Temperature response of photosynthetic capacity and carboxylase activity in Arctic marine phytoplankton

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ABSTRACT The temperature response of photosynthetic capacity was compared to that of 3 carboxylating enzymes in Arctic marine phytoplankton. Only the activity of ribulose-1,5-bisphosphate carboxylase (RuBPC) consistently exhibited an apparent activation energy equivalent to that of photosynthetic capacity. This is the first indication from field samples of phytoplankton that changes in the activity of RuBPC may be closely associated with changes in photosynthetic capacity. The maximum photosynthetic capacity attained by Arctic phytoplankton at a given *in situ* temperature appeared to increase from about 0.4 mg C mg Chl a^{-1} h^{-1} at $-1.5\,°C$ to an apparently constant value of about 2.0 mg C mg Chl a^{-1} h^{-1} at temperatures equal to and greater than $0.0\,°C$.

INTRODUCTION

The photosynthetic response and adaptation to temperature has been well studied in higher plants (Berry and Björkman, 1980; Patterson, 1980; Berry and Raison, 1981; Graham and Patterson, 1982) but not in unicellular algae (Eppley, 1972; Li, 1980). High latitude environments, especially marine ecosystems, are persistently cold. Phytoplankton inhabiting such systems are therefore particularly well-suited subjects for studies of photosynthesis at low temperatures.

In this paper, we examine the relation between photosynthetic capacity of Arctic phytoplankton and temperature of the water *in situ*. The measurements required to establish this relation are 'observations' in the sense that there is no interference with the metabolism of the cells except to sample and perform the measurements. These results pertain to the characteristics of the cells as they occur in nature. We also examine the short-term responses of photosynthetic capacity and carboxylase activities when cells are subjected to abrupt shifts in temperature. The results from these manipulative experiments pertain to the potential importance of the enzymes in the control of photosynthetic capacity at low temperatures.

MATERIALS AND METHODS

Photosynthetic rates were measured for phytoplankton sampled from the eastern Canadian subarctic (Labrador Sea) and Arctic (Baffin Bay, Lancaster Sound, Jones Sound, Smith Sound, Foxe Basin, Fury and Hecla Strait) during cruises to these areas from 1977 to 1981. Phytoplankton from various depths in the photic zone were collected in Niskin bottles. For each sample, the amount of $H^{14}CO_3^-$ taken up in 2 h was measured within a light gradient from about 1 to 800 W m^{-2} (PAR) in a temperature-controlled incubator, artificially illuminated by a 2,000 W tungsten-halogen floodlight. The temperature response of photosynthesis was determined on 10 occasions in the subarctic and on 12 occasions in the Arctic. For each sample, the photosynthesis-irradiance relation was established at each of four incubation temperatures. A detailed description of methods and the results of one such experiment have been published (Li and Platt, 1982). Photosynthetic capacity (P_m^B) is defined as the rate of ^{14}C fixation (P) measured at the irradiance resulting in the maximal (m) rate and normalized to phytoplankton biomass (B), expressed as the mass of chlorophyll *a*. Chlorophyll *a* was measured by the fluorometric

technique of Yentsch and Menzel (1963) as modified by Holm-Hansen et al. (1965).

The activities of 3 carboxylating enzymes known to occur in marine algae (Appleby et al., 1980; Kremer, 1981) were also measured. Ribulose-1,5-bisphosphate carboxylase (RuBPC, E.C.4.1.1.39) and phosphoenol-pyruvate carboxylase (PEPC, E.C.4.1.1.31) activities were determined radiometrically as described by Smith et al. (1983) by measuring the rate of incorporation of $^{14}CO_2$ (RUBPC) and $H^{14}CO_3^-$ (PEPC) into acid stable products by permeabilized cells *in vivo*. These assays were modified by the addition of L-α-lysophosphatidylcholine (Sigma, type I, 0.25 mg 1.3 ml^{-1} reaction mixture), the reduction of the concentration of Tris buffer from 0.4 to 0.1 M and the lowering of the pH from 8.0 to 7.5. Phosphoenolpyruvate carboxykinase (PEPCK, E.C.4.1.1.49) activity was determined in an assay system identical to that for PEPC except that Mg^{2+} was replaced by Mn^{2+} (2 mM) and ADP (5 mM). The temperature responses of the enzymes were determined on numerous occasions by incubating the samples at seven different temperatures, although, for logistic reasons, only 4 or 5 experimental temperatures were used on the earliest cruise. Four experimental and 2 control replicates were determined for each enzyme at each temperature. The controls were not affected by temperature and their values may represent an absorption phenomenon or non-acid labile impurities in the ^{14}C stock solutions. A typical example both of the closeness of the replicates and of the goodness of the approximation of the temperature response of these enzymes to the Arrhenius formulation is that for RuBPC at station X228 from Foxe Basin. When the linear regression of the natural logarithm of RuBPC activity (dpm l^{-1} h^{-1}) against the reciprocal of the absolute temperature was calculated, the slope of the line was $-7268 \pm 315\,°K$ (SE) and the intercept was 33.866 ± 1.103 (SE). The correlation coefficient was -0.977 for 26 degrees of freedom, the probability of this arising by chance being less than 10^{-5}

