TEMPERATURE AND PHYTOPLANKTON GROWTH IN THE SEA

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ABSTRACT

The variation in growth rate with temperature of unicellular algae suggests that an equation can be written to describe the maximum expected growth rate for temperatures less than 40°C. Measured rates of phytoplankton growth in the sea and in lakes are reviewed and compared with maximum expected rates. The assimilation number (i.e., rate of photosynthetic carbon assimilation per weight of chlorophyll *a*) for phytoplankton photosynthesis is related to the growth rate and the carbon/chlorophyll *a* ratio in the phytoplankton. Since maximum expected growth rate can be estimated from temperature, the maximum expected assimilation number can also be estimated if the carbon/chlorophyll *a* ratio in the phytoplankton crop is known.

Many investigations of phytoplankton photosynthesis in the ocean have included measures of the assimilation number, while fewer data are available on growth rate. Assimilation numbers for Antarctic seas are low as would be expected from the low ambient temperatures. Tropical seas and temperate waters in summer often show low assimilation numbers as a result of low ambient nutrient concentrations. However, coastal estuaries with rapid nutrient regeneration processes show seasonal variations in the assimilation number with temperature which agree well with expectation.

The variation in maximum expected growth rate with temperature seems a logical starting point for modeling phytoplankton growth and photosynthesis in the sea.

Temperature does not seem to be very important in the production of phytoplankton in the sea. For example, Steemann Nielsen (1960) has written, "Recent investigations have shown, however, that the direct influence of temperature on organic production in the sea is fairly insignificant." Other reviewers of photosynthesis in the sea likewise give little or no consideration to a role of temperature and Steemann Nielsen's statements find widespread endorsement in the published data on geographic and seasonal variation in marine phytoplankton photosynthesis.

In response to this, the reader may ask at least two questions: (1) Why is temperature of so little importance and (2) why would anybody write a review on temperature and phytoplankton growth in the oceans? Several answers to the first question have appeared in the literature and some of these will be discussed in this account. I have two answers for the second question. The purpose of this review is (1) to suggest maximum growth and photosynthetic rates which might be reasonably expected for natural marine phytoplankton and (2) to point out the interrelationship among growth rate, photosynthetic assimilation number (i.e., rate/chlorophyll), and carbon/chlorophyll *a* ratios in the phytoplankton.

What follows is an attempt to show that temperature sets an upper limit on phytoplankton growth rate and on the rate of photosynthesis per weight of chlorophyll, and that this upper limit can be predicted from a knowledge of temperature and the carbon and chlorophyll content of the plants.

It can perhaps be inferred, from above, that phytoplankton growth in the oceans seldom approaches the upper limits imposed by the temperature of the water and that temperature does not figure prominently in simulation models for primary production in the marine environment. Other factors effect reduced rates of growth and

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photosynthesis and diminish the potential production of phytoplankton. Nevertheless, earlier reviewers have been able to generalize on several aspects of the relation between phytoplankton growth and temperature (see especially Talling, 1957; Steemann Nielsen, 1960; Ichimura and Aruga, 1964; Yentsch and Lee, 1966; Ichimura, 1968). Culture experiments have revealed that clones of a species isolated from cold or warm seas may differ in their optimum temperature for growth (Braarud, 1961; Hulburt and Guillard, 1968).

VARIATION IN SPECIFIC GROWTH RATE (μ) WITH TEMPERATURE IN LABORATORY CULTURES OF UNICELLULAR ALGAE

Much of the available data on the specific growth rates of algae in culture have been assembled by Hoogenhout and Amesz (1965). Growth rates for marine phytoplankton fall in the same range of values as those for freshwater algae, and there are no obvious distinctions between marine and freshwater unicellular algae with respect to the variation of specific growth rate (μ) with temperature. Hence data for algae from the two media will not be segregated.

Specific growth rate is defined as the rate of increase of cell substance per unit cell substance $1/N\ dN/dt = \mu$. Since dN/dt depends upon the rate of metabolic processes, one expects some temperature variation of μ if conditions are otherwise favorable for growth (i.e., if light and nutrient supply are not growth-rate limiting). This variation can be seen in Figure 1. Data of Figure 1 were selected from Hoogenhout and Amesz (1965) as representing, as nearly as possible, growth rates measured under conditions such that temperature would be rate limiting. Figure 1 shows much variation in μ among species at a given temperature. Most of this results from differences in cell size (Williams, 1964; Eppley and Sloan, 1966; Werner, 1970) and in the concentration of photosynthetic pigments within the cells of the different species (Eppley and Sloan, 1966).

It has been mechanically impossible to identify each of the points on the Figure by species (approximately 130 species or clones were included, some for several temperatures). No doubt, by further literature search, the entire area beneath the line of maximum expected growth rate could be filled in. It is perhaps surprising and a tribute to the quality of the measurements from many laboratories that only three of nearly 200 values were rejected as being unrealistically high. Inclusion of these three spurious values would only be an embarrassment to the authors rather than a critique of the validity of the line of maximum expected growth rate presented.

Not plotted in Figure 1 are values of μ for *Chlamydomonas mundana* photoassimilating acetate (Eppley and Macias R., 1962), *Chlorella pyrenoidosa* 7-11-05 for which μ was computed for increase in cell substance uncoupled from cell division (Sorokin and Krauss, 1962), or for the photosynthetic bacteria listed by Hoogenhout and Amesz (1965). Values for these slightly exceed the line of maximum expected μ. Figure 1 is limited to algae growing photoautotrophically with carbon dioxide and water.

Two general trends are noted in Figure 1: (1) There is a gradual and exponential increase in μ with temperature up to about 40°C. Temperature data above 40°C, obtained with thermophilic, blue-green algae show no further increase in μ (Castenholz, 1969). Such temperatures are outside the range encountered in the ocean and will not be further discussed. (2) Values of μ below 40°C seem to fall within an envelope and it is possible to draw a smooth curve, i.e., a line of maximum expected value, to describe the upper limit of μ to be expected at a given temperature. An approximate equation for this line is:

$$\log_{10} \mu = 0.0275T - 0.070 \qquad (1)$$

where T is temperature in degrees Celsius.

Equation (1) gives a Q_{10} for growth rate of 1.88, slightly lower than expected from the Q_{10} for photosynthesis measured in natural waters (Talling, 1955, gives $Q_{10} = 2.3$; Williams and Murdoch, 1966, give $Q_{10} = 2.25$; Ichimura, 1968, gives $Q_{10} = 2.1$) or the Q_{10} for growth rate of laboratory cultures suggested earlier (Eppley and Sloan, 1966, give $Q_{10} = 2.3$).

