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Numerous studies of the growth of phytoplankton in the laboratory have demonstrated the dependence of cellular pigment concentration and growth rate upon light intensity, photoperiod, temperature, and nutrient supply. These same environmental parameters vary with season in the polar seas and presumably affect the growth rate and cellular pigment concentration of the phytoplankton crop. Unfortunately, there has not been a complete mathematical description of the interaction of all four environmental parameters. This study presents an approach to describing these interactions.

It can reasonably be assumed that the gross specific growth rate, g, is a function of the specific rate of light absorption:

$$g = \Pi\,\Gamma\,(1\text{-}\exp(-a_p\,\phi_{max}\,E_0/\Pi\,\theta)).$$

The dependent variables in this equation are g, the gross specific growth rate, Π, the maximum carbon-specific photosynthetic rate, and, θ, the ratio of carbon to chlorophyll. The value of all three dependent variables is constrained. The independent variables are E_0, the light intensity (assumed constant during the photoperiod), and Γ, the photoperiod (as a fraction of 24 hours) that the cells are illuminated. Π is the instantaneous capacity of the dark reactions to assimilate electrons, while the product $a_p\,\phi_{max}\,E_0/\theta$ is the instantaneous capacity of the light reactions to supply electrons. If the capacity for photochemistry exceeds the capacity for assimilation, dissipative processes occur, and the quantum yield is low.

We have applied this equation to the analysis of the growth and light absorption by *Skeletonema costatum* cultured under light, temperature, and nutrient limitation. Decreases in nutrient supply and temperature cause decreases in Π and increases in θ; thus both the capacity for electron supply and utilisation decrease. However, decreases in temperature decrease the capacity for electron assimilation more rapidly than the capacity for supply; quantum yield drops. Decreases in nutrient supply cause the capacity for supply and assimilation to drop in parallel; quantum yeield is maintained. Decreases in day length cause decreases in θ and increases in Π. The capacity to assimilate electrons and the capacity to supply electrons increase in parallel; quantum yield is maintained. Decreases in light intensity cause decreases in both θ and the capacity to supply electrons. Although the changes in Π with light intensity are difficult to assess, the capacity to assimilate electrons appears to be little changed by light limitation. Quantum yields increase with decreasing light levels.

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Introduction

A number of factors may limit the growth rate of phytoplankton in the sea. These include light intensity, day length, temperature, and nutrient supply. Given the large seasonal variability that exists at high latitudes, it is likely that the extent to which each of these four variables determines the growth rate may fluctuate. For example in the Barents Sea, which is between 70–80°N, the water temperature ranges over the year between 0 and 6°C, the day length ranges between 0 and 24 hours, midday incident photosynthetically available radiation ranges between 20 and 1000 μ E $m^{-2}\,s^{-1}$, and the concentration of nitrate ranges between 0.1 and 12 μmol kg^{-1}. Although the growth of phytoplankton is clearly influenced by this variability, there have been few, if any, publications describing the effects of all four variables – light intensity, day length, temperature, and nutrient concentation – upon growth rate.

In this study a tentative description of the regulation of phytoplankton growth by more than one or two environmental parameters is presented. Through examination of data on growth rate and

chemical composition obtained from the continuous cultures of phytoplankton where all four factors mentioned above have been varied, it is suggested that there are strong patterns in the responses of phytoplankton to variations in temperature, light, and nutrient limitation. This information has been incorporated into a model that provides a reasonably satisfactory description of the relationship between the light absorption, chemical composition, and growth rates of phytoplankton.

Model

Many models of the growth of phytoplankton are energy budgets (Ryther & Yentsch 1957; Webb et al. 1974; Jassby & Platt 1976; Geider 1990) that describe growth as a function of incident irradiance; photosynthetic efficiency and the amount of carbon that must be synthesized to make another cell. While such models are very useful, they do little to explain how environmental factors regulate growth and chemical composition of phytoplankton (Cullen 1990). Additional insight comes from descriptions of the effects of irradiance, day length, nutrients, and temperature on light absorption, photosynthetic efficiency, and chemical composition. Although these effects have been described many times, (Smith 1980; Laws & Bannister 1980; Fasham & Platt 1983; Kiefer & Mitchell 1983; Osborne & Geider 1986; Geider 1987; Falkowski et al. 1985), a comprehensive description is still lacking.