RESULTS

The relation between P_m^B of Arctic phytoplankton and *in situ* temperature is shown in Fig. 1 Most of the values for P_m^B are less than 2 and none greatly exceed 3 mg C mg Chl a^{-1} h^{-1}. In all cases here, the deviation of incubation temperature from that *in situ* was ≤ 1 C°. The significance of the dashed line (Fig. 1) is discussed below.

In experiments where the incubation temperature was manipulated away from that *in situ*, the temperature dependence of P_m^B and carboxylase activities (V)

was expressed according to the Arrhenius equation as follows:

$$\varrho = A\, e^{\left(-\frac{E_a}{RT}\right)} \tag{1}$$

$$\varrho' = A\, e^{\left(-\frac{E_a}{RT'}\right)} \tag{2}$$

$$\ln\left(\frac{\varrho'}{\varrho}\right) = -\frac{E_a}{R}\left(\frac{1}{T'} - \frac{1}{T}\right) \tag{3}$$

where ϱ = either P_m^B or V at the absolute *in situ* temperature T; ϱ' = either P_m^B or V at the absolute assay temperature T'; A = a constant; R = gas constant; E_a = apparent activation energy. Equation (3) is simply the logarithmic transform of the ratio $\varrho' : \varrho$ (i.e. Eq. [2] divided by [1]). Equation (3) expresses rates relative to that *in situ* and thus allows experiments conducted on phytoplankton collected at various temperatures (−1.5 to 4.5 °C) to be considered on a common basis. The validity of pooling data from separate experiments is indicated by the fact that E_a for P_m^B and for V of any of the enzymes were statistically uncorrelated ($P \geq 0.2$) with *in situ* temperature.

Plots of $\ln\left(\frac{\varrho'}{\varrho}\right)$ versus $\left(\frac{1}{T'} - \frac{1}{T}\right)$ are shown for P_m^B

(Fig. 2). RuBPC (Fig. 3), PEPCK (Fig. 4), and PEPC (Fig. 5). On the basis of linear regressions of the data (Fig. 2 to 5) according to Eq. (3), the values of $E_a \pm$ standard error (kcal mol^{-1}) were 16.9 ± 0.85 for P_m^B, 17.3 ± 0.67 for RuBPC, 6.0 ± 0.71 for PEPCK and 7.8 ± 1.03 for
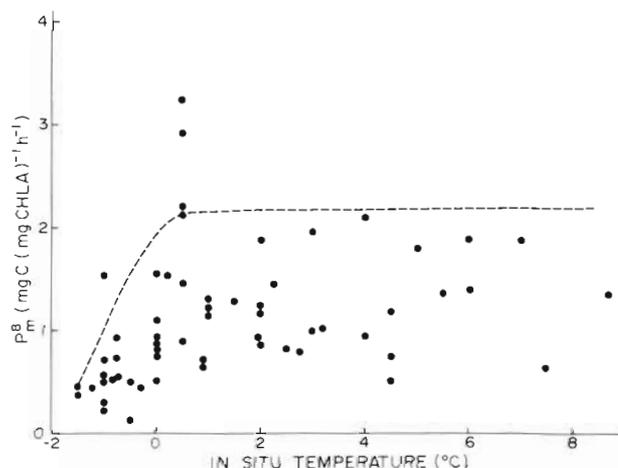

