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Nitrate Uptake in Marine Phytoplankton: Energy Sources and the Interaction with Carbon Fixation

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Abstract

Field studies of whole natural phytoplankton communities from Knight Inlet, B. C., Canada and laboratory cultures of the diatom *Skeletonema costatum* indicate inorganic carbon fixation may be temporarily suppressed following 10 to 15% enrichment with NO_3^- or NH_4^+. (This effect is suggested to be due to competition between inorganic carbon and nitrogen for adenosine triphosphate (ATP), and is reduced when chlorophyll *a* is increased intracellularly after 6 to 8 h.) Results imply that the source of ATP for nitrate uptake is primarily from Photosystem I (cyclic photophosphorylation) in the presence of light. It would appear that a transient nutrient-adaptive response occurs upon addition of extracellular nitrogen.

Introduction

The physiological role of ATP in the uptake of nutrients by marine phytoplankton remains unclear. Nutrients such as nitrate, ammonium, phosphate, and silicate often appear to be transported against their negative chemical concentration gradients and may be influenced by light. This implies that active transport may be one important mechanism for such ion uptake (Eppley and Rogers, 1969; Eppley *et al.*, 1971a, b; Hemmingsen, 1971; MacIsaac and Dugdale, 1972; Bates, 1974; Ullrich-Eberius and Yingchol, 1974). As such, active transport necessitates the utilization of a chemical reaction (a scalar quantity) to provide the driving force for the ion uptake (a vectoral quantity) (Katchalsky and Curran, 1967). Presumably this energy is made available through the hydrolysis of ATP or some other high-energy phosphate (Healy, 1973; Falkowski, in press).

Photosynthetic phytoplankton are capable of synthesizing high-energy nucleotides from at least 4 distinct metabolic pathways: (1) substrate phosphorylation; (2) oxidative phosphorylation; (3) non-cyclic photophosphorylation (Photosystem II); (4) cyclic photophosphorylation (Photosystem I). As the latter two processes are, in the presence of light energy, actively providing energy and reducing power for inorganic carbon fixation, nutrient uptake processes utilizing energy from photophosphorylation may compete for high-energy nucleotides with dark reactions. As a result, carbon fixation may be suppressed following the addition of inorganic nutrients.

This study was made to determine some of the parameters controlling the physiological role of ATP in nitrate and ammonium uptake by whole natural phytoplankton communities and cultures of the neritic diatom *Skeletonema costatum*.

Materials and Methods

Field Study

Two cruises on the C.S.S. "Vector" to Knight Inlet, a glacier-fed estuarine fjord ca. 180 miles north of Vancouver, B. C., were made in July and September, 1974. This inlet has been under study by one of us (D.P.S.) for 12 months. These two cruises corresponded to the recession of the spring bloom and peak of the secondary fall bloom, respectively, as determined by *in situ* chlorophyll *a* concentrations (Fig. 2). A control station (QC, Fig. 1) was chosen in Queen Charlotte Strait for comparison with inlet stations. Fig. 1 shows the relative positions of the sample stations.

Hydrocasts were made at each station at 2-m depth with 2-l Van Dorn bottles. Each sample was split into 3 equal parts. One part was enriched with 3 µg-at NO_3^-/l and one with 3 µg-at NH_4^+/l. The remaining sample was not enriched. Each subsample was incubated, in duplicate, in 250-ml Pyrex bottles, equipped with ground-glass stoppers. These were then innoculated with 2 µCi $Na_2C^{14}O_3$ and incubated at sea-surface temperatures in a simulated *in situ* deck incubator (Doty and Oguri, 1958). Banks of 40-W fluorescent tubes provided an incident maximum light intensity of 0.09 langleys/min. Neutral density filters were used to attenuate the light to 60, 30, 15, 1, and 0% of the incident radiation and one set remained at the maximum intensity (MacIsaac and Dugdale, 1972). After the desired incubation period (2 to 8 h), the samples were filtered on 0.45 µ Millipore filters at less than 12-cm Hg vacuum pressure, fumed for 15 sec over concentrated HCl, and dried in a desiccator. The filters were counted for radioactivity in a liquid scintillation counter ashore, using the channels-ratio method.

