Temperature effects on phytoplankton growth in continuous culture[1]

Abstract—Temperature has a strong influence on the chemical composition of marine phytoplankton. A common characteristic of several species is a minimum nutrient content (as nitrogen or carbon) per cell at the temperature optimum for cell division, with increasing cellular biomass at lower and higher temperatures. Hence, cell division and nutrient uptake rates are uncoupled with respect to temperature. This raises doubts concerning the role of temperature in phytoplankton ecology and the predictive value of existing models of kinetic growth and uptake.

Temperature strongly influences the outcome of phytoplankton competition in mass cultures maintained on wastewater-seawater mixtures (Goldman and Ryther 1976). Although that research was directed toward development of waste recycling-aquaculture systems (Ryther et al. 1975), several aspects of our results appear to be of importance to a more complete understanding of phytoplankton dynamics in natural aquatic systems.

[1] Contribution 3813 from the Woods Hole Oceanographic Institution. This research was supported in part by contract E(11-1)-2532 from the U.S. Energy Research and Development Administration and by NOAA Office of Sea Grant under grant 04-6-158-44016.

The direct influence of temperature on phytoplankton division rates is clear: within defined temperature limits division rates increase with increasing temperature (Eppley 1972; Goldman and Carpenter 1974). Yet, as discussed in detail by Eppley (1972), a number of species increase in biomass as temperature is lowered. Jorgensen (1968) first observed this phenomenon; in *Skeletonema costatum* lowered temperatures led to lowered division rates but to higher rates of carbon and nitrogen assimilation. Increased enzyme production as a result of a higher cellular protein concentration was suggested as an adaptive mechanism for maintaining high photosynthetic rates at the lower temperatures. Morris and Glover (1974) however showed that photosynthetic rates were independent of temperature only toward the end of batch growth, but they too found that biomass per cell (measured as dry weight) in *Phaeodactylum tricornutum* and *Dunaliella tertiolecta* was inversely affected by temperature; this effect was not evident in *Nitzschia closterium*.

In our mass culture experiments (Goldman and Ryther 1976), we found that temperature strongly influences cellular chemical composition, not only at the lower, but at the higher temperatures as well. We grew five phytoplankton species from the culture collection of R.R.L. Guillard at Woods Hole Oceanographic Institution [*Skeletonema costatum* (Skel), *Monochrysis lutheri* (Mono), *Phaeodactylum tricornutum* (TX-1), *Dunaliella tertiolecta* (Dun), and *Thalassiosira pseudonana* (3H)] in continuous monocultures at a constant dilution rate of 0.6 d^{-1} with constant lighting (about 0.03 ly min^{-1}, visible region) on enriched media consisting of 50% secondarily treated wastewater and 50% seawater. Steady state measurements were made in the temperature range 10°–30°C in 5°C intervals, for cell counts (CC) (Spencer bright-line hemacytometer), and particulate carbon (PC) and nitrogen (PN) (Perkin-Elmer 240 elemental analyzer). We suspected that light limitation controlled the steady state populations (Goldman and Ryther 1976), although a silica limitation may have been present in the *T. pseudonana* cultures (unpublished data).

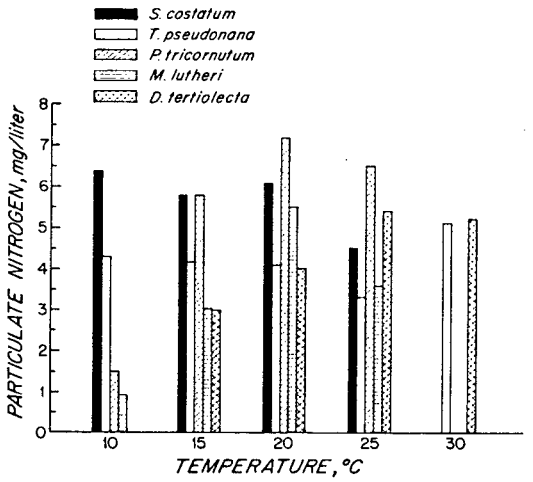

Fig. 1. Effect of temperature on steady state PN concentration for five phytoplankton species grown in continuous culture at a dilution rate of 0.6 d^{-1}.

The data for steady state PN values are shown in Fig. 1, cell numbers and PN:CC ratios in Fig. 2. The PN:PC ratios varied between about 5–7 (wt basis) for all species and temperatures, so the results can also be applied to PC variations with temperature (*see* Goldman and Ryther 1976 for PC data).