Fig. 1. Relation between photosynthetic capacity and *in situ* temperature for eastern Canadian Arctic marine phytoplankton. Temperatures during incubation were ± 1 C° of those *in situ*. See text for discussion of dashed curve
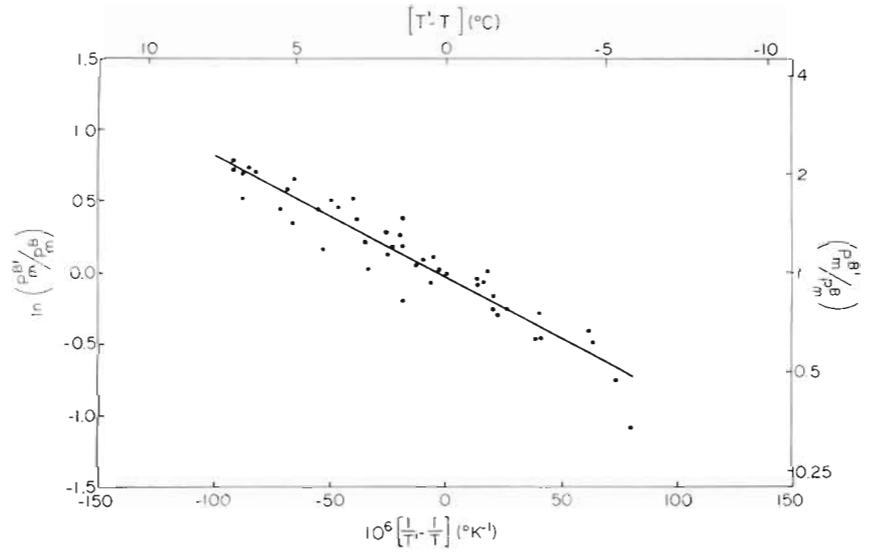
Fig. 2. Modified Arrhenius plot (Equation 3) of photosynthetic capacity in eastern Canadian Arctic marine phytoplankton
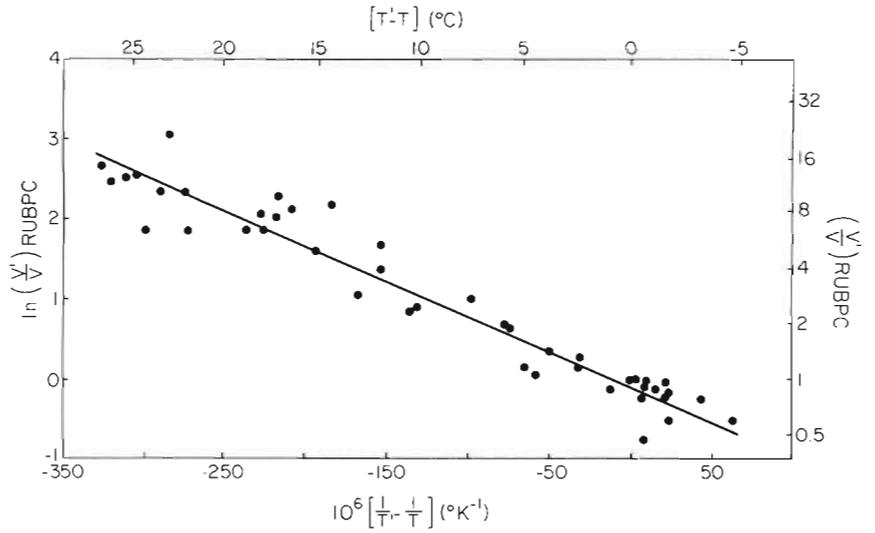

Fig. 3. Modified Arrhenius plot (Equation 3) of RuBPC activity in eastern Canadian Arctic marine phytoplankton
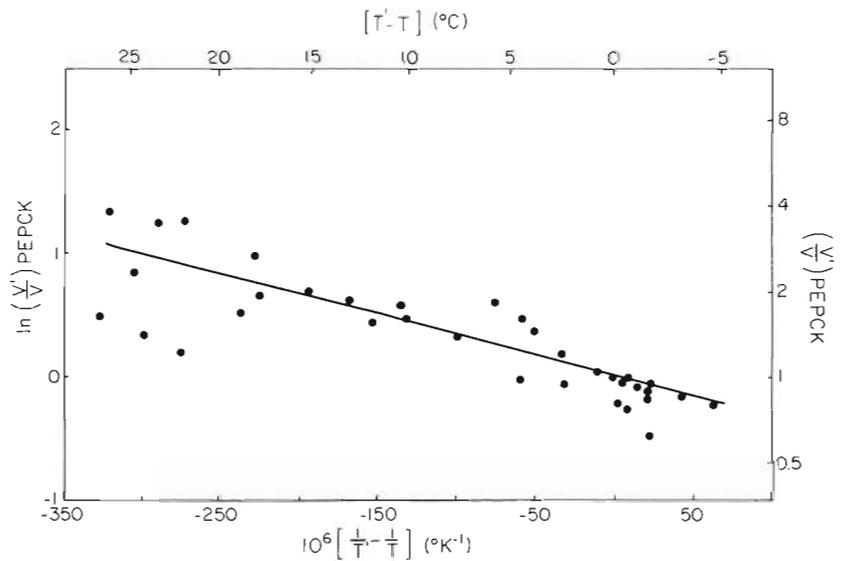