Chlorophyll *a* was determined in each sample prior to, and after each incubation by the trichromatic method (Strickland and Parsons, 1972). Estimates of the light extinction coefficient were made with a Secchi disc. In addition, vertical profiles of nitrate, phosphate, dissolved oxygen, chlorophyll *a*, temperature, salinity, and combined particulate material were made at each station. Whole phytoplankton samples from the 2-m depth were preserved with Lugol's solution for cell identification and counting.

Laboratory Study

Unialgal, but not axenic, cultures of *Skeletonema costatum* (University of British Columbia, Northwest Pacific Culture No. 18) were grown at 18°C on medium "f" (Guillard and Ryther, 1962) diluted to "f/2" with autoclaved seawater. Samples were grown with either NO_3^- or NH_4^+ as the sole inorganic nitrogen source, at initial concentrations of 28 µg-at N/l. Atmospheric ammonium contamination of the NO_3^- medium was prevented by prebubbling air entering the culture vessels through a saturated solution of $ZnCl_2$ (Caperon and Meyer, 1972). Microscopic examination with phase contrast indicated that few bacteria were present when cultures reach log phase.

Cultures, of 100-ml quantity, were placed in 250-ml Pyrex bottles and incubated with neutral-density filters at

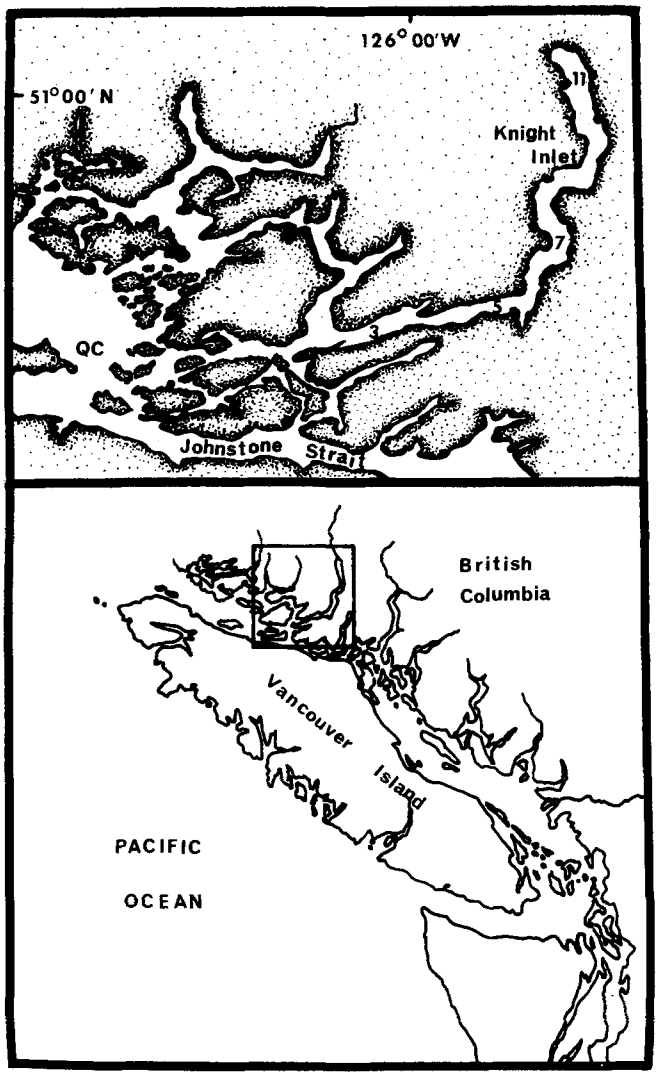

Fig. 1. Above, positions of sample stations within Knight Inlet; below, location of Inlet (insert) in relation to British Columbia coast. Distance between Stations QC and Kn 11 is 105 km. Description of physical oceanography of area is given by Pickard (1961)