By examining experimental data to specify how each environmental factor affects parameters of a simple model, this study aims at describing phytoplankton growth as regulated by light, temperature, and nutrients. The conceptual model used to relate the rate of light absorption by phytoplankton to the growth rate is based upon both a phenomenological description and a mechanistic description. The phenomenological description, which will be used to analyze the data presented in the following section, simply states that the specific growth rate of phytoplankton is the product of the rate of light absorption by the cell and the quantum yield of cellular carbon fixation. More specifically, the following can be stated:

$$g(E_0, \Gamma, T, N) = E_0\, \Gamma\, a_p\, \phi(E_0,T)/\theta(E_0, \Gamma, T, N). \quad (1)$$

g, which is the specific gross rate of photosynthesis and a dependent variable (units of day^{-1}), is a function of independent variables: light intensity, E_0; photoperiod, Γ; temperature, T; and nutrient concentration, N. g is equal to the sum of the specific growth rate, μ, and the specific respiration rate (Bannister 1979). In this study the light regime is rectified; the lights are on (units of mol m^{-2} day^{-1}) for a fraction, Γ, of each 24-hour cycle; T is in units of °C; N is in units of mg-at m^{-1}. a_p is the chlorophyll a-specific absorption coefficient (units of m^2 mg^{-1}) and is assumed here to be a constant. θ is the ratio of cellular carbon to cellular chlorophyll a (units of mg-at C mg Chl^{-1}) and is a dependent variable. ϕ is the quantum yield (units of mg-at C mol^{-1}) and is a dependent variable. Although the two dependent variables may be functions of all four independent variables, we will see that this is true only for θ;

Table of Symbols

g.	a dependent variable as indicated by equation 7, is the gross specific growth rate of the cells
Π.	a dependent variable, is the maximum, instantaneous, carbon specific rate of carbon fixation
Γ.	an independent variable, is the duration of the photoperiod as a fraction of a 24-hour day
E_0	an independent variable, is the light intensity during the photoperiod
a_p.	a constant, is the chlorophyll *a* specific absorption coefficient of the cell suspension
ϕ_{max}.	a constant and thus independent of light intensity, temperature, day length, and nutrient concentration, is the maximum quantum yield of carbon fixation
ϕ.	a dependent variable as indicated by equations (5) and (8), is the quantum yield of carbon fixation
θ.	a dependent variable, is the ratio of cellular carbon to chlorophyll *a*
fc.	a dependent variable as indicated by equation (2), is the maximum, light-limited, instantaneous, carbon specific rate of carbon fixation
Fc.	a dependent variable as indicated by equation (3), is the maximum, light-limited daily, carbon specific rate of carbon fixation
τ.a	dependent variable, is the minimum steady state turnover time of the photosynthetic electron transport system
σ_{II}.	a dependent variable, is the mean, effective absorption cross-section of photosystem II
η_{II}.	a dependent variable, is the ratio of the cellular concentration of photosystem II to carbon
jcc.	a constant which depends upon the chemical composition of the cell, is the ratio of the number of carbon atoms fixed to the number of electrons passed through the electron transport system

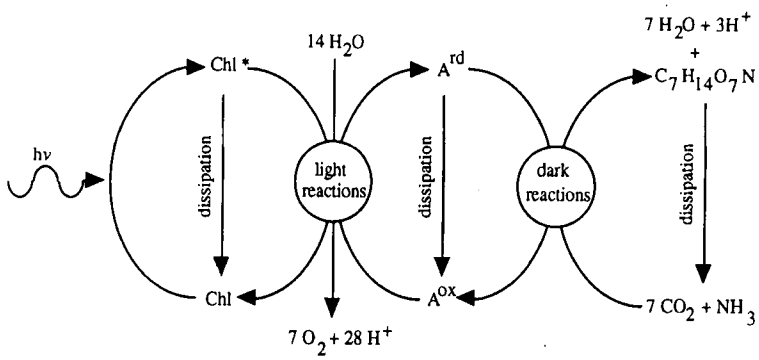

Fig. 1. A conceptual model of phytoplanktonic growth and regulation. Variations in light intensity, photoperiod, temperature, and nutrient supply will cause changes in both the rates of energy transformations and the cellular concentrations of the components shown in the figure. These components are the photosynthetic unit, the electron transport chain, and the enzymes of the dark reactions. The cellular concentrations of these three components are regulated so that the growth rate is maintained without excessive dissipation of energy.

ϕ varies with temperature and light intensity but is little affected by variations in day length and nutrient concentration.

We represent the maximum, light-limited instantaneous carbon specific rate of carbon fixation as fc (units of day^{-1}):

$$E_0\, a_p\, \phi_{max}/\theta = fc. \quad (2)$$

The maximum, light-limited, daily carbon specific rate of carbon fixation is Fc:

$$E_0\, \Gamma\, a_p\, \phi_{max}/\theta = Fc. \quad (3)$$

The mechanistic description is represented in Fig. 1. Photosynthetic growth is described in terms of the cycling of the pool of electron transport compounds, symbolized by A^{ox}/A^{rc}, the oxidized and reduced forms of the carrier pool. Electrons are supplied to this pool by the activity of photosystem II, symbolized by Chl_{II}/Chl^*_{II}, the ground and excited states of chlorophyll in the photosystem. Although not shown in the figure, each photosystem consists of an antenna and a reaction centre. Photosystem I is not shown but is assumed to be under metabolic control (Foyer et al. 1990) and does not restrict electron flow. While rates of electron supply will depend directly upon the size and cellular concentration of the photosystems and upon light intensity, rates will also be regulated by day length, temperature, and nutrient concentration. Although evidence is limited, it appears that the cellular concentration of the electron transport pool is proportional to the concentration of photosystem II (Sukenik et al. 1987). Electrons are lost from the electron transport pool by the assimilation of inorganic compounds such as carbon dioxide and nutrients. While the rates of electron assimilation will depend directly upon the cellular concentration of the enzymes of the dark reactions and temperature, rates will also be regulated by day length, nutrient concentration, and light intensity.