Each species responded to temperature variations somewhat differently. Four species (*T. pseudonana* excepted) showed an increase in nitrogen (and carbon) content per cell (PN:CC ratio) at the lowest temperatures at which steady state biomass was measurable (Fig. 2); the PN:CC ratios of *D. tertiolecta* and *P. tricornutum* were lowest at 20°C and increased at both higher and lower temperatures.

In the competition experiments in our mass culture study, we found (Goldman and Ryther 1976) that *S. costatum* at 10°C and *D. tertiolecta* at 30°C were the dominant and most efficient species in assimilating inorganic nitrogen and carbon. The anomalous feature of these results was that the PN (and PC) values and the corresponding nutrient uptake rates were high-

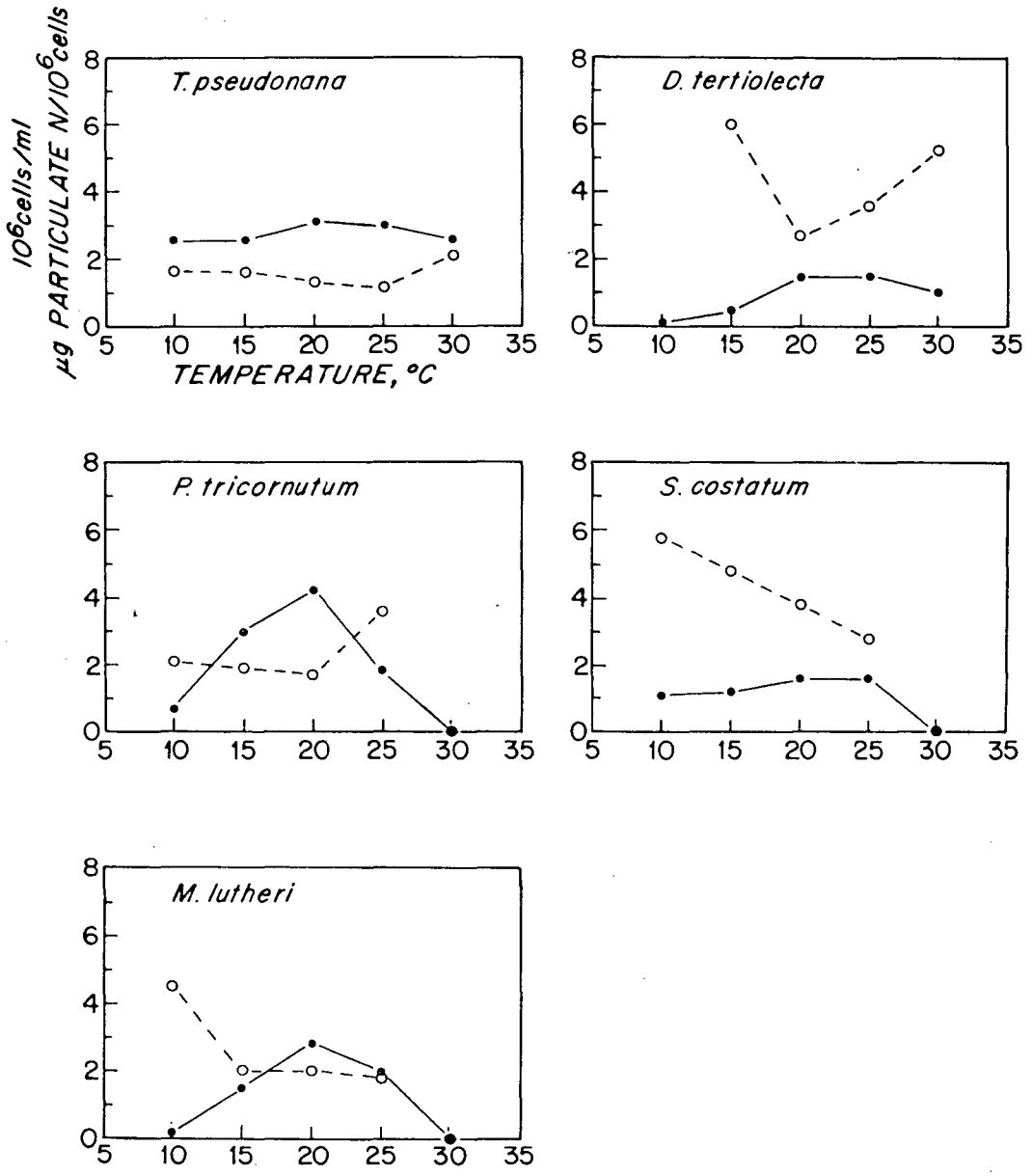

Fig. 2. Effect of temperature on steady state cell numbers (●) and PN : CC ratios (○) for five phytoplankton species grown in continuous culture at a dilution rate of 0.6 d^{-1}.

est when cell numbers were declining (Fig. 1).