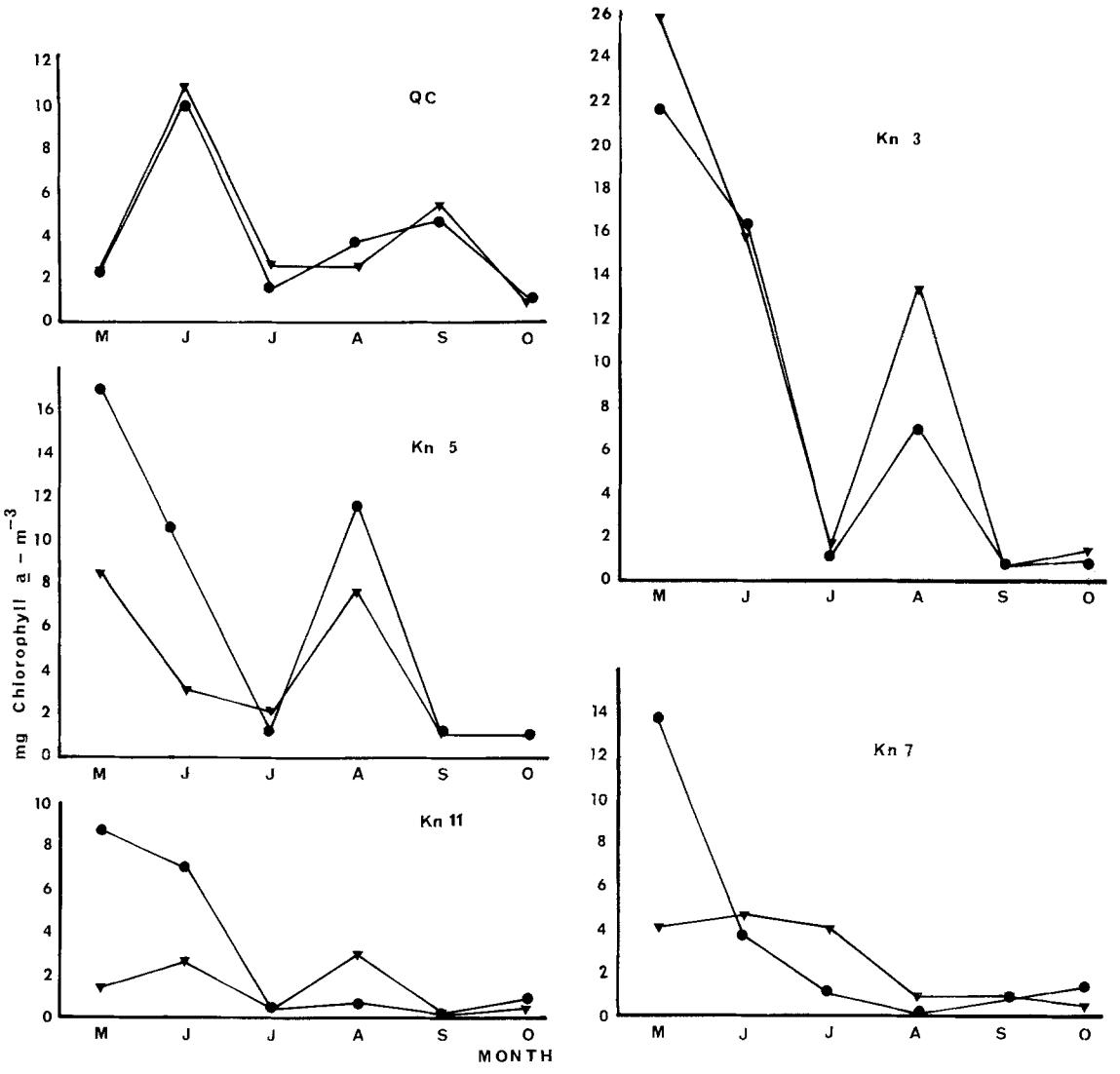

Fig. 2. Variation in chlorophyll *a* at sample stations during study period at 0 m (circles) and 5 m (triangles). Phytoplankton samples were taken in July and September, corresponding to recession of spring bloom and peak of secondary fall bloom, respectively, at Control Station QC

