growth (Fig. 5A). However, the coupling is not always a strict proportionality. Under balanced growth conditions, $Chl:N$ is inversely related to the light-saturation parameter (E_k) of the P–E_0 curve (Fig. 5B). The linearity in Fig. 5A arises because E_k does not vary significantly with the nutrient-limited growth rate (Herzig and Falkowski 1989).

As in our previous model (Geider et al. 1996), Chl *a* synthesis is regulated by the parameter ρ_{Chl} (Eq. 8), which reflects the ratio of energy assimilated to energy absorbed. For a discussion of the significance of this regulatory ratio see Geider et al. (1996). The ratio of Chl *a* synthesis to nitrogen assimilation is greatest under low irradiance, where photosynthesis is proportional to light absorption (i.e. where $P^C_{phot} = \alpha^{Chl}\theta^C E_0$) and declines as photosynthesis becomes light saturated and(or) nutrient limited (i.e. where $P^C_{phot} < \alpha^{Chl}\theta^C E_0$). The maximum coupling is given by the maximum value of the $Chl:N$ ratio achieved under extreme low light and designated θ^N_{max}. The rate of Chl *a* degradation is assumed to be proportional to the Chl *a* concentration, and is assumed to be small, consistent with observations for minimal Chl *a* turnover in phytoplankton (Redalje and Laws 1981; Goericke and Welschmeyer 1992; but also see Riper et al. 1979).

Energy storage reserves—Accumulation of energy storage reserves in bright light or under nitrogen-limiting conditions is treated as an excess of photosynthesis over nitrogen assimilation. The subsequent mobilization of these reserves in low light or darkness (Foy and Smith 1980; Cuhel et al. 1984) is treated as continued nitrogen uptake in the absence of photosynthesis. There are two components to this mobilization. First, the carbon skeletons required for amino acid synthesis are derived from energy reserve polymers. This is treated as an increase of $N:C$ associated with nitrogen assimilation. Second, energy required for nitrogen

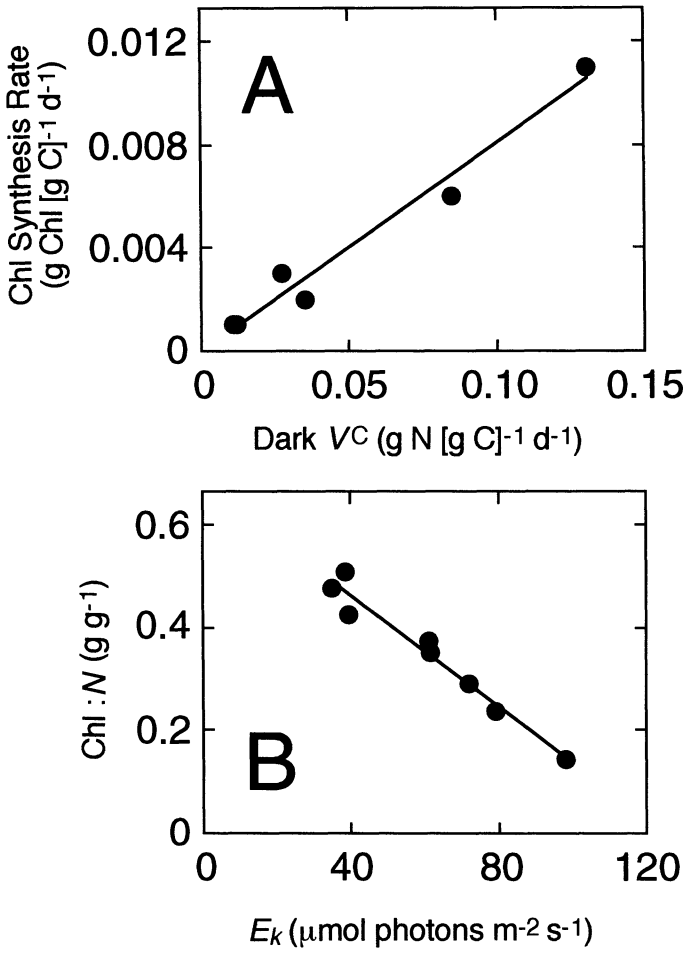

Fig. 5. A. The dependence of the Chl *a* synthesis rate on the nitrogen assimilation rate for *Phaeodactylum tricornutum* in chemostat cultures (Osborne and Geider 1986). The Chl *a* synthesis rate was calculated as the product of Chl:*C* and growth rate. The nitrate assimilation rate was calculated as the product of *N*:*C* and growth rate. B. The dependence of Chl:*N* on the light-saturation parameter E_k for nutrient-replete *P. tricornutum* (Geider et al. 1985).

uptake and amino acid synthesis is provided by respiration of particulate carbon (Fig. 1D). Thus, uptake of nitrogen in darkness results in an increase of *N*:*C* due to both an increase of *N* and an accompanying decrease of *C*. Nitrogen assimilation is also controlled by feedback as parameterized by the response of V^C_{max} to *N*:*C* (Eq. 7). The decline of V^C_{max} at high values of *N*:*C* (Fig. 4) arises because nitrogen uptake cannot occur unless the carbon skeletons used for amino acid synthesis are replenished from photosynthesis or carbohydrate energy reserve polymers (Hupe and Turpin 1994).

Temperature—Temperature is assumed to affect photosynthesis and nitrogen assimilation by modulating the maximum uptake velocities (P^C_{max} and V^C_{max}) and the maintenance metabolic rates (R^C, R^{Chl}, R^N) to the same extent. Thus, we do not consider the possible differences in the temperature-dependence of different metabolic processes (Raven and Geider 1988). We assume that both the half-saturation constant for nutrient uptake (Ahlgren 1987) and the initial slope of the P–E_0 curve (Post et al. 1985) are independent of temperature. We do not consider temperature further here, but have included it in the model equations for completeness.

Table 3. Parameter values used in simulations (by species). The values for P^C_{max}, V^C_{max} and Q_{max} have been chosen such that they are related through the identity $V^C_{max} = P^C_{max}Q_{max}$.

Parameter	Units	*Pavlova lutheri*	*Skeletonema costatum*	*Thalassiosira pseudonana*	*Isochrysis galbana*
P^C_{max}	d^{-1}	3.0	3.0	5.1	3.0
V^C_{max}	g N (g C)$^{-1}$ d^{-1}	0.6	0.6	1.0	0.5
α^{Chl}	10^{-5} g C m^{-2} (g Chl *a* μmol photons)$^{-1}$	0.46	1.38	1.0	0.46
$R^C = R^N = R^{Chl}$	d^{-1}	0	0	0	0.025
K_{nit}	μM	1	1	1	3
θ^N_{max}	g Chl *a* (g N)$^{-1}$	0.3	0.3	0.4	0.3
Q_{min}	g N (g C)$^{-1}$	0.04	0.04	0.04	0.04
Q_{max}	g N (g C)$^{-1}$	0.20	0.20	0.20	0.167
ζ	g C (g N)$^{-1}$	2.0	2.0	2.0	2.0