Fig. 4. Modified Arrhenius plot (Equation 3) of PEPCK activity in eastern Canadian Arctic marine phytoplankton
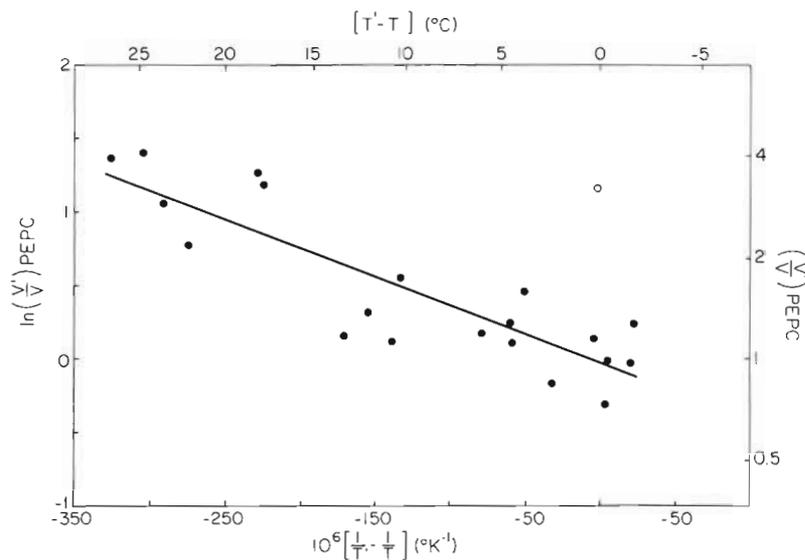
Fig. 5. Modified Arrhenius plot (Equation 3) of PEPC activity in eastern Canadian Arctic marine phytoplankton. Outlying datum (open symbol) was excluded from regression analysis
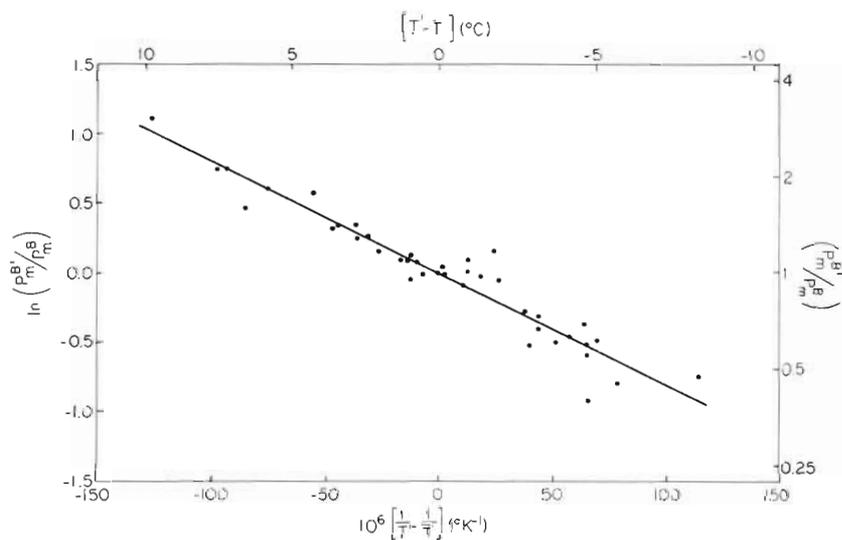

Fig. 6. Modified Arrhenius plot (Equation 3) of photosynthetic capacity in eastern Canadian subarctic (Labrador Sea) marine phytoplankton

PEPC. We have also determined the temperature dependence of P_m^B for eastern Canadian subarctic (Labrador Sea) phytoplankton (Fig. 6): it was statistically indistinguishable ($E_a = 16.0 \pm 0.64$ kcal mol^{-1}) from that of P_m^B for Arctic phytoplankton (Fig. 2).