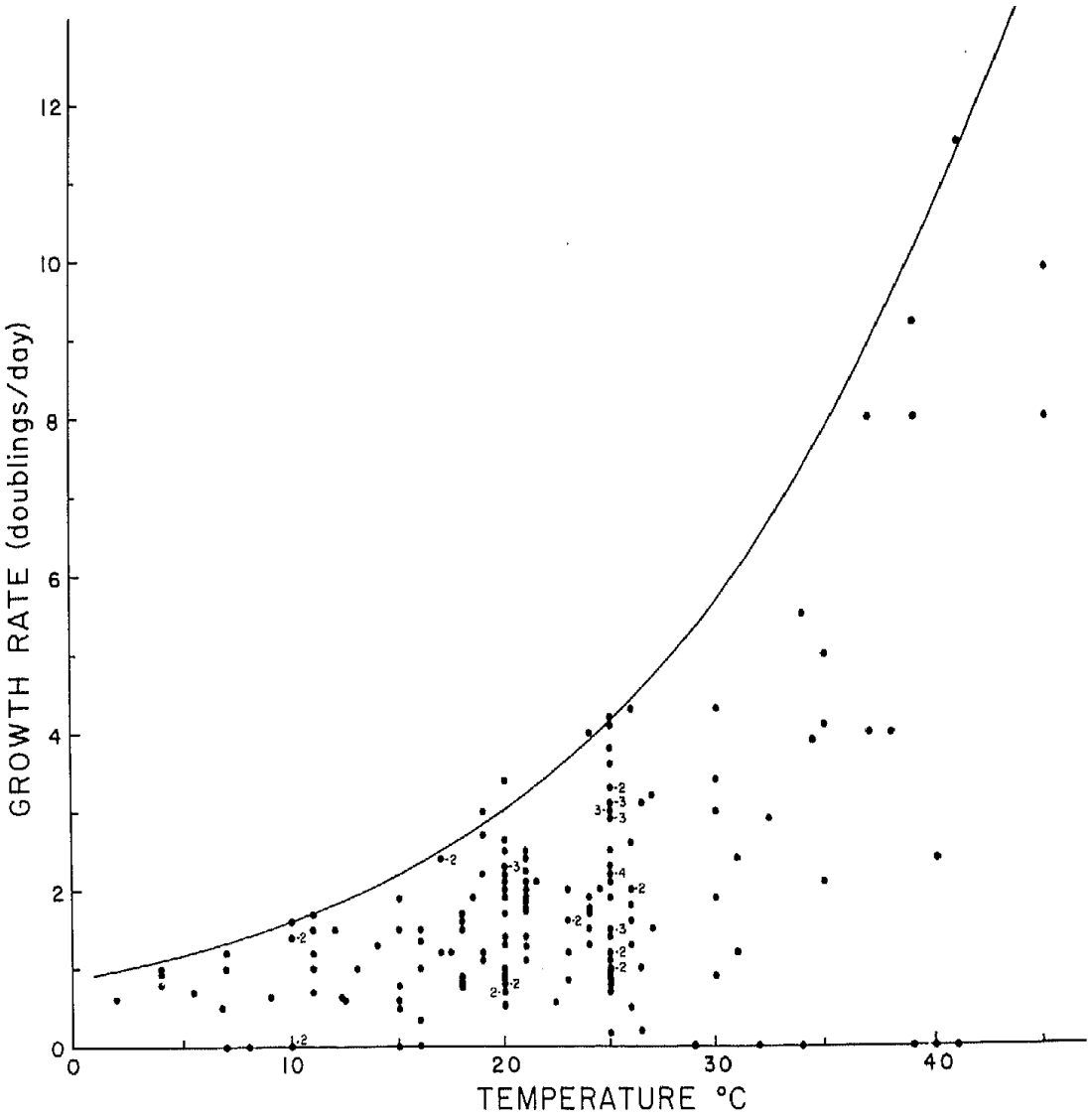

FIGURE 1.—Variation in the specific growth rate (μ) of photoautotrophic unicellular algae with temperature. Data are all for laboratory cultures. Growth rate is expressed in doublings/day. Approximately 80 of the points are from the compilation of Hoogenhout and Amesz (1965). That listing is restricted to maximum growth rates observed, largely in continuous light. The figure also includes additional data, mostly for cultures of marine phytoplankton, from the following sources: Lanskaya (1961), Eppley (1963), Castenholz (1964, 1969), Eppley and Sloan (1966), Swift and Taylor (1966), Thomas (1966), Paasche (1967, 1968), Hulburt and Guillard (1968), Jørgensen (1968), Smayda (1969), Bunt and Lee (1970), Guillard and Myklestad (1970), Ignatiades and Smayda (1970), Polikarpov and Tokareva (1970). The latter papers include about 50 strains of marine phytoplankton. The line is the growth rate predicted by Equation (1), i.e., the line of maximum expected μ. Small numbers by points indicate the number of values which fell on the point.

I will avoid speculation on possible reasons why such a curve would include algae from a wide variety of taxonomic groups, including both eucaryotic and procaryotic cell types, cells with different complements of photosynthetic pigments, and diverse morphologies. Nevertheless, the curve and Equation (1) appear to be useful as a generalization of maximum μ to be expected for photosynthetic unicellular algae.

Equation (1) is essentially a van't Hoff formula and can be expressed in the more typical form

$$\mu = 0.851\ (1.066)^T. \qquad (1a)$$

McLaren (1963) discussed the choice of a temperature function and preferred the formula of Bělehrádek

$$\mu = a\ (T - \alpha)^b \qquad (1b)$$

where a, b, and α are constants. A virtue of this equation, among the three monotonic functions discussed by McLaren (1963) is that α, the scale positioning factor, represents a "biological zero" for the process. A graph of log (μ) vs. log ($T - \alpha$) assumes linearity for appropriate values of α. Fitting values from Equation (1) at T = 0, 10, 20, and 30 degrees gave linear graphs if α were $\leqslant$ —40 degrees. For α = —40, a and b were approximately 2.46 $\times$ 10^{-6} and 3.45, respectively.

Figure 1 can be made more understandable by comparing μ vs. temperature curves for a few selected species for which fairly complete data are available (Figure 2). Each of these species has a different optimum temperature and the maximum growth rate for each approaches the line of maximum expectation. Such "μ vs. temperature" curves typically show a gradual diminution of μ as temperature decreases from the optimum, but an abrupt decline at supraoptimal temperatures.

Temperature optima and the upper critical temperature can be shifted somewhat by altering environmental conditions. For example, the salinity of the culture medium influences these parameters in euryhaline *Dunaliella tertiolecta* (Figure 3). Note, however, that only one salt concentration gives the unique maximum growth rate of about 5.0 doublings/day.

The figures can be criticized as being limited with respect to the number of species included. Furthermore many of them represent "laboratory weed" species and relatively few are ecologically significant ocean phytoplankton. Happily this shortcoming is temporary and information on important planktonic species is growing (see Figure 1 legend).

Use of Figures 1 and 2 or Equation (1) for insight as to maximum expected values of μ in the sea presumes that natural marine phytoplankton are autotrophic. But it is conceivable,

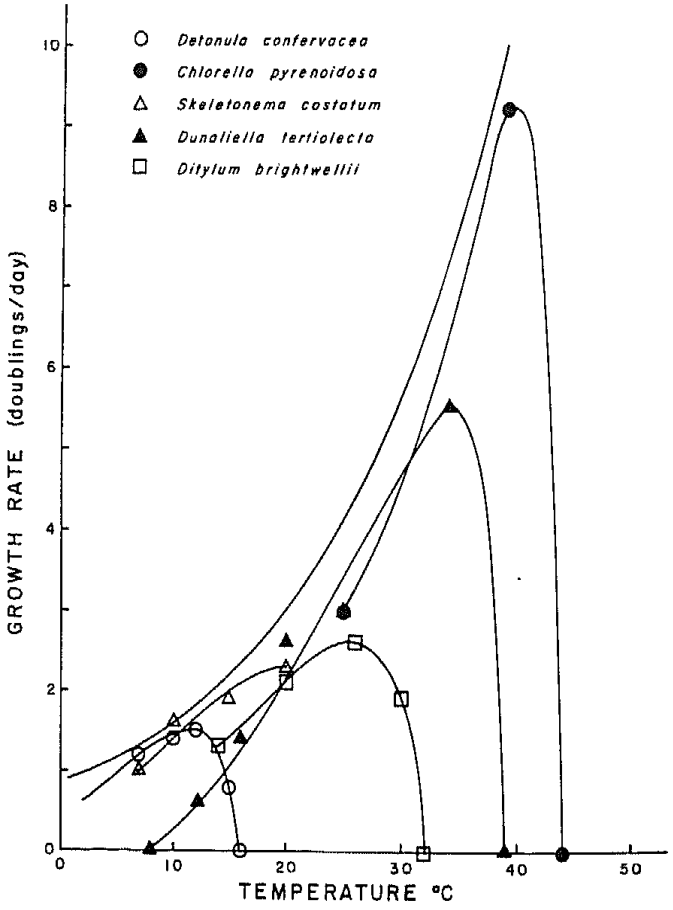

FIGURE 2.—Growth rate vs. temperature curves for five unicellular algae with different temperature optima: *Detonula confervacea* (Guillard and Ryther, 1962; Smayda, 1969), *Skeletonema costatum* (Jørgensen, 1968), *Ditylum brightwellii* (Paasche, 1968), *Dunaliella tertiolecta* (McLachlan, 1960; Ukeles, 1961; Eppley, 1963; Eppley and Sloan, 1966), *Chlorella pyrenoidosa* (Sorokin and Krauss, 1958, 1962).

although perhaps unlikely in the sea, that heterotrophic nutrition might lead to values of μ higher than predicted above, as appears to be the case when one compares doubling times of heterotrophic and photosynthetic bacteria or autotrophic vs. photoheterotrophic growth rates of the sewage alga *Chlamydomonas mundana*.

Equation (1) has been useful in this laboratory for predicting the maximum dilution rates ("washout rates") for continuous cultures. In the few organisms examined here the value of μ at washout was slightly higher than the maximum rate observed in batch cultures of the organism, but within the envelope of values predicted by Equation (1).

Rates of growth given by Equation (1) are much higher than those which permit the operation of mass cultures at maximum efficiency of light utilization or nutrient removal. Maximum production will be achieved when the product of μ and standing stock is a maximum, and light is likely to be limiting growth at some depth in the culture under these conditions (see, for example, Ketchum, Lillick, and Redfield, 1949; Myers and Graham, 1959).

The data of Figures 1 and 2 apply to cultures grown with continuous illumination (or with optimum daylength for those in which μ passes through a maximum at intermediate daylength [Castenholz, 1964; Paasche, 1968]). This lessens the utility of the data for predictive purposes with natural phytoplankton exposed to seasonally varying daylength since the daylength for maximum μ varies among species (Table 1). Efforts to generalize on the influence of daylength on μ have not been very successful since the daylength allowing maximum μ at a given temperature seems to vary with the intensity of illumination (Tamiya et al. 1955; Terborgh and Thimann, 1964). A proportion between μ and the number of hours of light/24 hr is often assumed but this can be only a first approximation.