Comparison of model with data

The model was allowed to run until balanced growth was achieved (i.e. until $[(1/C)(dC/dt)] = [(1/N)(dN/dt)] = [(1/\text{Chl})(d\text{Chl}/dt)]$) under a range of prescribed irradiances and nutrient concentrations and with the parameter values listed in Table 3. In this section, we compare the behavior of the model with observations for phytoplankton from cultures reported to be in balanced growth. We demonstrate that the behavior of the model is consistent with observations for *Pavlova lutheri* (Chalup and Laws 1990) and *Skeletonema costatum* (Sakshaug et al. 1989). For *P. lutheri,* we used the direct measurements of photosynthesis–light response curves to specify the value of the initial slope (α^{Chl}) and the dependence of light-saturated photosynthesis (P^C_{max}) on *N*:*C*. Unfortunately, this information was not available for *S. costatum.*

Growth rate vs. N:C—The model predicts that nutrient-limited growth rate (at constant irradiance and temperature) is a function of *N*:*C* (Fig. 6A). The form of this relationship is similar in shape to the Droop equation, which describes growth rate as a function of the cellular quota of the limiting nutrient (Droop 1983). The slight curvature predicted by the model for the relationship between μ and *N*:*C* may not be evident in experimental data (Wantanabe and Miyazaki 1996). The predictions of the light- and *N*:*C*-dependencies of growth rate are consistent with observations (Fig. 6B,C) for the chrysophyte *P. lutheri* (Chalup and Laws 1990) and the diatom *S. costatum* (data presented in Sakshaug et al. 1989), the only species for which growth in nutrient-limited chemostat cultures has been studied at more than one irra-

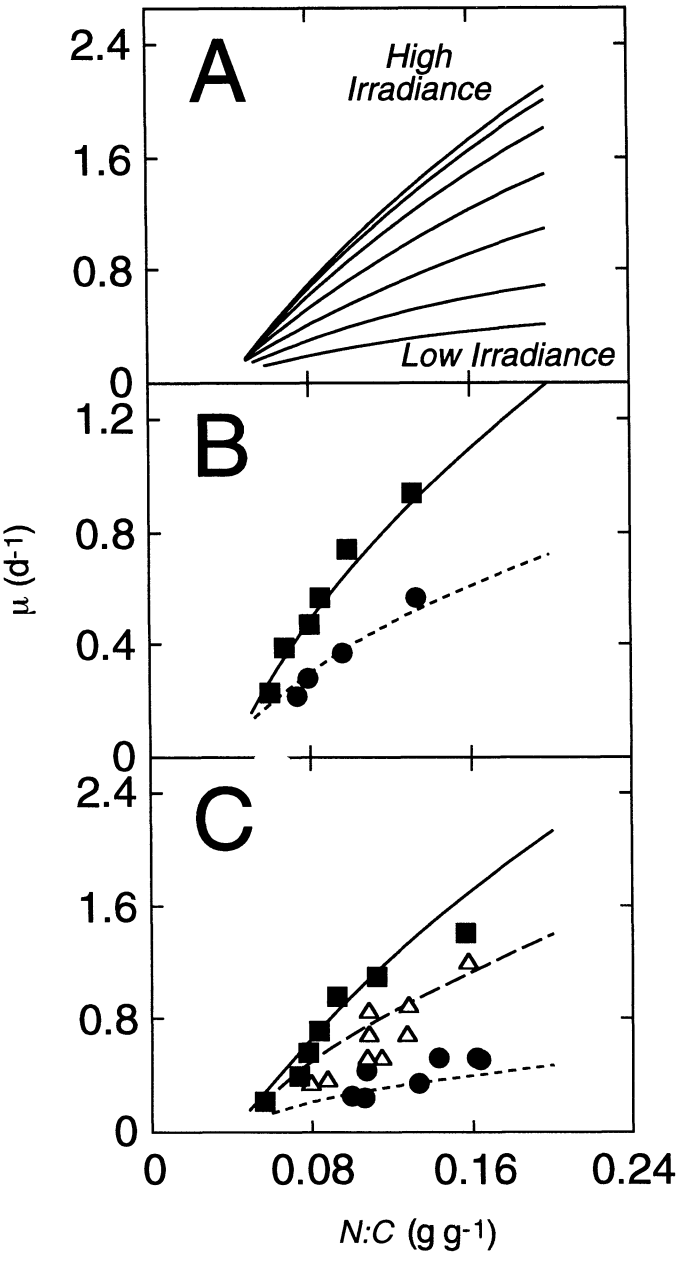

Fig. 6. The dependence of μ on $N:C$ for conditions of balanced growth. A. The relationships predicted by the model for the parameter values given in Table 3 for *Pavlova lutheri* at irradiances between 30 and 2,000 μmol photons m^{-2} s^{-1}. There is a factor of two change in irradiance between each treatment. The envelope of highest values from each curve represents the nutrient-replete condition. B. Observations and predictions (based on parameter values given in Table 3) for *P. lutheri* (Chalup and Laws 1990). *P. lutheri* was grown under nitrate-limited conditions at irradiances of 189 (■) and 63 (●) μmol photons m^{-2} s^{-1}. C. Observations and predictions (based on parameter values given in Table 3) for *Skeletonema costatum* (Sakshaug et al. 1989). *S. costatum* was grown under nitrate-limiting conditions at irradiances of 1,200 (■), 99 (△), and 12 (●) μmol photons m^{-2} s^{-1}.

diance. Similar interactions among irradiance, the cellular quota of the limiting nutrient, and growth rate have been documented for other limiting nutrients (Droop et al. 1982).

Chl:C *vs. growth rate*—The model predicts that Chl:*C* increases with increasing growth rate under nutrient-limiting conditions at constant irradiance. It also predicts that Chl:*C* at constant μ is inversely related to irradiance. The predictions (Fig. 7A) are consistent with observations (Fig. 7B,C). The model predicts slight departures from a linear dependence of Chl:*C* on nutrient-limited μ, especially under the combination of low nitrate and low irradiance.

Chl:N *vs. growth rate*—The Chl:*N* ratio varies significantly with irradiance under both nutrient-limited and nutrient-replete conditions (Fig. 8A), consistent with Chan's (1978) observations for the light-dependence of Chl *a*:protein in diatoms and dinoflagellates. However, Chl:*N* is predicted to be largely independent of nutrient-limited growth rate at constant irradiance, except at low growth rates where a decline is predicted (Fig. 8A). Again, predictions and observations (Fig. 8B,C) show good agreement. Note the decline of Chl:*N* at low, nutrient-limited growth rates predicted by the model and evident in the data for *P. lutheri* cultured at 189 μmol photons m^{-2} s^{-1} and *S. costatum* at irradiances ranging from 12 to 1,200 μmol photons m^{-2} s^{-1}. Such behavior is also evident in observations of *Isochrysis galbana* (Herzig and Falkowski 1989) and *Phaeodactylum tricornutum* (Osborne and Geider 1986).