18°C. The maximum light intensity of 0.10 langleys/min, supplied by cool white fluorescent tubes, was attenuated to 100, 60, 30, 15, 1, and 0%. After 2-h incubation, the cells were filtered on Whatman GF/C glass-fiber filters and the ATP was extracted as described by Holm-Hansen and Booth (1966). Using tracer ATP, the efficiency of extraction was estimated at ca. 80%. The samples were assayed for ATP with fresh luciferin-luciferase preparations (Sigma Chemical Co.) and the photon emittance was detected in a Unicam liquid scintillation counter, using one photomultiplier. Standard and background counts were performed in conjunction with each sample. Samples were assayed in triplicate and the mean of the three counts was used to calculate the intracellular ATP.

To determine the effect of temperature on the ATP pool size, the preceding method was performed at 8°, 18°, and 28°C at each of the 6 light intensities. Cells were grown at 18°C and transferred to the experimental temperature for 2 to 4 h prior to ATP extraction.

Cell counts were made in a Coulter Counter (Model B) after a 60-sec sonication period to break up the chains. Chlorophyll *a* was determined spectrophotometrically, following the equations of Strickland and Parsons (1972).

Results and Discussion

The results of the effects of light and temperature on the intracellular ATP pools are shown in Fig. 3. The intracellular ATP concentrations vary direct-

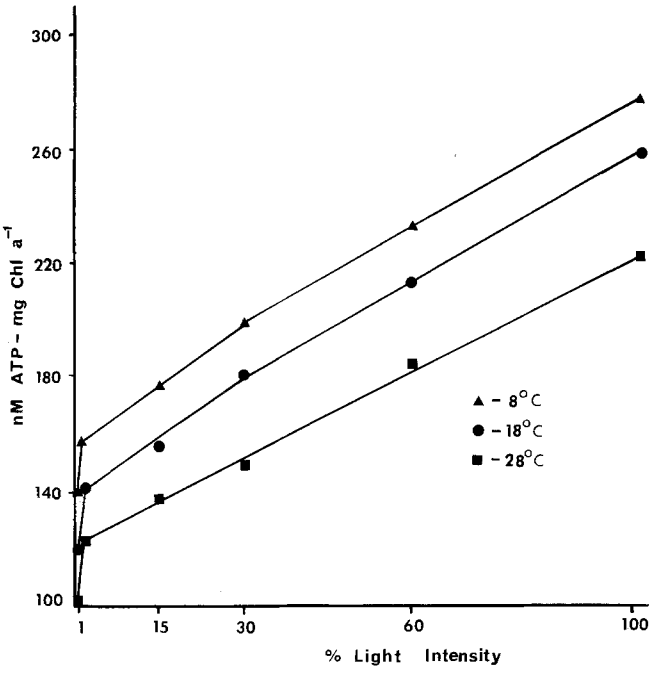

Fig. 3. *Skeletonema costatum*. Effects of light and temperature on the adenosine triphosphate (ATP) pool. Increased light intensity increased the ATP pool, while increased temperature decreased it. The interaction of these two parameters in overall ATP metabolism suggests that decreasing temperature lowers ATP catabolism at greater rate than ATP anabolism; difference is reflected by larger ATP pool at lower temperatures at all light intensities

ly with light intensity, presumably due to the contributions of the light reactions to the ATP pool. The ATP pool size was calculated per unit chlorophyll *a* to minimize the effects of short-term light adaptation and express more clearly the relationship between photoreactions and ATP pool sizes. In addition, only a 5% increase in chlorophyll *a* could be detected at 18°C in the 100% light bottle.

