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Questions on the Mechanism of Temperature Adaptation in Marine Phytoplankton

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Abstract

The rate of light-saturated photosynthesis in 3 marine algae [*Phaeodactylum tricornutum* Bohlin, *Nitzschia closterium* (Ehrenberg) Smith and *Dunaliella tertiolecta* Butcher] varies during growth in batch culture. The photosynthetic rate declines most rapidly during growth at the higher temperatures. Because of these changes in photosynthesis rate, the previously reported enhanced photosynthetic abilities caused by growth at lower temperatures (generally interpreted as evidence for higher enzyme levels) can only be observed when measurements are made late in the exponential phase or after the onset of the stationary phase of growth. When allowance is made for the earlier peak of photosynthetic ability in cultures growing at higher temperatures, there is no evidence for adaptation to lower temperatures being caused by increased levels of the enzymes required for carbon-dioxide fixation. When the changes due to growth in batch culture are taken into account, certain effects of temperature can be recognized. The dry weight: chlorophyll ratio of all 3 algae increases with decreasing growth temperatures. For *P. tricornutum* and *N. closterium*, growth at lower temperatures reduces the cellular content of chlorophyll *a*, but has little effect on the chlorophyll content of *D. tertiolecta*. The dry weight: cell-number ratio of *D. tertiolecta* and *P. tricornutum* increases with lower growth temperatures, but growth temperature has little effect on the cell mass of *N. closterium*. Growth of the 3 algae at lower temperatures does not increase their ability to photosynthesize at these lower temperatures. Rather, it reduces their ability to assimilate carbon dioxide at the higher temperatures.

Introduction

Recently (Morris and Farrell, 1971), we have tried to extend the observations of Steemann-Nielsen and his colleagues (Jørgensen and Steemann-Nielsen, 1965; Jørgensen, 1968; Steemann-Nielsen and Jørgensen, 1968a, b) on the nature of temperature adaptation in phytoplankton .In essence, Steemann-Nielsen and his co-workers suggested that algae adapt to sub-optimal temperatures by increasing their complement of enzymes required for the fixation of carbon dioxide. Their evidence was indirect, being based on a comparison of the rates of light-saturated photosynthesis with the protein contents of cells of *Skeletonema costatum* grown at different temperatures.

Our work with *Dunaliella tertiolecta* (Morris and Farrell, 1971) seemed to confirm this hypothesis. For example, we observed that algae grown at a lower temperature showed higher rates of light-saturated photosynthesis, and that this was true at all temperatures used for the measurements of photosynthesis (such a finding would be expected if the cells grown at the lower temperatures contained greater amounts of enzymes). We also observed that the cells grown at the lower temperatures contained higher activities of ribulose diphosphate carboxylase in cell-free extracts.

Now we wish to question the validity of this hypothesis. Our doubts arose originally from observations of changing rates of photosynthesis during growth of algae in batch culture. Because the pattern of these changes depended on the temperature at which the alga was growing, it seemed likely that the reported effects of different growth temperatures might relate to changes during batch growth and not to any phenomenon of temperature adaptation.

In this paper, the rate of light-saturated photosynthesis is used as a measure of the dark reaction and, thus, of the activity of photosynthetic enzymes. We describe the way in which this changes during batch growth, emphasizing the fact that similar results are obtained with several algae and with several different growth conditions. From these results it is concluded that the generally accepted hypothesis of temperature adaptation by algae is untenable. The latter parts of the paper emphasize those features which do not depend on the stage of growth in batch culture, but which truly depend on the growth temperature. It is asked whether there is a phenomenon which can be called "temperature adaptation" and, if so, what is its mechanism. Since the changing physiology of algae during batch growth has such a profound effect on our understanding of the response of algae to environmental factors, it is emphasized that further studies on such problems must be based on work with continuous cultures.

Materials and Methods

Growth of Organisms

Three marine algae were used in this study: *Phaeodactylum tricornutum* Bohlin was obtained from the Cambridge Culture Collection, *Nitzschia closterium* (Ehrenberg) Smith was kindly supplied by Dr. J.

Hayward, and *Dunaliella tertiolecta* Butcher by Professor C. S. Yentsch.