Dynamic behavior under variable environmental conditions

The ability of the model to describe the chemical composition of phytoplankton under conditions of balanced growth (Figs. 6–8) suggests that essential features of phytoplankton physiology have been adequately represented. However, a new feature of the model is that it also predicts the time course of changes in chemical composition and growth rate that occur when environmental conditions change. In contrast to previous treatments of the time-dependence of biomass accumulation and chemical composition (Cullen and Lewis 1988; Barkman and Woods 1996), our model does not require specification of acclimation rate constants. This is because the model is formulated in terms of rates of change of the biomass variables (Eq. 1–3). The time course of acclimation predicted by the model is determined by the net rates of Chl *a* synthesis, CO_2 assimilation, and NO_3^- uptake. In this section we describe the predicted behavior of Chl:*C*, Chl:*N*, and *N*:*C* under several nonsteady-state conditions. The conditions are (1) reciprocal step changes in irradiance of nutrient-replete cells, (2) nutrient-limited growth in a L/D cycle, and (3) the different growth phases of a batch culture.

Step changes of irradiance under nutrient-replete conditions—The dependencies of growth rate and Chl:*C* on irradiance in nutrient-replete *Thalassiosira pseudonana* and the response of *T. pseudonana* to reciprocal step changes of irradiance are illustrated in Fig. 9 and compared to the ob-

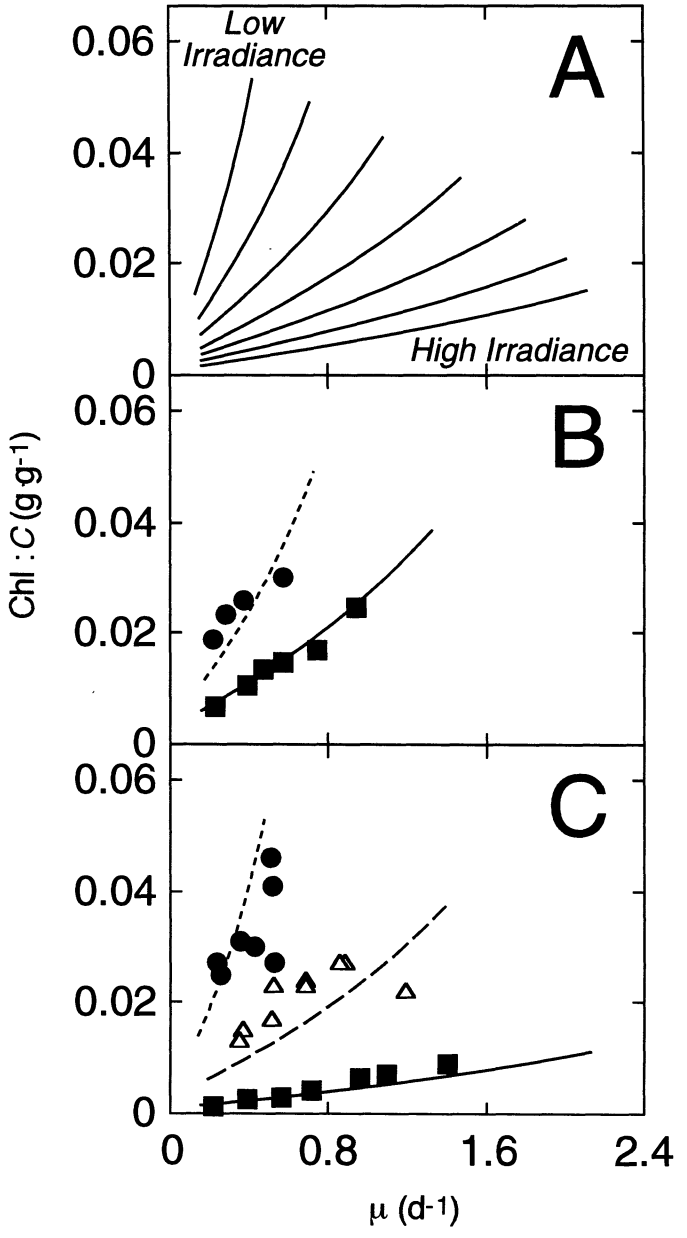

Fig. 7. The dependence of Chl:C on μ for conditions of balanced growth. A. The relationships predicted by the model for the parameter values given in Table 3 for *Pavlova lutheri* at irradiances between 30 and 2,000 μmol photons m^{-2} s^{-1}. There is a factor of two change in irradiance between each treatment. The envelope of highest values from each curve represents the nutrient-replete condition. B. Observations and predictions (based on parameter values given in Table 3) for *P. lutheri* (Chalup and Laws 1990). *P. lutheri* was grown under nitrate-limited conditions at irradiances of 189 (■) and 63 (●) μmol photons m^{-2} s^{-1}. C. Observations and predictions (based on parameter values given in Table 3) for *Skeletonema costatum* (Sakshaug et al. 1989). *S. costatum* was grown under nitrate-limiting conditions at irradiances of 1,200 (■), 99 (△), and 12 (●) μmol photons m^{-2} s^{-1}.