An increased ATP pool was observed at 8° and 18°C relative to the high temperature incubation (28°C). The change in ATP pool size was not determined per unit time (i.e., not expressed as a metabolic rate), but rather reflects a difference between input and output of the high energy triphosphate. Calculations of the Q_{10} (a rate-dependent coefficient) from these data would not be physiologically valid. It would seem that decreased temperature lowers ATP hydrolysis (e.g. protein synthesis) at a greater rate than ATP anabolic processes (e.g. photophosphorylation). This overall difference is reflected by a larger ATP pool at lower temperatures.

Field studies with natural phytoplankton communities indicate a 6 to 8 h, transitory decrease in carbon fixation per unit chlorophyll *a* (i.e., assimilation ratio). This effect was observed at all light intensities tested with NO_3^- or NH_4^+ enrichment (Fig. 4). As the enrichment only represents 10 to 15% of the *in situ* dissolved inorganic nitrogen concentration (Table 1), excess nutrient repression was not considered to be a cause of the decreased productivity. Following a 6-h preincubation with either nitrogen enrichment, addition of 2 µCi $Na_2C^{14}O_3$ indicated an increased assimilation ratio over control samples. This response, with a longer term exposure to nitrogen enrichment, was accompanied by ca. 20% increase in chlorophyll *a* per cell and is significantly greater than control samples ($P > 0.05$) (Table 2).

At Control Station QC, a 2-h incubation with either NO_3^- or NH_4^+ resulted in depression of carbon fixation (Fig. 4A), but this effect was reduced after a 6-h preincubation (Fig. 4B). The data for Stations Kn 3 and Kn 5 (Fig. 4C and D, respectively) are shown for a 6-h preincubation with nitrogen and suggest a difference in the rate at which the two communities responded to external nutrient enrichment. At Station Kn 7 (Fig. 4E), a 2-h incubation caused an altered light response; a linear relationship between light intensity and assimilation ratios was observed for the enriched samples, while the unenriched control indicated a hyperbolic relationship. At Station Kn 11 (Fig. 4F), inhibition above 60% light intensity was observed in all samples after a 2-h incubation. Further, at Station Kn 11, suspended particulate material decreased the light penetration so that the 1% light depth was estimated at less than 2 m. The response of the phytoplankton community at Station Kn 11 suggests the cells were more shade-adapted than the phytoplankton at Stations Kn 3 or Kn 5, where light penetration is much better (Tables 1 and 2).

On all cruises phytoplankton populations were low in the inlet and high in the adjoining Strait. The major species represented in the Strait were the diatoms *Chaetoceros debilis, Thalassiosira nordenskioldii,* and *Skeletonema costatum.* The inlet stations were not clearly dominated by any major species; *S. costatum* and assorted nanoplankton (less than 25 µ) were observed in the preserved samples.

The results of the nitrogen enrichment series at Knight Inlet suggests that a nutrient adaptive period of between 6 and 8 h is required by natural