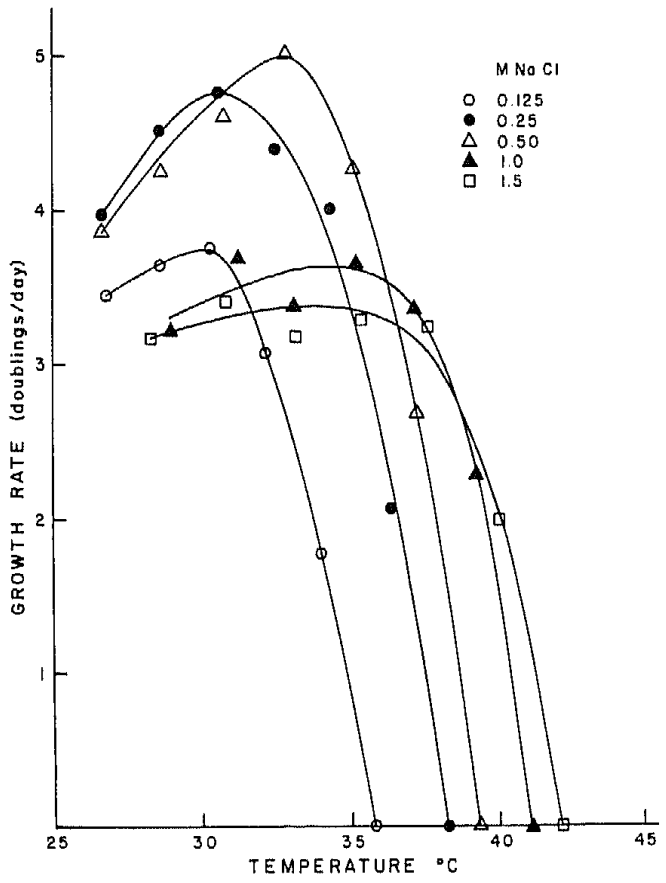

FIGURE 3.—Growth rate vs. temperature curves for *Dunaliella tertiolecta* measured in culture media containing different salt concentrations (R. W. Eppley and F. M. Macias, unpublished data).

TABLE 1.—Daylength resulting in maximum growth rate for some algae which show depressed growth rate in continuous light. Some species which showed maximum μ in 24 hr light/day are shown for comparison.

Organism	Daylength (hr)	Growth rate[1] μ_{max}	Temperature (°C)	Reference
Ditylum brightwellii	16	2.1	20	Paasche (1968)
Nitzschia turgidula	16-24	2.5	20	Paasche (1968)
Fragilaria sp.	24	1.7	11	Castenholz (1964)
Biddulphia sp.	15	1.5	11	Castenholz (1964)
Synedra sp.	15-24	1.2	11	Castenholz (1964)
Melosira sp.	15-24	0.7	11	Castenholz (1964)

[1] Units are doublings/day.

Use of Figure 1 and Equation (1) for insight on the behavior of natural phytoplankton requires the further assumption that the organisms present are reasonably adapted to ambient temperatures and are, preferably, at a temperature somewhat less than optimum. Aruga (1965a) has shown this to be so for the phytoplankton of a pond on the University of Tokyo campus. Smayda (1969) has discussed his own and earlier observations on the distribution of phytoplankton in nature where temperature optima for growth in laboratory cultures were invariably higher by several degrees than the water temperature in which the species flourish.

Figure 2 suggests that μ for suboptimal temperatures will be only slightly lower than would be predicted from the maximum μ for the species given a temperature coefficient (Q_{10}) for growth of about 2. However, some organisms show a critical lower temperature, above the freezing point of water, below which no growth occurs. Ukeles (1961) has listed such lower critical temperatures for several species, and see Smayda (1969) for another example. Temperatures in excess of the optimum for growth result in a much steeper decline in μ with increasing temperature than do suboptimal temperatures; growth in this thermal region would be risky

if the ambient temperature were subject to fluctuations of a few degrees.

ESTIMATES OF THE SPECIFIC GROWTH RATES OF PHYTOPLANKTON IN THE SEA

REVIEW OF METHODS

Measurement of the phytoplankton specific growth rate in nature is not a routine procedure both because of the lack of widely accepted methodology and because the utility of such data is not well appreciated. J.W.G. Lund, J. F. Talling, L. A. Lanskaya, T. J. Smayda, J. D. H. Strickland, and S. Ichimura and his colleagues have been the pioneers in such measurement in natural waters while R. W. Krauss and J. Myers have promoted the measurement of μ for laboratory cultures.

Minimal values of μ can be calculated from rates of increase of cell concentration or of chlorophyll during the spring bloom in temperate waters, although advection, diffusion, and grazing complicate their interpretation. Recent examples of this technique are provided by Bunt and Lee (1970), Pechlaner (1970), and Happey (1970). Samples of water can also be incubated in bottles for cell counting at intervals (see, for example, Talling, 1955; Smayda, 1957). In oligotrophic waters the period of growth necessary to allow a precise estimation is likely to result in the depletion of nutrients and the gradual diminution of μ with time. In rich water if growth were extensive, changes in μ would be expected as a result of the decrease in effective illumination in the bottles due to self-shading. Short-term incubations of less than 24 hr may be complicated by diel periodicity in the property measured, by synchronous cell division, or insufficient change for meaningful calculations. Such problems are eased in shipboard cultures provided with adequate nutrients for growth, but here rates may be unreasonably high if ambient nutrient or light levels in the natural water are not duplicated.

Estimates of μ are obtained routinely in terms of ^{15}N-nitrogen assimilation rate per unit particulate nitrogen in the sample, but such rates will underestimate μ to the extent that the particulate nitrogen analyzed includes detrital and other nonphytoplankton nitrogen (Dugdale and Goering, 1967).

Carbon assimilation rates per unit phytoplankton carbon have also been calculated but suffer from the errors inherent in measuring the latter as well as from the uncertain reality of incubation conditions (Riley, Stommel, and Bumpus, 1949; McAllister, Parsons, and Strickland, 1960; McAllister et al., 1961; Antia et al., 1963; McAllister, Shah, and Strickland, 1964; Strickland, Holm-Hansen, Eppley, and Linn, 1969). What is needed is an instantaneous method not confounded by the complexities of long incubation either in situ, in enclosed vessels, or in shipboard cultures. Unfortunately, no such method is in view.

In this laboratory two methods have been employed for estimating the carbon content of the crop. In the first of these, all the cells in the sample are counted and their dimensions measured so that the cell volume of each species can be calculated (see Kovala and Larrance, 1966, for dealing with cell shape problems). The carbon content of a cell is then computed from its volume, or "plasma volume," using empirical equations developed from laboratory culture (Mullin, Sloan, and Eppley, 1966; Strathmann, 1967). The carbon in each species is then obtained from the concentration of cells of that species, and the total carbon of all species is summed. Several applications of this method have been published (Strickland, Eppley, and Rojas de Mendiola, 1969; Holm-Hansen, 1969; Eppley, Reid, and Strickland, 1970; Reid, Fuglister, and Jordan, 1970; Zeitzschel, 1970; Beers et al., 1971; Hobson, 1971; Eppley et al., in press). In the second method, only recently put into practice, the adenosine triphosphate (ATP) content of particulate matter retained on a fine porosity filter is determined (Holm-Hansen and Booth, 1966). The ATP is apparently restricted to living cells but may include contributions from bacteria, protozoans, and other colorless microorganisms, as well as phytoplankton, even if larger animals are removed by passing the sample through netting. However, phytoplankton appear to be predominant in water samples from

the euphotic zone judged from the rough proportionality of ATP to chlorophyll. Estimates derived from ATP appear to agree well with those given by the first method (Holm-Hansen, 1969) and the ratio C/ATP approximates 250.

In determining an average μ for the phytoplankton the carbon content, as measured above, is taken at the beginning of the photosynthesis measurement to give phytoplankton carbon at time zero (C_0). The measured daily rate of photosynthetic carbon assimilation, assumed to represent net carbon assimilation (ΔC), is then added to the carbon content after a day's growth. The specific growth rate is then calculated as:

$$\mu = \frac{1}{t} \log_2 \left(\frac{C_0 + \Delta C}{C_0}\right) \qquad (2)$$

to give μ in doublings of cell carbon per day.

It should be straightforward to compute μ using ATP determined initially and after 24-hr incubation, and this has been done at least once (Sutcliffe, Sheldon, and Prakash, 1970). We have used chlorophyll *a* values, before and after 24- or 48-hr incubation, to compute μ but the results were poor due to the plasticity of cell chlorophyll *a* content and the difficulty of providing incubation conditions sufficiently close to those in nature to maintain constant cell chlorophyll *a* per cell or per weight of carbon (Eppley, 1968).

Increase in the total volume of particulate matter, determined with an electronic particle counting and sizing machine, can also be used to compute μ (Parsons, 1965; Cushing and Nicholson, 1966; Sheldon and Parsons, 1967). This method holds much promise when changes are large enough to be significant over background levels of particulates. The cost of the machines is a serious drawback to wider use, and the problems in proper incubation of the sample to mimic conditions in the sea are as serious here as in the other incubation methods.

Sweeney and Hastings (1958) used the percentage of paired dinoflagellate cells in cultures as a measure of the time of day of cell division and this has been used at sea (R. Doyle, Duke University, personal communication). A variation on this theme has allowed estimates of μ for *Pyrocystis* species in situ (E. Swift, University of Rhode Island, personal communication). Changes in cell morphology related to cell division probably give the least ambiguous estimates of μ where advection and sinking are not serious problems and when a parcel of water can be followed over time. The time course of change in valve diameter in diatoms seems to be out of favor for estimating μ since valve diameter in cultures may not decrease in a regular way or always be proportional to the number of cell divisions. Methods of measuring microbial growth rates were recently reviewed by Brock (1971).