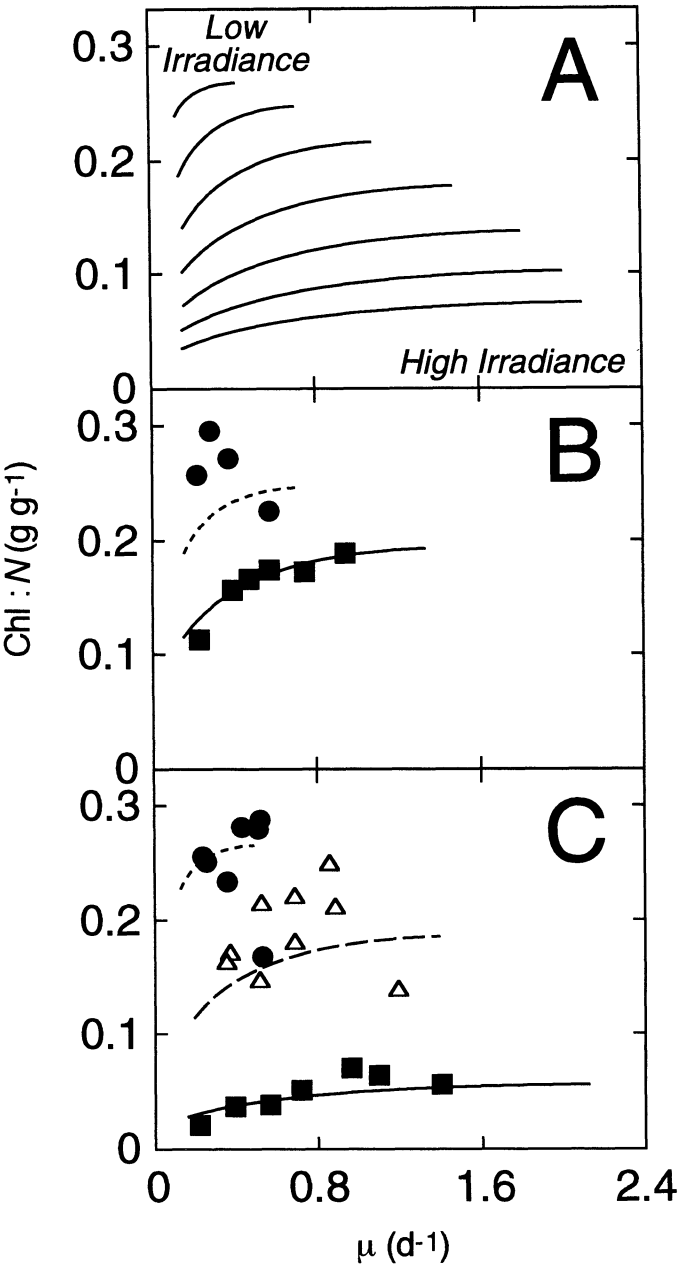

Fig. 8. The dependence of Chl:N on μ for conditions of balanced growth. A. The relationships predicted by the model for the parameter values given in Table 3 for *Pavlova lutheri* at irradiances between 30 and 2,000 μmol photons m^{-2} s^{-1}. There is a factor of two change in irradiance between each treatment. The envelope of highest values from each curve represents the nutrient-replete condition. B. Observations and predictions (based on parameter values given in Table 3) for *P. lutheri* (Chalup and Laws 1990). *P. lutheri* was grown under nitrate-limited conditions at irradiances of 189 (■) and 63 (●) μmol photons m^{-2} s^{-1}. C. Observations and predictions (based on parameter values given in Table 3) for *Skeletonema costatum* (Sakshaug et al. 1989). *S. costatum* was grown under nitrate-limiting conditions at irradiances of 1,200 (■), 99 (△), and 12 (●) μmol photons m^{-2} s^{-1}.

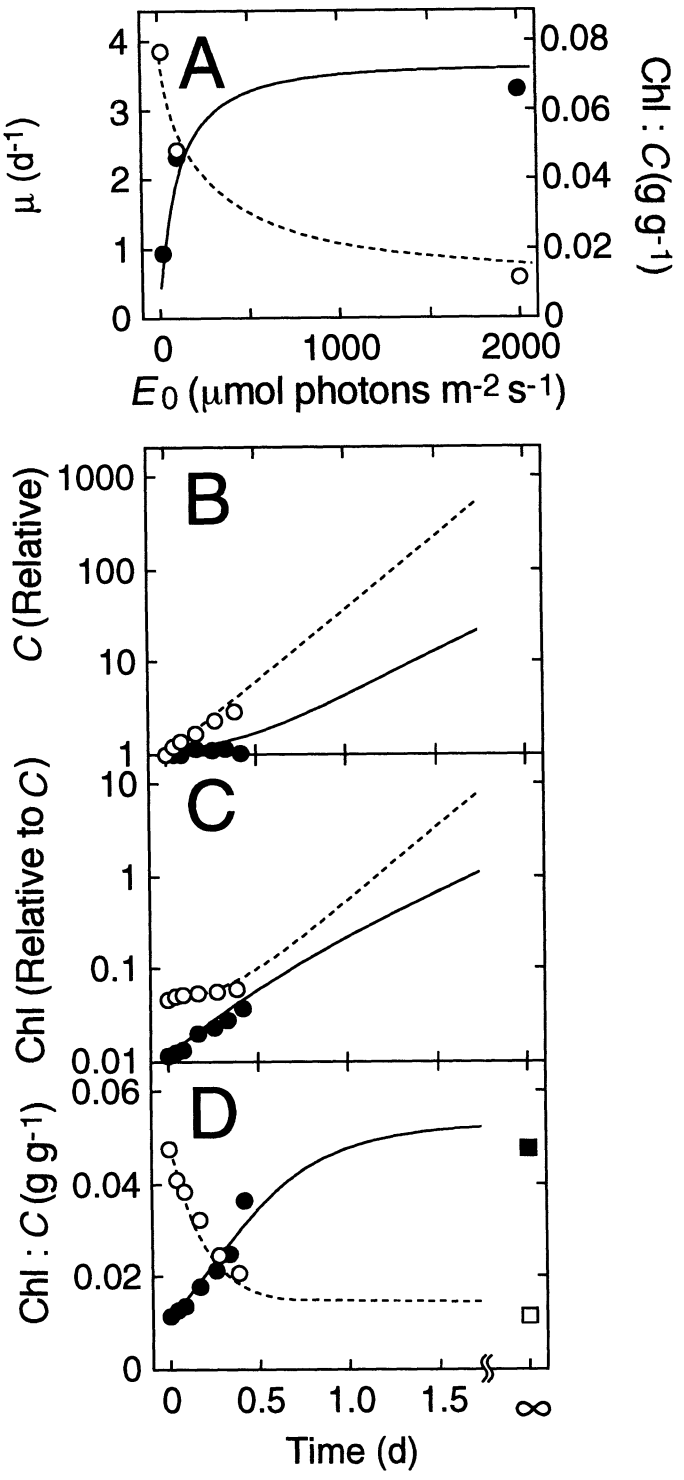

Fig. 9. A. The relationship between μ (solid line and closed symbols) or Chl:C (dashed line and open symbols) and growth irradiance (E_0) in nutrient-replete *Thalassiosira pseudonana* under conditions of balanced growth. The model predictions are based on the parameter values given in Table 3 and inorganic nitrogen concentration of 81 μM. B–D). The model predictions of the responses of C, Chl, and Chl:C to reciprocal step changes of irradiance between 2,200 and 100 μmol photons m^{-2} s^{-1}. The solid line and closed symbols are model output and data for the high light–low light switch and the broken line and open symbols are model output and data for the low light–high light switch. The open symbols at the right of panel D are the steady-state values of Chl:C at high and low irradiances. The model predictions are based on parameter values for *T. pseudonana* given in Table 3 and the data are from Cullen and Lewis (1988).

servations of Cullen and Lewis (1988). Parameter values were chosen to yield the observed dependencies of growth rate (μ) and Chl:C on irradiance for conditions of steady-state growth (Fig. 9A). These values were used to predict changes of C (Fig. 9B), Chl (Fig. 9C), and Chl:C (Fig. 9D) under non-steady-state conditions during reciprocal step shifts of irradiance between 100 and 2,200 μmol photons m^{-2} s^{-1}. Upon a step-up of irradiance, C increased exponentially, but Chl increased only after a lag of ~0.5 d. Chl:C decreased from the initial value to a new steady-state value over a period of ~0.5 d, closely resembling an exponential rate law.

Upon a step-down of irradiance, Chl was predicted to increase rapidly, consistent with observations. In contrast, C was predicted to increase more slowly, although the observations suggest no net increase during the first 10 h following the step-down. The response of Chl:C to a step-down of irradiance is much slower than to a step-up (1 d vs. 0.5 d). This is because the model stipulates strict coupling of Chl *a* synthesis to nitrate assimilation. Under conditions of low light, the rate of nitrogen assimilation is limited by the rate of photosynthesis through the requirement for carbon skeletons for amino acid synthesis.