All organisms were grown in the "f" or "f-1" medium of Guillard and Ryther (1962). In our earlier experiments, "Tris-HCl" buffer was omitted from the medium, and the pH increased to approximately 9.3 after 3 days growth. In later experiments, Tris was included at a final concentration of 1.0 mg/l and a pH of 8.1; this maintained a constant pH during growth.

The cultures were illuminated in constant-temperature cabinets with "Warm White" fluorescent tubes giving a light intensity of about 9,000 lux at the culture surface. In early experiments, the cultures were subjected to alternating 16 h light, 8 h dark. However, because of the possible induction of synchrony, the experiments were repeated growing the algae in continuous light. Most of the experiments reported in this paper are taken from these later experiments with continuous illumination.

The main cultures were inoculated with suspensions maintained at the respective growth temperature for 3 days. In some experiments the cells were previously maintained at the growth temperature for 2 to 3 weeks, in others they were maintained at 20 °C until the inoculum was established 3 days before beginning growth. There was no apparent difference resulting from these two pre-treatments. In our experiments there was no evidence of lag periods in growth of the algae at any temperature.

Measurement of Photosynthetic Carbon-Dioxide Assimilation

At various times during growth, the algae were harvested by centrifugation and resuspended in fresh growth medium. After adjusting the density to 2×10^5 cells/ml, the suspension was transferred to test tubes and these sealed with vaccine stoppers. After 20 to 30 min equilibration in the growth cabinets, sodium bicarbonate-^{14}C was added to give a final concentration of 5.0 mM and a specific activity of 1.0 μCi/μM. 1.0 ml samples were removed at various intervals over 1 h and added to 2 ml acidified ethanol (with 5% acetic acid) in a scintillation vial. After evaporating to dryness, scintillant containing 6 g Butyl-PDB in 750 ml toluene plus 250 ml methanol was added, and the vials counted in a Packard Tricarb Model 3000 liquid-scintillation counter, or in a Tracerlab Corumatic 200 spectrometer. The rates were calculated from the linear incorporation over the first hour.

In some experiments with *Phaeodactylum tricornutum* and *Nitzschia closterium*, we examined the light-saturation curves of photosynthesis of these algae grown at different temperatures. In these experiments, the sealed test tubes were incubated at different distances from a water-cooled tungsten lamp at a temperature of 22° to 23.5 °C. Incorporation of sodium bicarbonate-^{14}C was followed as described above.

Interpretation of the results depends entirely on the fact that the rate of photosynthesis is being measured at saturating-light intensities and, hence, can be interpreted as a measure of the dark reaction of photosynthesis. The light-saturation curves for *Phaeodactylum tricornutum* and *Nitzschia closterium* are presented in Fig. 1 A and B, respectively. For both species, photosynthesis saturates at 8 to 10,000 lux. This is unchanged by growing the algae at lower temperatures. Similar results have been obtained for *Dunaliella tertiolecta*. Thus, the light intensity used in our experiments — 9,000 lux — is at, or near, the saturating intensity.

Chlorophyll *a* concentrations were measured by the method of Lorenzen (1967). Between 25 and 100 ml of

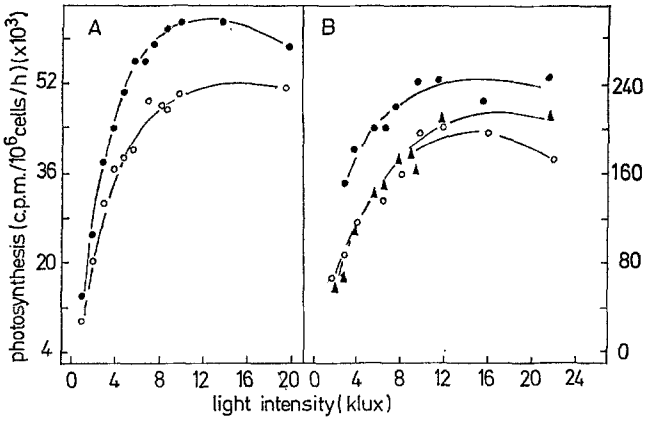

Fig. 1. Light-saturation curves for (A) *Phaeodactylum tricornutum*, (B) *Nitzschia closterium*, grown at 18 °C (filled circles), 12 °C (open circles) and 7 °C (triangles). Experimental temperature was 22° to 23 °C. c.p.m.: counts per min