Transformations of the system include the dissipation of free energy in photosystem II by fluorescence and heat production, the dissipation of heat from the electron transport system by short circuiting of electrochemical gradients, and the dissipation of heat and excreted compounds by the "photorespiratory" pathways of the dark reactions. Of course, such dissipation causes reductions in the quantum yield of carbon assimilation. We assume that the process of metabolic regulation involves adjustments to maintain growth rates and to minimize the costs that are associated with dissipation. (For example see Kiefer & Enns 1976 and Shuter 1979.) Such regulation can generally be achieved by adjusting the rate of supply of electrons from the light reactions with rates of utilization by the dark reactions. Specifically, this is achieved by varying the cellular concentrations of all three components shown in Fig. 1, photosystem II, the electron transport pool, and the enzymes of the dark reactions. At present we do not have a complete mathematical formulation describing the steady state, optimized condition.

A mathematical description of the relationship between light absorption and growth is most simply represented in terms of the cellular con-

centration of photosystem II, its effective absorption cross-section, and its minimum, steady state, turnover time. A similar derivation has been presented by Bannister (1979). The minimum, steady state, turnover time of photosystem II, τ, is the minimum time required for the reaction center to process an electron under steady state conditions (Myers & Graham 1971). The time required for charge separation by the unit is many times shorter. τ, which is a dependent variable (unit of days), can be defined as the quotient of the cellular concentration of photosystem II and the maximum carbon specific rate of photosynthesis:

$$\tau = \eta_{II}\, jce/\Pi. \tag{4}$$

η_{II}, a dependent variable (in units of m gm-at C), is the concentration of photosystem II normalized to cellular carbon (units of moles mg-at C^{-1}). Π, a dependent variable, is the maximum carbon specific rate of photosynthesis (units of day^{-1}). *jce*, which is a constant, is the stoichiometric coefficient of the number of carbon atoms fixed per electron that is passed through the transport chain (units of gm-at C mole e^{-1}). Increases in the concentration of reaction centers tend to increase the turnover time while increases in the maximum rate of carbon assimilation tend to decrease the turnover time. If the time between the capture of photons by photosystem II is less than the minimum turnover time of the photosystem, the photosynthetic quantum efficiency will be reduced. This relationship is expressed by the Poisson distribution function (Dubinsky et al. 1986; Peterson et al. 1987; Cullen 1990):

$$\phi = \phi_{max}\,(1-\exp(-\sigma_{II}\,\tau\,E_0))/\sigma_{II}\,\tau E_0. \tag{5}$$

ϕ_{max}, a constant, is the maximum photosynthetic quantum yield; its value can be measured when the time between each capture of a photon by the photosystem is much longer than the minimum turnover time. σ_{II} is the effective cross-section of photosystem II (units of m^2/mole) (Ley & Mauzerall 1982).

The mean specific absorption coefficient, a_p, is assumed to be contributed solely by the photosynthetic pigments of photosystems I and II. If the effective absorption by the two photosystems is equal, one writes:

$$a_p = 2\,\eta_{II}/\sigma_{II}\theta. \tag{6}$$

By appropriate substitution within equations 1, 4, 5, 6, one eliminates the two dependent variables, n_{II} and σ_{II} and obtains an equation for gross specific growth rate in terms of two constants, ϕ_{max} and a_p, two independent variables, E_0 and Γ, and two dependent variables, Π and θ:

$$g = \pi\Gamma\,(1-\exp(-a_p\,\phi_{max}E_0/\pi\cdot\theta)). \tag{7}$$

The quantum yield is

$$\phi = \Pi\theta\,(1-\exp(-a_p\,\phi_{max}\,E_0/\pi\cdot\theta)/a_p\,E_0. \tag{8}$$

Equation (7) is the exponential form of photosynthetic response curve. $\theta\Pi/a_p\phi_{max}$ is Ik, g θ is P_m^B. If it is assumed that a_p and ϕ_{max} are constants, then variations in quantum yield that are effected by temperature, day length, and nutrient concentration must result from changes in the product $\Pi\theta$. As mentioned earlier, it appears that this product is sensitive to changes in light intensity and temperature but not to changes in day length and nutrient concentration.