Growth and chemical composition of cells grown on a L/D cycle—We modeled diel changes of biomass (C, N, and Chl) and chemical composition (Chl:N and N:C) over 12:12 L/D cycles for cells growing at 350 μmol photons m^{-2} s^{-1} in cyclostat cultures at a range of dilution rates (Fig. 10). N:C declines during the day when carbon assimilation exceeds nitrate uptake, and increases in darkness as nitrogen assimilation continues in the absence of photosynthesis. Model predictions of diel variability of C, N:C, and NO_3^- compare favorably with observations (Fig. 11) for *P. lutheri* (data of Laws and Caperon 1976). Chl:N remained stable in a L/D regime when we assumed that the value of ρ_{Chl} in darkness equaled the value calculated for the end of the preceding light period. This assumption was necessary to prevent an unrealistic buildup of Chl:N in darkness (when ρ_{Chl} would equal θ^N), and is consistent with the observation that phytoplankton do not photoacclimate to darkness (Falkowski and La Roche 1991). It would be more realistic to structure the model in such a way that inertia is built into ρ_{Chl} (*see* Geider et al. 1996), consistent with evidence for transcriptional control of photoacclimation (La Roche et al. 1991; Escoubas et al. 1995). One approach to this problem would be to assume that ρ_{Chl} at any instant is determined by a weighted mean over a suitable period. More experimental work is required to address this problem.

Growth and chemical composition of batch cultures—Phytoplankton are often grown in batch cultures in the lab-

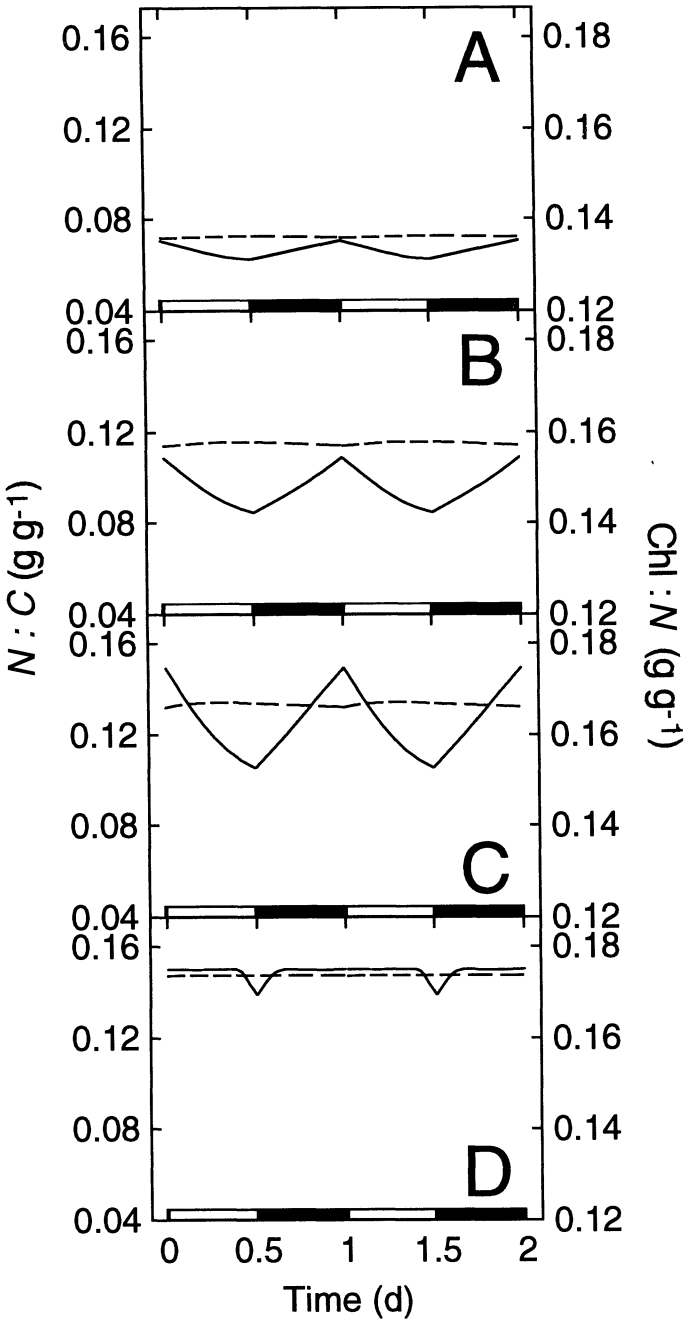

Fig. 10. The model predictions of diel changes of Chl:N (– – –) and N:C (———) for cells cultured on a 12:12 L/D in cyclostat cultures with input NO_3^- concentration of 50 μM and irradiance of 350 μmol photons m^{-2} s^{-1}. Simulations at dilution rates of 0.2 (A), 0.4 (B), 0.6 (C) and 0.8 d^{-1} (D) are shown. The parameter values used are those given for *Pavlova lutheri* in Table 3 except that Q_{max} was set at 0.15 g N (g C)$^{-1}$ and V^C_{max} was set at 0.45 g N (g C)$^{-1}$ d^{-1}.