suspension were filtered through glass-fibre discs moistened with a drop of saturated magnesium-carbonate solution. The algae were broken with a "Potter" homogenizer for 1 min in 3 ml 90% (v/v) acetone. After washing with 1 ml of 90% acetone, the broken suspension was centrifuged and absorption of the supernatant measured at 665 nm with a Unicam SP 1800 before and after adding a drop of 1 N HCl (the "acid ratio" was generally slightly less than 2.0). The concentrations were calculated using the equations of Lorenzen (1967).

The dry weight:cell-number relationships were determined by filtering 30 to 150 ml of suspension through weighed glass-fibre discs and drying at 100 °C to constant weight.

Results

Changing Rates of Photosynthesis During Batch Growth

The rate of photosynthesis (expressed per unit number of cells) did not remain constant during the

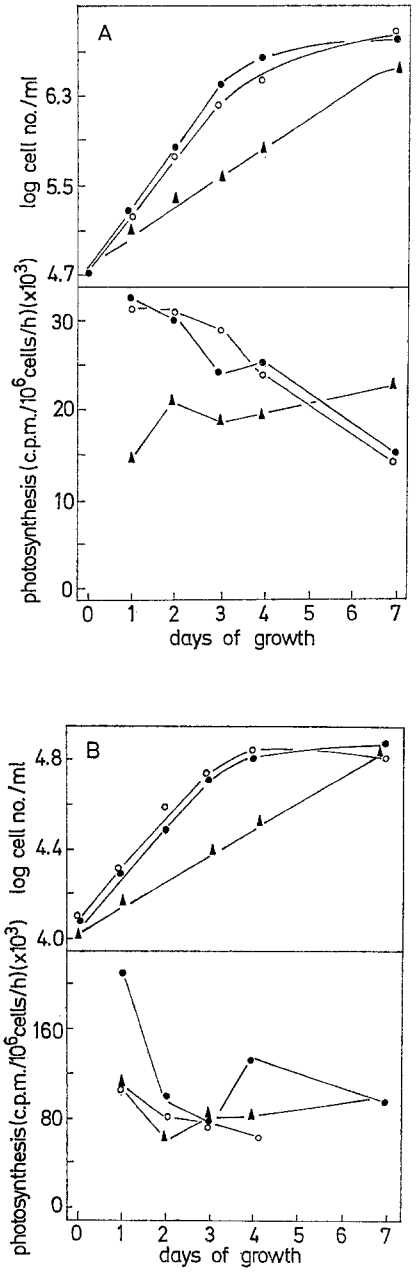

Fig. 2. Growth (upper) and photosynthetic rates (lower) of (A) *Phaeodactylum tricornutum*, (B) *Nitzschia closterium* grown in "f-1" medium (i.e., with "Tris" buffer present) under continuous illumination at 18 °C (filled circles), 12 °C (open circles), and 7 °C (triangles). Photosynthesis was measured at 12 °C and expressed per cell number

batch growth of any of the algae examined. In all batches, maximum photosynthesis occurred early in the exponential phase of growth, after which a decline was generally observed. The decline in photosynthetic rate depended on the growth temperature. This is shown for *Phaeodactylum tricornutum*, *Nitzschia closterium*, and *Dunaliella tertiolecta* in Figs. 2A, B and 3, respectively.

Although the details differed from one alga to another, a basic phenemenon was common to all three. The decline in photosynthetic ability was most marked during growth at higher temperatures so that those cultures grown at lower temperatures displayed a greater rate of photosynthesis only when comparison was made relatively late in the growth curve. When allowance was made for the earlier maximum in cultures at higher temperatures this difference disappeared.