RESULTS OF GROWTH RATE MEASUREMENTS IN THE NATURAL PHYTOPLANKTON AT DIFFERENT TEMPERATURES

In their classic paper of 1949, Riley, Stommel, and Bumpus expressed photosynthetic rate as the daily carbon assimilation per unit plant carbon, a measure readily calculated as μ in doublings/day. They used Baly's equation as a model. This equation includes temperature as a variable influencing photosynthetic rate. The constants in the equation were computed from Baly's compilation of data on *Chlorella* cultures and detached leaves, and from Jenkin's 1937 data for a culture of *Coscinodiscus* incubated at various depths in the sea. I have calculated expected values of μ using their Equation 6 for different levels of total incident radiation (Figure 4). It is seen that the Baly equation is relatively insensitive to temperature, in comparison to Figure 1, and gives values inconsistent with the results from laboratory cultures.

Bunt and Lee (1970) provide a unique set of data on the photosynthetic rates of Antarctic phytoplankton which grow under the ice layer, an environment with low ambient light and with temperature approximately —2°C. They also provide seasonal values of the particulate carbon and chlorophyll *a* concentration. A maximum, midsummer, value of μ was less than 0.5 doublings of cell carbon/day.

Most of the data which allow estimates of μ are from nutrient-poor waters, such as are found

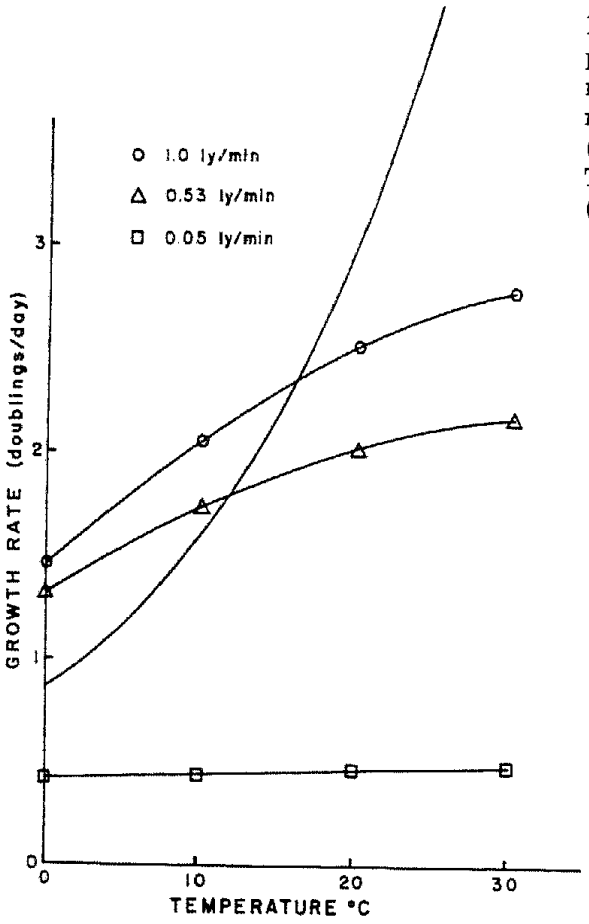

FIGURE 4.—Growth rate vs. temperature relationship predicted by the Baly equation as used by Riley, Stommel, and Bumpus (1949). Three different levels of total radiant energy are included for the Baly equation: 1.0 (circles), 0.53 (triangles), and 0.05 ly/min (squares). The line of maximum expectation predicted by Equation (1) is drawn for comparison (no symbols).

in the Sargasso Sea, the Eastern Tropical Pacific, and southern California coastal waters. Exceptions are μ estimates obtained from upwelling regions off Peru (Strickland, Eppley, and Rojas de Mendiola, 1969; Beers et al., 1971) and southwest Africa (Hobson, 1971) where nutrient limitation is not a factor reducing μ.

A summary of estimated values of μ, as average doublings of cell carbon/day in the euphotic zone, is provided in Table 2. The recent data are based upon simulated in situ techniques usually involving 24-hr incubation in order to obtain photosynthetic rates free of errors resulting from diel periodicity in metabolism. The list of values given is not inclusive but is, hopefully, representative. Mean values of μ in the Peru Current showed little variation and averaged about 0.7 doubling/day. Values of this magnitude are consistent also with estimates from ^{15}N-labeled nitrate assimilation rates measured by R. C. Dugdale, J. J. Goering, and

TABLE 2.—Some estimates of the average specific growth rate of phytoplankton in the euphotic zone for various regions. Temperatures indicated are for the surface or the average in the mixed layer.

Location	Temperature (°C)	Growth rate as doublings/day		Reference
		Measured	Max. expected	
Oligotrophic waters				
Sargasso Sea	--	0.26	--	Riley, Stommel, and Bumpus (1949)
Florida Strait	--	0.45	--	Riley, Stommel, and Bumpus (1949)
Off the Carolinas	--	0.37	--	Riley, Stommel, and Bumpus (1949)
Off Montauk Pt.	--	0.35	--	Riley, Stommel, and Bumpus (1949)
Off southern California				
July 1970	20	0.25-0.4	1.5	Eppley et al. (in press)
Apr.-Sept. 1967	12-21	0.7 avg	0.9-1.6	Eppley et al. (1970)
Nutrient-rich waters				
Peru Current				
Apr. 1966	17-20	0.67 avg	1.5	Strickland, Eppley, and Rojas de Mendiola (1969)
June 1969	18-19	0.73 avg	1.4	Beers et al. (1971)
Off S.W. Africa	--	1.0 avg	--	Calculated from Hobson (1971)
Western Arabian Sea	27-28	>1.0 avg	2.4	Calculated from Ryther and Menzel (1965b)

[1] From Equation (1) assuming μ will be one-half the value calculated as expected if daylength is 12 hr and μ is directly proportional to the number of hours of light per day.

co-workers (University of Washington, 1970) in the Peru upwelling region.

The maximum values of μ observed in depth profiles off Peru approached those expected from Figure 1 if the effect of daylength is considered (Figure 5) but were lower as a result of low insolation brought about by continuous cloud cover. Depth profiles of μ roughly parallel those for photosynthetic rate per weight of chlorophyll *a* and both show diminished rates with depth as a result of decreasing light.

Figure 5 also shows a depth profile of μ for the North Central Pacific where μ was depressed because of low ambient nutrient concentrations. Enrichment experiments suggested that growth rate was limited at two stations by low concentrations of both nitrogen and phosphorus and at a third station by nitrogen alone (Perry, in press).

Thomas (1970b) and Thomas and Owen (1971) reported values of μ for 10 m depths in the eastern tropical Pacific Ocean. In situ μ was estimated to be about 0.2 doubling/day resulting from low ambient nitrogen concentration. Shipboard cultures were enriched with various concentrations of nitrogen (nitrate and ammonium), and the variation of μ with nitrogen concentration was determined (Thomas, 1970b). Maximum values of μ were 1.1-1.5 doublings/day.

In many cases nutrient limitation (in the upper surface waters) or light limitation (in deeper waters and in nonstratified water where vertical mixing may reduce the effective light level to which the phytoplankton are exposed) appears to decrease μ. The values expected from Figure 1 are not realized under such conditions and μ shows little or no temperature-dependence.

Table 3 presents growth rates measured by three different methods (i.e., from the velocity of nitrogen assimilation per unit particulate nitrogen, from the photosynthetic carbon assimilation rate per unit phytoplankton carbon, where the carbon content of the phytoplankton crop was determined from ATP, and from cell concentration and cell volume). Growth rates from the three methods usually agree within a factor of two, but more precise methods are desirable. The value from ^{15}N assimilation rate