Growth and light absorption in cultures

The laboratory studies used to examine the model presented above provide information on changes in two (g and θ) of the three dependent variables which are effected by variations in light intensity, day length, temperature, and nutrient supply. Two studies which describe the steady state growth of *Skeletonema costatum* will now be examined. One study by Yoder (1979) examined the cellular concentration of chlorophyll *a* and growth rate of cells limited by light intensity and temperature. The other study by Sakshaug et al. (1989) examined cellular concentration of chlorophyll *a* and growth rate of cells limited by light intensity, day length, and rates of nutrient supply. Cultures in these studies were grown at 15°C. It will be seen that g, Π, and θ vary with temperature, nutrient concentration, light intensity, and day length. It will also be seen that although the product $\Pi\theta$ varies little with day length and nutrient concentration, it does vary with temperature. Thus, only light intensity and temperature effect the steady state quantum yield of carbon assimilation.

Yoder (1979) grew *Skeletonema costatum* in turbidostat at five temperatures (0, 5, 10, 16, and 22°C) and at five light intensities. Although cultures were also grown under a number of different photoperiods, values for the ratio of cellular carbon to chlorophyll *a* were reported only for

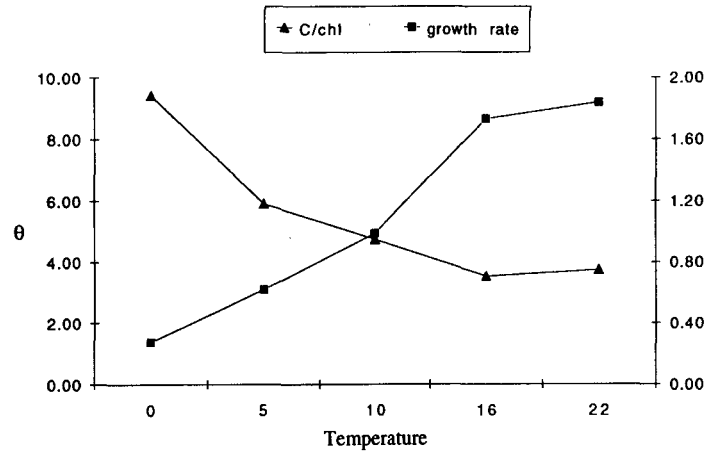

Fig. 2. Variations in specific growth rate, μ (d^{-1}), and the cellular ratio of carbon to chlorophyll, θ (gm-at C gm Chl^{-1}, of *Skeletonema costatum* caused by variations in temperature. The five cultures were grown under light intensities of about 130 μmol m^{-2} s^{-1} and a photoperiod of 12 hours.

a 12-hour light and 12-hour dark cycle. Sakshaug et al. (1989) grew *Skeletonema costatum* continuously by daily dilution with a medium with an elemental composition that ensured nitrogen limitation. The cultures were maintained at 20°C, at six light intensities, ranging from 12 to 1200 μE · m^{-2} · s^{-1}, 3 photoperiods, 6 h light, 14 h light, and 24 h light, and from 4–6 rates of dilution. The matrix of light intensities, dilution rates, and photoperiods was not complete. Both studies include measurements of the temperature, light intensity, day length, specific growth rate, μ, and the ratio of cellular carbon to chlorophyll *a*, θ. The data from these two studies have been analyzed by introducing values for the measured independent and dependent variables into equation (7). a_p has been assigned a value of 0.016 m^2 mg Chl^{-1} and ϕ_{max} a value of 0.10 g-at mol^{-1}. Since neither g nor the specific rate of respiration in the dark was measured, we assumed that g was equal to μ and that dark respiration was only a small fraction of μ. This assumption is questionable for cultures grown at very low light intensities or very short photoperiods.

Growth rates and cellular concentrations of chlorophyll a

Figs. 2, 3, 4, and 5 summarize the changes in growth rate and cellular chlorophyll *a* concentration that occurred with limitation by the four independent variables, light intensity, day length, temperature, and nutrient supply. Temperature limitations (Fig. 2) causes decreases in growth rate that are accompanied by increases in the ratio of cellular carbon to chlorophyll *a*. Such decreases in growth rate have been interpreted to result from decreases in the maximum specific