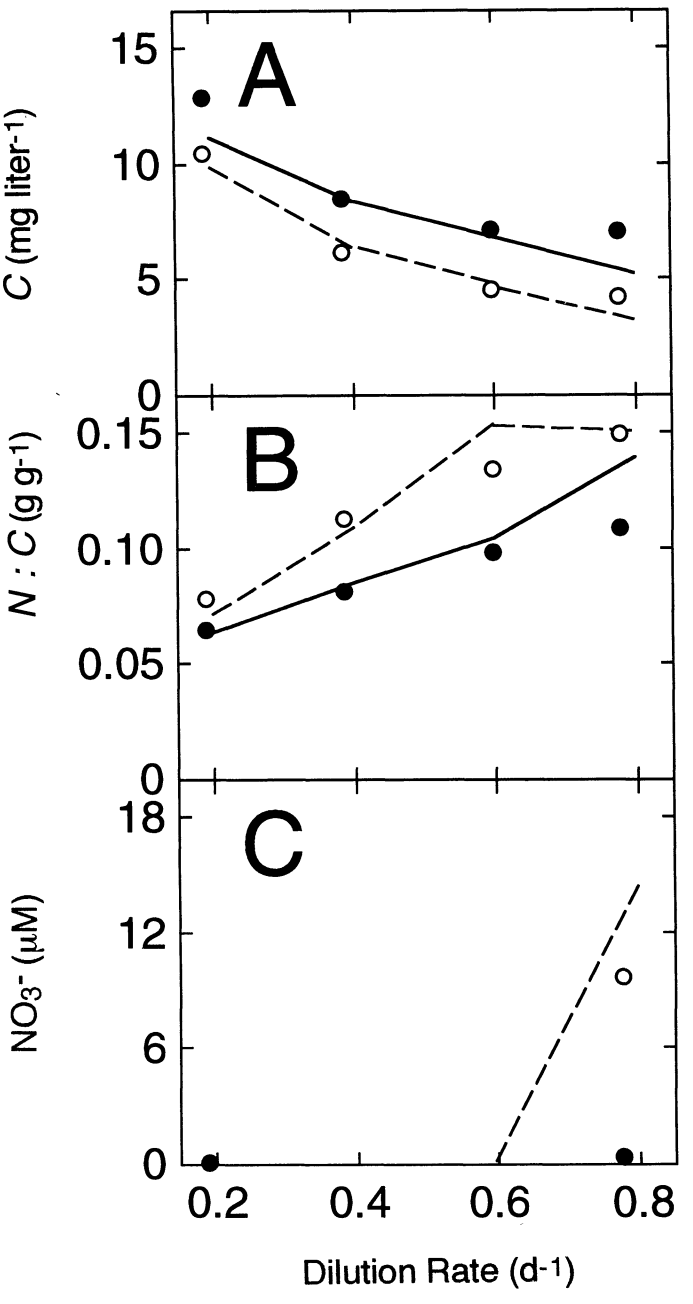

Fig. 11. Comparison of model predictions and observations of diel variability of C, N:C, and NO_3^- in cyclostat cultures with input NO_3^- concentration of 50 μM and irradiance of 350 μmol photons m^{-2} s^{-1}. The model predictions for the start (– – –) and end (———) of a 12-h light period are from Fig. 10. The observations at the start (■) and end (●) of a 12-h light period are for *Pavlova lutheri* (data of Laws and Caperon 1976).

oratory. However, because of the non-steady-state conditions and associated changes in cell physiology that occur as cells enter stationary phase, batch cultures are rarely used to specify the coefficients of conventional phytoplankton growth models. Our model allows growth and chemical composition of phytoplankton to be specified in both balanced and unbalanced growth. As such, it yields predictions of changes of μ, Chl:C, and N:C that occur in batch cultures.

We estimated model parameters that describe observations of *Isochrysis galbana*. Flynn et al. (1994) grew *I. galbana* at 18°C on a 12:12 L/D cycle under incident illumination of 100 μmol photons m^{-2} s^{-1} and with ammonium as the

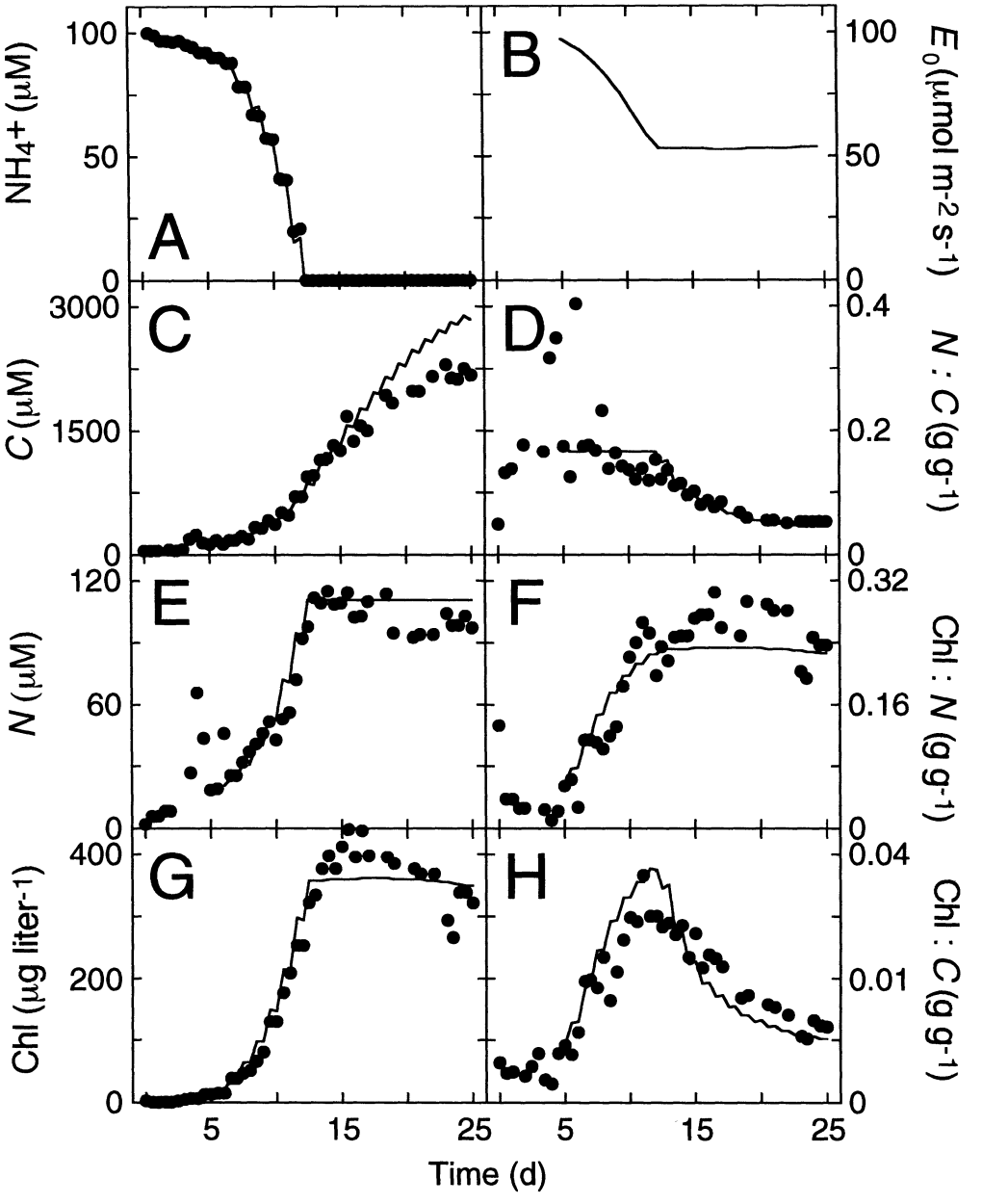

Fig. 12. Comparison of model predictions (solid lines) for *Isochrysis galbana* grown in a batch culture with the parameter values given in Table 3 and observations (●) for growth of *I. galbana* (data of Flynn et al. 1994). The model was run starting on day 5 using observed concentrations of 1,288 μg NH_4^+ liter^{-1}, 260 μg *N* liter^{-1}, 1,490 μg *C* liter^{-1}, and 14 μg Chl liter^{-1}. It was necessary to start the simulation on day 5 because the initial lag phase in the data could not be replicated by the model. Predictions and observations of the changes of (A) NH_4^+, (B) irradiance (E), (C) C, (D) $N:C$, (E) N, (F) Chl:N, (G) Chl and (H) Chl:C. The model predictions of changes in the mean irradiance within the culture were based on predicted Chl assuming an attenuation coefficient of 16 m^2 g^{-1} Chl *a* and a 0.25-m depth culture vessel illuminated from above.

nitrogen source. We accounted for changes of ammonium (N_1) and phytoplankton nitrogen (N) concentrations using a mass balance ($N + N_1$ = constant). We assumed that growth was a function of the mean irradiance in a 0.25-m-deep batch culture illuminated from above. The mean irradiance was calculated assuming that light attenuation was due exclusively to phytoplankton with a Chl *a*-specific light attenuation coefficient of 16 m^2 g^{-1} Chl *a*. The behaviors of biomass (N, C, Chl), irradiance (E_0), ammonium concentration (N_1), and composition ratios (Chl:N, Chl:C, $N:C$) are illustrated in Fig. 12. An extended lag phase was evident in the dataset (Fig. 12) that could not be accommodated in our model; therefore, we started our simulation on day 5, using the values of $N_{1,N}$, C, and Chl reported for that day.