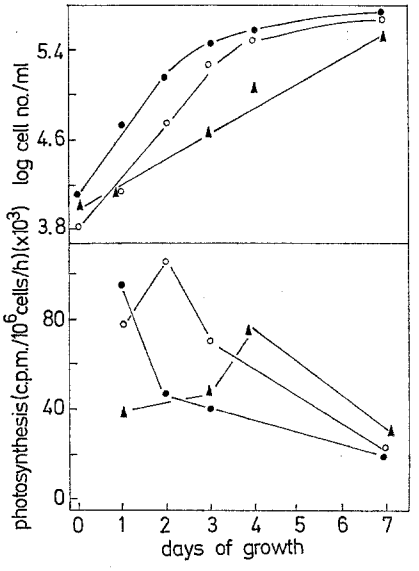

Fig. 3. *Dunaliella tertiolecta*. Growth (upper) and photosynthetic rates (lower) of culture grown at 24 °C (filled circles), 18 °C (open circles), and 12 °C (triangles). Photosynthesis was measured at 18 °C. For further details see legend to Fig. 2

This basic result was confirmed by several experiments with each alga. Change in growth conditions affected the details but did not alter the essential result. The experiments were repeated with growth medium lacking "Tris" buffer. During growth in the absence of buffer, the pH of the medium increased from about 8.2 to a maximum of 9.3 to 9.5 after 3 days; the main effect of this was to increase the rate of decline in photosynthesis in cultures growing at the higher temperatures. This is demonstrated in *Phaeodactylum tricornutum* in Fig. 4. In other experiments the algae were grown under alternating light-dark cycles. Although we had no evidence to suggest that the cultures were synchronized, the cell counts were not sufficiently frequent to rule out this possibility completely. Measurements were made at the same time each day, thus minimizing any complicating effects due to synchronized growth. The essential result was the same as that already outlined; cells grown at

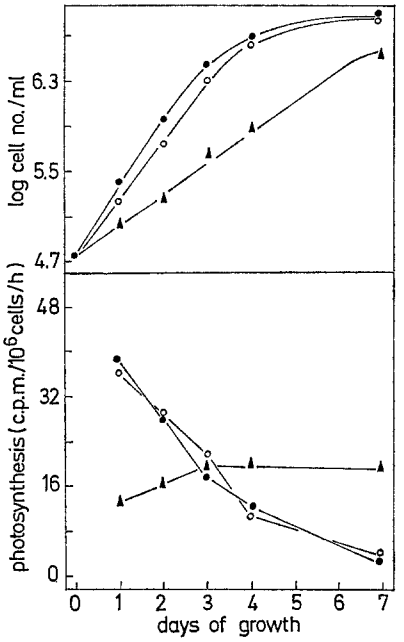

Fig. 4. *Phaeodactylum tricornutum.* Growth (upper) and photosynthetic rates (lower) of culture grown in "f" medium (i.e., in the absence of "Tris" buffer). For further details see legend to Fig. 2

illustrated by comparison of Figs. 2A and 5. Fig. 2A shows changing rates of photosynthesis during growth of *Phaodactylum tricornutum* with photosynthesis measured at 12 °C; in Fig. 5, photosynthesis was measured at 7° and 18 °C. Thus, whatever temperatures were used for the measurement of photosynthesis, algae grown at lower temperatures only displayed higher rates when comparison was made late in the growth curve.

One of the implications of the published model for temperature adaptation (Steemann-Nielsen and Jørgensen, 1968a; Morris and Farrell, 1971) is that growth at lower temperatures indicates photosynthesis at these lower temperatures to approximate photosynthesis at higher temperatures by algae grown at these higher temperatures. However, Fig. 5 shows this to be true only when measurements are made towards the end of the growth curve.

Chlorophyll a Content of Algae Grown at Different Temperatures

The chlorophyll *a* content of *Phaeodactylum tricornutum* and *Nitzschia closterium* depend on growth temperature (Table 1); those cells grown at the lowest temperatures contain least chlorophyll *a*. This was most marked in *N. closterium*, the effect being apparent