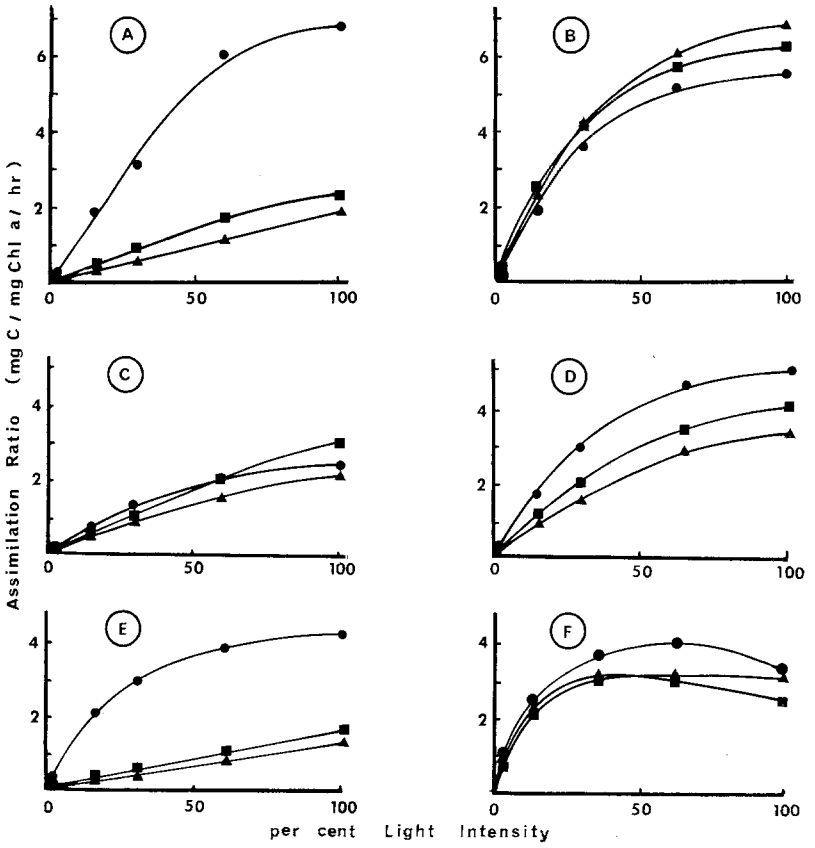

Fig. 4. Comparison of effects of NO_3^- (triangles) and NH_4^+ (squares) enrichment with unenriched (circles) samples on photosynthetic assimilation ratios. (A) and (B) Control Station QC; (C) - (F) Stations Kn 3, Kn 5, Kn 7, Kn 11. Details are given in text for each station

Table 1. Salinity, nitrate and 1% light depth at sample stations in July and September. Pronounced halocline is observable at all stations in Inlet, especially in upper 5 m. At Stations Kn 5, 7 and 11, mixed layer is deeper than 1% light depth, and reduction of dissolved inorganic nitrogen can be detected above this layer. Samples of phytoplankton were collected at 2-m depth at all stations for determinations of assimilation ratios, regardless of light extinction coefficient

Station	Depth (m)	Salinity (‰)		NO_3^- (µg-at/l)		1% Light depth	
		July	Sept.	July	Sept.	July	Sept.
QC	0	31.06	31.02	20.21	15.92	16 m	20 m
	5	31.08	31.09	20.21	20.45		
	10	31.27	31.39	19.49	21.45		
	30	31.68	31.73	19.97	24.17		
Kn 3	0	16.70	22.19	16.64	17.03	10 m	16 m
	5	24.48	27.62	13.91	18.42		
	10	29.23	29.73	15.18	18.81		
	30	30.22	20.44	19.28	-		
Kn 5	0	8.64	11.28	3.47	4.44	6 m	5 m
	5	26.08	13.08	17.64	18.86		
	10	26.66	25.86	23.75	24.31		
	30	30.31	30.49	23.64	-		
Kn 7	0	3.27	3.82	1.09	2.38	4 m	3 m
	5	20.92	24.59	14.08	6.86		
	10	26.99	27.91	19.62	19.03		
	30	29.86	30.11	24.09	24.41		
Kn 11	0	0.57	0.89	1.36	1.33	0.2 m	1 m
	5	20.43	20.59	12.55	7.04		
	10	27.87	26.97	19.30	20.18		
	30	29.93	30.03	22.20	22.55		

phytoplankton communities in response to changes in the external concentrations of nitrate and ammonium. The adaptive response does not depend upon light adaptation *per se*. The depression of assimilation ratios with nitrogen enrichment was observed at all stations for the first 2-h incubation. The samples were obtained from the same absolute depth despite changes in light extinction coefficients. Although it is difficult to characterize the physiological nature of the adaptation, it is accompanied by increases in photopigment concentrations per cell.