The observed and simulated changes of N_t, N, C, and Chl show good agreement (Fig. 12). The rate of decline of N_t and rates of increase of N, Chl, and C compare well over days 5–12. However, the model overestimates C, N, and Chl after day 17. A decline of N between days 17 and 25 is evident in the data, but not in the model. The observed decline of N may indicate a systematic error in the data such as wall growth, or a systematic error in the model such as neglect of release of dissolved organic nitrogen. Although the data also show a marked decline of Chl from day 17 to day 20 that is not predicted by the model, constancy of Chl : N after day 12 is evident in the data and predicted by the model.

We predict a large reduction of mean irradiance within the culture vessel. As a consequence, Chl : C and Chl : N are predicted to increase initially due to self-shading under nutrient-replete conditions. The model slightly underestimates the increase of Chl : N and overestimates the response of Chl : C. Upon exhaustion of ammonium, Chl : N remains constant, consistent with observations that nitrogen-limited cells cannot photoacclimate (Prezelin and Matlick 1983). The declines of Chl : C and N : C from day 12 to 25 appears to be a consequence of buildup of energy reserve polymers (i.e. continued net photosynthesis) despite nitrogen limitation.

Caveats regarding model formulation—Several potentially important processes are excluded from the model. The model does not account for changes in the Chl a-specific light absorption coefficient that may arise from changes in accessory pigment concentration or the package effect (Berner et al. 1989). It does not allow for reductions in the quantum efficiency of photosynthesis that may be associated with photoinhibition or nutrient limitation (Droop 1983; Kolber et al. 1988). There is no differentiation between nitrate and ammonium assimilation (McCarthy 1980; Flynn et al. 1997). The model does not include possible delays in biosynthesis that may arise from filling and emptying of metabolite/intermediate pools (Dortch 1982; Goericke and Welschmeyer 1992; Flynn et al. 1997) or that may arise from the finite rate of signal transduction associated with transcriptional or other molecular controls (La Roche et al. 1991; Escoubas et al. 1995). Diel variations or circadian rhythms of physiological rates (Eppley et al. 1971; Prezelin 1992) are not considered except as they arise as a consequence of diel variability of Chl : N and N : C. The model does not treat the causes of interspecific variability of growth and photosynthesis rates (Chan 1978, 1980). Finally, we note that the invariance of α^{Chl} (Fig. 2B) and the functional relationships between P^C_{max} and N : C (Fig. 2A), V^C_{max} and N : C (Fig. 4), dark respiration and nitrogen assimilation (Fig. 3), and Chl a synthesis and nitrogen assimilation (Fig. 5) were obtained for the condition of balanced growth. We have assumed that these relationships apply under all growth conditions. Despite these limitations, the model output compares favorably with published data for light- and nutrient-limited phytoplankton cultures.

Variability of quantum efficiency of photosynthesis and Chl a*-specific light absorption*—The model treats α^{Chl} as a constant, assuming invariance of the maximum quantum efficiency of photosynthesis (ϕ_{max}) and the Chl a-specific light absorption coefficient (a^{Chl}). However, variations of ϕ_{max} with growth rate have been observed in nutrient-limited chemostat cultures (Droop et al. 1982; Kolber et al. 1988; Geider 1992) and with nitrate concentration in oceanic phytoplankton (Sathyendranath et al. 1996). In addition, there are well-documented changes in the Chl a-specific light-absorption cross section (a^{Chl}) that accompany variations of intracellular pigment content and Chl : C ratio in response to variations in light, nutrient availability, and temperature. To correct for these possible deficiencies, it may be necessary to consider α^{Chl} as the product of a light-absorption efficiency (a^{Chl}) and a maximum light-limited quantum efficiency of photosynthesis (ϕ_{max}). For example, we could have treated a^{Chl} as a decreasing function of Chl : C (Falkowski et al. 1985; Geider 1992), and ϕ_{max} as an increasing function of N : C (Herzig and Falkowski 1989). These changes would allow a variety of behaviors of α^{Chl}.

Discussion

Phytoplankton growth requires coordination of light harvesting with carbon dioxide fixation and nutrient assimilation over the time-scales associated with cell growth and division. However, these processes are typically uncoupled in nature because cells are continuously exposed to varying environmental conditions. Uncoupling carbon from nitrogen assimilation allows phytoplankton to exploit encounters with limiting resources on short (<1 h) time-scales. On longer time-scales (>1 h), phytoplankton pigment content changes, and this brings light harvesting into a closer balance with photosynthetic carbon assimilation. We have addressed the problem of light–nutrient interaction by formulating a model that considers the interdependencies of the energy, carbon, and nitrogen metabolism of phytoplankton. We limit our model to one limiting nutrient in a spectrally invariant light field although it can be extended to other nutrients and made fully spectral. The model is based on feedback between elemental composition and physiological rates, and includes regulation of pigment synthesis by energy supply and demand. The model allows photosynthesis to become temporarily uncoupled from nitrogen assimilation. In addition, the kinetics of acclimation to variable light, nutrient concentration, and(or) temperature are implicit within the model and require no additional rate constants. In other words, the time-courses of acclimation of N : Chl, N : C, P^{Chl}_{max}, and μ are determined by the variations in the rates of CO_2 assimilation, NO_3^- uptake, and Chl a synthesis as defined by Eq. 1, 2, and 3.

How many parameters are required to describe phytoplankton growth in ecosystem models?—Steele and Henderson (1992) used a two parameter model of phytoplankton growth to study the effects of interannual variability of mixed layer depth on phytoplankton–zooplankton dynamics. Riley (1947) described the annual production cycle on George's Bank using a model that required four parameters to account for the light-, nutrient-, and temperature-dependencies of phytoplankton growth. Fasham et al. (1990) used six parameters to describe phytoplankton nitrogen dynamics

in a one-dimensional mixed-layer model. Clearly, the number of parameters required for a phytoplankton model varies with the purpose of the model. The number of parameters that need to be specified will depend on the number of environmental variables (at least one parameter per independent variable) and the number of biomass variables (again at least one parameter for each pair of independent variables). Nonlinearities in resource response functions will increase the number of parameters required, as will accounting for deviations from constant chemical composition. The challenge is to describe biological acclimation adequately with a minimum number of additional parameters.

We developed a model to account for acclimation of chemical composition, carbon fixation and nitrogen assimilation to light, and nutrients and temperature in both constant and variable environments. The model requires the specification of 10 parameters to describe the dependencies of $N:C$, Chl$:N$, and μ on irradiance (E_0), nutrient concentration (N), and temperature (T). The 10 parameters are the minimum and maximum $N:C$ ratios (designated $Q_{\min}$ and $Q_{\max}$); the values of maximum carbon-specific photosynthesis (P^{C}_{ref}) and nutrient uptake (V^{C}_{ref}) rates at a reference temperature; the maintenance respiration rate ($R^{C} = R^{N} = R^{Chl}$, all treated as one maintenance metabolism parameter); the maximum Chl a : nitrogen ratio (θ^{N}_{max}); the initial slope of the photosynthesis–light curve (α^{Chl}); the cost of nitrogen assimilation (ζ); the temperature coefficient (A_E); and the half-saturation constant for nitrate uptake (K_{nit}). The physiological plasticity of phytoplankton and the requirement for coordination of carbon and nitrogen metabolism are reflected in the fact that 10 parameters are required to describe phytoplankton dynamics in the model.