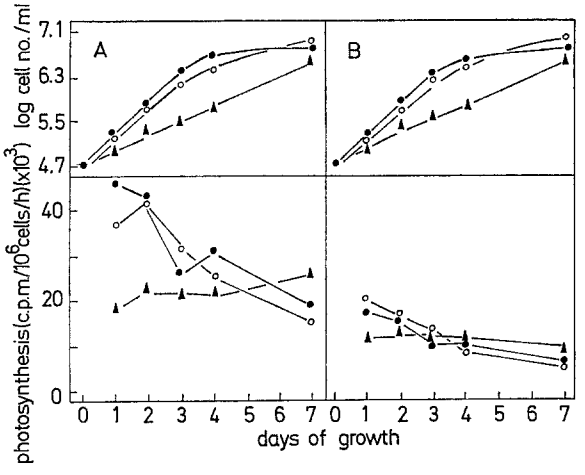

Fig. 5. *Phaeodactylum tricornutum.* Growth (upper) and photosynthetic rates (lower) of culture grown under conditions described in legend to Fig. 2. In (A) photosynthesis was measured at 18 °C, in (B) at 7 °C

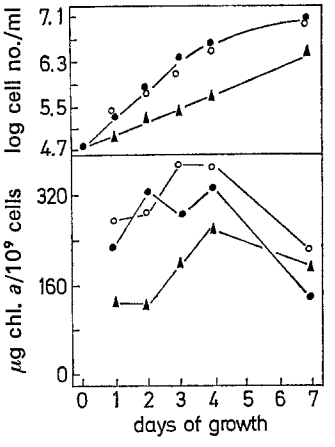

Fig. 6. *Phaeodactylum tricornutum.* Growth (upper) and chlorophyll *a* content (lower) of culture grown in "f-1" medium at 18 °C (filled circles), 12 °C (open circles), and 7 °C (triangles)

lower temperatures had greater photosynthetic rates only when comparison was made relatively late during batch growth.

In the experiments described so far, photosynthesis was measured at a particular temperature. The basic result, presented above, was independent of the temperatures used to measure photosynthesis. This is over all 3 temperatures and over the entire growth curve. In *P. tricornutum* such difference was apparent only between 7 °C and the other temperatures, not between 12° and 18° C. After 7 days growth at 7 °C, cells of *P. tricornutum* did not contain less chlorophyll than those grown at 18 °C (Table 1 and Fig. 6). There was little consistent difference in the chlorophyll

Table 1. *Chlorophyll a content (μg/10⁹ cells) of 3 marine algae grown at various temperatures*

Growth temperature (°C)	*Phaeodactylum tricornutum* Days growth			*Nitzschia closterium* Days growth			*Dunaliella tertiolecta* Days growth		
	1	4	7	1	4	7	1	2	4
24	—	—	—	—	—	—	870	900	712
18	232	337	168	1615	1580	1870	860	855	842
12	272	399	264	1030	795	1425	510	923	992
7	174	216	184	870	725	1060	—	—	—

content of cells of *Dunaliella tertiolecta* grown at various temperatures (Table 1).

The changing rates of photosynthesis presented in the previous section have been expressed per unit number of cells. Similar changes during batch growth could be observed when the photosynthetic rates were

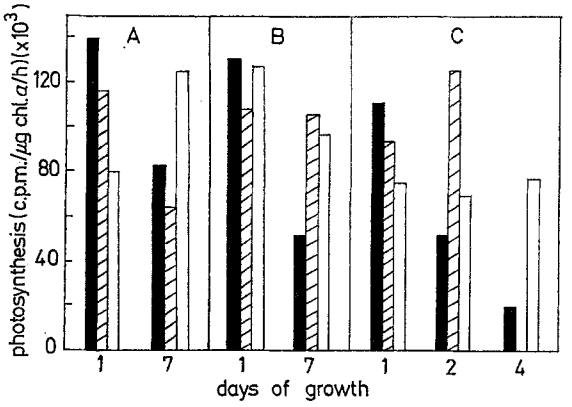

Fig. 7. Rates of photosynthesis, expressed on chlorophyll basis, by (A) *Phaeodactylum tricornutum*, (B) *Nitzschia closterium*, (C) *Dunaliella tertiolecta*. For *P. tricornutum* and *N. closterium*, photosynthesis was measured at 12 °C after 1 and 7 days growth, for *D. tertiolecta* at 18 °C after 1, 2, and 4 days growth. For *P. tricornutum* and *N. closterium*, growth temperatures were 18 °C (filled columns), 12 °C (hatched columns) and 7 °C (open columns); for *D. tertiolecta* they were 24° (filled columns), 18 °C (hatched columns) and 12 °C (open columns)

expressed per unit chlorophyll concentration (Fig. 7), with one difference: When expressed on a chlorophyll basis, the maximum rates of photosynthesis (measured at any single temperature) were approximately the same for cultures grown at all 3 temperatures. However, with the two diatoms (but not with *Dunaliella tertiolecta*), cultures grown at the lower temperatures could not achieve the same maximum rate of photosynthesis — expressed on a cell-number basis — as could those grown at the higher temperatures.