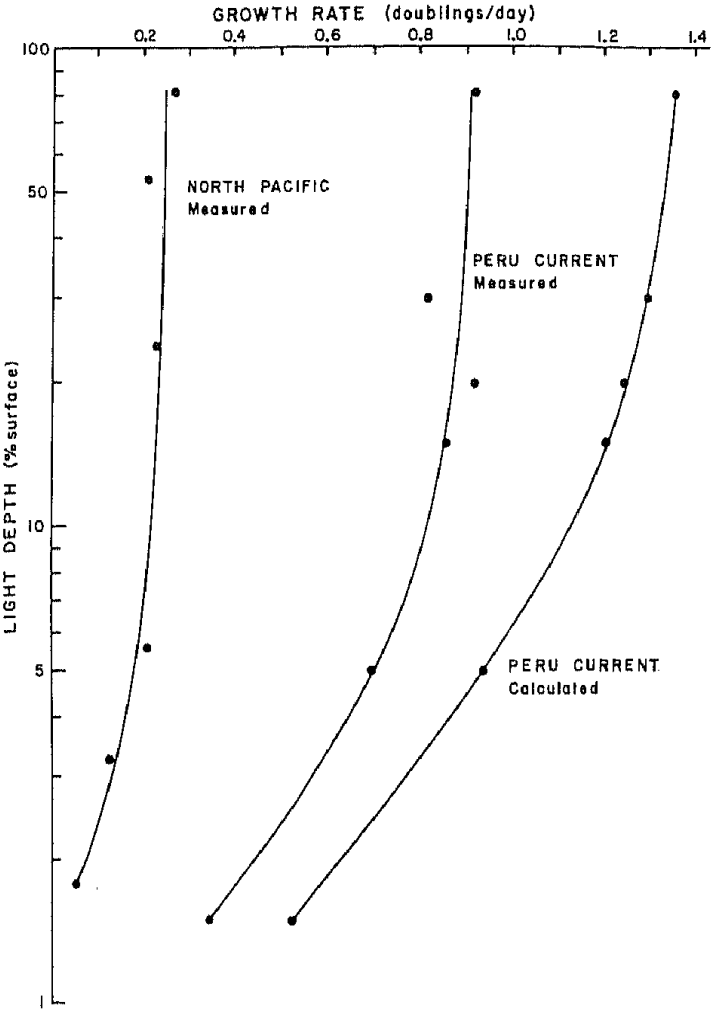

FIGURE 5.—Variation in growth rate of natural marine phytoplankton with depth in the Peru Current, June 1969, and in the subtropical North Pacific central gyre, November 1971 (this laboratory, unpublished). The "light depth" of the ordinate was calculated as the radiant energy at depth as a percentage of that at the surface so that data from the two regions, with euphotic zone depths of about 30 and about 150 m, could be compared. The calculated line is based on Equation (1) for 19°C with the assumption that light limits growth rate below the surface. The μ_{max} from Equation (1) was multiplied by $(I/2.5 + I)$ where I is the radiant energy at depth as percent of surface. The half-saturation constant of 2.5% is low (see Rodhe, 1965) and suggests that the Peru Current phytoplankton were "shade adapted." Hence, measured μ would be less than expected from Equation (1), in spite of abundant nutrients. In the North Pacific study enrichment experiments and other data suggested limitation of phytoplankton growth rate by both nitrogen and phosphorus concentration (Perry, Renger, Eppley, and Venrick, unpublished data). There the temperature in the mixed layer was 22°C and the maximum expected value would be slightly greater than shown for the Peru Current.

TABLE 3.—Some comparison of the average growth rate of phytoplankton in the euphotic zone in southern California coastal waters using different methods of estimation.

Month	Station	Photosynthetic rate (g C/m²/day)	Standing stock (g C/m²)		Growth rate (doubling/day) by method[1]		
			From ATP	From cell vol.	(a)	(b)	(c)
June 1970	4	0.53	2.4	2.0	0.28	0.33	0.13
	7	1.05	3.1	3.25	0.42	0.40	--
July 1970	1	1.37	8.4	--	0.26	--	0.19
	6	1.10	4.4	--	0.32	--	0.22
	10	0.36	3.6	--	0.13	--	0.21
	19	1.76	5.9	5.38	0.37	0.40	0.15

[1] Methods: (a) μ from photosynthetic rate and ATP × 250 = standing stock as carbon.
(b) μ from photosynthetic rate and standing stock carbon computed from cell numbers and cell volumes.
(c) μ computed from assimilation rate of nitrate + ammonium + urea per unit particulate nitrogen. Data for method (c) from McCarthy (1971) and Institute of Marine Resources (1972, see text footnote 2). Other data are unpublished values from this laboratory. Surface water temperatures were 18°-20°C. Maximum expected growth rates would be about 1.5 doublings/day.

tends to be lower than those from ^{14}C assimilation rate because no correction was made for the detrital nitrogen in the particulate matter, while detrital carbon is not a complication in the other methods. Low growth rates in these samples resulted from nitrogen limitation.

Rates of nitrogen assimilation per weight of particulate N were measured in the Sargasso Sea and Peru upwelling regions (Dugdale and Goering, 1967; Dugdale and MacIsaac, 1971), and in the eastern tropical Pacific Ocean (Goering, Wallen, and Nauman, 1970) which allow estimates of μ.

As is readily seen from the above discussion and the values of Tables 2 and 3 we have very little data at hand to properly evaluate the role of temperature in determining maximum rates of phytoplankton growth in the sea, and whether Figures 1 and 2 and Equation (1) are useful guides for field work. It is hoped that this lack will stimulate more effort to make growth rate measurements. Most needed are μ values for cold waters and warm, nutrient-rich waters.

Meantime let us turn to lakes and ponds. Additional growth rate data are available and the influence of temperature on growth rate is often apparent. Since growth rates seem comparable in laboratory cultures for freshwater and marine unicellular algae, as noted earlier, μ vs. temperature in lakes should be of equal interest to limnology and oceanography. Some data are given in Table 4 which confirm low μ values in cold water and a variation in μ with temperature in outdoor ponds.

The phytoplankton growth rates in lakes which show a variation in μ with temperature were usually measured in the spring as the waters were gradually warming but before nutrients were depleted to levels limiting to the rate of phytoplankton growth (cf. Cannon, Lund, and Sieminska, 1961). Presumably similar data could be gathered for nutrient-rich estuaries or for temperate, coastal sea areas where sufficient warming occurs to obtain a reasonable range of temperatures before stratification and nutrient depletion become severe. The seasonal succession of phytoplankton in coastal ocean waters has been much studied, and the change in the phytoplankton crop from predominantly diatoms to flagellates, with the onset of nutrient depletion, would be accompanied by a marked decrease in growth rate. One may judge the magnitude of change from the comparison of μ in the Peru Current with μ in the North Pacific central gyre (Figure 5).

INTERRELATION BETWEEN SPECIFIC GROWTH RATE OF PHYTOPLANKTON AND ASSIMILATION NUMBER

The specific growth rate of phytoplankton in laboratory cultures is often measured from the rate of increase in the concentration of cells in the culture when cell counts are determined over a time interval, i.e.,

$$\mu = \frac{1}{\Delta t} \log_2 \left(\frac{N_2}{N_1}\right). \qquad (3)$$

This can also be expressed as

$$\mu = \frac{1}{\Delta t} \log_2 \left(\frac{N_1 + \Delta N}{N_1}\right) \qquad (4)$$

where N_1 is the initial cell concentration, N_2 the cell concentration after an interval of time, Δt, and ΔN is $N_2 - N_1$. To determine μ from analogous carbon units one needs the initial carbon content of the phytoplankton (C_1) and either the carbon content after a time interval Δt, i.e., C_2, or a measure of carbon assimilation by the phytoplankton during the time interval, i.e., ΔC. It will be assumed that the ^{14}C method of measuring phytoplankton photosynthesis (Steemann Nielsen, 1952) in fact measures ΔC, the net increase in particulate carbon in the phytoplankton. This is indicated by several studies with laboratory cultures which include two or more independent measures of the rate of carbon assimilation by the phytoplankton cells (Antia et al., 1963; McAllister et al., 1964; Eppley and Sloan, 1965; Ryther and Menzel, 1965a; Strickland, Holm-Hansen, Eppley, and Linn, 1969). Then μ can be calculated from carbon data from Equation (2). The evaluation of μ requires a measurement of photosynthetic rate as carbon and an estimate of the carbon content of the phytoplankton at the initiation of the measurement. Direct methods for the latter are not usually suitable because of detrital carbon in natural waters and indirect methods must often serve (see earlier discussion of methods of measuring μ). A convenient way of expressing photosynthetic rate per unit phytoplankton standing stock is the "assimilation number," i.e., the rate of photosynthetic carbon assimilation per weight of chlorophyll *a*. The terms "assimilation ratio" and "photosynthetic index" are common synonyms for assimilation number. If the carbon/chlorophyll *a* ratio in the phytoplankton is known, its carbon content can, of course, be calculated from chlorophyll measurements. Usually this is not the case and considerable effort has been expended to derive such estimates (see, for example, Harris and Riley, 1956; Cushing, 1958; Wright, 1959; Steele and Baird, 1961, 1962; Lorenzen, 1968; Eppley, 1968; Zeitzschel, 1970; Hobson, 1971). An equation expressing μ (as doublings of cell carbon/day) in terms of the assimilation number per day and the carbon/chlorophyll ration of the phytoplankton can be derived from Equation (2) as

$$\mu = \frac{1}{\Delta t} \log_2 \left(\frac{\text{C/Chl. } a + \Delta\text{C/Chl. } a}{\text{C/Chl. } a}\right). \qquad (5)$$

This equation is useful in that it directly relates the assimilation number, i.e., the photosynthetic rate per weight of chlorophyll (ΔC/Chl. *a*), the carbon/chlorophyll *a* ratio of the phytoplankton

TABLE 4.—Phytoplankton growth rates in lakes and ponds.