DISCUSSION

Measurements of the short-term temperature response of inorganic carbon fixation for unicellular algae from high latitude seas (Bunt, 1964; Li and Platt, 1982; Neori and Holm-Hansen, 1982; Jacques, 1983) indicate that such habitats are invariably at temperatures suboptimal for photosynthesis. Extensive studies on higher plants (Berry and Björkman, 1980; Berry and Raison, 1981) suggest that whereas at near optimal temperatures the rate of photosynthesis is principally

limited by the capacity of chloroplast membranes for electron transport, it is most likely the activities of enzymes such as RuBPC and fructose bisphosphate phosphatase that are limiting to photosynthesis at suboptimal temperatures. The potential importance of an enzyme in relation to photosynthetic capacity at suboptimal temperature may be indicated by its responsiveness to abrupt shifts in temperature away from that to which the plant is acclimated. Thus, a comparison of the apparent activation energy for photosynthesis and that of possible rate-limiting enzymes may be useful in this context (Berry and Raison, 1981). Björkman and Pearcy (1971) reported that for various species of higher plants, apparent activation energies (E_a) of photosynthetic capacity and RuBPC activity were in close agreement. Similarly in the present study, of the enzymes examined, only RuBPC consistently exhibited a value of E_a equivalent to that of photosynthetic

capacity (Fig. 2 and 3). These results are consistent with the view that changes in RuBPC activity may be the predominant response of the photosynthetic machinery elicited by temperature changes in the suboptimal range (Berry and Björkman, 1980; Berry and Raison, 1981).

In comparing the temperature response of the β-carboxylating enzymes (PEPCK and PEPC) and P_m^B, we do not imply that these enzymes necessarily function in primary carbon fixation in Arctic phytoplankton. The precise role of C_4 metabolic reactions in algae is not fully resolved (Benedict, 1978; Morris, 1980; Kremer, 1981). Our measurements of relatively low apparent activation energies for these enzymes suggest that their role in the control of photosynthetic capacity at low temperatures is less than that of RuBPC.

By themselves, measurements of short-term responses to abrupt shifts in temperature indicate little about the rate of physiological processes that would be found after the organisms had been exposed to a new ambient temperature for an extended period. In general, for ectotherms, the following sequence occurs after a shift from low to high temperature (Prosser, 1964): depending on the abruptness and the extent of the shift, there may be an initial 'shock reaction' leading to an overshoot in metabolic rate; following this, over a period of minutes or hours, a 'stabilized state' prevails during which metabolism is sustained at an elevated rate; finally, over a period of days or weeks, an 'acclimated state' prevails during which compensatory mechanisms have acted to reduce metabolism, at the higher temperature, to a rate near to that occurring before the shift. Measurements such as those in Fig. 2 to 5 and those of Olson (1980) and Neori and Holm-Hansen (1982) most likely pertain to the 'stabilized state'. It is therefore misleading to speak of phytoplankton *growth* (a property of the 'acclimated state') being limited by temperature, based on measurements of uptake of nitrogenous nutrients (Olson, 1980) and CO_2 (Neori and Holm-Hansen, 1982) as functions of short-term changes in temperature. The results from a laboratory experiment on the marine planktonic diatom *Phaeodactylum tricornutum* illustrate this point (Li and Morris, 1982): different values of Q_{10} were obtained for growth rate, 'stabilized state' P_m^B and 'acclimated state' P_m^B.

We now turn our attention to the effect of temperature on the values of P_m^B in the 'acclimated state'. For this, it is essential that the measurements be made at a saturating (but not inhibiting) irradiance and at the *in situ* temperature. These requirements were met in our measurements (Fig. 1). We interpret the variation of P_m^B at any temperature as being due to diel changes (Mac-Caull and Platt, 1977; Harding et al., 1982), light history (Yentsch and Lee, 1966; Beardall and Morris,

1976), cell size and species composition (Malone, 1971; Durbin et al., 1975; Glover, 1980; Côté and Platt, 1983) and nutrient conditions·(Thomas, 1970; Glover, 1980). To assess the influence of temperature alone, only the highest P_m^B measured at each temperature ($\hat{P}_m^B$) should be considered. Operationally, this might be achieved by forming a curve that envelops the scattergram (e.g. Yentsch et al., 1974). The upper limit of our scattergram (Fig. 1) is not sufficiently well-defined to form a unique envelope. Nevertheless, we have indicated a possible form for the envelope (dashed line in Fig. 1) by comparison with similar plots (Yentsch et al., 1974; Li, 1980) which indicate a progressive decrease in the dependence of P_m^B as *in situ* temperature increases: in other words, the curve 'flattens out'.