Falkowski (in press) has pointed out that nitrate uptake in *Skeletonema costatum*, as well as other species of marine phytoplankton, is primarily due to active transport. The process is characterized by a (NO_3^-, Cl^-)-activated adenosine triphosphatase on the plasmalemma. (Isolated membrane fractions of *S. costatum* exhibit enzymatic ATP hydrolysis in the presence of NO_3^- and Cl^-.) The apparent saturating concentration of NO_3^- for this enzyme is ca. 50 µM, and may be species-specific. The results of ATP determinations on cultures of *S. costatum* imply that light and temperature influence ATP pools significantly. It seems reasonable to suggest that the addition of NO_3^- extracellularly, below saturating NO_3^- concentrations (i.e., ca. 50 µM), causes increased hydrolysis of ATP, reducing the ATP pool. Results of nitrate enrichment studies are consistent with this hypothesis (Healy, 1973; Falkowski, unpublished data). The process would appear analagous to the addition of extracellular potassium to the ($Na^+ + K^+$)-activated transport ATPase (EC 3.6.1.3) (Glynn, 1962).

In 1972, MacIsaac and Dugdale demonstrated that NO_3^- and NH_4^+ uptake kinetics in natural phytoplankton populations are light-dependent and obey Michaelis-Menten kinetics. Bates (1974) has observed that NO_3^- uptake may be accompanied by changes in chlorophyll *a*/cell concentrations. The source of energy for NO_3^- and NH_4^+ uptake would imply contributions of the light reactions.

Of the 4 major ATP sources for NO_3^- transport (i.e., substrate phosphorylation, oxidative phosphorylation, cyclic photophosphorylation, non-cyclic photophosphorylation), the observed dependence of NO_3^- uptake on light suggests that Photosystems I and/or II (PS I, PS II) are directly involved. Consistent with this hypothesis, Eppley and Coatsworth (1968) failed to inhibit NO_3^- uptake with KCN, a potent inhibitor of oxidative phosphorylation. However, these latter authors also reported that inhibition of non-cyclic photophosphorylation with 3 (3,4-dichlorophyenyl)-1,1-dimethylurea

Table 2. Effects of nitrate and ammonium on intracellular chlorophyll *a* in mixed phytoplankton population from Knight Inlet. Data are taken from September samples from 2 m after 6 to 8 h preincubation with either nitrogen source. Cell counts were made on preserved samples (Lugol's solution) within 1 week of collection; unfortunately, small flagellates are lost by such procedure. (An inverted microscope was used to count 100 random fields at 250X) Chlorophyll *a* (Chl *a*) data are mean values and are intended for intrastation comparison only

Station	Condition[a]	Cells/l ($\times 10^6$)	Chl *a*/cell ($\times 10^{-7}$ µg)	% change Chl *a*/cell
QC	A	4.27	4.21	-
	B	4.32	4.30	+2
	C	4.51	4.93	+18
	D	4.71	4.87	+13
Kn 3	A	2.11	8.06	-
	B	2.19	7.66	-5
	C	2.40	8.71	+8
	D	2.61	8.63	+7
Kn 7	A	2.97	6.02	-
	B	3.05	5.89	-2
	C	3.09	6.48	+7
	D	3.26	6.31	+5
Kn 11	A	0.33	9.10	-
	B	0.41	8.72	-4
	C	0.37	10.88	+19
	D	0.37	10.31	+13

[a] A: original samples; B: unenriched; C: NO_3^- enriched; D: NH_4^+ enriched.

(DCMU) does not inhibit NO_3^- uptake in *Ditylum brightwellii*. Ahmad and Morris (1964) were able to inhibit NO_3^- uptake in *Ankistrodesmus braunii* with 1 mM dinitrophenol, however the multiple effects of this inhibitor do not clearly establish either oxidative phosphorylation or photophosphorylation as the primary energy source for NO_3^- uptake. We can report the inhibition of NO_3^- uptake in *Skeletonema costatum* with the addition of 100 µM carbonyl cyanide chlorophenylhydrozone, CCCP (Fig. 5). CCCP is an uncoupler of the two light reactions (i.e., PS I and PS II) and has been used to infer that cyclic photophosphorylation is a primary energy source for NO_3^- uptake (Healy, 1973; Raven, 1974).