Dry-Weight Cell-Number Ratios of Algae Grown at Different Temperatures

One of the pieces of evidence supporting the hypothesis that algae grown at lower temperatures contain higher levels of photosynthetic enzymes was the observation of Jørgensen (1968) that cells of *Skeletonema costatum* grown at lower temperatures contained more protein, and were larger. Because of this, we have examined the cell mass — expressed as dry weight — of the 3 algae, grown at various temperatures (Table 2). For *Phaeodactylum tricornutum* and *Dunaliella tertiolecta*, the dry weight of cells grown at lower temperatures was significantly greater than of those grown at the higher temperatures. For *Nitzschia closterium*, there was no reproducible effect of temperature on dry weight.

Expressed on a dry-weight basis, the rate of photosynthesis by cells grown at lower temperatures was no greater than the maximum attained by those cultures grown at higher temperatures. This is illustrated on *Phaeodactylum tricornutum* in Table 3. Since the dry-weight:cell-number ratio of *P. tricornutum* declined during growth, the rate of photosynthesis expressed on a dry-weight basis was approximately the same after 7 days growth at lower temperatures as in the early part of exponential growth in cultures grown at the higher temperatures. In other words, in this alga the decline in photosynthesis per cell number is related, in part at least, to the decline in cell mass during batch growth.

Relative Rates of Photosynthesis at Different Temperatures by Algae Grown at Various Temperatures

In most of the results presented so far, we have generally measured photosynthesis at one particular temperature. In this section we examine whether growth of algae at particular temperatures affects their relative photosynthetic abilities at the different temperatures. One way of doing this is to examine whether the ratio of photosynthetic rate at a higher to that at a lower temperature changes with different

Table 2. *Phaeodactylum tricornutum, Nitzschia closterium, and Dunaliella tertiolecta. Dry weight (μg/10⁶ cells) of algae grown at various temperatures*

Growth temperature (°C)	*Phaeodactylum tricornutum* Days growth			*Nitzschia closterium* Days growth			*Dunaliella tertiolecta* Days growth
	2	4	7	1	3	4	2
24	—	—	—	—	—	—	25.8
18	54.5	29.1	27.1	237	219	251	51.5
12	77.8	61.1	21.1	240	233	282	101.0
7	94.7	77.1	33.9	338	230	246	—

growth temperatures (Table 4). Essentially, *Phaeodactylum tricornutum* grown at 18 °C fixed carbon dioxide about 2.70 times as rapidly at 18 °C as at 7 °C. However, the cells grown at the lower temperature

Table 3. *Phaeodactylum tricornutum. Rates of photosynthesis (cpm/μg dry weight/h) during growth at different temperatures. Photosynthesis rate was measured at 12 °C*

Days of growth	Growth temperature 18 °C	12 °C	7 °C
2	550	395	220
4	860	470	238
7	555	667	690

Table 4. *Ratios of photosynthesis (PS) at 18 °C to photosynthesis at 7 °C* $\left(\frac{PS\,18\,°C}{PS\ 7\,°C}\right)$ *by cultures of algae grown at 18° and 7 °C. (The ratio was measured at various points during the growth curves; figures in brackets: extreme values reached during growth of batch culture)*

Alga	Growth temperature (°C)	Ratio of $\frac{PS\ 18\,°C}{PS\ 7\,°C}$
Phaeodactylum tricornutum	18	2.70 (3.20—2.28)
	7	1.87 (2.63—1.52)
Nitzschia closterium	18	2.82 (3.01—3.76)
	7	2.04 (2.27—1.64)
Dunaliella tertiolecta	18	2.46 (2.83—2.02)
	7	1.47 (2.20—1.23)

assimilated carbon dioxide only 1.87 times as rapidly at 18 °C as at 7 °C. A similar effect of growth temperature could be seen for both *Nitzschia closterium* and *Dunaliella tertiolecta*. Although there was considerable variation in these ratios during growth (figures in parenthesis in Table 4) most of the extreme values occur at the end of the growth period, and should not obscure a reproducible effect of growth temperature on these ratios.