Organism	Temperature (°C)	Growth rate as doublings/day		Reference
		Measured	Max. expected[1]	
		1-m depth only		
Asterionella formosa	5	0.8	1.2	Talling (1955)
		Average in the lake		
Stephanodiscus hantzschii	2-4	0.3	1.1	Pechlaner (1970)
Asterionella formosa	5	0.3	1.2	Happey (1970)
Stephanodiscus rotula	8	0.25	1.4	Happey (1970)
	15	0.7	2.2	Happey (1970)
		In outdoor ponds		
Chlorella ellipsoidea	7	0.15	1.3	Tamiya et al. (1955)
	15	0.65	2.2	
	25	1.4	4.1	

[1] From Equation (1).

(C/Chl. a), and μ. Figures 6 and 7 show this relationship graphically where the calculated assimilation number per day (Figure 6) or per hour (Figure 7) is graphed as a function of μ for different carbon/chlorophyll a ratios in the crop. Carbon/chlorophyll ratios of Figures 6 and 7 are typical of the Peru upwelling region (C/Chl. a 30-40) (Lorenzen, 1968; Strickland, Eppley, and Rojas de Mendiola, 1969; Beers et al., 1971) and the Western Arabian Sea (Ryther and Menzel, 1965b), or low-nutrient surface waters off southern California (90-100) (Eppley, 1968; Strickland, 1970); and of surface waters in the North Pacific central gyre (120-150) (Institute of Marine Resources, unpublished data). The marked dependence of the assimilation number upon the carbon/chlorophyll a ratio of the phytoplankton is noteworthy, although little discussed in the literature. It is interesting that assimilation numbers greater than about 15 per hour (see Figure 7) are rarely reported in the literature and one wonders whether this is because of disbelief in the validity of the data or because high μ and high C/Chl. a are somehow mutually exclusive in nature. The latter is most likely since such high assimilation rates and high μ would place extreme demands for nutrients, such as N and P, on the environment and could not long be sustained without massive nutrient input. Even at southern California sewage outfalls where high rates of nutrient input prevail we found low values for μ. These low values apparently result from the buildup of high phytoplankton crops which maintain low-nutrient levels in the surface waters such that growth rate is nitrogen-limited (Institute of Marine Resources).[2] Furthermore, high C/Chl. a ratios seem to be typical of nutrient depleted cells which grow slowly. For example, carbon/chlorophyll a ratios increased from 30 to over 150 with increasing nitrogen limitation of growth in N-limited chemostat cultures of marine phytoplankton (Thomas and Dodson, in press; Institute of Marine Resources[2]).

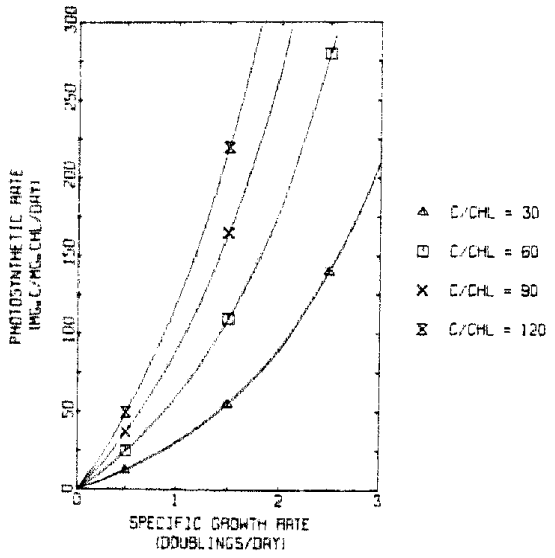

FIGURE 6.—Photosynthetic rate (assimilation number/day) vs. the specific growth rate of the phytoplankton computed from Equation (5). Photosynthetic rate is expressed as milligrams carbon assimilated per day per milligram chlorophyll a and is shown for several values of the ratio carbon/chlorophyll a in the phytoplankton crop (30, 60, 90, and 120 g/g).

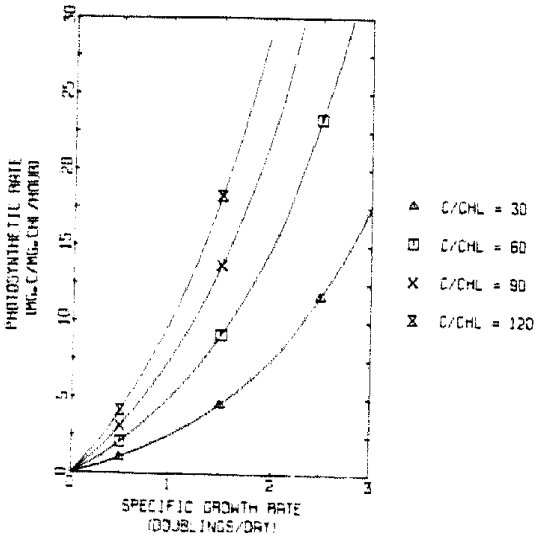

FIGURE 7.—Same as Figure 6, but photosynthetic rates (assimilation numbers) were calculated per hour, rather than per day, assuming 12 hr light per day (i.e., values of Figure 6 were divided by 12).

[2] Institute of Marine Resources. 1972. Eutrophication in coastal waters: nitrogen as a controlling factor. Final Rep. U.S. Environ. Prot. Agency, Proj. #16010 EHC. Inst. Mar. Resour., Univ. Calif., San Diego. 67 p.

THE VARIATION OF ASSIMILATION NUMBER WITH TEMPERATURE IN THE SEA

The maximum expected values of μ at different temperatures, from Equation (1), can be used to predict maximum assimilation numbers to be expected in the sea (as grams carbon/gram chlorophyll *a* per time). Combining Equations (1) and (5) gives rise to Figures 8 and 9 to show assimilation numbers per day and per hour for different C/Chl. *a* ratios in the phytoplankton. Actual rates would be lower than those shown for the reasons already discussed and would require the growth of small-celled phytoplankters with light essentially saturating for photosynthesis and with adequate nutrient concentrations. Aruga (1965b) presents graphs of assimilation numbers vs. temperature, with various light levels, for *Scenedesmus* sp. grown at 20°C. His curves resemble these in form.

The question of the influence of daylength upon μ is ignored in Figure 8 and needs further investigation before generalities may be drawn. In Figure 9 it was assumed that μ in natural phytoplankton assemblages will be one-half the value calculated from Equation (1) since that function assumes continuous light rather than natural illumination of, on the average, 12 hr light and 12 hr dark.

There are several reasons why the dramatic potential effects of temperature on assimilation number are not often observed in oceanic studies and why so little variation in assimilation numbers has been observed (cf. Ryther and Yentsch, 1958; Curl and Small, 1965). One of these is that growth at different temperatures results in shifts in the chemical composition of phytoplankton. Increased C/Chl. *a* ratios at low temperature would tend to increase assimilation numbers in cold waters over those predicted by Figures 8 and 9 and a constant C/Chl. *a* ratio cannot be assumed.

Steemann Nielsen and Jørgensen (1968a, b) point out that while the lowering of the temperature of a culture of *Skeletonema costatum* reduced the growth rate (by an amount to be expected from Figure 1 and Equation (1)), the

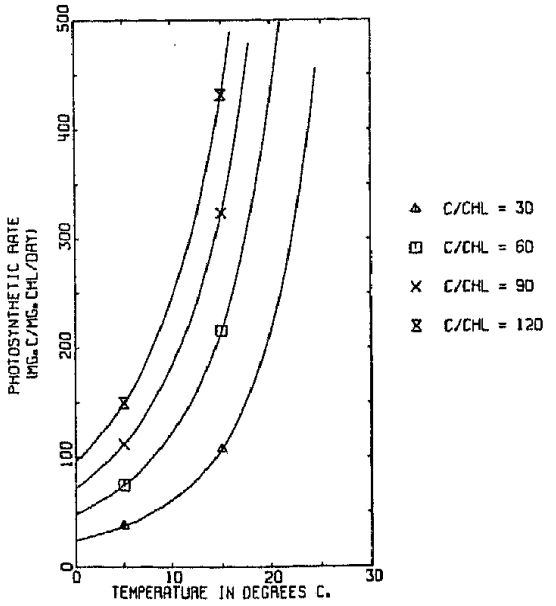

FIGURE 8.—The variation in maximum expected rate of photosynthesis (assimilation number) with temperature. Rates were computed by combining Equations (1) and (5) and are expressed as milligrams carbon/milligram chlorophyll *a*/day. Continuous light was assumed.