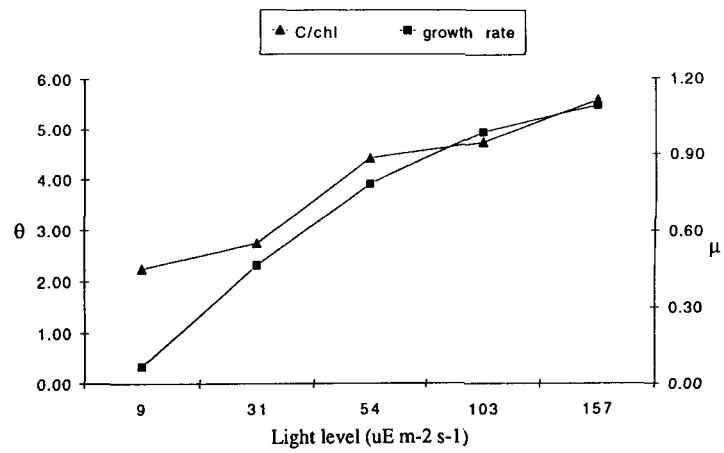

Fig. 3. Variations in specific growth rate, μ (d^{-1}), and the cellular ratio of carbon to chlorophyll, θ (gm-at C gm Chl^{-1}), of *Skeletonema costatum* caused by variations in light intensity. The five cultures were grown at 15°C, under a photoperiod of 12 hours, and with a rapid supply of nutrients.

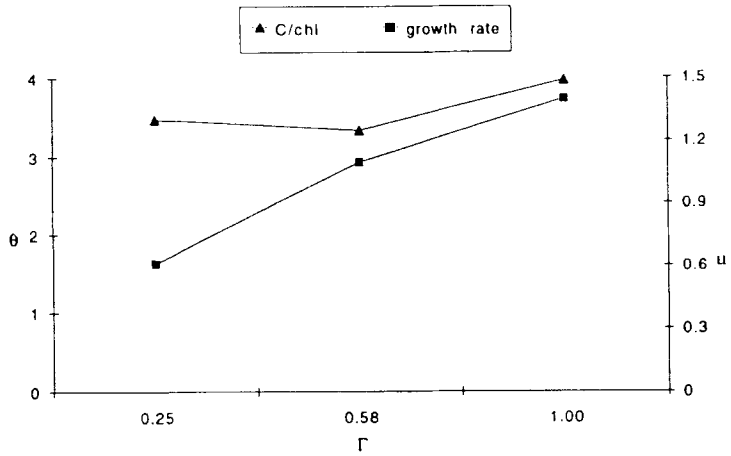

Fig. 4. Variations in specific growth rate, μ (d^{-1}), and the cellular ratio of carbon to chlorophyll, θ (gm-at C gm Chl^{-1}), of *Skeletonema costatum* caused by variations in photoperiod, Γ. The three cultures were grown at 15°C and under a light intensity of 100 μmol m^{-2} s^{-1} and with a rapid supply of nutrients.

activity of enzymes of the dark reactions. Limitations by light intensity (Fig. 3) cause decreases in growth rate that are accompanied by decreases in the ratio of cellular carbon to chlorophyll *a*. Growth rate declines with E_0 because the cellular concentration of chlorophyll *a* does not increase sufficiently with decreasing intensity. Limitations by day length (Fig. 4) cause decreases in growth rate that are accompanied by little change in the ratio of cellular carbon to chlorophyll *a*. Since the instantaneous rate of cellular light absorption remains constant for the three photoperiods, the decreases in growth are simply caused by decreases in the daily rate of light absorption. Limitations by rates of nutrient supply (Fig. 5) cause decreases in growth rate that are accompanied by increases in the ratio of cellular carbon to chlorophyll *a*.

Growth rates and maximal daily rates of photochemistry

The data from the two studies can be further analyzed by examining the relationship between the specific growth rate of the cultures, μ, and the cell's maximal daily capacity to supply electrons, Fc of equation (3). In the case of temperature and light limitation to growth the relationship is complicated by an absence of linearity. As shown in Fig. 6, growth rate is a curvilinear function of Fc. Furthermore, this relationship is clearly a function of temperature; temperature decreases

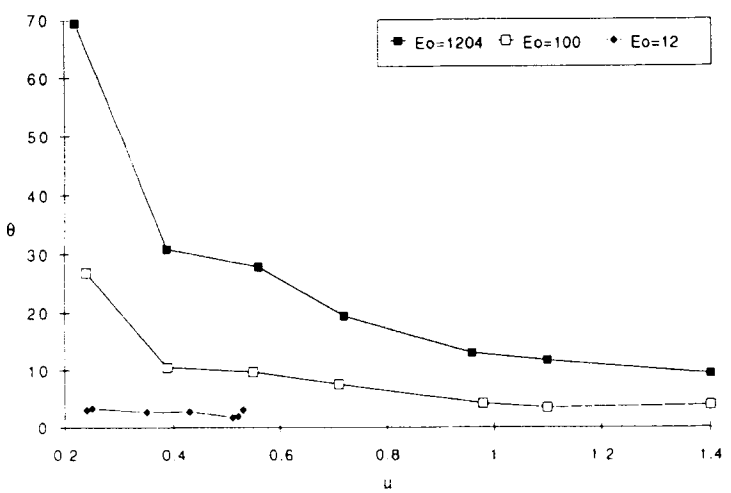

Fig. 5. Variations in the cellular ratio of carbon to chlorophyll, θ (gm-at C gm Chl^{-1}), of *Skeletonema costatum* caused by variations in specific rates of nutrient supply. The cultures were grown at 15°C, at the light intensities shown (μmol m^{-2} s^{-1}), and under a photoperiod of 24 hours.