It is postulated on the basis of these experiments that natural phytoplankton communities may respond to external nutrient concentrations in a relatively short time (less than a generation) by increasing the output of ATP from PS I through increased chlorophyll *a* synthesis. During the acclimation period there appears to be competition between NO_3^- and inorganic carbon for ATP.

Knight Inlet has not been found to be nitrogen-limited, even during the spring bloom. The extent of nutrient adaptation of a phytoplankton community to nitrogen enrichment from this area may not be applicable to nitrogen-limited systems (Thomas, 1969). Glooschenko and Curl (1971) have shown that NO_3^- enrichment may increase carbon fixation in a nitrogen-limited system. In fact, increased assimilation ratios after the addition of a "limiting" nutrient have been taken as evidence of nutrient limitation (e.g. Thomas, 1969).

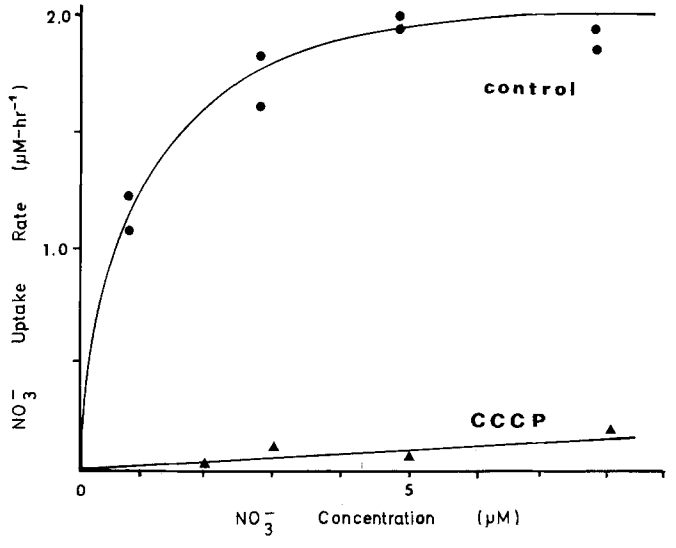

Fig. 5. *Skeletonema costatum*. Inhibition of NO_3^- uptake with 10^{-4}M carbonyl cyanide chlorophenylhydrozone (CCCP). Hydrozone is uncoupler of Photosystems I and II, and these data suggest cyclic photophosphorylation is a major energy source in the presence of light

In conclusion, it would appear that a major physiological feedback mechanism in nutrient adaptation in phytoplankton may be through regulation of chlorophyll *a*. Zgurovskaya and Kustenko (1968a, b) have shown rapid changes in chlorophyll *a/c* ratios upon addition of nitrite or ammonium. Glooschenko and Curl (1971) have demonstrated a synergistic effect on carbon fixation with simultaneous enrichments of iron and nitrogen. It is well known that iron is an important component of cytochromes and ferridoxin (Lehninger, 1970) and may also be a factor in nitrate reductase (Beevers and Hageman, 1969). Unfortunately, Glooschenko and Curl did not report NO_3^- uptake in their studies, but their data, and those of Hayward (1968) are consistent with increased chlorophyll *a* synthesis, upon addition of iron.

The nutrient-adaptation response appears similar to the light-shade adaptation reported by Ryther and Menzel (1959) in that changes in chlorophyll *a*/cell are observed in both cases. One effect of increased chlorophyll *a*/cell is apparently an increase in light-trapping ability and hence ATP synthesis. This increase in ATP production with pigment accumulation represents a considerable energy gain. It has been estimated that a green plant cell can form 30 times as much ATP by photophosphorylation as a cell kept in the dark can by oxidative phosphorylation (Giese, 1968). Hence, changes in chlorophyll *a* concentrations, in response to light or external nutrients, may be an efficient means of supplying sufficient energy for inorganic nutrient assimilation.

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