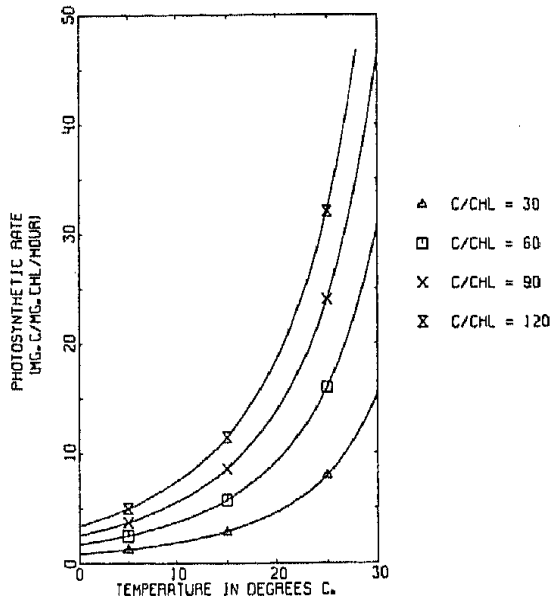

FIGURE 9.—Maximum expected photosynthetic rate (assimilation number) from Equations (1) and (5) with the assumption that the growth rate will be one-half the value predicted by Equation (1) to adjust for natural daylength averaging 12 hr light/day. Photosynthetic rates are expressed as milligrams carbon assimilated/milligram chlorophylll *a*/hour. This figure gives values more in line with ocean measurements than does Figure 8.

photosynthetic rate at light saturation was decreased by a lesser amount. Assimilation numbers for *S. costatum* at 2° or 8°C were higher than would be expected from Figure 9, if it were assumed that a constant C/Chl. *a* ratio was maintained at all temperatures. They observed that cells at low temperature contained greater amounts of photosynthetic enzymes and of organic matter than at higher temperatures. For example, *S. costatum* assimilated 10.2 picogram (pg) carbon/cell in one generation at 20°C, but 19.5 pg at 7°C (Jørgensen, 1968). The carbon content of a cell nearly doubled between 20° and 7°C. *Dunaliella tertiolecta* cells were likewise larger at low temperature than at high temperatures as were cells of *Ditylum brightwellii* (Table 5). This phenomenon seems to be general for mesothermal marine phytoplankton, but data for cold water species are not available. Fluctuations in C/cell and in the C/Chl. *a* are about twofold over the 10°-15°C range studied (Table 5). Steele and Baird (1962) reported high C/Chl. *a* ratios in winter in Loch Nevis and suggested that they resulted from low light "etiolation." One wonders if low winter temperatures might also play a role in this.

We have seen that low temperature reduces the assimilation number and promotes increased carbon/chlorophyll *a* ratios. Similar effects result from nutrient deficiency and were well documented by McAllister, et al. (1964). An influence of nutrient deficiency on μ was shown also in Figure 5 for the North Pacific and was noted in the eastern tropical Pacific (Thomas, 1970b). Low assimilation numbers for phytoplankton photosynthesis in nutrient-impoverished waters are well known (Curl and Small, 1965) and are clearly shown by Ichimura (1967; see his graph of assimilation number vs. phosphate concentration in the waters of Tokyo Bay). Caperon, Cattell, and Krasnick (1971) reported 10 year increases in assimilation numbers in Kaneohe Bay, Oahu, Hawaii (from approximately 6-8 to 11-13 between 1960 and 1970) which attended increased rates of waste discharge into the bay. Hepher (1962) found assimilation numbers of about 4 in unfertilized fish ponds while values in fertilized ponds averaged about 7.6. Furthermore, there are many examples of enhanced ^{14}C-assimilation rates in shipboard enrichment experiments in response to nutrient additions. A recent report is that

TABLE 5.—Carbon content of a cell and carbon/chlorophyll *a* ratios in phytoplankton cultured at different temperatures.

Organism	Carbon/cell	C/Chl./*a*	Temperature	Reference
Skeletonema costatum	19.5	--	7	Jørgensen (1968)
	16.5	--	10	Jørgensen (1968)
	12.7	--	15	Jørgensen (1968)
	10.2	--	20	Jørgensen (1968)
Ditylum brightwellii[1]	1600	41	5	Checkley (1972)[2]
	1500	48	7.5	Checkley (1972)[2]
	1330	50	10	Checkley (1972)[2]
	720	25	15	Checkley (1972)[2]
	--	20	14.5	Strickland, Holm-Hansen, Eppley, and Linn (1969)
	680	14	20	Eppley, Holmes, and Paasche (1967)
Dunaliella tertiolecta[3]	41.8	38	12	Eppley and Sloan (1966)
	35.6	29	16	Eppley and Sloan (1966)
	25.9	25	19.5	Eppley and Sloan (1966)
	28.2	24	20	Eppley and Sloan (1966)
	25.3	26	21	Eppley and Sloan (1966)
	22.5	16	25	Eppley and Sloan (1966)

[1] *D. brightwellii* was cultured with irradiance 0.05 cal/cm²/min with periodic illumination 12L : 12D by Checkley (1972, see footnote 2 below). Values are for samples at the beginning of the light period.

[2] Checkley, D. 1972. The effect of the variation of growth temperature on the ratio of carbon to chlorophyll *a* in a laboratory culture of *Ditylum brightwellii*. Univ. Calif., Inst. Mar. Resour., La Jolla, Calif. (Unpubl. manuscr.)

[3] *D. tertiolecta* was cultured under continuous light with irradiance 0.07 cal/cm²/min.

of Glooschenko and Curl (1971). These authors, and Thomas (1969, 1970a), found no enhancement in waters in upwelling regions, but assimilation numbers were increased in response to nutrient additions in oligotrophic subtropical water. Malone (1971a, b, c) found assimilation numbers in eutrophic waters to be nearly an order of magnitude greater than those in oligotrophic surface waters of the subtropical and tropical Pacific.

It has so far proved difficult to sort out the effects on assimilation number of low light and low temperature in seasonal studies of natural waters. Phytoplankton cultures grown with either low light or low temperature show low maximum photosynthetic rates per chlorophyll *a* at light saturation (P_{max}) and low saturating intensity (I_k) for photosynthesis (Talling, 1957; Steemann Nielsen and Hansen, 1959, 1961; Ichimura, 1960; Yentsch and Lee, 1966). Thus some of the effects on assimilation number usually attributed to low light levels may, in cold waters, result also from low temperature. Bunt and Lee (1970) were able to sort out the two variables in their study of diatom growth under the ice in Antarctica by comparing a station with clear ice to one with snow cover. Photosynthetic rate and growth rate were considered to be light-limited at the station with snow cover but temperature-limited at the clear ice station (see also Saijo and Sakamoto, 1964, for photosynthesis vs. depth curves in ice-free and ice-covered lakes).

Assimilation numbers in Antarctic waters are low. Many values are less than 1.0 per hour (Mandelli and Burkholder, 1966; Horne, Fogg, and Eagle, 1969; Bunt and Lee, 1970). Saijo and Kawashima (1964) found an average value of 1.2 mg C/mg Chl. *a*/hr which they attributed to low temperatures and to a deep mixed layer (resulting in a low average irradiance seen by a cell). Water temperature in these studies was usually in the range —2° to 1°C. El-Sayed and Mandelli (1965) gave a range of 1.0 to 3.6 for the assimilation number in surface samples over a temperature range —1.75° to 6.0°C. Assimilation numbers of 4-5 were found in Drake Passage and Bransfield Strait where water temperature was usually about 1°C (El-Sayed, Mandelli, and Sugimura, 1964). All these values are compatible with assimilation numbers predicted by Figure 9.

Besides shifts in carbon/chlorophyll *a* ratios with temperature and the effects of nutrient limitation and light on assimilation number there is yet another factor which tends to obscure the expected seasonal changes in assimilation number with temperature. This comes about as a result of the variation in growth rate and assimilation number with cell size. By passing a water sample through netting one can conveniently separate the phytoplankton into two size categories: the larger cells and diatom chains retained by the net (the netplankton) and the smaller cells and chains which pass through the net (the nanoplankton). Malone (1971a, b, c) has recently compared assimilation numbers of the two size fractions and cites earlier studies. Invariably, the nanoplankton showed higher assimilation numbers than the netplankton, as would be expected from laboratory studies (cited earlier) which show a regular diminution in growth rate with increasing cell size. He further showed that netplankton are relatively more abundant during upwelling in coastal waters off California (Malone, 1971b). Chain-forming diatoms seem to be characteristic of the rich waters of temperate regions during the spring bloom. Yentsch and Ryther (1959) have shown a progressive increase in the ratio nanoplankton/netplankton with seasonally increasing temperature off New England. Tropical, warm, oligotrophic waters have been shown repeatedly to contain a high proportion of nanoplankton (see references cited by Malone and by Sutcliffe et al., 1970).

The causes of such seasonal succession of phytoplankton species is one of the significant problems in the study of marine phytoplankton. One can only speculate on possible contributing factors. For example, the high (relative) sinking rates of large-celled species and long diatom chains suggest that suspension and buoyancy are more significant problems for large cells than small (Munk and Riley, 1952; Smayda, 1970). Hence stratification, reduced mixing, and the imposition of a seasonal thermocline would tend to discourage large forms. Perhaps the most ele-

gant work in such problems is that of Lund and colleagues on diatom succession in the English lakes. Artificially mixing a lake in summer, when it would normally be stratified, permitted a bloom of *Melosira italica*, a diatom which usually sinks out of the water column upon the formation of a thermocline in late spring (Lund, 1971).