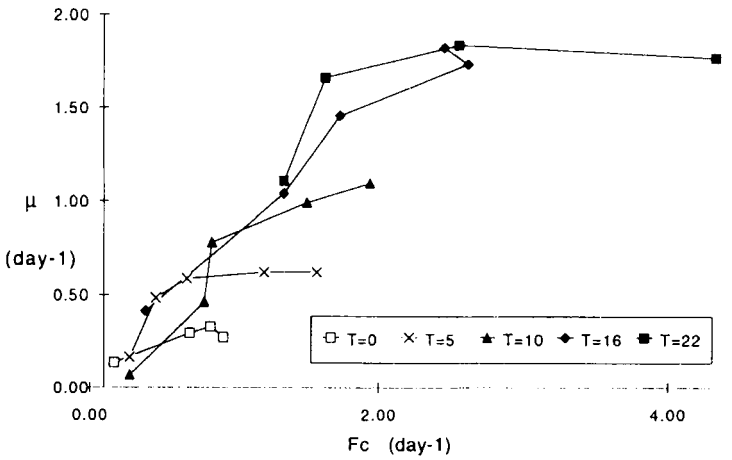

Fig. 6. Variations in specific growth rate, μ, of *Skeletonema costatum* with variations in cellular, daily capacity of electron supply, Fc of equation 3. The variations between cultures that were grown at the temperatures shown in the legend were caused by variations in light intensity. The photoperiod for all cultures was 12 hours.

cause decreases in rates of electron supply that saturate growth. It is apparent from this figure that at 5°C a daily rate of electron supply of 0.5 d^{-1} is sufficient to meet a rate of assimilation of about 0.6 d^{-1}. At 22°C a daily rate of electron supply of 2.0 d^{-1} is needed to meet maximal daily rates of assimilation of about 1.8 d^{-1}.

In the case of limitations to growth by light intensity, day length, and nutrient supply, the relationship appears to be linear. As shown in Fig 7, when *Skeletonema*'s growth rate at a given light intensity is plotted as a function of its daily capacity for photochemistry, the relationship is linear despite changes in day length and rate of nutrient supply. The slope of this line, which in fact is the proportional to quantum yield, increases with increasing light intensity.

Quantum yields and growth rates

The variations in quantum yield implied in Figs. 6 and 7 are explicitly presented in Figs. 8 and 9. When the quantum yields for growth at a given light intensity are plotted as a function of growth rate, there is evidenced a clear distinction between the adaptation to limitation by temperature and the adaptation to limitation by either day length or rate of nutrient supply. As shown in Fig. 8, decreases in the temperature-dependent growth rate at a given light intensity are

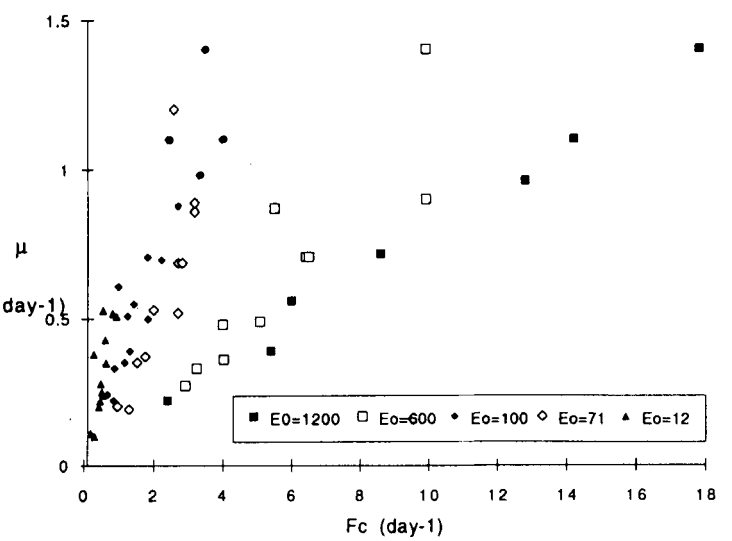

Fig. 7. Variations in specific growth rate, μ, of *Skeletonema costatum* with variations in cellular, daily capacity for electron supply, Fc of equation (3). The variations between those cultures that were grown under the light levels, E_o (μmol m^{-2} s^{-1}), shown in the legend were caused by variations in both rates of nutrient supply and photoperiod. The temperature was 15°C.