The results in Table 4 show how growth at a lower temperature reduces the effect of temperature on photosynthesis. The results do not, however, show whether this occurred because of enhanced photosynthetic ability at lower temperatures or because of reduced ability at higher ones. The answer to this is shown in Table 5. The photosynthetic rates expressed in Table 5 are the maximum values reached during growth at each temperature. Growth at lower temperatures did not have a significant effect on photosynthesis at those lower temperatures; rather, it reduced the ability to photosynthesize at the higher temperatures. This was true whether photosynthesis was expressed on a cell number basis or per unit amount of chlorophyll (Table 5). The results presented in Table 5 also emphasize the point made earlier: when expressed on a cell-number basis, the maximum rate of photosynthesis attained by the two diatoms (*Phaeodactylum tricornutum* and *Nitzschia closterium*) grown at the lower temperatures is less than that attained by cells grown at the higher temperatures.

Discussion

The data presented in this paper do not permit critical comment on the reason for the changing photosynthetic abilities during growth of the algae in batch culture. From the limited evidence available, it is clear that the precise nature of the changes depends, in part at least, on the pH control and on the question of whether the algae are grown in continuous light or in alternating light-dark periods. However, although we have little idea of what causes changes in the photosynthetic abilities during batch growth, such changes are not without parallel. For example, Slater and Morris (1972) have recently emphasized the importance of changing photosynthetic rates during batch growth of the photosynthetic bacterium *Rhodospirillum rubrum*. The changes reported here are similar to those ob-

Table 5. *Maximum rates of photosynthesis (counts/min × 10^3/h) at different temperatures by algae grown at different temperatures. (Maximum rates were reached on following days: Phaeodactylum tricornutum, 18 °C-grown, Day 1; 12° and 7 °C-grown, Day 2; Nitzschia closterium, 18°-, 12°- and 7 °C-grown, Day 1; Dunaliella tertiolecta, 24 °C-grown, Day 1; 18 °C-grown, Day 2; 12 °C-grown, Day 4)*

Growth temperature (°C)	Incubation temperature (°C)	*Phaeodactylum tricornutum*		*Nitzschia closterium*		*Dunaliella tertiolecta*	
		per 10^6 cells	per µg chlorophyll	per 10^6 cells	per µg chlorophyll	per 10^6 cells	per µg chlorophyll
24	24	—	—	—	—	109	125
	18	—	—	—	—	96	110
	12	—	—	—	—	54	62
18	24	—	—	—	—	110	128
	18	46.1	205	260	161	106	124
	12	32.6	145	210	130	86	100
	7	17.2	76.5	88	54.5	—	—
12	24	—	—	—	—	84	85
	18	41.5	145	170	165	76	77
	12	31.8	111	110	107	55	55.5
	7	20.9	73.5	76	73.8	—	—
7	24	—	—	—	—	—	—
	18	22.2	132	120	138	—	—
	12	21.2	125	110	126	—	—
	7	13.0	76.5	58	66.7	—	—

served by Slater and Morris. Griffiths (1973) has recently described the same phenomenon in *Phaeodactylum tricornutum*.

Although we do not understand the mechanism behind these changes during batch growth, it is nevertheless clear that they must radically alter our idea of temperature adaptation in algae. The apparent higher rate of photosynthesis by cells grown at lower temperatures arises because the photosynthetic rate by these cultures is more stable during batch growth. However, there is no evidence to suggest that the maximum photosynthetic rate reached by algae growing at lower temperatures is any greater than the maximum rate reached by cells growing at the higher temperatures. We feel it important to emphasize that this basic result has been observed for all three algae growing under a range of conditions, and must question the hypothesis that algae adapt to sub-optimal temperatures by synthesizing greater amounts of the photosynthetic enzymes (Steemann-Nielsen and Jørgensen, 1968a; Morris and Farrell, 1971).