How does the number of parameters in the model compare with the number of parameters in conventional models? Conventional models require specification of at least six physiological constants to describe the irradiance-, nutrient-, and temperature-dependencies of phytoplankton growth. These are the light-saturated growth rate, the initial slope of growth–light curve, the respiration rate, the half-saturation constant for nutrient uptake, the temperature coefficient, and the Chl a : biomass ratio. These parameters have counterparts in our model. To specify biomass in terms of both nitrogen and carbon requires a seventh parameter (i.e. a fixed $N:C$). Unfortunately, conventional seven-parameter models cannot be used to describe the known variability in Chl$:C$ and $N:C$. Knowledge of the variations in these ratios is crucial for understanding the coupling of carbon export from the euphotic zone to nitrogen import and for translating pigment fields into biomass fields. Additional parameters are required to capture such behavior. At least one additional parameter must be specified to capture variability of Chl$:N$ empirically and another to capture variability of $N:C$ for cells in balanced growth, bringing the total number of parameters to nine. Once variability in Chl$:C$ and $N:C$ ratios is allowed, it is necessary to account for the rate of acclimation of these ratios to variations in light, nutrients, and temperature. Models of the dynamics of photoacclimation in variable light require specification of at least one acclimation rate constant (Cullen and Lewis 1988), bringing the total number of parameters required for a conventional model of carbon, nitrogen, and chlorophyll dynamics in fluctuating environments to at least 10. Thus, the model requires no increase in the number of parameters over conventional models.

Applications of the model—We envisage that the model can be applied to a number of current problems in phytoplankton ecology. Here we describe three such problems: the Spring bloom, vertical migration in stably stratified waters, and episodic events.

Most of the export production and much of the annual production of phytoplankton in temperate regions is supported by a spring bloom. The spring bloom occurs during the period in which the seasonal thermocline develops, trapping water with high nutrients near the surface. The export of particles following the spring bloom can be seen in the deposition of phytodetritus on the seabed at depths in excess of several thousand meters (Deuser and Ross 1990) and may draw down the partial pressure of CO_2 below air-equilibrium values (Taylor et al. 1991). Changes in the light and nutrient environment during the spring bloom can be dramatic. In addition, the day and night mixing depths can be highly variable (Barkmann and Woods 1996), resulting in the intermittent exposure of phytoplankton to limiting and saturating irradiances during bloom development. Under such conditions, physiological adjustments of Chl$:N$ and $N:C$ ratios, with consequent effects on phytoplankton growth, are to be expected. The Chl$:N$ and $N:C$ ratios are expected to decline between low-light/high-nutrient conditions characteristic of prebloom to the high-light/low-nutrient conditions during the bloom decline.

Vertical migration may be an important strategy followed by phytoplankton in stably stratified waters where irradiance is most intense near the surface and nutrients are supplied by upward diffusion from a deep reservoir. Buoyancy is regulated in freshwater cyanobacteria, allowing populations to migrate over relatively short distances between the nutrient-rich hypolimnion and the nutrient-poor epilimnion (Oliver 1994). Vertical migration may contribute to dinoflagellate blooms in stratified estuaries and to dinoflagellate growth in the open sea (Rivkin et al. 1984). Recent evidence points to the potential importance of vertically migrating diatoms in the nitrogen dynamics of oligotrophic open-ocean environments typical of the subtropical gyres (Villareal et al. 1993) where the nutricline may be found at depths of 100–150 m in extremely low-light conditions (1% of surface irradiance). Mixing of nutrients to the surface is extremely low under such stably stratified conditions, and penetration of light in quantities that can support maximum photosynthesis is typically limited to <50 m by the opacity of water. One way for phytoplankton to overcome light and(or) nutrient limitation in highly stratified environments is to cycle between the high-light/low-nutrient environment of the surface mixed layer and the low-light/high-nutrient environment of the nutricline. Such migrations appear to occur in dinoflagellates (Rivkin et al. 1984) and diatoms (Villareal et al. 1993; Villareal and Lipschultz 1995). Modeling the dynamics of vertically migrating phytoplankton requires the simultaneous treatment of nutrient, light, and temperature interactions, as well as explicit consideration of energy storage and nutrient storage. Our model may be applicable to vertically migrating

phytoplankton provided that vertical velocity can be parameterized as a function of $N:C$. Carbohydrate ballasting provides a mechanism that can account for an inverse relationship between buoyancy and $N:C$ (Oliver 1994; Moore and Villareal 1996; but see Fisher and Harrison 1996).

A similar case for vertical migration can be made for microphytobenthos, which are significant contributors to shallow-water productivity (MacIntyre et al. 1996). Many microphytobenthos migrate through a large light gradient with a rhythm determined by diel–tidal interactions (Serodio et al. 1997) and can be exposed to significant changes in temperature at the sediment surface on the same time-scales (Blanchard et al. 1996). Although there is unlikely to be a nutrient effect because of diagenesis in the sediments, a case can be made that light and temperature effects are more pronounced than in the water column.

It has long been recognized that phytoplankton productivity is determined by a balance between injection of nutrients into the euphotic zone and stability of the water column trapping cells in a high light environment. Intense vertical mixing can stimulate productivity by transporting nutrients to the surface or reduce productivity by transporting phytoplankton into darkness. Alternating periods of intense mixing and stabilization of the water column on storm-event or upwelling-event time-scales can lead to high primary productivity. Modeling phytoplankton growth under these conditions involves accounting for the ability of phytoplankton to store nutrients when nutrients are abundant and to accumulate energy reserve polymers when nutrients are limiting. The model should allow theoretical investigations of growth under these conditions.

Conclusions

Phytoplankton growth in the sea can be regulated by both bottom-up and top-down processes. Bottom-up regulation depends on the physiological ecology of phytoplankton whereas top-down regulation depends on the feeding behavior and population dynamics of zooplankton. Significantly, zooplankton feeding, excretion, and fecal pellet composition may depend on the nitrogen-to-carbon ratio of the phytoplankton food source (Anderson 1994). Understanding the interaction of bottom-up and top-down controls on trophic dynamics and biogeochemical cycles in the sea requires realistic models of phytoplankton and zooplankton responses.

The important features of our new model for improving understanding of the role of phytoplankton in biogeochemical cycles are (1) parameterization of the links between carbon and nitrogen metabolism in terms of the nitrogen-to-carbon ratio, and (2) linking pigment synthesis to nitrogen assimilation. Although the specific details of our parameterization may prove to be incorrect, we think that including links among pigment synthesis, carbon assimilation, and nutrient uptake will prove to be of general applicability.

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