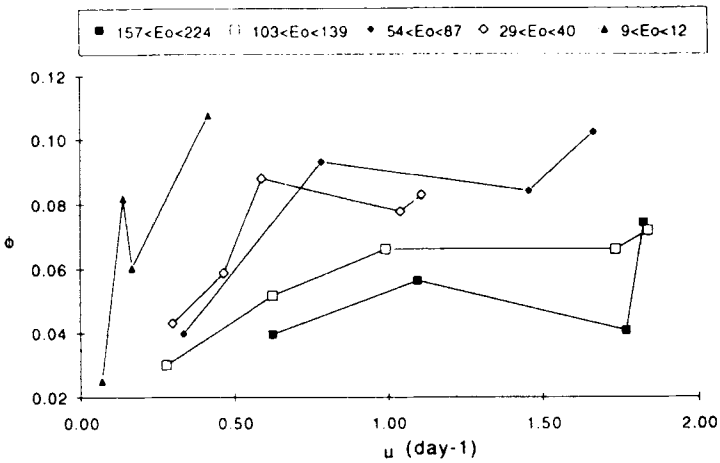

Fig. 8. Variations in the photosynthetic quantum yield, ϕ (gm-at C E^{-1}), of *Skeletonema costatum* with variations in specific growth rate, μ. The variations between those cultures that were grown under the light levels, E_0 (μmol m^{-2} s^{-1}), shown in the legend were caused by variations in temperature. The photoperiod was 12 hours.

accompanied by decreases in quantum yield. Each of the five categories of light intensity display a trend of decreasing yield with decreasing growth rate. One also notes by comparing the five categories that quantum yields tend to decrease with increasing light levels.

Decreases in growth rate at a given light level effected by decreases in nutrient supply or day length do not appear to be accompanied by decreases in quantum yield (Fig. 9). An examination of the six categories of light levels indicates that in four of the six categories there is little or no covariation between quantum yield and growth rate. The two exceptions are the categories of the lowest light levels, 12 and 41 μmol m^{-2} d^{-1}, where decreases in quantum yield appear to parallel decreases in growth rate. Again, it can be noted that quantum yields decrease with increases in light levels.

Capacity for instantaneous electron supply and assimilation

The final analysis of the two studies of *Skeletonema* consisted of introducing values for E_0, Γ, and θ, into equation (7). The equation is then solved for Π, the maximum, instantaneous, specific rate of carbon fixation, by introducing

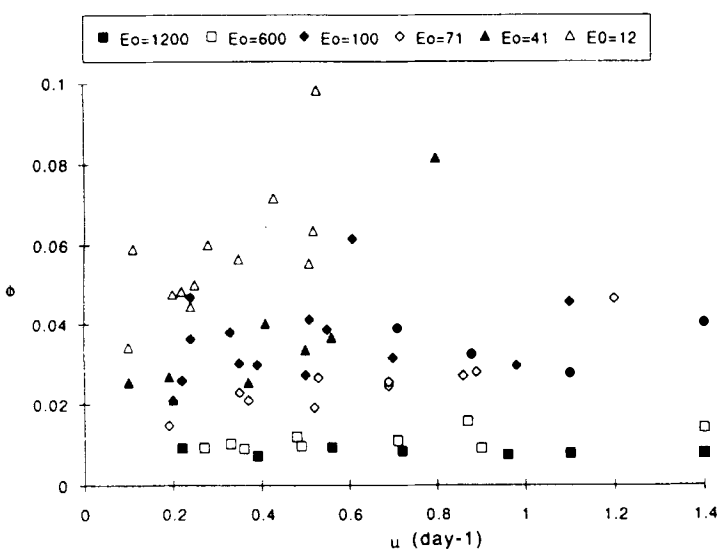

Fig. 9. Variations in the photosynthetic quantum yield, ϕ (gm-at C E^{-1}), of *Skeletonema costatum* with variations in specific growth rate, μ. The variations between those cultures that were grown under the light levels, E_0 (μmol m^{-2} s^{-1}), shown in the legend were caused by variations in nutrient supply and photoperiod. The temperature was 15°C.

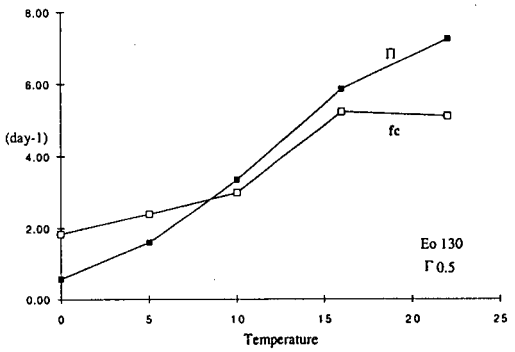

Fig. 10. Variations in the cellular, instantaneous capacity for electron supply by the light reactions, fc of equation (2), and the instantaneous capacity for electron assimilation by the dark reactions, Π, with variations in temperature. The five cultures were grown under light intensities of about 130 μmol m^{-2} s^{-1} and a photoperiod of 12 hours.