The question remains, however, as to whether the growth temperature does affect the physiology of planktonic algae over and above any effects of batch growth. From our results it appears that there are 3 main effects of growth temperature.

Firstly, in the two diatoms *Phaeodactylum tricornutum* and *Nitzschia closterium*, growth at lower temperatures reduces the cellular content of chlorophyll *a*. There appears to be little effect of growth temperature on the chlorophyll content of *Dunaliella tertiolecta*. This agrees with the observations of Eppley and Sloan (1966), who observed only a slight increase in the chlorophyll content of *D. tertiolecta* with increasing growth temperature. The effect of temperature on the chlorophyll content of the two diatoms means that the maximum rate of photosynthesis per cell number attained by those cells growing at lower temperatures is less than the maximum rate attained by those growing at higher temperatures. When expressed on a chlorophyll basis, the maximum rates achieved are approximately the same for all growth temperatures.

The second effect relates to the cell mass of algae grown at different temperatures. In our studies we have not emphasized this aspect, but the data we do have support the published conclusions of several authors. For example, Jørgensen (1968) observed increased carbon content in cells of *Skeletonema costatum* grown at lower temperatures, and Eppley and Sloan (1966) reported increasing carbon : cell and carbon : chlorophyll *a* ratios in *Dunaliella tertiolecta* with decreasing growth temperatures. Eppley (in press) has also shown similar effects for *Ditylum brightwellii*. In our own experiments, we have observed increasing dry weight : chlorophyll ratios for all 3 algae we have studied and have also observed increasing dry-weight : cell-number ratios with lower growth temperatures of *Phaeodactylum tricornutum* and *Dunaliella tertiolecta*. Thus, one general effect of growth at reduced temperatures seems to be an increase in cell mass (volume, dry weight, or carbon content) relative to the chlorophyll *a* content. However, it must be stressed that this cannot be interpreted as resulting from increasing enzyme content producing increased rates of light-saturated photosynthesis.

The third effect is common to all three algae we have studied. Growth at the lower temperatures reduces the ability of the algae to assimilate carbon dioxide at the higher temperatures (temperatures not so high as to reduce the growth rate), but does not enhance the ability to photosynthesize at the lower temperatures. This effect can be seen whether photosynthesis is expressed per cell number or on a chlorophyll basis. Although the mechanism of this effect is not clear (our light-saturation curves do not support the idea that light intensity is too low to observe maximum expression of the photosynthetic ability of the algae grown at lower temperatures), we feel that it is basic to understanding the effects of temperature on algae. To some extent the question of whether this effect can be called "adaptation" is largely semantic. When grown at sub-optimal temperatures, the algae do not gain any ability to utilize these lower temperatures; rather, they lose some ability to utilize fully the more optimal conditions of a higher temperature. There is no reason why this should not be thought of as an "adaptive" response. Future elucidation of the biochemical mechanism for this effect must depend on the use of continuous cultures. Without this the effects can be too easily obscured by changes occurring during growth in batch culture.

Summary

1. The photosynthetic ability of 3 marine algae [*Phaeodactylum tricornutum* Bohlin, *Nitzschia closterium* (Ehrenberg) Smith, and *Dunaliella tertiolecta* Butcher] changes during growth in batch culture. The decline in photosynthesis is most marked during growth at higher temperatures.

2. Because of these changes, we suggest that the hypothesis that algae adapt to lower temperatures by increasing their complement of photosynthetic enzymes is untenable, and results from the fact that the measurements have been made relatively late in the growth curve.

3. In all 3 algae, growth at lower temperatures increases the dry weight: chlorophyll ratio of the cells.

4. In two of the algae (*P. tricornutum* and *N. closterium*) growth at lower temperatures decreases the cellular content of chlorophyll *a*. In *D. tertiolecta* and *P. tricornutum*, growth at lower temperatures increases the dry-weight: cell-number ratio.

5. In all 3 algae studied, growth at the lower temperatures does not enhance their ability to photosynthesize at those lower temperatures. Instead, it reduces their ability to assimilate carbon dioxide at the higher temperatures.

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