Another factor which tends to select against large-celled species in low-nutrient waters results from a low surface/volume ratio and a consequent inability to absorb nutrients from low concentration (Munk and Riley, 1952). This generalization has been confirmed in laboratory experiments on the kinetics of nutrient absorption where large-celled species showed higher half-saturation constants (K_s) for nitrate and ammonium uptake than small-celled species (Eppley, Rogers, and McCarthy, 1969). Similarly, the K_s for assimilation of vitamin B_{12} by phytoplankton depends on cell size (Carlucci, 1972).[3]

The argument with respect to netplankton vs. nanoplankton and the expected seasonal changes in assimilation number with temperature can be summarized as follows: (1) Nanoplankton show higher assimilation numbers (and growth rates) than do netplankton. This generalization results both from observations of natural phytoplankton and from studies of variations with cell size in laboratory cultures. (2) Increasing insolation in the spring results in increased water temperatures, and often in stratification and seasonal thermoclines. Nutrients in the mixed layer then tend to be depleted and often rather quickly, except in very shallow water where regenerative activities of microorganisms in sediments can maintain adequate nutrient levels for rapid phytoplankton growth. (3) Stratification of the water column tends to discourage the growth of large-celled species and long chain diatoms, because (a) reduced vertical mixing may result in their sinking out of the water column and (b) they are less effective in absorbing nutrients from low ambient concentrations than are nanoplankton. (4) Both seasonal increase in temperature and in the ratio of nanoplankton/netplankton should increase assimilation numbers for photosynthesis except where growth and photosynthetic rates are reduced by nutrient limitation.

Nanoplankton would be expected to be more abundant, relative to netplankton, in oligotrophic waters because of their lower sinking rates and lower K_s values for nutrient absorption. Hence, phytoplankton of warm, oligotrophic tropical waters would be expected to show high assimilation numbers (and growth rates) except for effects of nutrient limitation. One can begin to understand from all this why a graph of assimilation number vs. temperature for observation of natural phytoplankton usually fails to show the relationship expected from Figure 9, and why so much current work emphasizes the role of nutrient concentrations in phytoplankton growth in the sea.

Some exceptional marine waters which do show the expected relationship between assimilation number and temperature are shallow coastal estuaries where nutrient regeneration on the bottom maintains a high nutrient input to the overlying water. Examples reported for the east coast of the United States are Barlow, Lorenzen, and Myren (1963), Williams and Murdoch (1966), and Mandelli et al. (1970). Both of the latter papers show graphs of assimilation number vs. temperature which match beautifully the relation expected in Figure 9. Williams and Murdoch's data fall between the C/Chl. *a* 30 and 60 lines, with an indication of higher C/Chl. *a* ratio in winter, as expected. Mandelli et al. present two graphs, one for diatoms and the other for dinoflagellates. Assimilation numbers of the latter are higher than those for diatoms and fall on the line in Figure 9 for C/Chl. $a = 30$. They also show the seasonal change in relative numbers of diatoms and dinoflagellates; the latter are more abundant at higher temperatures.

Williams and Murdoch (1966) cite several other studies which show parallels between phytoplankton production in shallow marine waters and temperature over the seasons. The Danish

[3] Carlucci, A. F. 1972. Saturation constants for vitamin assimilation by phytoplankton. (Unpubl. manuscr.)

results are reviewed also by Steemann Nielsen (1960). Few of these earlier works included chlorophyll *a* measurements, however, and assimilation numbers are not reported.

Ichimura (1967) found a close relation between temperature and assimilation number for a station well within Tokyo Bay, but not at a station in deeper water. Nutrient limitation was postulated for the outer station.

Some of the values for assimilation number and its variation with temperature which can be conveniently summarized are provided in Table 6. One might have hoped, by comparison of the data with values expected from Figure 9, to check up on the quality of one's colleagues' work and to find some reported values outside the bounds of reasonable expectation. Happily, only one of the papers reviewed gave unrealistically high assimilation numbers and these were not repeated in subsequent studies by that author.

IMPLICATIONS FOR SIMULATION MODELS OF PHYTOPLANKTON PRODUCTION

As pointed out by Patten (1968) and others, mathematical models are usually designed to be accurate or alternatively, realistic, but seldom are both. It can be seen from the preceding discussion that attempts to compute photosynthetic rates from temperature would generally be inaccurate, and unrealistic as well, unless radiant energy and concentrations of essential nutrients were also considered. In the past, models of photosynthesis have often included a term for the maximum rate of photosynthesis at light saturation which is widely acknowledged to be temperature-dependent. In Steele's (1962) model P_{max} is a constant and is expressed in units "carbon assimilation rate per unit plant carbon"

TABLE 6.—Assimilation numbers measured in different ocean regions in comparison with maximum expected values taken from Figure 9. A similar table is given by Saijo and Ichimura (1962) for pelagic and coastal seawaters and lakes.

Region	Assimilation number (mg C/mg Chl./hr)				Temperature (°C)	Source
	Measured	Max. expected if C/Chl. =				
		30	60	90		
Cold Seas						
Antarctic	avg <2.5	1.0	2.0	3.0	−2-2	(1)
Subarctic North Pacific	0.4-2	1.4	2.7	4.0	2-6	(2)
North Atlantic	3.5	1.4	2.7	4.0	4-6	(3)
	3.5	1.7	3.4	5.1	9	(3)
	4	3.1	6.3	9.4	16	(3)
Upwelling Regions						
Peru Current	<7.5	4.6	9.2		17-20	(4)
Peru Current	5	4.6	9.2		[1](20)	(5)
S.W. Africa	<6.5	4.6	9.2		[1](20)	(6)
Cromwell Current	5.3	5.1	10.3		21	(7)
	10	8.0	16.0		25	(7)
Tropical Seas						
Madagascar	avg 3.8	8.0	16.0		[1](25)	(8)
Caribbean	avg 6.3a avg 3.7b	8.0	16.0		[1](25)	(9)
Tropical Pacific	avg 2.3a avg 1.5b	8.0	16.0		[1](25)	(9)
Off Puerto Rico	<13	8.0	16.0		[1](25)	(10)
Western Arabian Sea	avg 4.4	11.7	23.4		<28	(11)

[1] Assumed temperature.

Sources: (1) Saijo and Kawashima, 1964; El-Sayed and Mandelli, 1965; Mandelli and Burkholder, 1966; Horne et al. 1969; Bunt and Lee, 1970; (2) Biological station, Nanaimo (1970. Biological, chemical and physical data First Canadian Trans-Pacific Oceanographic Cruise March to May 1969. Fish. Res. Board Can., Manuscr. Rep. 1080, 92 p). (3) Steemann Nielsen and Hansen, 1959, for light-saturated rate; (5) Lorenzen, 1968, average over the euphotic zone; (7) Barber and Ryther, 1969, average over the euphotic zone; (8) Sournia, 1968; (9) Malone, 1971a. Values designated by "a" are for nanoplankton, "b" values for netplankton; (10) Burkholder, Burkholder, and Almodóvar, 1967; (11) Ryther and Menzel, 1965b, average for euphotic zone.

and is equivalent to a specific growth rate of about 1.1 doublings/day. Such a value would be appropriate for temperate waters, but probably not for polar or eutrophic tropical waters. But to make P_{max} a function of temperature would probably add unnecessary complexity for modeling purposes, although it would add realism. However, the use of constant values makes the model restrictive geographically (see, for example, Parsons and Anderson's, 1970, use of the model of Steele and Menzel, 1962, for the subarctic North Pacific).

A plant physiologist would perhaps prefer to approach modeling phytoplankton growth in the sea in as physiologically realistic way as possible and to let the computer handle the complexity. But it is questionable how realistically this can now be accomplished or what insight would thereby result.

Equation (1) of this paper can be considered a model of sorts and its apparent universality is appealing. Comparing its predictions as to growth rate and assimilation number with data from natural phytoplankton shows, moreover, the magnitude of difference between potential plant growth and reality, as it is now best estimated. The gulf between real and maximum expected values shows how significant are the other environmental factors which affect phytoplankton: radiant energy, nutrient concentrations, grazing, and mixing processes. All of these parameters have been successfully treated in models since the 1940's (see Patten's summary review, 1968; Parsons, Giovando, and LeBrasseur, 1966; Dugdale and Goering, 1967).

A physiologically realistic model might begin with a relation between temperature and maximum expected growth rate, as in Eppley and Sloan (1966). In that paper the variations in growth rate among species were rationalized by including the chlorophyll concentration per unit cell volume (a parameter not readily measurable in assemblages of mixed species, but susceptible to averaging). This parameter seemed also to compensate for the sun-shade alterations of phytoplankton photosynthesis when used to calculate radiant energy absorbed by a cell's pigments. However, the problem of daylength could not be adequately handled for species which grow faster with a few hours darkness each day than in continuous light.

None of the models proposed for primary productivity simulation has attempted to treat diel periodicity in the metabolic processes of phytoplankton. Nor is the alteration of chemical composition attendant to growth with limiting concentrations of nutrients or to variations with irradiance or temperature treated.

One suspects that the simple models now available can be satisfactory for describing the major features of regional phytoplankton production. Realistic physiological models will probably remain in the "special purpose" category for the insight of those familiar enough with the subject to use them as guide to their own research. Nevertheless, it is admitted, given the current popularity of modeling, that neither the reader nor the author may be able to resist for long the temptation to combine Equation (1) with a realistic function for nutrient assimilation rate vs. ambient concentration, a function for the dependence of μ and assimilation number upon light, and a suitable function for describing effects of mixing, in line with critical depth theory, and to try it with his favorite set of oceanic data.

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