values of μ for g. Changes in Π with temperature, light level, day length, and nutrient supply are then compared with changes in maximum instantaneous rates of photochemistry, fc, defined in equation (2). Such a comparison provides insight into the differences in adaptation to the four environmental variables. Decreases in temperature at a given light level and photoperiod (Fig. 10) cause decreases in both the maximal rates of photochemistry and maximal rates of assimilation. Of most importance is the rate of change in assimilation with temperature which is significantly greater than the rate of change in photochemistry. While at 15°C and above, the specific capacity for electron supply is comparable to the specific capacity of electron assimilation; at 0°C the capacity for supply is about three times greater than the capacity for assimilation. The large decreases in quantum yield with decreases in temperature are explained by the differences between the two slopes. Decreases in nutrient supply (Fig. 11) cause decreases in both the capacity to supply and assimilation electrons. However, in the case of nutrient limitation, decreases in capacity for supply are paralleled by decreases in assimilation. Thus, unlike temperature adaptation, adjustments of the light and dark systems to nutrient limitation help to maintain the constancy of the quantum yield.

Decreases in light intensity cause decreases in the cellular instantaneous capacity to supply electrons but have little effect on the capacity to assimilate electrons (Fig. 12). Thus, quantum yields increase with decreasing light levels. Unfortunately, values of Π calculated from equation 7 for light limitation are too variable to allow us to confidently conclude that there is no trend. On the other hand, there is abundant evidence that quantum yields increase with decreasing light levels, and thus cellular capacity for electron supply must drop more rapidly with light level than cellular capacity for electron assimilation.

Finally, unlike decreases in light intensity, decreases in day length cause increases in both

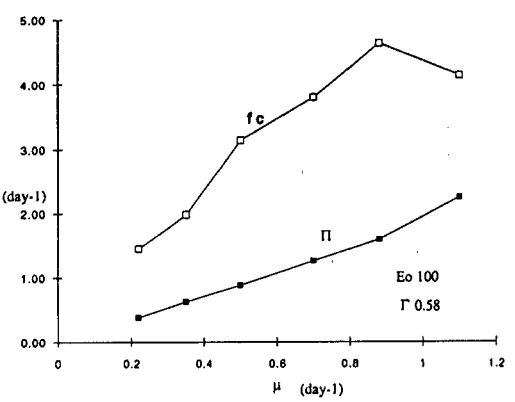

Fig. 11. Variations in the cellular, instantaneous capacity for electron supply by the light reactions, fc of equation 2, and the instantaneous capacity for electron assimilation by the dark reactions, Π, with variations in specific rates of nutrient supply, μ. (μ = dilution rate). The six cultures were grown under a light intensity of about 100 μmol m^{-2} s^{-1} and a photoperiod of 14 hours.

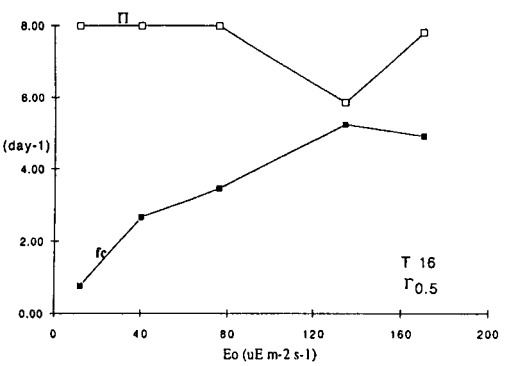

Fig. 12. Variations in the cellular, instantaneous capacity for electron supply by the light reactions, fc of equation (2), and the instantaneous capacity for electron assimilation by the dark reactions, Π, with variations in light intensity, E_0. The five cultures were grown at 16°C and under a photoperiod of 12 hours.

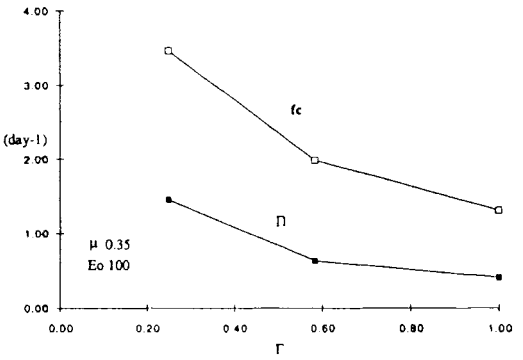

Fig. 13. Variations in the cellular, instantaneous capacity for electron supply by the light reactions, fc of equation (2), and the instantaneous capacity for electron assimilation by the dark reactions, Π, with variations in photo-period, Γ. The three cultures were grown at 15°C under light intensities of about 100 μmol m^{-2} s^{-1} and at a dilution rate of 0.35 d^{-1}.

the cellular instantaneous capacity to supply and assimilate electrons (Fig. 13). Since changes in both capacities parallel each other, photosynthetic quantum yields are little affected by changes in day length. These results indicate that adaptation to day length is to a large extent independent of adaptation to light intensity.

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