For the sake of discussion, we assume for the moment that the dashed curve indeed represents the temperature response of $\hat{P}_m^B$ for eastern Canadian Arctic phytoplankton in the 'acclimated state'. At *in situ* temperatures $\geq \approx 0\ °C$, $\hat{P}_m^B$ remained constant at ≈ 2 mg C mg Chl $a^{-1}\,h^{-1}$. A partial explanation may be that the cellular content of chlorophyll a is reduced at low temperatures (Li, 1980). In *Phaeodactylum tricornutum*, partial compensation of photosynthesis to low temperature ($\geq \approx 10\ °C$) was evident even after the reduction of cellular chlorophyll a had been taken into account; compensation appeared to be related to an increase in RuBPC activity at low temperature in the 'acclimated state' (Li and Morris, 1982). The parallelism between the 'acclimated state' temperature response of arctic phytoplankton and cultures of *P. tricornutum* extends to very low temperatures. In both cases ($< 0\ °C$ in the former, $< 10\ °C$ in the latter), $\hat{P}_m^B$ decreased with temperature (Fig. 1, Li and Morris, 1982). In *P. tricornutum*, there was a decrease in RuBPC activity at $< 10\ °C$. Berry and Björkman (1980) suggested that 'an improvement in photosynthetic effectiveness at a given low temperature . . . is likely to require an inordinately large investment in rate-limiting enzymes with only a marginal photosynthetic gain'.

In view of (a) the apparent parallelism between the 'acclimated state' temperature response of Arctic phytoplankton and *Phaeodactylum tricornutum*, (b) the apparent adaptive nature of RuBPC activity changes in *P. tricornutum* and (c) the apparent importance of changes in RuBPC activity when Arctic phytoplankton are abruptly shifted away from *in situ* temperature, we suggest that during 'acclimated state', RuBPC activity and $\hat{P}_m^B$ bear the same relationship to each other in arctic phytoplankton as they do in *P. tricornutum*. However, we must caution that this suggestion remains tentative until a more secure envelope of $\hat{P}_m^B$ vs. *in situ* temperature can be established.

Finally, we question whether the values of P_m^B for

Arctic phytoplankton are substantially different from those for temperate phytoplankton at low temperatures. In independent compilations of Soviet (Vedernikov, 1975) and Canadian (Harrison and Platt, 1983 which includes the data shown in Fig. 1) measurements in Arctic waters, the most frequently observed values of P_m^B were from about 0.7 to 1.2 mg C mg Chl a^{-1} h^{-1}; maximum recorded values were about 5.0 mg C mg Chl a^{-1} h^{-1}. These values are similar to those of temperate phytoplankton at low temperatures (e.g. Williams and Murdoch, 1966; Mandelli et al., 1970; Yentsch et al., 1974; Durbin et al., 1975), suggesting a lack of genotypic adaptation to 'overcome' the limitation of low temperature on enzymatic rates of photosynthesis.

This is supported by the values of specific rates of nutrient uptake by high latitude phytoplankton. If measurements of CO_2 and nitrogenous nutrient uptake are made under the condition that incubation and *in situ* temperatures are the same, specific rates are easily calculated by normalizing the uptake rates to phytoplankton biomass in units of carbon and nitrogen respectively. In cases where this has been done (e.g. Holm-Hansen et al., 1977; Slawyk, 1979; Olson, 1980; El-Sayed and Taguchi, 1981; Harrison et al., 1982; Neori and Holm-Hansen, 1982), the specific rates are almost always equal to or less than the specific rates of growth (cell divisions) predicted by Eppley (1972) for temperate phytoplankton at low temperatures. Caution is required to interpret such comparisons because the critical assumption of balanced growth (rates of nutrient uptake and cell division are equal) is probably met only infrequently under natural conditions (Eppley, 1981). Nevertheless, even when division rates are directly measured in culture, growth of high latitude algal isolates (Bunt, 1967; Seaburg et al., 1981; Palmisano and Sullivan, 1982; Jacques, 1983; van Baalen and O'Donnell, 1983) is not very different from growth, at low temperatures, of 'cold water species' isolated from temperate waters (Smayda, 1969; Durbin, 1974; Baars, 1981, 1982). This contrasts with the distinctly different temperature response of growth between temperate and tropical isolates (Braarud, 1961; Guillard and Kilham, 1977; Hulburt, 1982).

A plausible explanation to account for low photosynthetic rates in high latitude seas (and therefore also for the common observations of the substantial discrepancy between the temperature *in situ* and that at which photosynthesis is optimized) is that large increases in enzymes at low temperatures might be energetically cost ineffective (Berry and Björkman, 1980): this remains to be tested.

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