Nutrient uptake rates can be expressed on a per unit cell basis:

$$\rho_c = \mu Q = \mu \Delta S \, CC^{-1}, \qquad (1)$$

in which ρ_c is the nutrient uptake rate of an individual cell, μ is the specific growth rate (unit $time^{-1}$), Q is the cell quota, or amount of nutrient assimilated per cell, and ΔS is the amount of nutrient assimilated by the total cell population. The uptake rate

can then be described for the whole cell population by

$$\rho_B = \rho_c CC = \mu \Delta S, \quad (2)$$

in which ρ_B represents the gross nutrient uptake rate of the total cell population.

Because the dilution rate D in a continuous culture (flow rate culture volume^{-1}) is virtually equal to μ, and because D was kept constant at 0.6 d^{-1} in the experiments, the PN results from Fig. 1 and the PN:CC ratios from Fig. 2, when multiplied by 0.6 d^{-1}, represent the uptake rates ρ_B and ρ_c. Thus, for *S. costatum*, although the cellular uptake rate ρ_c decreased from 3.5 to 2.3 μg PN 10^6 CC^{-1} d^{-1} as the temperature increased from 10° to 20°C, the net effect was that ρ_B (3.5–3.8 mg PN liter^{-1} d^{-1}) was virtually independent of temperature.

It is tempting, but perhaps fruitless, to speculate on the role of this temperature-dependent cellular uptake phenomenon (i.e. ρ_c) in influencing species competition at the temperature extremes at which most natural marine populations grow (about 0° and +30°C). It may or may not be coincidental that *S. costatum*, which strongly displays this uptake at lower temperatures, is often found in coastal marine waters during winter (Curl and McLeod 1961; Braarud 1962; Smayda 1973). Malone (1976) in fact found that the assimilation ratio of natural populations in the New York Bight decreased with decreasing temperature down to 8°C, but showed a dramatic rise at lower temperatures when *S. costatum* was dominant.

Two observations appear noteworthy. First, for a given growth rate actual biomass production measured as PN or PC appears to be fairly independent of temperature over a broad range. As seen in Fig. 1, the peak amount of PN produced was similar between 10° and 30°C (5.3–7.2 mg liter^{-1}). The only major effect of temperature seemed to be on individual species growth: *S. costatum* grew well at the lowest temperatures (10°–15°C), *P. tricornutum* in the median range (15°–25°C), and *D. tertiolecta* at the highest temperature (30°C).

Second, we see here a classic example of the uncoupling of cell division and nutrient uptake. For a fixed growth rate, and depending on the species present, cellular uptake rates for both nitrogen and carbon varied widely with temperature. Williams (1971) developed a model to demonstrate that the temperature optima for division and biomass production were not necessarily the same after he found a U-shaped response of the biomass:cell ratio (as dry weight) to temperature changes for the freshwater species *Chlorella*. Our results for *D. tertiolecta* and *P. tricornutum* are identical to those of Williams, and suggest that this type of response to temperature may be characteristic of many algal species. In fact, it is conceivable that the PN:CC ratio of *M. lutheri* and *S. costatum* would have swung back up between 25° and 30°C had the temperature intervals been <5°C, since these two species could not grow at 30°C (Fig. 2). On the other hand, there appears to be a tight coupling between division and nutrient uptake, at least with respect to temperature, for species such as *T. pseudonana* (Fig. 2) and *N. closterium* (Morris and Glover 1974).

In conclusion, the role of temperature in phytoplankton ecology is poorly understood. Much emphasis is being placed on nutrient uptake and internal pool models (Droop 1973; Dugdale 1977). In light of the present findings, it appears that the usefulness of these models will be severely limited until the opposing temperature effects on cell division and nutrient uptake are accounted for. Because it is now evident that there are widely divergent and species-dependent responses to temperature, generalized use of such models, even with temperature functions included, may have limited predictive value. The simple insertion of a temperature factor into growth rate equations, as was done by Eppley (1972) and Goldman and Carpenter (1974), is obviously not sufficient.

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Submitted: 26 July 1976
Accepted: 14 February 1977